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VOLUME 2

Perception, Learning, and Cognition

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Contents

Volume 2: Perception, Learning, and Cognition

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PART I

PERCEPTION, ATTENTION, AND MEMORY

CHAPTER 1

ANIMAL PSYCHOPHYSICS: THE STUDY OF SENSATION IN NONVERBAL ORGANISMS

John Malone

"Had psychophysics been a modern child, it would be permanently in an institution for the mentally deranged. It was an unwanted child of its father; adored, praised, and occasionally harassed by its childhood friends; virtually ignored in adolescence; senile in young adulthood" (Candland, 1968, p. xi). Thus Candland began his foreword to the textbook *Classical Psychophysics and Scaling*. Candland went on to admit that "classical psychophysics does, indeed, seem dull to us today," and though you may consider it "among life's more dull and tedious adventures, the fact remains that psychophysical and scaling methodology is the foundation of psychology" (p. xi).

Stevens (1958), writing a decade earlier, agreed, charging that psychophysics had become dull because pedants had transformed a fascinating topic into a fetish-like concern with categorization of methods and general consistency of definitions, which is what pedants do. He cited "a distinguished committee" dealing with issues that "few people care about" as representative of this practice. Stevens saw psychophysics as a far more "nutritious subject" than such people have suggested.

Actually, neither Candland nor Stevens could have meant that *classical psychophysics* remains a foundation on which something now rests. Although one can argue that it was the mainstay of the early psychological laboratories, the truth is that Fechner's 1860 thesis inspired others to search for a metric to legitimately scale "mental sensations" into physical units. Because nothing mental was, has been, or ever could be scaled, the term *psychophysics* itself acts as a reminder that prescientific thinkers have found it difficult to shed the ancient belief in mind and body as two different things. And too often, the attempt to translate sensation to physical units has suffered from the criticism that Boring placed on Herbart's work and that applies to much current research in many fields:

> The not uncommon case in science in which inadequate data are treated with elaborate mathematics, the precision of which creates the illusion that the original data are as exact as the method of treatment. (Boring, 1950, p. 260)

CHAPTER OVERVIEW

Psychophysics is a classificatory term, a key word to guide readers to research or theory related to the vast field of sensory processes. Work in psychophysics is often technically demanding and we might expect researchers to be expert only in their restricted domains. Yet, perhaps more than in other areas of the life sciences, we find reports that display wide vision, surprising us with philosophical insights about life and epistemology.

I begin this chapter with a comment on the nature of sensation and a brief overview of the origin of psychophysics with Weber and Fechner, which includes a section on the classic

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I am very grateful to Hannah Snelling for her many hours spent gathering hundreds of studies for possible inclusion in this chapter—she will recognize some of those in these pages. Her wit, artistry, and discernment are missed.

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psychophysical methods, with illustrations of work with primates, sea turtles, goldfish, and pigeons and a note on the recent reassessment of Fechner's aims. Comparative psychophysics was surprisingly advanced by 1914 with Watson's *Behavior: An Introduction to Comparative Psychology* serving as a convenient summary of its status at that time. It also serves as a cue for a discussion of a very important issue—the question of the merits of ethological (descriptive/behavioral) treatments versus cognitive explanations that have been popular in psychology. The next section details changes in the concept of the threshold, beginning with Stevens's refutation of Fechner's theory and his own eclipsing by the revolution in psychophysics wrought by communication engineers in midcentury practical projects, with an illustration from pigeon research. I follow that with notes on empirical work in stimulus generalization and adaptation-level theory. The final section of the chapter summarizes the work of three eminent researchers: Hodos's treatment of achromatic avian visual acuity, Neumeyer's work with color vision in the goldfish, and James Land's remarkable application of the ophthalmoscope to the study of salticid spiders.

THE NATURE OF EXPERIENCE

Psychophysics concerns the general question of epistemology, the "what do we know and how do we know it," that depends on what we see, hear, and otherwise sense for its answer. That is the source of our experience and we are curious about the experiences of other people, though we can never really know what our "red" looks like to another viewer. We learn to be satisfied to see that others learn to stop at red lights and to judge blue as their favorite color, just as we do. By the same token, we are curious about the experience of nonhuman animals and ask whether a dog or a spider can know color as we do, reminding ourselves that we can only infer such things through observations of their behavior, the same method we apply to other people and even to ourselves (see Malone, 2009). The scientific study of sensation, the origin of our experience, began with Weber and Fechner in Leipzig almost 200 years ago.

WEBER AND FECHNER: THE SHORT STORY

Weber showed that discriminating the difference between two stimulus values on the same continuum was always a ratio judgment (see Chapters 23 and 25, this volume), but that in itself it had nothing to do with sensation, only with ratios of physical stimuli. Gustav Fechner called the ratio the *just-noticeable difference* (JND), declared that all JNDs were subjectively equal whatever the sensory modality or experimental procedures, and thereby believed that he had created a way to legitimately scale sensations in JND units (see Boring, 1950; Malone, 2009, for details). This fulfillment of his dream of calibrating the mental and physical was, in his opinion, as general and fundamental a law as was the law of gravitation (Fechner, 1860/1966). That is, for sensation to increase in equal intervals, stimulus intensity must increase geometrically and the increase seemed to be a logarithmic one, so that $S = k\log_{10} R$ where R refers to *Reiz* (stimulation). S is sensation in JND units and k is a *Konstant* (meaning a non-constant variable to adjust the fit of data to the equation). This conclusion rested on the assumption that all JNDs are subjectively equal, thus allowing an equal interval scale. It took 100 years to refute Fechner's equation.

The methods Fechner used to collect data for his 1860 *Elements of Psychophysics,* ascending and descending limits, right and wrong cases (constant stimuli), and adjustment were not his or anyone's "invention"; Boring (1942) listed experimenters using these methods as "the most natural way" at least 150 years before Fechner and others must have done so. Fechner's interpretations of his data have been controversial from the beginning. For example, Thurstone (1927) was a respected reviser of Fechner's logic and rejected the reality of JND as a sensory unit, because "now, as a matter of fact, everyone who works at all seriously in psychophysics knows that just noticeable differences have never been found" (pp. 421–422). That is, the assumption that there are real and stable thresholds and difference thresholds was mistaken; thresholds vary too much with circumstances. However, Thurstone not only retained Fechner's R (*reiz*) to refer to stimulus, but he still believed that we could scale (mental) sensation, though the JND must be probabilistic, as a discriminal dispersion, and he believed his method could be applied widely, to attitude scaling and beyond. Stevens (1958, 1961) disagreed with Thurstone's revision as well as with Fechner's logic, and argued that organisms can make direct judgments of ratios of sensation, even between modalities, so that the whole JND method is unnecessary.

METHODS AND TERMINOLOGY

Despite that debate, the methods Fechner used continue to be employed for many purposes with many variations. The following are descriptions of only the generic versions, along with definitions of several terms commonly used in animal psychophysics. There are apparent differences in definitions of these methods among several sources; Stevens (1958) pointed out that the methods are not clearly distinguishable and therefore they are subject to great variation in details. He saw this as a good thing and was critical of overdoing attempts to arrange methods in a tidy taxonomy and Fechner would have surely agreed.

It may be surprising for the modern reader accustomed to pictorial presentations to find that Fechner did not include a single figure plotting data on Cartesian (X-Y) axes in his 1860 book; all data appeared in tables. Early 20th century books followed the same practice.

Sensory Threshold

This seemingly-simple expression is actually a very contentious concept with a long history and many interpretations, as we find when trying to define it. For practical purposes, the *sensory threshold* is defined as that minimum stimulus value or change in stimulus value which a subject correctly detects 50% of the time for absolute thresholds and 75% of the time for difference thresholds, as explained in the following section.

Psychophysical Function: "How Often Can You Detect Each of These Stimuli?"

The plot of percentage detections arranged as an increasing or decreasing series of stimulus values or detections of differences comprises a *psychophysical function*. The specifics of the methods used to obtain such functions are so varied that Stevens, founder of Harvard's Psycho-Acoustics Laboratory, suggested that "many readers would find clarity improved if special names for procedures were banned and authors were forced to frame their descriptions in conventional English" (1958, p. 178). Figure 1.1 shows a psychometric function representing judgments of the duration of tones by human infants (*Homo sapiens*) after training to respond differently to brief (500 ms) and long (1,500 ms) 440 Hz tones (Provasi, Rattat, & Droit-Volet, 2011). The plot shows percentage judgments of long tones when five different durations were presented. The authors estimated 854 ms as the bisection (50%) point, which theoretically could not be discriminated as short or long by the infants and a JND of .39 s, compared with .23 s typically shown by rats and .17 s by adult humans.

Method of Limits: "Signal When You No Longer (Or Can Now) Hear the Tone"

Fechner (1860) placed the "method of just noticeable differences" or *method of limits* first on his brief list of psychophysical methods. This procedure is used to assess absolute thresholds for detection of a stimulus and usually is applied as an ordered ascending and descending series of stimulus values that is

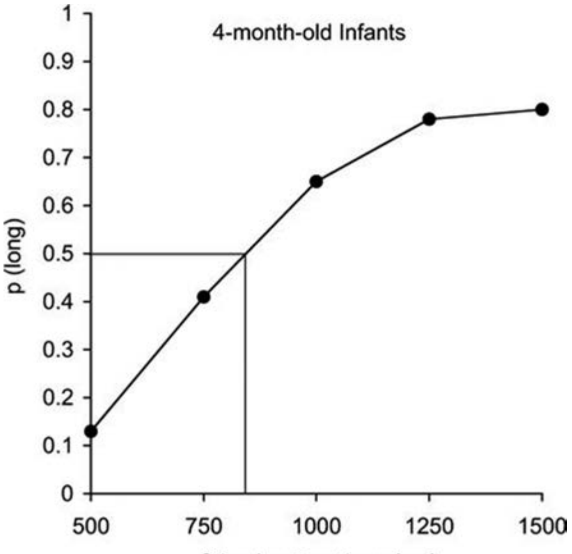
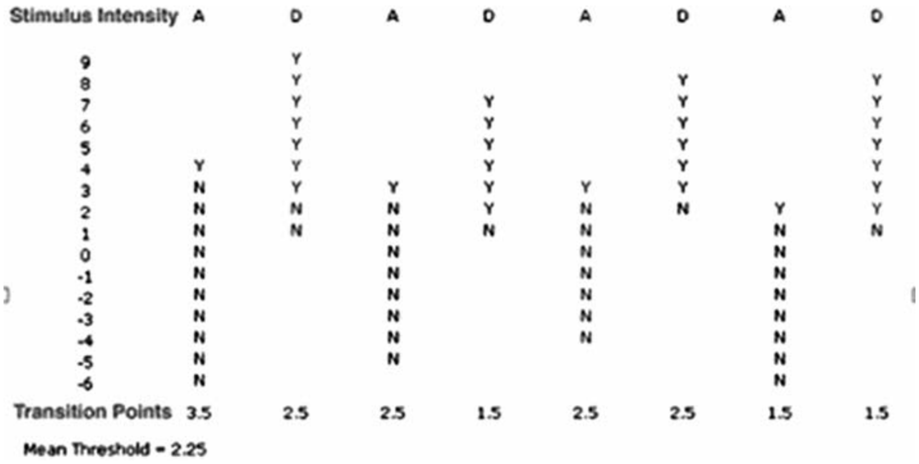


FIGURE 1.1. An example of a psychophysical function. From "Temporal Bisection in 4-Month-Old Infants," by J. Provasi, A. Rattat, and S. Droit-Volet, 2011, *Journal of Experimental Psychology: Animal Behavior Processes, 37*, p. 110. Copyright 2010 by the American Psychological Association.



Stimulus Intensity	A	D	A	D	A	D	A	D
9		Y						
8		Y				Y		Y
7		Y		Y		Y		Y
6		Y		Y		Y		Y
5		Y		Y		Y		Y
4	Y	Y		Y		Y		Y
3	N	Y	Y	Y	Y	Y		Y
2	N	N	N	Y	N	N	Y	Y
1	N	N	N	N	N		N	N
0	N		N		N		N	
-1	N		N		N		N	
-2	N		N		N		N	
-3	N		N		N		N	
-4	N		N		N		N	
-5	N		N				N	
-6	N						N	
Transition Points	3.5	2.5	2.5	1.5	2.5	2.5	1.5	1.5

Mean Threshold = 2.25

FIGURE 1.2. The method of limits.

meant to minimize effects due to presentation order of stimuli. This is the familiar method used by ophthalmologists and audiologists to test our visual acuity or range of pitch perception. Figure 1.2 shows a sample of the procedure; columns A and D represent ascending and descending series of stimulus intensities and the Y and N entries show the subject's detection yes/no responses. The threshold is taken as the average of the transition points. An example of the use of a common variation of the method of limits in assessing color vision in juvenile sea turtles follows.

The method of limits can be modified with a staircase procedure so that the stimulus strength does not simply decrease and increase, it adjusts to the subject's response. For example, Figure 1.3 shows a decrease in stimulus intensity over the first series of presentations until the subject reports no detection on the fifth. The experimenter then increases the stimulus intensity in steps until it is detected twice at the same intensity (trial 8) and then decreases intensity until it is not detected at trial 12. In this specific method, two detections must be made before intensity is decreased, but one failure leads to an increase on the next trial. An example of the staircase variation of the method of limits was provided by Young, Salmon, and Forward (2012), in their assessment of color vision in hatchling loggerhead sea turtles (*Caretta caretta*).

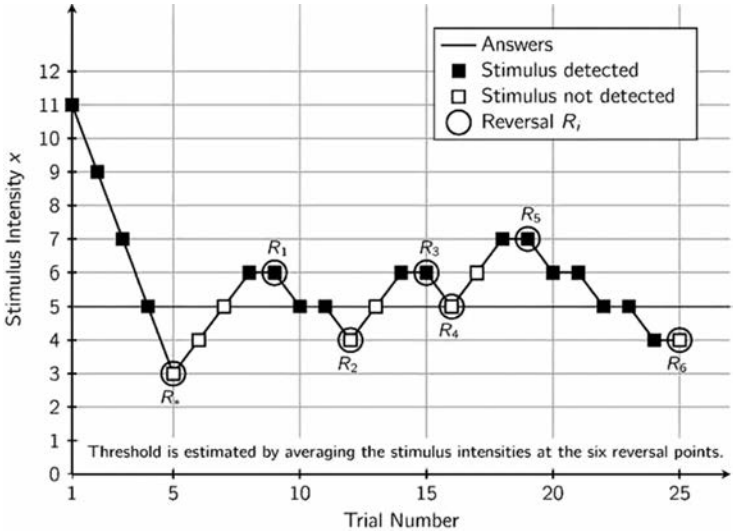


FIGURE 1.3. A staircase version of the method of limits. From *Haptische Unterscheidbarkeit mechanischer Parameter bei rotatorischen Bedienelementen* (p. 49), by M. L. Kühner, 2014. Copyright 2014 by M. L. Kühner. Adapted with permission.

Young et al.'s (2012) subjects were 401 hatchlings taken from 32 nests and individually tested for phototaxis color sensitivity after adaptation to (artificial) light; all testing took place between 11:00pm and 12:00am, when hatchlings usually move from the dark sands and dunes toward the brighter ocean surface. Hatchlings were placed individually in a Y-maze in seawater to determine the minimum brightness of blue (450 nm), green (500 nm), and yellow (580 nm) light back projected on a frosted panel that would be chosen over a dark alternative. For each of the three colors, brightness was decreased in measured staircase steps until the turtles' chose the dark arm of the Y as often as the lit arm. That was followed by a staircase of increases in brightness step by step until the subjects chose the lit arm. Each turtle was light adapted for at least 15 min so that rod vision was eliminated and only cones were operating. The lowest light intensity that evoked attraction was set as the phototaxis threshold for that wavelength and for these turtles the most effective was 500 nm, what humans report as the green light.

With few exceptions, studies of wavelength discrimination (color vision) in turtles have not convincingly controlled for brightness differences, which is an essential step. Failure to appreciate the effect that differences in reflected light intensity can have led to decades of debate about the very existence of color vision in dogs and cats. In the case of colored stimuli viewed under water the measure of the relative brightness at the animals' receptors is an almost impossible task. Young et al. (2012) overcame that difficulty in an ingenious way during a wavelength discrimination in the final condition of their study. Watson (1914) had referred to the method that these authors used but it has almost never been used to assess turtle vision in modern research. The procedure was to pair color target lights in the Y-maze, presenting one (S+) color with food and varying the intensity of one of the pair of lights during each trial. The turtles' excellent discrimination performance clearly showed that they could respond to wavelength alone. For example, when food was paired with a blue target light versus a green light, the turtles swam to blue, whether it was brighter or dimmer than the alternative. Their data showed clearly that loggerhead juveniles have trichromatic vision and the ability to learn discriminations among wavelengths independent of brightness.

The Method of Constant Stimuli: "Does This Tone Sound the Same as the Last One?"

The most common method to determine difference thresholds is, the *method of constant stimuli*, named by Fechner (1860/1966) the "method of right and wrong cases." It features presentation of a standard stimulus value, such as a 30 dB 1,000-Hz tone followed by other intensity levels, such as 35 dB, and asking the subject whether the second loudness was the same as the first, which required a simple "yes/no" response. The response to a number of comparison values allows us to plot a psychometric function with percent same/different correct judgments on the vertical axis and loudness on the horizontal. The difference threshold is appropriately set at 75% correct, because 50% would simply reflect random responding. If absolute thresholds are all that is wanted the method becomes a version of the method of limits; different stimulus values are presented in random order, rather than in graded series, and a present/absent judgment is made. In that case the threshold value may be set at 50% correct judgments. The time-estimation procedure discussed previously (Figure 1.1) can be viewed as a variation of the method of constant stimuli, because the two training values were presented in an unpredictable series with the test stimuli to yield the overall psychophysical function.

Another version of the method of constant stimuli was used by Yan and Popper (1991) to yield an audiogram for goldfish (*Carassius auratus*). Their procedure was unique, because the usual methods either make it difficult to control sound pressure level (SPL) as the fish swam around a tank and/or used electric shock paired with tones to cause cardiac and ventilator suppression as the measure—thus stressing the fish and rendering the data suspect. Yan and Popper trained their fish to touch a small paddle, turning on a tone through a system that targeted its maximum SPL at that spot. The fish then touched a second paddle adjacent to the first and received a food pellet. On trials when no tone was present a response led to a 90 s blackout period that deterred false alarms. Their audiogram shows the thresholds for their two subjects along with data points from other studies using electric shock. Their SPL scale is not the familiar decibel (dB) corresponding to human judgments of loudness; rather, it reflects the power of the amplifier relative to its maximum, which is zero on their scale. Decibel is not something scaled, it is a ratio that is of the same kind as percentage.

Method of Adjustment: "Can You Match That Loudness?"

The *method of adjustment* is what Fechner (1860) called the "method of average error" and requires the subject to control a stimulus so that it is intense enough to be detected (absolute thresholds) or so that it matches a standard stimulus value (differential thresholds). Human subjects can be given instructions to adjust the brightness of a light, the loudness of a tone, or the length of a line; analogous training can serve as instructions for nonverbal subjects. An animal application lies in tracing the course of dark adaptation. Suppose that a light is made gradually dimmer when the subject reports that it is visible and gradually brighter when it has become invisible to the subject. That is a version of the method of limits and is one way that the course of dark adaptation is assessed with a human subject; this has been duplicated with animal subjects. Blough (1956) published an account of the procedure and results. A pigeon (White Carneaux, bred from *Columbia livia*) was trained to peck one response key when a light was shown and to peck another key when it saw no light; Figure 1.4 is his sketch of the apparatus. The brightness of the light was controlled by an optical wedge that adjusted when the bird pecked, so as it varied the intensity of the light the bird answered the question, "Do you see the light?" by pecking the corresponding key. Each peck increased or decreased the light intensity, corresponding to the pigeon's "yes/no" pecks and a pen traced the responses and so determined the threshold, paralleling the method of adjustment used with human subjects.

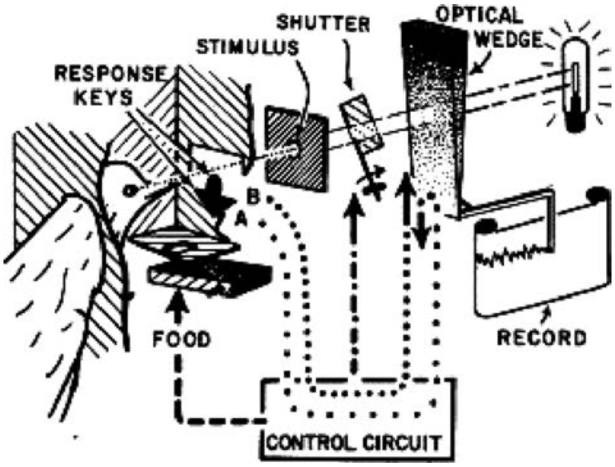


FIGURE 1.4. Depiction of Blough's apparatus. Reprinted from "Dark Adaptation in the Pigeon," by D. Blough, 1956, *Journal of Comparative and Physiological Psychology, 49,* p. 426. Copyright 1956 by the American Psychological Association.

REASSESSMENT OF FECHNER'S AIMS

Johnson (1978) summarized the development of psychophysics of vision as the quest for the definition of the word *light* and its quantification as sensation:

> Before attention was given to sensory mechanisms, two worlds, an inner and an outer, seemed necessary—and also sufficient. The boundary between them, for vision, was first taken to be the pupils. Scholars later pushed the boundary back to the retina; then, growing cunning in their sophistication, to the "sensorium," whatever that might be . . . the word light can be defined by reference to . . . sensitivity functions . . . "bright" and "dim," and "light" and "dark" related to quantity of light. Such terms were quantitative precisely to the degree that they were useful in communication. Each was an element in a verbal model of the world. . . . In due course these conceptualizations of the world succumbed to *measurement*. And when the physicist measured light in terms of a standard candle at a distance of 1 m, and when he specified points in the spectrum, the way was opened to . . . the "facts" of color mixture, and more. (pp. 3–4).

But where does psychophysics, in Fechner's sense, come in? What did Johnson think was actually being measured? He wrote that although the experience of other organisms may be forever unknowable, psychophysical measures still give us something:

> We emphasize that psychophysics, while related to experience, is not a scheme or set of procedures for directly describing or translating the experiences of one person in terms of those of another. Psychophysics gives us objective data for comparison with other objective data. . . . The data of psychophysics . . . serve as additional grist for the private mills that grind out, for each of us, our personal understandings and beliefs. (Johnson, 1978, pp. 4–5)

Of course that does not mean that what we think of as private experience is unknowable or that the subjective world of others is completely beyond our ken. Wundt knew that experience doesn't come as inner/outer (Malone, 2009) and so did sensory physiologist Floyd Ratliff. Concerning objectivity, he wrote,

> We have, of course, no procedures for complete dissociation of observer and object observed.. . . "My toothache" is the classic example of a private phenomenon, but the fact of the matter is that my toothache which I feel . . . is, strictly speaking, no more private than is "my light," which I see when I turn on a lamp. (Ratliff, 1962, p. 475)

Consider a different viewpoint, one that jibes with uninformed common sense and holds that our sensations are private and are different in kind from a real external world. This is the view that the media breathlessly presents to us when it announces breakthroughs in neuroscience. It is the mental/physical schism that we learned from our parents even before we could read.

EARLY 20TH CENTURY APPROACHES TO ANIMAL PSYCHOPHYSICS: JOHN B. WATSON

When Fechner, Cattell, and Thurstone referred to psychophysics they meant it literally; they believed that they were calibrating physical stimuli, like the intensity of a light or sound source, into sensation units and thus were "measuring the mental." Subsequent researchers held no such beliefs and realized that the real goal was to determine what they could about the behavioral reactions of humans and other animals to various kinds of stimulation. As example of early work on animal psychophysics, I chose the much maligned and misunderstood John B. Watson, whose *Behavior, An Introduction to Comparative Psychology* (1914), gives the reader a good picture of animal sensory research a century ago (see Volume 1, Chapter 2, this handbook).

Watson was a true pioneer in the study of animal sensory phenomena; not only did he personally carry out research with a variety of species, he reviewed dozens of research reports on the subject in his role as editor of journals. He criticized the extremely anthropocentric methods of the day that were based on introspective reports and "introspection by analogy." However, he did not advocate purely biological methods and warned that one could be "lost in a general biological mirage." Ideally, comparative psychology required "histology, physiology, and experimental zoology . . . preceded by training in chemistry and physics" (Watson, 1914, p. 56).

His purpose was the same as that of most modern researchers, who really don't want to find exact absolute and difference thresholds for a sense modality of a specific organism. The more likely question raised is along the lines of whether domestic cats or dogs are sensitive to the same visual spectrum and how does that compare to the vision of birds? What about color vision in marine mammals at varying ocean depths? How can porpoises and especially seals and sea lions see well when out of water, whether diving or sunning on a rock? How can we know that our animal subject sees stimuli that we are presenting? Watson (1914) referred to prisms and filters comprising a proto-monochrometer and explained that

> Our interest is not psychophysical here but methodological. We need to know for subsequent control of behavior, what difference in intensity one has to maintain between two reds of the same wavelength to afford a basis for a difference in response. (p. 35)

"The majority of mammals tested . . . are insensitive to light of long wavelengths" (Watson, 1914, p. 335). That was the first sentence in Watson's coverage of animal psychophysics, and it took decades to realize that many vertebrates (and invertebrates, like jumping spiders) are unable to distinguish reds from darkness or gray (see Chapter 3, this volume). Frisch's demonstration of trichromatic vision in some fish is included in Watson's survey, so a lot was known a century ago. Watson listed an interesting set of questions concerning all the senses, including sensitivity of birds to air columns' moisture content and pressure, as well as to air currents, including possible olfactory cues, which could play a part in homing of birds (p. 42). According to a review published 89 years later, it is likely that olfactory guides are important in bird navigation (Wallraff, 2004).

Watson (1914) reported data obtained from a wide variety of species and with a variety of methods, all in the last four chapters of his book, comprising about 100 pages. The level of description is general and often confined to one or a few reports. The following example is typical:

> From C. Hess we learn that when a light-adapted chick is taken into a dark room and placed before grains illuminated by the whole spectrum (spectrum of medium intensity) and allowed to peck freely, it will begin with the grains illuminated by the red and orange rays. It pecks continuously until the blue-green region is reached, beyond which point it refuses to peck further. A well dark-adapted chick in a spectrum of the same intensity will always begin to peck at the grains illuminated by the red; then in order, orange, yellow, green, and blue-green. . . . The behavior of the pigeon under the same conditions is closely similar to that of the chick. The range at the red end for it is normal, but at the violet end it is even more contracted than is the case with the chick. (p. 336)

Hess also examined color vision in birds with "twilight vision," including the kestrel, house hawk, small owls and great horned owls, finding a similar reluctance to feed when illumination was solely short-wavelength light (Watson, 1914). These birds have more rods than cones, but may share the human insensitivity to blue light owing to the small number of short-wavelength receptors (S-cones). Watson reported that Hess studied dark-adapted fish (*Atheria*), finding that they tended to gather in middle-wavelength (green to yellow-green) lit areas, whereas long-wavelength lit areas were treated as darkness. Turtles showed greatest response to the same wavelengths, that is, middle values of the human-visible spectrum. All of the findings Watson described correspond reasonably well with recent findings.

Watson (1914) considered the course of dark adaptation and, as he often did, described a truly comparative experiment—after an hour in darkness, "a human being, a chick, and a white pigeon were tested simultaneously" (p. 333). Complete adaptation was achieved in an hour for all three species. But there was one difference:

> It is interesting to note that chicks, when long dark-adapted, are not blinded by strong light. Small grains placed before a dark-adapted chick and then suddenly illuminated by bright sunlight, are picked up readily by the birds. Birds and turtles stand in interesting contrast to man in this respect. Man is blinded by strong light after darkness-adaptation. Whether this is due to the fact that man possesses rods, and hence visual purple, is not clear at present. (pp. 333–334)

Fish show a "one-thousand-fold" increase in visual acuity after 15 min of dark adaptation and the course of adaptation for the all-cone turtle matches that of the human with an orange glass over the eye "to compensate for the absorptive effect of the red oil globules" (p. 345). A method Hess used to study dark adaptation simultaneously in oneself and in a turtle or other animal subject is as follows:

> An interesting way to test the process of light-adaptation in such animals is for the observer to light-adapt only one eye. This eye is kept in the bright light for the same length of time that the subject's

> eyes are light-adapted. Then when the animal is taken into the dark room the experimenter, with his dark-adapted eye, can arrange the apparatus, while with his light-adapted eye he can test the course of adaptation in himself and compare it directly with that of the animal under observation. (pp. 345–346)

Which animals showed evidence for spectral sensitivity according to researchers in Watson's time? Monkeys, both Rhesus and Cebus, clearly showed that they distinguished colors though we will see following that Cebus color vision is complicated. In dogs the situation was different—in every case where differential responses to color are found, differences in brightness/intensity are the effective stimulus and the dog's color sensitivity must be very rudimentary if it exists at all, a conclusion that is still drawn by Jacobs (2009), authority on vertebrate color vision. Similarly, cats show different responses to standardized color papers, but in every case, a gray can be found to substitute for what seems differential response to spectral values.

Rats, mice, and rabbits all showed no evidence of color vision, but hens "pass the test with the ease of the human being normal in color vision" (Watson, 1914, p. 350). That according to Hess, who used colored grains, with reddish ones fastened down and found that his hens learned to peck the green and gray seeds "with astounding quickness and sureness" (Watson, 1914, p. 350). Similar effects were found with other arrangements and contrasted with the poor performance of a red–green colorblind human. A Purkinje effect appears in behavioral testing of birds but Watson found that it probably did not occur in fish, though conflicting reports had appeared. Frogs (and turtles) showed a clear preference for mid- to short-wavelength illumination and readily moved from red to orange, orange to green, and green to blue waters.

However, in all of these cases the reader should be cautioned, Watson (1914) wrote. Throughout his discussion of research in vision, he scolded authors for their often-shoddy methodology and, more often, for their careless interpretations. For example, some writers in his day concluded that cryptic/mimic behavior involving color change meant that the animals involved must have color vision. Watson seemed exasperated by such thinking and criticized the authors of such speculation at some length.

He provided a *very* detailed description of the auditory organs (see Chapter 2, this volume) in fish, birds, and mammals, accompanied by diagrams of each and described in (perhaps) too much detail the results of various surgeries performed on the auditory system of dogs. The subsequent dozen pages summarized research on hearing in raccoons, bats, frogs, and fish, much of it anecdotal. Watson's final chapter dealt with smell, taste, and the common chemical sense (see Chapter 4, this volume). So by 1914, a substantial amount of research had been done and more knowledge gained than we might expect. But, then and now, readers must be careful in drawing conclusions.

ANIMAL PSYCHOPHYSICS, COGNITION, AND PRIVATE EXPERIENCE: CONTROVERSY

Behaviorism and Psychophysics

Watson (1914) held that we could study sensory processes in animals and in humans with no reference to consciousness, mind, sensation, or the other terms used in folk psychology. He never wrote that that mind exists but is unmeasurable and never denied the reality of private experience (see Malone, 1990; Malone & García-Penagos, 2014 for a full account). In addition, though he was an expert in biology, Watson shunned recourse to postulated biological causes and his books featured no brain sections or cortical maps since, as remains true, they give the reader the impression that they explain more than they do. The suggestion that our brains work as calculating machines would have been quickly dismissed by Watson, but many modern writers disagree with his opinions on cognitive theorizing (see Volume 1, Chapter 28, this handbook).

Contemporary Rejection of Watson's Behaviorism and of Comparative Ethology

Wasserman (2012) is representative of those who advocate the application of vocabularies proven popular in cognitive psychology to the study of animal behavior, so treatments cast in cognitive terminology, such as *processing*, *working memory search*, *attention allocation*, and many others are acceptable if they have currency in cognitive psychology. His version of cognitivism also explicitly excludes the mention of subjective experience in humans, though Wasserman assumes that "other people experience the same thoughts and feelings that we do in similar circumstances" (p. 94). That does not hold for our dealings with animals, because he cautioned against anthropomorphic analogy as promoted 130 years ago by George Romanes, who was famous for overdoing the attributing of mental states in animals. Inferred cognitive machinery is good, whereas inferring private experience is improper. But as the "cognitive revolution" in psychology shows its age, it becomes more obvious that use of its terminology does not benefit comparative psychology and neither does Wasserman's thesis.

First, Wasserman's (2012) interpretation of Romanes has been seriously questioned (Malone, 1982), and in his recent rendition of von Uexküll (1934/1957) Wasserman denied that von Uexküll urged that we consider animals' experience/viewpoint insofar as possible. The starling and the fly and the other magical *umwelten* von Uexküll described should make Wasserman's error clear to any reader. But for Wasserman's cognitive psychology, taking the animal's viewpoint is off limits, even "mentalist," and he claims that is what von Uexküll really meant (2012). Burghardt (1997, 2007) argued convincingly for the legitimacy of taking the animal's viewpoint, while realizing that the best we can get is Paul's "a view through a darkened glass" (1997, p. 259).

Wasserman (2012) goes further than denying mention of animal experience and rejects the "central interpretative technique of yesterday's comparative psychologists and many of today's cognitive ethologists" (p. 95). Ironically, he repeatedly scolded those who follow convention (2012), while illustrating his own conformity with the mainstream cognitive approach. There is a learning opportunity here. What if we applied cognitive terminology to the behavior of organisms with no neurons? We can witness the application of cognitive language to phenomena that are actually interesting even without the cognitive "dressing up."

Cognitive psychophysics and nonneuronal animals. Reid, Garnier, Beekman, and Latty (2015) published an article in the respected journal *Animal Behaviour,* reviewing research on psychophysics and decision making by nonneuronal organisms, including bacteria, trees, fungi, and protists in general, excluding all organisms that feature neurons. The reviewed research appeared in top-tier journals, including *Science, Nature, Proceedings of the National Academy of Sciences,* and *Philosophical Transactions of the Royal Society* and the argument for adaptive "behavior" in these organisms is persuasive, but the descriptive language would be excessive if it were describing the most complex human reasoning.

Reid et al. (2015) dare not attribute subjective experience to beings that are *sans neurons,* but like Wasserman, they are eager to impute cognitive processing mechanisms to fungi and flagellites. Their nonbrained organisms comprise the

> vast majority of all life . . . [and] face many of the same decision-making challenges as organisms with a brain: they must search for resources, choose between resources of varying quality, adapt to changing conditions and search for suitable microclimates to inhabit. (Reid et al., 2015, p. 44)

I might add that they must also deal with predation, competition, toxins, and, perhaps, mating/reproductive issues. Hence, slime mold, amoebae, and peach trees use information for decision making via multiple sensory channels, evaluate attributes to which they assign values; calculate, select, and integrate information (making multiattribute decisions); use compensatory strategies; make trade-offs; and use many "computationally-intensive strategies." Indeed, one cannot help but recall the title of Rachlin's (1978) commentary, "Who Cares if the Chimpanzee Has a Theory of Mind?" and his proposal that one can infer cognitive processes in a heated pail of water, as it "signals" that it is about to boil by emitting bubbles. Positing cognitive processes is an irresistible pastime that we enjoy. Barrett (2011) thoroughly, entertainingly, and authoritatively exposed the folly in such abject anthropocentrism, belief in folk psychology, and cognitive processing reverence. The following section is one of many examples that I think illustrate her point: simple brains can show intelligent behavior and explanations couched in cognitive processing jargon are superfluous.

The bee shows what a simple brain can do. In 2005, Dyer, Neumeyer, and Chittka showed that honeybees (*Apis mellifera*) can be trained to choose a photographed human face when it is presented on a large wheel along with other similar-appearing faces. Their procedure was simple, as previously-marked honeybees came to their outdoor choice wheel, having been fed a rich sucrose solution there, and hovered a few seconds before choosing a photo. Choices were rewarded or punished with sucrose or with quinine and the bee was then lured onto a clear plastic spoon with more sucrose, moved a meter away, and turned from the display. While so distracted, the display wheel was turned so that the target face was in a new position and the bee was free to choose again in a nonrewarded test trial. Two bees never caught on and after repeated doses of quinine they "lost interest" (p. 4710) and flew away. But five bees did catch on quickly and chose the target face on over 90% of the trials. Two bees tested two days later remembered their lesson well and flew to the target face on over 80% of the trials. The target photo was a man in his mid-thirties who could easily be confused with the paired negative choices. A six-month old child would likely score no better than did the bees.

The evidence for such capabilities of bees seems convincing and the authors did not try to explain their findings by reference to cognitive mechanisms. But some critics contest such findings, even in the face of these and other authors' fine reputations. Adrian Horridge (2012), who has approached vision from a "reverse engineering" standpoint that he seemed proud to claim is not "comparative psychology, and far from ethology" (p. 188). He is particularly critical of claims of any sort of higher-order learning in bees since, "these wild guesses. . .led to confusion for years and failure to make the proper tests" (p. 187). According to his "mechanistic" analysis, bees are even incapable of any kind of pattern perception! One wonders whether he even admits that they can fly. I return here to the basis of psychophysics.

EVOLUTION OF THE CONCEPT OF THE THRESHOLD

In the early 19th century, Johann Herbart proposed the concept of *threshold* to refer to the boundary between conscious experience (apperception) and an ever-changing mass of unconscious ideas, struggling to gain access to consciousness. He was reviled by subsequent writers, from Fechner to William James, but the vocabulary he used was adopted by many, including modern writers (see Boring, 1950; Malone, 2009). It was the concept of the threshold that proved to be Gustav Fechner's obsession.

When Fechner examined the sensory abilities of his human subjects he could present a very weak stimulus, such as a light or a tone, and ask his subjects to give simple answers, like "yes/no," "more/less," "brighter/dimmer," or other variations of dichotomous answers. His subjects shared his language and he had no reason to believe that they answered dishonestly. It's easy to duplicate his methods and Fechner offered simple examples showing how easy it is to demonstrate, for example, that JNDs are constant ratios of stimulation. If one looks at a cloud and identifies that part of its edge that is a just-noticeable difference from its background and then interpose a gray glass or a sunglass lens to darken the whole image, we see that the same edge is still just-noticeably different, showing that it is the ratio, not the absolute difference, that is important (Boring, 1942).

Stevens and Direct Scaling: Fractionation and Magnitude Estimation

Stevens was born in Ogden, Utah, and did his Mormon missionary work during 3 years in Belgium and France before graduating from Stanford and entering Harvard's College of Education. He served as Boring's research assistant before receiving a PhD in philosophy and spending the rest of his career at Harvard running the psycho-acoustic laboratory. He became almost synonymous with psychophysical scaling in America and wanted to be remembered for his refutation of Fechner, described in 1961, a century after Fechner's "Elements of Psychophysics."

Fechner had assumed that we cannot directly judge magnitudes of sensation, because we have no metric to go by. When you hear a loud sound, we can measure the physical stimulus as SPL at your ear, but how can you or your animal subject place that intensity on a numeric scale of sensation as "loudness?" So Fechner's three methods rely on the subject judging less, equal, or more, yielding an indirect estimate of sensation and no one seriously challenged him until Stevens came along.

Why not scale judgments of sensation directly? Stevens proposed two methods of magnitude estimation and fractionation—asking subjects to adjust a stimulus to half its intensity, then half of that, then double that, and so on. People can do this and produce psychophysical functions that are reliable and that show that Fechner's log function and assumption of equal JNDs was mistaken. Although Fechner had claimed that sensation magnitude grew arithmetically as stimulus strength grew geometrically (by a constant ratio), Stevens showed that judged sensation increases in ratios, just as does stimulation, leading to his famous power law, $S = KI^a$ where I is stimulus intensity and a is an exponent corresponding to the power to which I is raised. When plotted as ratios on log-log paper, these psychophysical functions appear as straight lines.

Rather than scale sensation indirectly, via Fechner's methods, Stevens argued that we can make direct estimates of sensation if given an anchor, sometimes called a "modulus," and subjects can reliably scale stimulus intensity. For example, using the method of magnitude estimation, a starting SPL may be presented and called a "four" by the experimenter or even by the subject. As intensity is raised or lowered, the subject responds "five," "three," "seven," and so on, corresponding to the SPL intensity presented. The resulting psychophysical function turns out to be fit by a power function with an exponent of about 0.6 and such relations have been found for dozens of continua where intensity is varied, though the exponents vary greatly. Numbers need not be used and subjects were able to adjust their squeeze on a hand dynamometer in accord with changes in stimulus intensity. Further, they could scale brightness intensities by choosing corresponding loudness intensities.

There are critics of Stevens's interpretations but the fact of the power law is indisputable. Stevens was by no means a behaviorist, but he shared their goal—the discovery of functional relationships. Teghtsoonian (2001) described Stevens's outlook, which suggests what would be a very beneficial revision of current practices:

> Much of his time in the laboratory was spent plotting and replotting data in the pursuit of clarity and simplicity . . . A corollary of this belief was an attitude toward sampling theory and statistical testing that ranged from indifference to disdain. The object for him was not to see whether 80 dB tones received an average loudness judgment greater than did 60 dB tones (at the 5 percent level of significance), the equivalent of what most of his contemporaries were doing. What was important to Stevens was whether a lawful relation could be seen when data were plotted in a thoughtful way. Large numbers of experimental subjects were not needed to reveal the kind of robust relations he sought; a few colleagues or students recruited in the hallways were enough for most of his purposes. (p. 15107)

Teghtsoonian saw Stevens as a transitional figure and that is true partly because of the increasing emphasis on the neural bases of sensation since his death in 1973 and partly because of the recognition that psychophysics itself changed with the advent of signal detection theory.

Signal Detection Theory: Threshold as a Continuous Function

Boring dedicated his classic 1942 volume to Hermann Helmholtz, who contributed to the understanding of sensation and perception in many ways (see Boring, 1942, 1950; Malone, 2009). Not the least of his durable contributions was his scientific rendition of John Stuart Mill's theory of belief as the doctrine of "unconscious inferences," the fact that what we call sensation is a minute part of what is actually sensed/perceived/noticed. Our expectations play a far larger part than Fechner realized and, ironically, it was Fechner's writings on colored shadows that remain colored after the causal illumination is changed that convinced Helmholtz of that. Other examples abound: We unconsciously infer phantom limbs and misjudge distances if sensations from the stump of a limb or clearness of air lead to customary sensations of limbs or distance.

Since we now recognize that expectations and motivation play a very large part in psychophysical data, the notion that organisms act as more or less pure detectors of physical stimuli has been dismissed. This was made especially clear when a chain of British coastal radar stations was set up to detect German bombers before 1940 and difficulties arose in distinguishing airplanes from flocks of birds. The same problem arose in America as communications engineers analyzed the intelligibility of messages in noise in long-distance telephone lines. These practical problems of accurate detection led to *signal detection theory* (SDT; see Volume 1, Chapter 30, this handbook), which separates the sensitivity (d') of the detecting organism (or a machine) from the criteria for target detected (β). This is plotted as a receiver-operating characteristic curve, that tracks correct detections versus false alarms and shows changes in threshold as a function of criterion changes.

The theory was described in detail by Green and Swets (1966). Nevin (1969) reviewed their book soon after its appearance after analyses had already been applied in animal research. A review of animal research applications was later provided by Alsop (1998). Figure 1.5, taken from Blough (1967), shows a pigeon's (White Carneaux, *Columbia livia*) response to wavelength stimuli. The axes are equivalent to hits (Y-axis) and false alarms (X-axis), as the pigeon pecked "yes, this is 482 nm" (yellow to a normal human eye), as that color and other wavelengths were presented. The data points closer to the diagonal reflect lack of discrimination (small d') and those bowed up in the upper left corner show better discrimination (larger d') as high percentages of hits and low incidence of false alarms. Each of those curves is actually a threshold, corresponding to a color representing the pigeon's varying tendency to say "yes."

John Swets was a founder of SDT and titled a 1961 article, "Is There a Sensory Threshold?" He argued that the very concept of a threshold has been based on analogy with the neuron's all-or-none reaction and that Fechner himself clearly recognized the difficulties associated with the whole idea. Fechner knew that the data never reflected purely sensory processes and that the subject's motivation/response criterion was important. In fact, the simplest psychophysical method, ascending and descending limits, was specifically devised to cancel out the subject's tendency to commit "errors" of habituation and anticipation. Swets felt that sensation (the threshold) is a continuous variable and that is why Fechner proposed the existence of negative sensations, or partial thresholds (Malone, 2009), bodily responses below the threshold of awareness. Such phenomena were ignored by subsequent psychophysicists, a fact that Swets deplored.

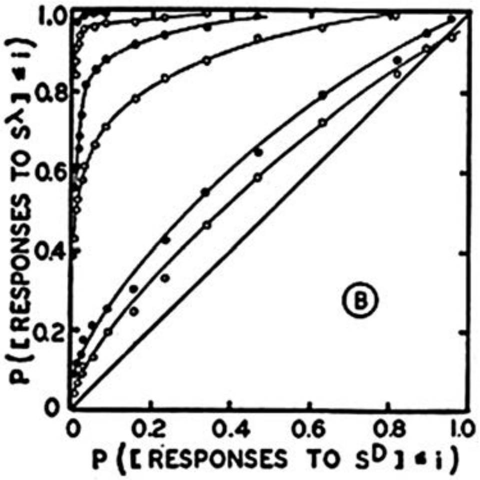


FIGURE 1.5. Blough's data in SDT form. From "Stimulus Generalization as a Signal Detection in Pigeons," by D. Blough, 1967, *Science, 158*, p. 641. Copyright 1967 by The American Association for the Advancement of Science. Reprinted with permission.

Empirical Stimulus Generalization Gradients

The study of stimulus generalization and discrimination is fundamental to an understanding of behavior and operant methods have proven particularly useful in this area (see Chapter 15, this volume). Indeed, in what was perhaps B. F. Skinner's last reference to this method he pointed to the pivotal pigeon work of Guttman and Kalish (1956), who pioneered the use of empirical stimulus generalization gradients (Malone, 1999). They paired food access with pigeons' (*Columbia livia*) pecking a disc illuminated with a specific wavelength, such as 550 nm, that looks greenish yellow to humans. Then during test sessions in extinction many brief presentations of a range of wavelengths were presented without food, producing a gradient of response centered around the training stimulus, giving a rough index of the pigeon's judgment of similarity.

Their work was the impetus for many subsequent studies, perhaps culminating in that of Honig and Day (1962), who used generalization testing as a psychophysical tool in the demonstration that stimulus differences in wavelengths of two filter-produced colors can serve as a discriminable continuum, so that pigeons' responding during extinction testing varied according to the difference in wavelength of two simultaneously-presented hues. That is, a difference of 40 nm was designated as S+ during pretraining and responses to differences in pairs of stimuli of 10nm, 15nm, 35nm, and so on to 70nm formed a gradient during testing, just as stimuli presented alone produce standard gradients of response.

Of course, testing in extinction (food withheld) meant that the gradient changes through a session as responding fades and the average response rate was often taken to represent the whole session. Work with human and animal subjects has led to a bewildering array of variables that influence the shape of generalization gradients and Rosemary Pierrel (1958) introduced an improved method, steady-state training, in which food (or other payoff) remains available for responses to the training stimulus as various other stimuli on the same continuum are added.

Figure 1.6 illustrates that technique used by Blough (1967) that depicts the SDT data in Figure 1.5 plotted in conventional generalization gradient form. Such gradients can be maintained over days, weeks, and months as changes in stimulus conditions are made (see Blough, 1975; Malone & Staddon, 1973).

One factor that is often, if not always, influential in determining gradient form and sensory judgments in general is the particular set of stimuli used—the "context" of stimulation and sequential effects among stimulus presentations (e.g., Malone & Cleary, 1986; Nevin & Shettleworth, 1966; Malone & Rowe, 1981). The importance of sequential effects in determining sensory judgments was shown by the work of Harry Helson, who developed a framework for analyzing context effects.

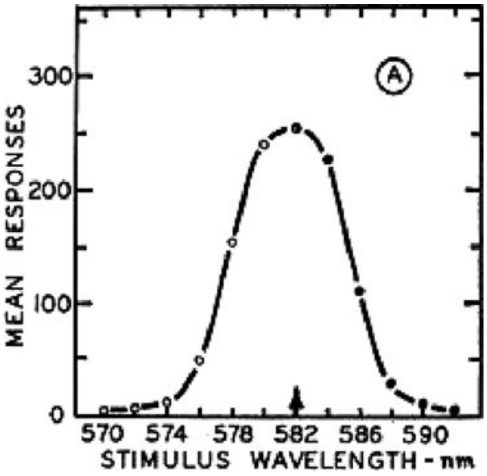


FIGURE 1.6. Blough's data in generalization gradient form. From "Stimulus Generalization as a Signal Detection in Pigeons," by D. Blough, 1967, *Science, 158*, p. 641. Copyright 1967 by The American Association for the Advancement of Science. Reprinted with permission.

Adaptation Level Theory

Helson (1964) showed that judgments of stimuli used in psychophysical experiments, as well as judgments of esthetics and of the tastes, smells, and sights of daily life are always dependent on context. They are all made in reference to an *adaptation level* (AL). If judgments are made of the values of stimuli arranged along a simple continuum, such as brightness, loudness, or flicker frequency, stimuli below AL tend to be judged as weaker (less intense, fainter) than values above AL, which are judged as stronger than their ordinal position warrants.

AL is not fixed—it is set and reset by stimuli immediately present (focal stimuli), background stimuli (e.g., those comprising a large set presented during a session) and residual stimuli (e.g., representing the pooled effects of past experience). Adaptation-level accounts vary in complexity; Helson's (1964) version required the calculation of weighted log means of values of stimulation during, immediately preceding, and long preceding the presentation of a stimulus value. Only then could an AL be calculated and the effect of a current stimulus be determined

More recently Viktor Sarris (2006) argued for what he calls relational psychophysics and urged comparative studies that take into account more than simple sensory effects. To underscore the comparative aspect, the cover of his book features a baby in a high chair facing a large chicken standing on the tray The data gathered by his research group led him to a multiple-stage perceptual-cognitive theory that he proposes as better than current frame of reference theories like Helson's. But Sarris's theory loses the appealing simplicity of AL theory.

Simpler definitions of AL are more common in the literature. Malone et al. (2004) showed that AL effects are easy to show using a flickering-light continuum of seven frequencies ranging from 13 Hz to 34 Hz in 3-Hz steps. They found that pigeons' responding to an ascending series of stimuli when S+ was the center of the series (25 Hz) was elevated at 22 Hz, the value preceding S+, and during the descending series 28 Hz brought peak responding. They proposed that an AL produced by the lower frequency flickers during the ascent increased the effective frequency of 23 Hz and the reverse, high AL caused by the descent (34 Hz and 31 Hz) rendered 28 Hz effective.

CONTEMPORARY ANIMAL PSYCHOPHYSICS: SELECTIONS FROM VISION RESEARCH

Three exemplars of recent work in animal psychophysics provide a glimpse of research with three very different animal groups. William Hodos is well known for his work with birds' achromatic vision, and Christa Neumeyer is authoritative in goldfish color vision. I finish this section with a sketch of some of the amazing work of Michael Land, whose landmark study of the vision of jumping spiders remains a model of ingenuity.

"What Birds See and What They Don't"

That is the title of a 2012 lead chapter by Hodos, who probably knows more about avian vision than anyone, past or present. His attention is limited here to achromatic vision and visual acuity, not the much wider and complex topic of avian color vision.

Assessing spatial acuity. In addition to the three classic psychophysical methods, Hodos (2012) described the two methods currently used to assess visual acuity (see Chapter 3, this volume). The quickest method is the electroretinagram (ERG) that requires only a single session. A recording electrode is placed on the cornea and the retinal response to brief light flashes can be assessed. By varying the intensity of the light, using the method of limits, a threshold can be estimated. To determine spatial acuity, a patterned grid stimulus may be presented, comprising a field of lines with varying spacing so that "minimum separable acuity" can be found (Hodos, 2012, p. 14).

The line pattern is a grid and these have been used to estimate spatial frequency discrimination, allowing us to estimate the visual image resolution of a variety of animals, including human infants. Hodos (2012) argued convincingly that sine wave (sinusoidal) grids are far better than step function (square wave) grids, even though the step looks like a simple, clean light/dark transition and the sine wave seems a blurred or smudged product. But appearances are deceiving, because a 1 kHz sine is the clean display, comprising a single frequency. If we superimpose a 3 kHz signal on the original and then add a 7 kHz wave, our oscilloscope will show that we are approaching a square wave and we realize that a step-function grid is composed of who knows what sine waves, just as a Fourier analysis shows that any sound is decomposable to sine waves of many frequencies.

Birds seem to have poor acuity. A person's thumb at arm's length subtends about 2° visual angle and if it covered the grating of Figure 1.7 it would comprise about 5.5 cycles per degree visual angle which is in the range of greatest acuity for humans. If we are asked to discriminate that grating from gray, we find that our ability decreases as frequency increases, with a limit of about 30 cycles per degree (30 c/d). Surprisingly, birds have poor vision if achromatic acuity is the standard. Their maximum spatial resolution, on the basis of contrast sensitivity, ranges from 6–8 cycles/degree (c/d) in generic owls to 12–18 c/d in pigeons, and 15–33 in corvids, contrasted with 30 c/d in humans. That seems a poor showing for birds until we consider raptors. The acuity of falcons ranges from 40–73 c/d and eagles score an incredible 120–143 c/d. A kestrel, with an acuity of 43 c/d can hover at an altitude of 12 m and detect a stationary prey .25cm long. An eagle with spatial acuity of 130 c/d can spot the same tiny prey from 35 m, roughly the height of a ten-story building. These feats are possible because of the raptors' high density of photoreceptors and a deeply-pitted fovea that acts as a sort of telephoto lens. But an ordinary bird, like the songbirds we see every day, has an acuity far inferior to our own, according to contrast sensitivity data. However, maximum spatial resolution is not the only measure of acuity—there is the matter of contrast thresholds with fixed spatial frequency. But, for most birds, Hodos (2012) finds that the degree of contrast between light and dark bars on a grid must differ by 10-20%, assessed either by sinusoidal grid or ERG, whereas for humans, the Weber fraction can be less than 1%.

Incredibly, human visual acuity seems better than a pigeon's in bright light and almost as good as an owl's in low light. It is only when the illumination is very low that the owl shows its superiority and that is because of the greater light gathering capacity afforded by larger pupil size. In camera lens terms, the human f 2.0–2.5 is no match for the owl's f 1.2–1.4 or even the pigeon's f 1.7. Hawk and eagle f stops are no better than ours, because their depth of field is less a concern.

Critical fusion frequency. A tapping sound becomes a tone once a critical frequency is reached, say 55 Hz, depending on intensity, and a flickering light appears steady at about the same frequency (this happens at a far lower frequency in patients with dementia). The critical fusion frequency (CFF) also depends on the intensity of the flashing light and on the species of the observer. All birds tested for CFF with light exceed human capacities, so that a chicken can distinguish a flicker of 105 Hz and a pigeon can distinguish a flicker of 77 Hz from a steady light. Pigeons were found to quickly learn to discriminate flicker frequencies from 13 to 34 Hz, in 3-Hz steps; under similar conditions, human observers see 34 Hz as a steady light (Malone et al., 2004).

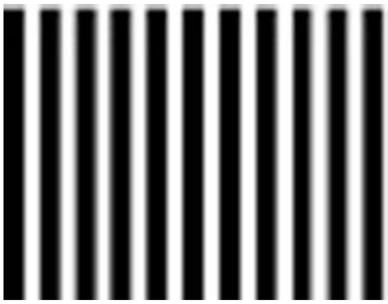


FIGURE 1.7. A grid used in assessing discrimination of spatial frequency.

Cautions in making interspecies comparisons. Hodos (2012, p. 11) warns us that despite the countless studies using many kinds of gratings and luminances, the acuity ranges cited previously can be no more than rough approximations. Spatial frequency of gratings and luminance do not tell us what the illumination of the retina is (that is, in trolands, or cd/m^2 through a 1 mm^2 pupil), because pupil diameter is almost never reported. Also neglected is the axial length of the eyes, which also affects illumination, so that the short axial length of a small bird's eye is illuminated more than is the retina of a larger eye. Greater illumination and the larger image of the small eye and the small birds' ability to focus on much closer targets could compensate for apparently poor acuity when confronted with a grating. More important, these acuity estimates are always done with achromatic stimuli and that deprives the bird of chromatic vision, which is vitally important to most birds. But that aspect of sensory science has been best studied in goldfish, not birds.

Color Vision: Neumeyer and "Goldfish White"

Christa Neumeyer (2012) believed that the only way to study color vision (see Chapter 3, this volume) is through behavioral experiments. And even if an animal shows reliable choice with brightness held constant, the response may be dependent on a receptor's sensitivity to polarization, motion, or just a general phototaxis. In all these cases there could be a "wavelength-specific behavior," but no true color vision, which must involve all known photoreceptor types.

One of many examples of careless misinterpretation that I add to her account lies in the color vision of the mantis shrimp (*Odontodactylus scyllarus*). This creature has 12 or more chromatic receptors per eye and it was easy to assume, as media reports did, that its world of color was far richer than ours, limited as we are to three cones. When careful behavioral testing was carried out by Thoen, How, Chiou, and Marshall (2014), who trained the shrimp to respond to ten wavelengths, ranging over 400–650 nm, testing showed that they were able to discriminate pairs separated by 50–100 nm, but could not distinguish wavelengths separated by 12 or even 25 nm. This poor color acuity showed that it is not the number of wavelength-specific receptors that is important, it is the capacity to deal with patterns of inputs from however many individual receptors.

The goldfish as model. Behavioral studies are essential, but difficult and time consuming, so it is helpful to choose a good subject and procedure. Neumeyer (2012) recommends the goldfish, which is tame, smart, and has a retina that is well understood. Indeed fish have served as subjects in vision research since at least the 1913 work of Karl von Frisch, who demonstrated that minnows can discriminate all the colors that humans do. Other fish, amphibians, and reptiles have served as subjects, particularly in studies of the retina, because their photoreceptors can be ten times the size of those found in birds and mammals.

In a typical experiment, the goldfish faces a pair of adjacent wavelength fields equated for brightness and saturation at one end of its tank; it is fed for swimming toward one and nosing a lever. Alternatively, a specific wavelength display may be presented at lower and lower intensity until the fish cannot distinguish it from darkness and then made gradually more intense until discriminable, using the method of descending and ascending limits. Neumeyer (2012) used such a method to show that goldfish cones' peak sensitivities lie at approximately 660 nm, 530 nm, and 400 nm, corresponding to red, green, and blue, and the 350 nm ultraviolet cone means that the color triangle that describes human color vision becomes a tetrahedron to include the color combinations possible in goldfish vision. She noted that the UV capability was actually demonstrated 60 years ago but, as is often the case, that report was ignored.

Because the combination of three primary colors produced by incandescent light and filters produces a human's experience of white, a xenon light must be added to produce the UV for "goldfish white." Neumeyer (2012) described the methodology required to show true tetrachromacy in goldfish; that is, she could match any color for the fish only with four primaries. This required a daunting course of research during the 1990s, described in general form throughout her 2012 chapter. Like humans, goldfish show color constancy, treating a color as unchanged despite great differences in the illuminant (e.g., when the yellow of morning becomes the blue of evening). And, like humans, their opponent color system means they also do not see red-green. But goldfish do "see white," though it is xenon-white and they can distinguish it from our tungsten white.

Vertebrate color vision in general. Neumeyer (2012, pp. 35–39) supplied us with a succinct summary of color vision in vertebrates that appears as up to date as that offered in other current sources (e.g., Jacobs, 2009). I further summarize in the following paragraphs.

Neumeyer (2012) explained that twenty thousand species of fish (half of all vertebrates) live in myriad environments, from muddy ponds to clear coral reefs, and sensory equipment varies greatly. We find fish with monochromatic vision and others with up to four cone types. Perhaps a third have UV capability and often that offers protection from harmful short-wavelength light. Even rods may vary and at least three kinds of rods have been reported in fish. Amphibians are difficult to handle in testing environments, but are usually trichromatic, with UV sensitivity.

Reptiles and birds have oil droplets associated with their cones, as Watson reported in 1914, and they probably act as cutoff filters modulating cone activity. The droplet attached to the S (blue) cone is clear, that with the M cone is yellow and the L cone has an orange/red droplet. The common red slider turtle's color vision includes UV sensitivity, as shown in color matching, and a color range of 400–600 nm, but unlike goldfish, acuity between 450 and 520 nm (which humans see as blue/green) is lacking.

The first UV receptors were found in vertebrates, not in insects. Pigeons not only show a range of at least 380 nm to 600 nm, but have two functional foveae, a frontal view with red droplets and a lateral with yellow droplets and better UV sensitivity.

In color naming using a MTS (matching to sample) procedure they exceed all other nonprimate species. Their four-cone retina is common to many bird species.

Mammals are not color blind, but it has taken a lot of research to show it (e.g., Jacobs, 2009). Dogs, deer, ground squirrels, pigs, and many other mammals are dichromatic, lacking the long-wavelength (L/red) cone, with sensitivity peaking at 500 nm (green) but without UV sensitivity. Mice and rats are sensitive to UV, and to middle-wavelength stimuli. Old-world monkeys are trichromatic like humans, but new world monkeys seem all to be dichromatic with the exception of some females, which can be trichromatic.

Marine mammals are difficult subjects for psychophysical research. Whales and seals have no short-wavelength cones, much less UV sensitivity. They appear to possess only an M (mid-wavelength, green) cone, which has seemed odd to many investigators, because the deep ocean is blue and green seems better suited to coastal waters. In any event, one cone is not enough to allow any kind of color vision, because color is the product of the pattern of response of at least two kinds of chromatic receptors. This led to speculation by Griebel and Peichl (2003) that perhaps some M-cone/rod interaction allows some color vision and accounts for the finding that aquatic mammals can discriminate blues and greens from all shades of gray.

Color vision is common in vertebrates and probably originated as tetrachromacy and trichromacy that disappeared in mammals and reappeared in old world primates; Jacobs (2009), the expert on this issue, provides details. The standard reference to trichromatic vision as an adaptation to allow primates to distinguish ripe and unripe fruit or berries and leaves is certainly not the case or, at best, is simple-minded. Color vision adds a huge amount to overall visual content for primates as well as for goldfish, reptiles, and many other species that have no commerce with fruit or leaves.

Along Came a Spider: Ophthalmoscopy in Salticids

Salticid (jumping) spiders may be tiny, yet their amazingly acute vision and eerily-intelligent predatory behavior have made some of them, like *Portia labiate*, assume an African lion aspect, inspiring authors like Barrett (2011) and Harland, Li, and Jackson (2012) to compare them to carnivore vertebrates. Those authors emphasize that Salticids show what can be done with a tiny nervous system, though it is a mistake to assume that the spiders perceive a world in any way like the one that humans have constructed.

Land's ingenious procedure. Helmholtz invented the ophthalmoscope to show his medical students that light enters and exits the eye and in so doing enabled viewing of the retina in a living organism. Modern devices work a bit differently, but one researcher used a method similar to Helmholtz and constructed an ophthalmoscope to apply to spider retinas. This astounding feat was accomplished by Michael Land in 1969 when he was a postdoctoral fellow at Berkeley. The device that he built required almost no funding and 36 years later he said that "Bugs and humans are both cheap, compared with cats and monkeys . . . and I like to do my own work. So I'm cheap to run" (Land, 2005, p. R281). His subjects in 1969 were jumping spiders, the largest of which (*Phidippus johnsoni*) may reach 11mm long, and his findings remain a standard reference for researchers such as Harland et al. (2012).

Salticid spiders are known for visual equipment that provides incredible spatial acuity equal to a pigeon's, and color vision with "true form vision" in eyes with no more than a few thousand photoreceptors (Land, 1969). Land was concerned with only the two forward-facing principal eyes, not the six secondary ones that serve an accessory function. The main eyes have a corneal lens mounted in two eye tubes with a secondary lens that produces a telephoto effect. Land knew that the eyes were movable, show nystagmus, and can distinguish prey from potential mates at distances of at least ten body lengths, meaning that an image covering 100 receptors at most can be assessed by the spider. This could only be possible if repeated scanning occurred and Land showed that the retinae move back and forth across the target, while simultaneously partially rotating around the visual axes of the eyes.

Land's (1969) ophthalmoscope comprised a 6v car headlight bulb source passing light through a collimated (light-aligning) lens, a focusing lens, a second collimator, and finally focusing on the cornea/lens of the spider, which was tethered. A beam splitter allowed the observer, at right angles to the beam, to see either the corneas or the retinas of the spider's eyes. Various stimuli to evoke eye movements were inserted just past the initial lens and projected into the eyes. Though its direction of gaze was fixed and the spider stuck to a waxed card, it could move, because it "held a light card ring between its feet, round which it could move at will without moving its body" (p. 473). The observer tracked the movements of the two anterior eyes by moving a grid line in the image plane that he kept aligned to the inner edges of the retinas. As the eyes moved, two pens recorded the eyes' positions as he followed them.

Through the jumping spider's eyes. Through this remarkable method and the dissection of several specimens, Land (1969) was able to show that the eyes (or eye tubes) are controlled by six muscles on each eye with each muscle controlled by a single neuron. The eyes move together, though not connected, and rotate as much as 30° right and left so that constant movement, including saccades, seems to effectively compensate for the lack of number of photoreceptors. The fields of view of the two retinas do not overlap, though they do superimpose on a stimulus dot that is moved into their view and they track it as it moves. When it stops, scanning movements begin as regular periodic horizontal movements, along with slower rotation of the eye tubes and retinas.

Though these spiders have no real fovea, the centers of their boomerang-shaped retinas have ten times the density of the periphery and four layers of cells, whereas there are only two in the periphery. Thus, the retinal peripheries, as well as the six side eyes respond so as to bring a new moving stimulus to the front, followed by a saccade to place the target in the center of the retinas. The scanning that comes next is "without parallel in any other visual system" (Land, 1969, p. 489) and is followed by "watching" the target for a few seconds and then one of five general actions. The spider may move toward the target and attack, begin a courtship dance (male), remain still (if female), flee, or walk away. How the spider discerns prey from mate from predator has puzzled every researcher who has studied these animals and previous work led Land to propose that the geometry/form of the object is key. If it is small, dark, and moves, the spider will be prone to attack, unless the target has a pair of oblique lines on each side, meaning that it is another salticid. The scanners seem to be looking for those "spider-leg" lines. Perhaps each retina has an oblique-line detector, similar to the bar detectors in the cortex of higher vertebrates.

That cannot be the whole story, because the simple cells and their elaborations in the visual cortex of cats, monkeys, and humans do not begin to account for perception—perhaps the amphibian "bug detector" is a more apt analogy. Further, Land (1969) knew that jumping spiders can recognize spider-like targets rotated through 90° and 180°, so the comparison with cortical edge detectors is misplaced. But at least we now know how it sees, if not how it knows what it sees.

CONCLUSION

Animal psychophysics is an integral part of sensory science and far too vast a field to summarize compactly; I take some comfort in the fact that previous authors have had the same difficulties that I experienced. Needless to say, my inclusion of exemplars and even of references had to be arbitrary, since the number of excellent options seems endless. But the most useful reports remain those that are written in the way that S. S. Stevens preferred. That is, they come in plain language, detailing the procedures that were involved and drawing conclusions that seem justified without use of jargon or anthropocentric interpretation. They do not depend on wildly speculative neural bases or use cognitive processing language as an appeal to the popular media.

Any treatment of psychophysics must include Weber and Fechner and the simple psychophysical methods that are still useful even if we are not trying to prove mind and body identity. Stevens showed that Fechner was wrong and that judgments of sensation intensity increase geometrically, not arithmetically, as stimulus intensity increases geometrically, so a power function replaced Fechner's classic equation. Stevens's reformulation and direct scaling methods might have had more influence if not for the revolution brought by signal detection theory in the 1960s, which showed that the subjects' criteria for detection could be more important than the strength of stimuli to be detected.

The final section is meant to convey examples of research programs that are models for the kind of work that advances understanding in comparative psychophysics. Hodos (2012) and Neumeyer (2012) exemplify the kind of painstaking long-term focused research that ignores the pressure of appeals for presentations that the media can present as "breakthroughs." Thankfully, theirs are not the only examples of such programs. The final section illustrates what can be accomplished by a lone researcher with a small budget. Land's construction and use of an ophthalmoscope for *in vivo* research with spiders the size of a small kernel of corn, as well as his subsequent work on vision has inspired a host of subsequent researchers.

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CHAPTER 2

HEARING AND COMMUNICATION

Georg M. Klump

Acoustical signaling forms the basis for many important communication mechanisms not only in humans, but also in many nonhuman species. The complexity of speech and the large repertoires of song elements produced by some birds provide prime examples for the complex and highly evolved acoustic communication in social interactions (see ten Cate, 2014; see also Volume 1, Chapters 26 and 30, this handbook). Repertoires of bird song elements can include more than 1,000 items (J. M. Moore, Székely, Büki, & Devoogd, 2011) and bird song has been demonstrated to have a syntax resembling the syntactical structure of human speech (e.g., Berwick, Okanoya, Beckers, & Bolhuis, 2011). In addition, the majority of bird species learn their songs by vocal imitation that in many aspects resembles human vocal learning (Doupe & Kuhl, 1999). These striking parallels in the processes underlying human and bird communication have provided the motivation to often put birds in the focus of comparative studies of hearing and communication (see Volume 1, Chapter 26, this handbook).

Evolution has adapted signal structure to specific functions (see Volume 1, Chapter 30, this handbook). Territorial signals have evolved structures that support broadcasting the sounds over a large distance (Brumm & Naguib, 2009), whereas some alarm signals are mainly for private communication of prey avoiding detection by a distant predator (Klump, Kretzschmar, & Curio, 1986). Signals serving to attract mates are also optimized for good transmission and often have features that advertise the signaler's quality (e.g., W. Fitch & Hauser, 2003). However, some signals are not necessarily honest to best serve their functions.

Adaptations for acoustic communication not only occur on the sender's side but also in the receiver's auditory system. Ears have evolved that can detect both faint signals and at the same time, function for processing signals with levels ranging over six orders of magnitude (e.g., Manley, 2000; Nobili, Mammano, & Ashmore, 1998). High sensitivity is especially important for nocturnal predators detecting prey, and the most sensitive hearing among all vertebrates has been found in owls and cats (e.g., Dyson, Klump, & Gauger, 1998; Neff & Hind, 1955; see Figure 2.1).

Usually, however, the hearing system has to function well above the absolute hearing threshold of the ear. This suprathreshold hearing determines how well communication is possible in the natural, noisy world. Tree-frog (*Hyla spp.*) choruses, in which a female chooses a mate on the basis of his advertisement signals, are among the loudest acoustic environments created by the cacophony of hundreds of males acoustically competing for the female (e.g., Gerhardt & Klump, 1988; Schwartz & Bee, 2013). Need for communication in noisy cocktail-party situations is not limited to human subjects (Bee & Micheyl, 2008). Environmental noise because of wind or traffic also has a profound impact on the receiver's ability to detect and recognize signals above auditory threshold (Brumm & Slabbekoorn, 2005). Humans and animals have developed a remarkable ability to cope with

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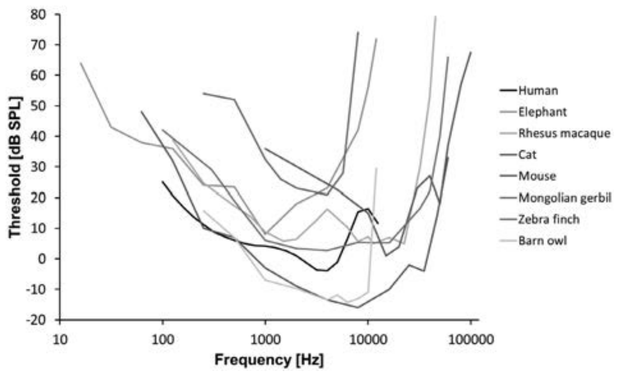

FIGURE 2.1. Auditory threshold of some representative animal species obtained in quiet (human: International Organization for Standardization, 1961; Indian elephant: R. Heffner & Heffner, 1982; Rhesus macaque: Pfingst et al., 1978; cat: Neff & Hind, 1955; mouse: Ehret, 1974; Mongolian gerbil: Ryan, 1976; zebra finch: Okanoya & Dooling, 1987; barn owl: Dyson, Klump, & Gauger, 1998).

complex acoustic scenes with sounds from many sources, an ability termed *auditory scene analysis* (ASA; Bregman, 1990). ASA mechanisms allow the receiver to separate sounds from different sources and group sounds from each source thus providing for an improved ability to analyze signals broadcast by each sender separately.

One chapter cannot cover every facet of hearing and acoustic communication in detail but can only provide an introduction to the basics. Throughout the chapter, I provide the reader with additional references that provide a deeper insight. After introducing the physical features of sounds, I provide insight on the constraints in acoustic signal production and transmission, and discuss signal features that affect detection and discrimination. Next, communication is looked at from the receiver's perspective. The functional principles of hearing organs are elucidated, as well as the general processing mechanisms in the neuronal auditory pathway leading to perception. Finally, the study of perception in animal models is illustrated using examples related to detection, discrimination, localization, and the analysis of signals in complex acoustic scenes with many active sound sources. General introductions to human communication and auditory perception are provided by B. C. J. Moore (2012) and Plack (2014).

PHYSICAL FEATURES OF ACOUSTIC SIGNALS

The physics of acoustic signals makes these ideal for communication. Acoustic communication does not require a line of sight between the sender and the receiver because sound waves can travel around obstacles on their path from sender to receiver. The transmission distance can be adjusted by setting the sound pressure level (SPL) of the signal broadcast by the sender and by the choice of spectral composition of the signal (Brumm & Naguib, 2009). SPL is measured in decibel (dB) which is proportional to the logarithm of a ratio of two sound pressures:

Sound pressure level [dB] = 20 * log10
(pressure 1/ pressure 2)

If pressure 2 has the value of $2 * 10^{-5}$ N/m^2 (i.e., Pa), which is the sound pressure at approximately the human absolute hearing threshold, the unit of sound pressure is dB SPL. It has a value of 0 dB SPL at about the normal absolute hearing threshold of human subjects and ranges up to values of 120 dB SPL for very loud sounds that can damage sensitive ears. Loudness is the perceptual entity that represents sound pressure.

The spectrum of a signal is characterized by the SPL of each tone frequency contributing to the signal. The frequency of communication signals that different animal species use (see Figure 2.2) may vary from less than 30 Hz (termed *infrasound frequency range* with respect to the lower frequency limit of human hearing) to up to 200,000 Hz (termed *ultrasound frequency range*, relative to the upper limit of human hearing of about 18 kHz). Most other mammals have a higher upper frequency limit of hearing than humans and thus can use a larger frequency range for signaling (H. Heffner, Heffner, & Heffner, 1998). Infrasound sensitivity is only found in some exceptional cases, for example, in elephants that have been shown to use very low frequency communication signals (R. Heffner & Heffner, 1982; Payne, Langbauer, & Thomas, 1986; see Figures 2.1 and 2.2B). Tonal signals mainly contain spectral energy at one frequency. However, the sound producing apparatus often creates signals with multiple frequency components that are either

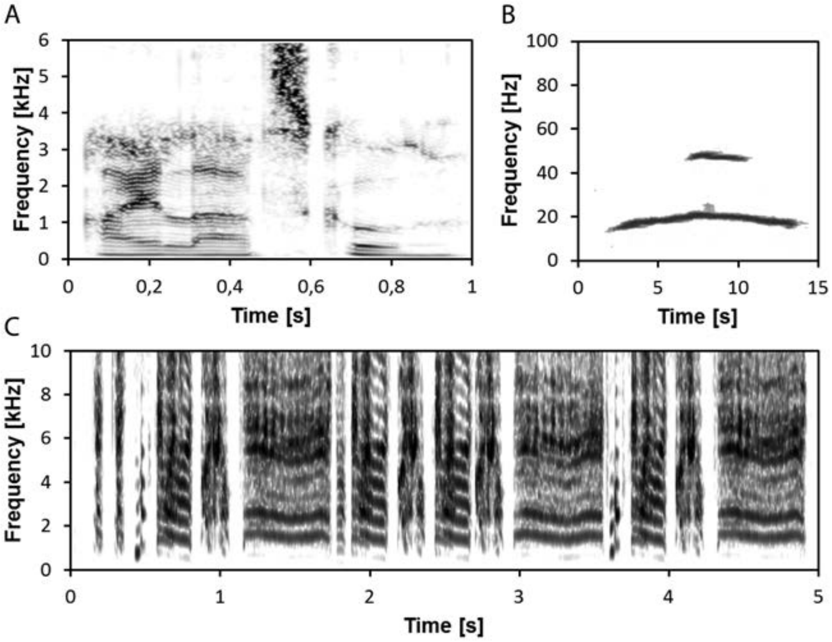

FIGURE 2.2. Spectrograms of exemplary communication sounds: (A) human speech (male subject uttering the sentence "I love school"), (B) infrasonic call of Indian elephant (data from Payne et al., 1986), and (C) zebra finch song (data from ten Cate, 2014). In the spoken sentence and in the bird song sequence, harmonic complex signals can be seen (parallel line in the spectrum) with components starting simultaneously.

integer multiples of the fundamental frequency (termed *harmonic frequencies*; see Figure 2.2A and 2.2C) or it produces noisy sounds that include a range of nonharmonic frequencies (see Figure 2.2A). Pitch is the perceptual entity that represents the frequency of a tonal signal. The pitch of a harmonic complex tone represents the frequency of the fundamental. Noisy sounds have no clear pitch. As with harmonic complex tones, noisy signals can elicit a perception of timbre (i.e. a sound quality in perception that is related to the shape of the spectrum).

Besides the spectral composition, temporal patterns of signals can be relevant for communication. Overall signal duration is relevant for detecting signals: Long signals can more easily be detected because these contain more sound energy than short signals (e.g., Pohl et al., 2013). Variation of the SPL over time, which can be described by the spectrum of the signal envelope, is characteristic for many signals. Speech, for example, has envelope frequencies of a few Hz. Regularly repeating rapid envelope variation is typical for sinusoidally amplitude modulated (SAM) sounds. Up to envelope frequencies of about 100Hz, SAM communication sounds are mainly analyzed in the time domain by the auditory system. At higher envelope frequencies, the auditory system processes the SAM in the frequency domain (Joris, Schreiner, & Rees, 2004). The shape of the signal envelope (e.g., the "ramps and damps") is also of perceptual relevance (e.g., Irino & Patterson, 1996). We experience this if we reverse a recorded sound and play it back. In some frogs, ramps have been shown to be relevant for species recognition (Gerhardt & Schul, 1999). Recently, there is an increased interest in the temporal fine structure of signals, that is, the temporally repeating patterns that characterize the carrier on which the amplitude modulation is impressed (B. C. J. Moore, 2014). Temporal fine structure analysis can enhance speech perception in noise or support localization of sound sources. Sharp transients of signal level at onset and offset may also support sound localization.

These physical features of communication sounds described as separate entities are often integrated in perception (e.g., in the segregation of sound sources in complex acoustic scenes). The apparatus producing communication sounds automatically will create common onsets and offsets of the frequency components that will then be grouped in perception on the basis of common level transients (e.g., Figure 2.2C). Harmonic tone complexes used in communication are produced by the sound source (e.g., the vocal folds), emitting pulse trains. Thus, harmonicity that is due to the physics of the sound producing mechanism has established itself as a strong grouping cue for frequency components of sounds originating from one source (e.g., Darwin, 2008).

PHYSICAL CONSTRAINTS TO ACOUSTIC COMMUNICATION

To address the intended audience, the signaler has to take the laws of physics, which affect optimal signal design, into account. The receiver can also make use of these fundamental physical principles for improving perception, especially if signals are degraded or masked. How physics constrains sound production, transmission, and perception is outlined in the sections that follow.

Sound Production

The frequency range for efficient sound production (important for long-range communication) is constrained by the mechanics of the sound producing structures, their acoustic resonance, and the coupling of the sounds to the medium through which it is transmitted from the sender to the receiver. Factors such as the size, the stiffness, and the mass of vibrating structures as well as the size of resonant cavities involved in producing the sounds will affect the frequency spectrum of the signals. For example, smaller body size confines an animal to producing higher frequencies than a competitor with a larger body size, because production of low frequencies is constrained by the size of the sound producing structures. This forms the basis for the signal frequency spectrum being an "honest" reflection of body size in animal communication (W. Fitch & Hauser, 2003). Resonances of sound producing structures serve to enhance a narrow range of frequencies or shape the spectrum of a sound produced with a wide range of frequencies (Riede, Suthers, Fletcher, & Blevins, 2006). The resonance frequency of the wings of a cricket will determine the frequency spectrum of its advertisement songs for attracting mates (Mhatre, Montealegre, Balakrishnan, & Robert, 2012). In human speech production, the resonance characteristics of the vocal tract and the mouth determine the frequency peaks in the spectrum of sounds (termed *formants*) that are used to categorize different vowel sounds (Peterson & Barney, 1952). Only the sound energy that is coupled to the medium for transmission and that is also monitored by the receiver is relevant for communication. For example, some stridulating bugs will transmit the sound through the stems of a plant to attract mates while effectively avoiding attracting acoustically hunting birds using airborne sound (e.g., Virant-Doberlet & Čokl, 2004). Underwater sounds are restricted to the body of water and are not efficiently crossing the water surface to be converted to airborne sounds that humans can perceive well. This limit is due to the impedance mismatch between water and air and isolates humans from animals communicating in the water.

Sound producing structures are rarely omnidirectional (Larsen & Dabelsteen, 1990). Emission of high-frequency sounds usually is more directional than the emission of low-frequency sounds. Directionality can be a disadvantage if there is no preferred direction (e.g., in sounds used for attracting mates). One strategy to overcome this disadvantage would be turning the sound source during production, as can be observed in many birds singing. If, however, a high directionality is advantageous, morphological structures allow forming a sound beam for emission of signals. Such a sound beam can be used to address specific receivers or, in echolocation, to inspect certain structures in the environment (Surlykke, Ghose, & Moss, 2009).

Sound Transmission

The modifications of the sounds on the transmission path from the sender to the receiver limit the detectability of sounds and the utility of some of the physical features for recognizing signals (Klump, 1996; Wiley & Richards, 1982). Sound level decreases with increasing distance from the sound source, which provides a major limitation to the detectability of communication sounds. This decrease because of attenuation by geometric spreading (in theory, for an omnidirectional source) amounts to 6dB per doubling of distance. This change in level, however, can be modified by a deviation from the omnidirectionality of the source and by frequency specific effects of absorption of sound energy, sound reflections on surfaces, and diffraction. If, on the one hand, the transmitted sound is confined to one segment in the environment (for examples, see Bass & Clark, 2003; Wiley & Richards, 1978) the reduction in level with distance can be lower than 6 dB per doubling. Diffraction of sound affected by the density of the medium (e.g., because of temperature gradients and reflections on surfaces) may help to confine the sounds to a layer parallel to the surface of the earth resulting in a reduced attenuation. On the other hand, water molecules in the air absorb sound in a frequency-dependent manner which produces a major obstacle to long-range communication in terrestrial environments. Absorption of sound is low for frequencies up to 4 kHz and increases with increasing frequency above this level. The combined effects of absorption by the medium transmitting the signals, the frequency-specific reflections from surfaces, and the diffraction are usually summarized by the value for *excess attenuation* that characterizes the deviation from the attenuation being due to geometrical spreading of sounds from an omnidirectional source alone (Dabelsteen, Larsen, & Pedersen, 1993). Excess attenuation is especially important if one considers large transmission distances. Because attenuation also depends on reflections that may lead to constructive or destructive interference (resulting in a sound level increase or decrease, respectively), a range of distances should be used to obtain an estimate that reflects the environmental conditions in general.

Besides affecting the level of the sound in a frequency-specific manner, sound transmission also limits the usefulness of temporal features of signals for long-range communication. Air turbulence modulates the envelope patterns of sounds, resulting in rapid level fluctuations (Richards & Wiley, 1980). Reverberations because of reflections from surfaces will fill silent intervals within sounds with acoustic energy and add echoes, thus obscuring temporal structure. Thus, rapid amplitude modulation of sounds and sharp amplitude transients are not well preserved in long range transmission.

However, the degradation of signals with transmission distance can also provide useful information for communication for determining the distance of a receiver from the sound source (Brumm & Naguib, 2009). Such ranging of communication signals is useful (e.g., for evaluating the distance of a competitor in territorial conflicts). It has been demonstrated in field experiments that birds fly a larger distance if a degraded competitor's song rather than a nondegraded song is played back to them suggesting that birds make use of degradation cues in their natural behavior (e.g., Naguib, Klump, Hillmann, Grießmann, & Teige, 2000).

Masking

If a signal is broadcast by the sender in the presence of other simultaneously active sound sources providing background noise, the relative level of the signal in relation of the level of the background noise determines signal detectability (for a review of masking effects see Klump, 1996). In general, a signal embedded in a steady-state background noise becomes audible if its level in a frequency filter of the auditory system is similar to or above the level of the background noise in that frequency filter (i.e., a signal with a relative level greater than 0 dB). This type of energetic masking is due to the interaction of signal and masking background noise at the sensory cells in the ear (see Figure 2.3). Fortunately, many sound sources in the natural environment produce signals that rapidly vary in level with time. This variation results in peaks and dips in the envelope of background noise that can be exploited for improving signal detection. Air turbulence on the transmission path will also create level fluctuations of masking noise over a wide range of frequencies, and a signal of interest that originates from another source will carry different envelope fluctuations than the noise background. These fluctuations can be exploited to lower detection thresholds, a perceptual effect that has been termed *comodulation masking release* (CMR; Hall, Haggard, & Fernandes, 1984;

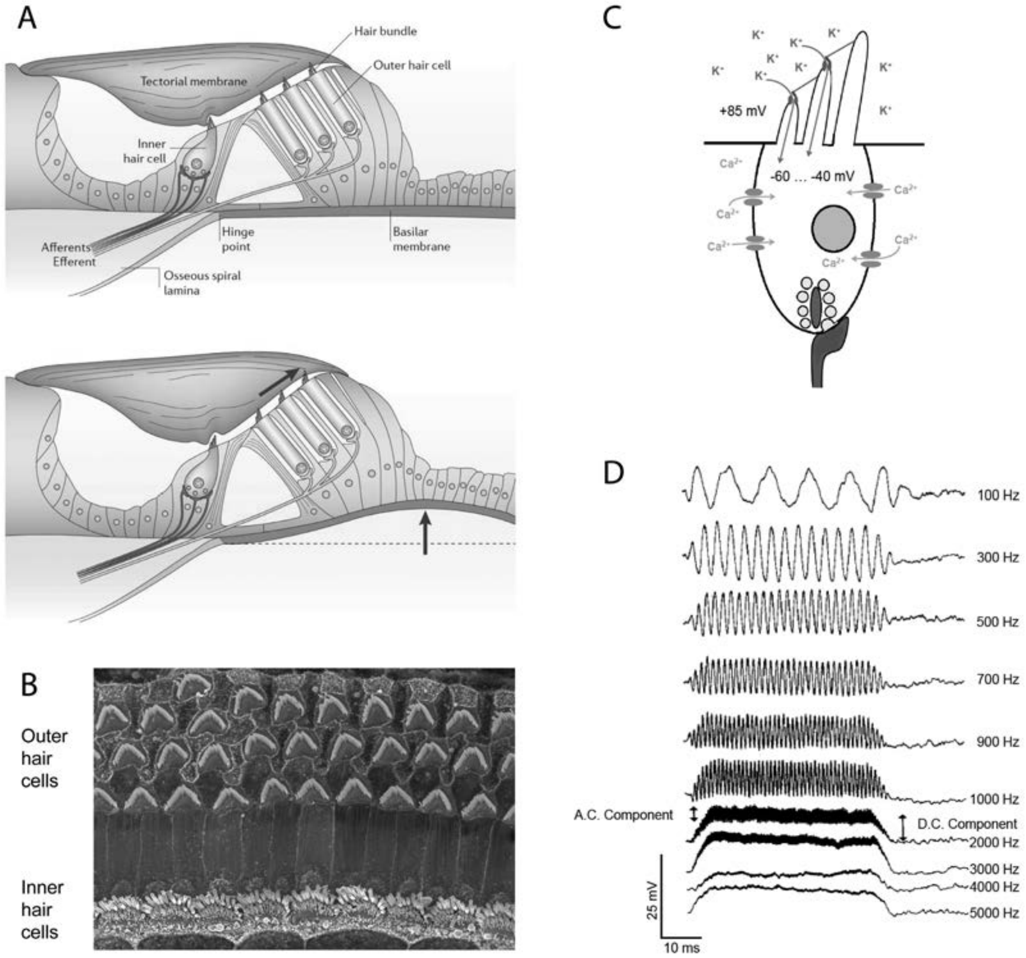

FIGURE 2.3. Mechanism of sound transduction in the mammalian inner ear. (A) Cross section through the organ of Corti. Due to the sound-generated bulging of the basilar membrane, the stereovilli (hair) bundles of the sensory cells are deflected and the membrane potential of the sensory cells changes. From "The Sensory and Motor Roles of Auditory Hair Cells" by R. Fettiplace and C. M. Hackney, 2006, *Nature Reviews Neuroscience, 7,* p. 22. Copyright 2006 by Macmillan Publishers. Reprinted with permission. (B) Scanning electron micrograph of the mouse organ of Corti showing a top view on the stereovilli bundles of outer and inner hair cells (provided by Karim Boustani & Dr. Jing Chen, King's College London). (C) Transduction mechanism of the hair cell. Deflection of the bundle causes the opening of potassium channels, which results in a change of the membrane potential. This change triggers a sequence of events leading to a transmitter release at the ribbon synapse that is enabled by the calcium ions in the hair cell and results in action potentials in the auditory nerve. (D) Depending on the stimulus frequency the two components of the membrane potential vary. At low frequencies, the membrane potential follows every cycle of the stimulus (A.C. component) resulting in phase locked action potentials. At high frequencies, the membrane potential cannot follow the stimulus cycles and only a D.C. is observed that precludes the phase locking of the action potentials in the auditory nerve fiber (data from Palmer & Russel, 1986).

Verhey, Pressnitzer, & Winter, 2003) or *comodulation detection difference* (CDD; Cohen & Schubert, 1987). Signal detection can improve by 10 to 20 dB in fluctuating noise maskers, an effect that can make communication possible in noisy environments (e.g., a busy pub, a bird morning chorus) and can vastly increase communication distance in the natural environment (Klump, 1996). CMR and CDD have been demonstrated in birds and mammals, indicating that the mechanisms underlying improved signal detection in fluctuating noise must be widespread (Klink, Dierker, Beutelmann, & Klump, 2010; Klump & Langemann, 1995; Langemann & Klump, 2007). Several hypotheses have been proposed regarding the mechanisms underlying CMR and CDD. The auditory system can exploit time periods of low masker amplitude (i.e., dip listening) and the comparisons across separate frequency filters in the auditory system to reduce masking (Verhey et al., 2003). Furthermore, the nonlinear representation of sound level by the ear (i.e., the compression of the representation of sounds in the inner ear at intermediate sound levels) can explain part of the release from masking (Buschermöhle, Verhey, Feudel, & Freund, 2007).

Spatial separation of sound sources can be exploited to obtain a release from masking. If a source broadcasting a signal of interest and an interfering sound source are spatially separated, the directionality of each ear and the comparison of sounds from the left and right ear help to segregate the sound of interest from the interfering background. Two effects have primarily been studied in this respect: (a) the binaural masking level difference (BMLD) and (b) spatial release from masking (SRM). The BMLD describes an improved detection of a signal arriving at the two ears 180 degrees out of phase (i.e., simulating a signal coming from the side) compared to detecting the same signal arriving at the ears in phase (i.e., simulating a signal coming from the front and having no interaural time difference) in a noise masker that arrives at the ears at the same time (i.e., is identical at both ears simulating a source in front of the listener). BMLD has been described for humans and for animal subjects (Early et al., 2001; Hirsh, 1948). BMLD mechanisms can improve low-frequency signal detection in background noise by up to 15 dB. SRM denotes the improved detection of signals from one location in a masker originating from a different location. SRM can result mainly from analyzing the sound with the ear having the best signal-to-masker ratio of the sound level (i.e., a better ear effect) or from true binaural comparison in the auditory pathway of the brain. SRM has been investigated in a range of animals and humans (Bronkhorst & Plomp, 1988; Dent et al., 2009).

Energetic masking occurs if signals of interest and maskers stimulate the same sensory cells in the ear at the same time because of the physical interaction between the stimuli in the ear. Considerable masking can also occur if there is no energetic masking. This “informational masking” results from the inability to focus on the signal of interest and to analyze it separately from other signals that cram the acoustic scene and function as distractors (Kidd, Mason, Richards, Gallun, & Durlach, 2007; Watson, 2005). Two effects determine the amount of informational masking: (a) the similarity between the distractors and signals of interest and (b) the uncertainty, or variability, of important features of a signal that needs to be analyzed. If the distractors are processed in the same auditory stream as the signals of interest and show a large variability, then informational masking is high. For example, it is difficult to detect a tone signal of a specific frequency if many distracting signals of the same duration but with a different frequency are presented simultaneously. Furthermore, it is difficult to discriminate features of signals of interest if distractors processed in the same auditory stream vary considerably in these features. If distractors and signals of interest are processed in different auditory streams, informational masking can be completely abolished if the receiver can parse an acoustic scene and focus on the stream of interest. Informational masking has been demonstrated for processing of acoustic signals in humans and in animal subjects (Dolležal, Tolnai, Beutelmann, & Klump, 2013).

Signal Variability

Variability of signals may hamper recognition. It is easier to recognize and classify signals if the physical features of the different signal types have distinct means and distributions that show little overlap. Signal-detection theory can explain the effects of signal variability on the animals’ detection and recognition of communication sounds (Wiley, 2006). Field studies on song recognition by birds revealed that they treat signals as being different from the species’ own song if the stimulus characteristics of the songs deviate by two standard deviations or more from those of the species’ average (Nelson & Marler, 1990). Although in the field, stimulus variability appears to limit discrimination, in most laboratory studies it likely is the noisy internal representation that determines the discrimination threshold.

PHYSIOLOGY OF AUDITION

The perceptual performance of the receiver is determined by mechanisms operating on different levels in the auditory system. In the auditory periphery, the ears have evolved to achieve a high sensitivity for the different features of communication signals. Specialized computational mechanisms in the auditory pathway serve to further improve the segregation of signals from the ubiquitous background noise in the natural environment. Some of the most important functional principles will be described in the sections that follow.

Ears

Ears are signal transducers that produce a pattern of neural activity on the basis of the sound waves impinging on the hearing organs. Ears must function over a large range of sound pressures varying more than six orders of magnitude. This requires a high sensitivity for sound with a low sound pressure, and a reduced sensitivity for sounds with a high sound pressure (Nobili et al., 1998). Three general types of ears can be found: (a) *antennal* or *bristle ears* that process the velocity of air particles, (b) *tympanic ears* that process sound pressure waves in air, and (c) *otolith ears* that process sound waves transmitted through water. Although these types of ears look quite different, their general functional principles regarding sensory cells are remarkably similar. A general overview on the mammalian ear and auditory pathway is provided by Pickles (2012).

Antennal or bristle ears are found, for example, in insects (Robert & Göpfert, 2002). In the fruit fly (*Drosophila melanogaster*), the sound of the courtship song produced by vibrating the wing moves the distal segment of the antenna that is mounted in a cup so that it can be deflected to all sides (Göpfert & Robert, 2002). The movement of segments mechanically stimulates the sensory cells that transmit information via the antennal nerve fibers to the brain. To achieve high sensitivity, the insect antennal ear involves active amplification as has been observed in vertebrate ears (Göpfert & Robert, 2001; Robert & Göpfert, 2002). Tuning is due to the mechanical properties of the antenna. For example, the physical dimensions of the antenna of male mosquitos tune it to the wing beat frequency of the female with a resonance making it especially sensitive (Göpfert, Briegel, & Robert, 1999; Göpfert & Robert, 2001).

Tympanic ears are typically found in land vertebrates (e.g., amphibians, reptiles, birds, mammals). Often, external structures such as pinnae guide the sound into the ear canal that is terminated by the tympanic membrane (in some ears, e.g., in frogs, no external structures are found and the tympanic membrane is right at the surface of the head). Airborne sound impinges on the membrane which has bones attached that transmit the sound through the middle ear into the liquid-filled inner ear. These bones form a lever that increases the sound pressure at the oval window, a small membrane that forms the entrance to the inner ear. The ratio between the tympanic membrane surface and the oval window surface plus the leverage provided by the middle ear ossicles matches the impedance between the airspace outside the tympanum and the watery liquid in the inner ear. Without such an impedance matching, little sound energy would reach the inner ear. Birds, reptiles, and amphibians have only one ossicle (the columella), whereas mammals have a chain of three middle ear ossicles (malleus, incus, and stapes) forming the leverage system in the middle ear (Manley, 2010). Birds, reptiles, and amphibians have another special development of the middle ear structures: The cavities of the left and right middle ear, in which the auditory ossicles are positioned, are well connected by an air space (Christensen-Dalsgaard, 2011). In birds this air space is formed by the spongiform space within the bone of the skull, whereas in reptiles and amphibians the air space is formed by the mouth cavity and the Eustachian tubes (the tympana can be seen from the inside the mouth of a frog). The connection between the two middle ear spaces creates a pressure-gradient receiver that produces a large directional response of the tympanic membrane without any external ear structures. It is especially helpful for producing directionality if the wavelength of the sound is much larger than the diameter of the head and the distance between the ears. In mammals, the tympana operate as pure pressure receivers of the sound impinging from the outside and mostly the external structures determine the directionality of the ears.

Otolith ears that are found in water-dwelling animals, such as fish, lack external and middle ear structures (Popper & Fay, 2011). Sound travelling underwater enters the body of an animal with little attenuation (i.e., the body is transparent to the sound) and no impedance matching is necessary. The otholiths have a higher density than the surrounding tissue and will thus be "rocked" by the sound waves and stimulate the sensory cells in the ear through their motion. As in the case of antennal/bristle-type ears, the otholith motion is related to the angle of sound incidence. Thus, the vibrations of the structures in these types of ears represent not only the sound pressure but also the direction of the sound source (Fay, 2005).

Whereas sounds are transmitted to the sensory cells via solid structures in the antennal/bristle and otholith ears, sounds in the tympanic ears of the vertebrates are transmitted from the oval window to the sensory cells via the watery liquids in the inner ear. Generally, the sensory cells are organized in a flat tissue, the sensory epithelium residing on a vibrating membrane, the *basilar membrane* (Raphael & Altschuler, 2003; see also Figure 2.3). Each sensory cell on the one end has extensions that vibrate when stimulated with sound and on the other end has synapses releasing transmitters that excite the nerve fibers sending the sound-induced action potentials to the brain. The extensions (called *stereovilli* or *stereocilia*) look like hairs and, therefore, the sensory cells are called *hair cells* (Fettiplace & Hackney, 2006; Gillespie & Müller, 2009; Raphael & Altschuler, 2003). The tips of the stereovilli are the site of mechanically driven potassium channels that open and close when the bundle of stereovilli moves. If the hair bundle moves in the direction of the longest stereovilli, the filaments attached to the channels are strained and the channels open, and moving in the other direction releases the tension and the channels remain closed. The change in the hair cells' membrane potential follows the time pattern of the movement of the bundle (AC potential) up to sound frequencies of 2-4 kHz, whereas a general slow change of the membrane potential (DC potential) dominates at higher frequencies (Palmer & Russell, 1986; see Figure 2.3D). The AC potential triggers a phase-locked release of a transmitter by the hair cell and phase-locked action potentials in the auditory nerve. Phase locking represents the temporal fine structure and timing of transients in the sounds enabling deducing the sound frequency from the time interval between phase-locked action potentials. The hair cells not only respond passively to the vibration of the stereovilli bundle but also are able to actively move the bundle and change their form (mammalian hair cells can do so on the basis of conformational changes in the membrane protein prestin; see Dallos, 2008). This active motion is the source of amplification of actions by the sound wave traveling in the inner ear, and the motion-driving system has been named the *cochlear amplifier*. Without the action of the cochlear amplifier, the ear is about 40 dB less sensitive which is a major cause of hearing deficits in older humans (Nobili et al., 1998).

Hair cells in the sensory epithelia are not randomly positioned and oriented. In antennal/bristle ears, the sensory cells surround the vibrating structure (e.g., the bristle), representing the direction of the movement by the distribution of activity in the population of sensory cells (Göpfert & Robert, 2002). Sensory epithelia in otholith ears have two populations of hair cells with opposing orientation (Popper & Fay, 1973). Because the orientation of the bundle determines the hair cell's response, such structures also may encode the direction from which the sound impinges on the ear. In tympanic ears, the direction of the sound source is determined by neural computations higher up in the auditory pathway. In mammals, a distinct row of inner hair cells, having mainly afferent innervation, and three rows of outer hair cells, having mainly efferent innervation, are found. The inner hair cells transmit the information upward on the auditory pathway, and the outer hair cells serve to construct the cochlear amplifier (Nobili et al., 1998). Birds have many more rows of hair cells, and there is a gradual transition between hair cells functioning similarly to the mammalian inner hair cells and hair cells functioning similarly to the outer hair cells

(Manley, 2000). In the mammalian tympanic ear, in general, vibrations at the oval window elicit traveling waves on the basilar membrane that will peak at a specific location related to the frequency of the sound. This peak occurs close to the oval window for high frequencies (basal end of the basilar papilla) and at the far end of the basilar papilla (apical end) for low frequencies. Thus, frequencies are mapped on spatial coordinates (Greenwood, 1990). This tonotopic map of frequencies can be found throughout the neuronal structures in many parts of the auditory pathway. The cochlear amplifier resulting from the activity of the outer hair cells creates a sharp peak reflecting the sharp frequency tuning of the hair cells at low SPLs. If the cochlear amplifier is dysfunctional the sensitivity drops and the bandwidth of the frequency tuning of the hair cells is increased.

Central Pathways

The action potentials in the population of auditory-nerve fibers elicited by the hair cell population provide the input for neuronal computations at various levels in the auditory pathway (Grothe, Pecka, & McAlpine, 2010; Malmierca & Hackett, 2010). Here, I focus on the mammalian auditory pathway, concentrating on binaural processing, and add some information for the birds (Carr & Code, 2000), because these have been subjects in many studies on perception (see Chapter 1, this volume). At the first stage, auditory-nerve fibers diverge and target different subunits in the cochlear nucleus that form the starting points of partially parallel, specialized auditory pathways. The first pathway rooting in the *dorsal cochlear nucleus* (DCN in mammals; the avian counterpart is the *nucleus angularis*) specializes on processing the spectral cues; that is, its neurons represent the distribution of sound levels across different frequencies. By a combination of excitation and across-frequency inhibition neurons in the DCN will preferentially fire if stimuli have certain spectral notches or other marked spectral characteristics. The second pathway rooting in the *ventral cochlear nucleus* (VCN in mammals; the avian counterpart is the *nucleus magnocellularis*) specializes on representing the temporal structure of the sound, such as onset transients, amplitude modulations, or the temporal fine structure of the waveform. In mammals, VCN neurons project to the first stage of binaural interaction, the superior olivary complex, in which the *medial superior olive* (MSO in mammals; the avian counterpart is the *nucleus laminaris*) and the *lateral superior olive* (LSO in mammals; the avian counterpart is the *nucleus ventralis lemnisci laterale, pars posterior*) are the targets. The MSO receives excitatory inputs from the anterior VCN from both sides and its neurons operate as coincidence detectors for phase-locked action potentials originating from both ears. These coincidence detectors will fire, if action potentials from both ears arrive at the same time. To compensate for the different times of arrival of sounds at the two ears that is due to the sound source being placed to the right or the left, the axons reaching the MSO form a delay line that counteracts the physical *interaural time difference* (ITD). By an orderly arrangement of these delay lines, the MSO neurons create a topographic map of ITDs. Although the bird nucleus laminaris functions in the same way, there has been a debate in the past years whether an exactly timed inhibition plays an additional role in the processing of ITDs by the MSO. As a result of the inhibitory circuit function, in the mammal the slopes of the neurons' ITD tuning functions rather than their preferred ITD appear to be evaluated by the auditory midbrain to represent a position of a sound source in space, whereas in the owl the peaks of the response function represent the ITD (Ashida & Carr, 2011; Grothe et al., 2010).

The LSO compares the input from the left and right ear that is related to the interaural level differences (Tollin, 2003). The output of LSO neurons reflects the interaction of ipsilateral excitation provided by the VCN and contralateral inhibition provided by the medial nucleus of the trapezoid body in representing the *interaural level difference* (ILD). Because both inputs supply action potentials that are locked to the temporal pattern of the stimulus waveform, the output of the LSO neurons may also be affected by ITDs in addition to being affected by overall ILDs (e.g., Tollin & Yin, 2005). The analysis by the LSO and MSO contributes to the generation of a map of auditory space in the mammalian *superior* *colliculus* (SC). In mammals, the *inferior colliculus* (IC), also being the target of MSO and LSO cells, has neurons tuned to spatial cues. However, there is no clear spatial map in the IC, although it does show maps featuring other cues such as frequency or modulation frequency of a sound (Malmierca & Hackett, 2010). In the barn owl (*Tyto alba*), however, the external part of the IC has neurons with small well-circumscribed spatial receptive fields that integrate the inputs from the ILD and ITD pathways. Similar to the SC of mammals, neurons in the optic tectum of the owl are bimodal representing corresponding parts of visual and auditory space (Konishi, 2003).

The auditory pathway reaches to the cortex. Cortical neurons not only represent a variety of stimulus features but also adapt their processing to specific tasks. Recordings from awake, behaving ferrets demonstrated rapid changes of the spectrotemporal receptive fields of cortical neurons that are correlated with the task and the attention of the animal (Fritz, Elhilali, & Shamma, 2005, 2007). Thus cortical neurons go beyond the pure representation of the stimulus features, especially in secondary cortical areas.

AUDITORY PERCEPTION

The performance of physiological mechanisms given the constraints of environmental acoustics will determine the limits of perception. The perceptual limits for certain features of sound signals will be illustrated in the sections that follow.

How to Study Perception in Animals

Perceptual studies rely on differential behavioral responses in different stimulus conditions. Human psychophysics uses subjective evaluation of the stimuli and objective measurement of responses in which detection or discrimination performance in a task is evaluated. Animal psychophysics is bound to applying objective psychophysical methods on the basis of detection or discrimination (see Chapter 1, this volume). The major difference in working with animals is the ineffectiveness of using verbal instructions in animals and the limited repertoire of behavioral responses available to animals. However, similar analysis methods and metrics for evaluation of responses can be used in studies with humans and animals that enables comparing results across species. A signal-detection theoretical approach (Macmillan & Creelman, 2005) has been commonly applied in animal and human studies, and the sensitivity measure from signal-detection theory (i.e., d prime [d']) can be compared across testing procedures and across species.

Animal studies have used different types of behavioral paradigms (Klump, Dooling, Fay, & Stebbins, 1995). The prepulse inhibition (PPI) paradigm is based on the natural startle reflex and has attracted some interest because it does not require the animal to be conditioned behaviorally (e.g., Ison, 2001). The startle response is a reflexive contraction of the muscles in response to a short sound with a high SPL (typical startle stimuli can have levels of 105 dB SPL) that makes the animal's body twitch. In PPI, the change in a stimulus presented prior to the startle stimulus (i.e., the prepulse) reduces the strength of the twitching (thus, the term *prepulse inhibition*). Although the PPI procedure has been widely applied, it has some drawbacks (Behrens & Klump, 2015). First, there is an optimum delay between the stimulus change (i.e., the start of the prepulse) and the beginning of the startle stimulus that maximizes the reduction of the startle. This must be determined for each specific prepulse and species or strain. Typically, this prepulse-startle onset delay is in the range from 50 to 200 ms. Shorter delays may create facilitation of the startle response whereas longer delays may show little effect of the prepulse on the startle. Mostly, perceptual processing of the change of simple stimulus features, such as sound level increments or decrements (Ison, Agrawal, Pak, & Vaughn, 1998) or tone frequency (Clause, Nguyen, & Kandler, 2011) has been studied with PPI and only few studies have used more complex stimuli (R. Fitch, Threlkeld, McClure, & Peiffer, 2008). The short time period between the onset of the change and the onset of the startle stimulus prevents the study of the perception of long, complex stimuli with PPI. Furthermore, startle responses can be quite variable which limits the sensitivity of that procedure for determining sensory thresholds. Failure to determine a threshold with PPI because of the high

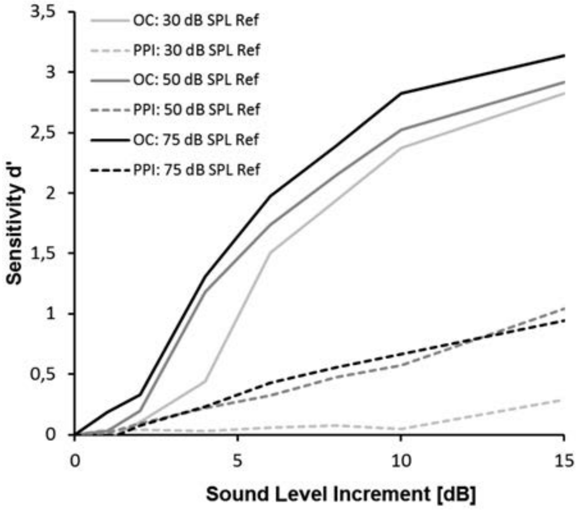

FIGURE 2.4. **Sensitivity for detecting an increment in sound level determined with an operant conditioning (OC) and prepulse inhibition (PPI) procedure (mean values of N = 12 mouse subjects). Results are shown for different reference sound pressure levels. The same mice were tested in all conditions and procedures. Sensitivity was much higher for the operant procedure.**

variability of the response does not preclude successfully using an operant conditioning procedure for threshold measurement (Behrens & Klump, 2015; see Figure 2.4). In addition, with different inbred mouse strains the genetic constitution may affect startle responses (e.g., Paylor & Crawley, 1997). The PPI paradigm can be an option for studying auditory perception, but often it does not provide the most sensitive and most accurate perceptual thresholds.

Classical conditioning has less frequently been applied for studying auditory perception. For example, by pairing a specific acoustic stimulus with an electric shock in a fear conditioning paradigm, a heart rate change can be used as a response indicator. The sensitivity of that procedure appears to be moderate compared to operant conditioning procedures (e.g., see Bräucker & Schwartzkopff, 1986; Sinnott, Sachs, & Hienz, 1980). The lack of sensitivity of heart rate conditioning may lie in that the stressful situation in which the animal finds itself will also affect the heart rate and may drive it to a ceiling with the stimuli no longer affecting it.

The most common method for studying auditory perception in animals uses operant conditioning, either providing rewards (e.g., food or water) or aversive stimuli (e.g., an electric shock). A common form of aversive operant procedure relies on the animal licking a spout to obtain water (or food) and suppression of the licking if a change in the stimulation occurs (e.g., H. Heffner & Heffner, 1995). The procedure has the advantage that by licking the opening of the spout the animal fixes its position in space, making it possible to calibrate the sound field for stimulating. Alternative aversive procedures have used a shuttle box in which the animal subject needs to change the side (e.g., by crossing a hurdle dividing the cage in two compartments; e.g., Wetzel, Wagner, Ohl, & Scheich, 1998). Aversive conditioning has been used for studying detection and discrimination of sounds. The disadvantage of the aversive procedures is that the animal may generalize the stimuli, making it less discriminating than in an operant procedure using rewards.

Operant conditioning with rewards generally results in sensitive thresholds for detection and discrimination. If rewards are used, the animal can be trained to position itself in a controlled way to allow calibration of the sound field (e.g., by only starting with stimulus presentation if a specific position is taken). Reward-based conditioning allows one to use go/no-go procedures and alternative forced choice procedures (Klump et al., 1995). Procedures with a delayed response can be used to determine the integration of stimulus patterns over extended time periods (e.g., MacDougall-Shackleton, Hulse, Gentner, & White, 1998). Motivation to respond can be monitored by providing trials with salient stimuli and sham trials in which no change is presented. In sham trials the false-alarm rate is determined. The animal subjects can obtain their daily food and water by responding to the stimuli, so generally a large number of trials can be conducted each day. If the false-alarm rate was too high (above 20%), studies have used negative reinforcement in addition to positive rewards. Usually, timeouts that prevent the animal from rapidly proceeding to the next trial have been applied. Often, a secondary reinforcer (e.g., a "food light") is paired with the primary reinforcer so that after some training it can replace the primary reinforcer in a fraction of the trials, allowing one to collect more data without the animal becoming satiated.

In the behavioral procedures, two methods of presenting the stimuli have been used: the method of limits and the method of constant stimuli. In the method of limits, an adaptive staircase procedure is used for presenting the stimuli (e.g., Leek, 2001). Presentation starts with a salient suprathreshold stimulus, and stimulus features are made progressively less salient on hit responses and more salient on misses. This yields the stimulus tracking threshold. A 2-down/1-up staircase is often used that results in tracking the threshold of 70.7 % in a 2-alternative forced choice procedure (Levitt, 1971). Thresholds can be determined as the average value of the stimulus parameter under study at the switching points of the staircase (Leek, 2001). Within the threshold range, steps can be reduced to obtain a more precise threshold estimate. A disadvantage of adaptive tracking procedures is that subjects are presented for a long time with stimuli that are not very salient (because these are close to threshold). This may result in a loss of stimulus control of the response. Animal subjects may also "track" a more salient above-threshold value not reaching the actual threshold (Klink, Bendig, & Klump, 2006). In the method of constant stimuli, values of the stimulus parameters are drawn at random from a set of stimuli with parameter values ranging from below to above threshold. By choosing values that result in about a third of the stimuli being below threshold, a third within the threshold range, and a third well above threshold, respectively, the responses can be kept under stimulus control. Commonly, trials are organized in blocks with each stimulus parameter value occurring once per block to avoid long time periods without salient stimuli. When animals have been tested with adaptive staircase procedures and with the method of constant stimuli, the latter has yielded lower thresholds (Klink et al., 2006).

Signal-detection theory has been applied to derive a measure of sensitivity d' from hit and false-alarm rates (Macmillan & Creelman, 2005). Thresholds have been defined by estimating the value of the stimulus parameter that results in a preset sensitivity. Typical values for d' at threshold are 1 or 1.8 (the former being less conservative but more commonly used, the latter being more conservative and having the advantage that stimuli at threshold are quite salient). Measures of sensitivity can be obtained for behavioral responses and for neuronal responses. Thus, sensitivity allows one to directly compare the processing of sounds by the brain and the resulting behavior using a similar measure. In addition to simply recording hits, misses, correct rejections, and false alarms, animal studies of auditory perception have also recorded *response latency*. Response latency can be used as an input variable to multidimensional scaling analysis that reveals perceptual distances in the organization of the perceptual space (e.g., Seeba & Klump, 2009).

Detection of Signals

Before any other analysis by the auditory system is possible a signal must be detected (see Volume 1, Chapter 30, this handbook and Chapter 1, this volume). If no relevant masking noise is present, detection is limited by the absolute sensitivity of the ear. Absolute threshold sensitivity of the tympanic ears of vertebrates is due to the sensitivity of the ear's hair cells including the action of the cochlear amplifier, the transfer function of the middle ear, and the transfer function of the outer ear that includes the effects of head and body, pinna, and ear canal. If the hearing system functions as a pressure gradient receiver, the connection between the ears may modify the ear's absolute sensitivity. The cochlear amplifier makes the largest contribution. If it fails, the sensitivity at the corresponding frequencies can be reduced by more than 40 dB (Nobili et al., 1998). External structures such as pinnae may increase the sensitivity of the ear considerably. If the cochlear function is intact, the middle ear transfer function mostly determines the low-frequency roll-off of the absolute hearing threshold curve. In addition to the high-frequency roll-off of the middle ear transfer function, the upper limit of hearing is mostly determined by the frequency tuning curves of the hair cells representing the highest frequencies at the base of the cochlea. Best absolute thresholds for nonspecialized tympanic ears range from 0 to 20 dB SPL. If the amplification contributed by the outer ear structures (e.g., by the facial ruff of the barn owl; Keller, Hartung, & Takahashi, 1998) are added, thresholds may improve to -20 dB SPL (see Figure 2.1). Thus, animal ears can be more sensitive than the best measuring equipment for sound levels and often have a wider frequency range of sensitive hearing than humans. This has to be kept in mind when designing experiments measuring auditory perception.

In the natural environment, however, because of the commonly occurring background noise, absolute thresholds are rarely important. Thresholds are elevated by the masking of signals provided by the background noise (Klump, 1996). Masking by a steady-state noise increases thresholds to a value corresponding to a signal-to-noise ratio of about 0 dB in the auditory frequency filters. This signal-to-noise ratio with normalization to frequency bandwidth has been defined as the critical masking ratio (e.g., Kittel, Wagner, & Klump, 2002). Masked thresholds obtained with a steady-state noise of the level typical in nature are up to 20 dB to 30 dB higher than the absolute threshold. Because background noise has a frequency spectrum that emphasizes low frequencies, masked thresholds are more relevant at low frequencies than at high frequencies (Pohl, Leadbeater, Slabbekoorn, Klump, & Langemann, 2012). Fortunately, the auditory system can exploit the temporal pattern of variation in the background noise because of fluctuations in level produced by the signalers and by the effect of air turbulence on sound transmission. The improvement in sensitivity achieved by exploiting the variation of the masker for signal detection can be more than 20 dB (Klump & Langemann, 1995; Langemann & Klump, 2001). The physiological basis of the improvement has been investigated with the CMR and CDD paradigms.

In the natural environment, detection thresholds and measures of attenuation of sound on the path of transmission are critical for determining the maximum communication distance between a signaler and the receiver. If in addition to these measures the SPL of the background noise, its frequency spectrum, and its pattern of temporal fluctuation are known, the maximum distance over which signals of a known level at the source will be detectable can be calculated. This distance has implications for interaction of animal subjects in the natural environment (Gerhardt & Klump, 1988; Klump, 1996).

Discrimination of Signals

Recognition of communication signals requires higher SPLs than detection threshold levels. At least a 3 dB increase above the detection threshold is necessary (Klump, 1996). Many communication signals are processed at a SPL much higher than the detection threshold. For such signals, the whole pattern of excitation across the cochlear frequency range is available for analysis and thousands of auditory-nerve fibers may provide information to the auditory pathway. The information about the acoustic scene is not only represented by the neurons' firing rate, it also is represented in part by the temporal structure of the neurons' firing in both ears. In a typical study to determine the sensitivity for discrimination, signals are presented at least 20dB to 30 dB above the detection threshold. Discrimination tasks have focused on signal frequency (determining the frequency difference limen), the level of the signal (determining the intensity difference limen), or the location of signal source (the minimum audible angle). Precaution must be taken that artifacts providing cues other than those that are intended for study are avoided. For example, in measuring the discrimination of sound frequency, variation of the SPL at the subject's ear because of the acoustics of the testing room and the transfer function of the sound presenting system must be avoided, because these could provide an indirect cue to detecting a frequency change. Rarely can such effects totally be excluded. Therefore, customarily one randomizes the parameters that may interfere with the desired measurement. If the threshold for frequency discrimination is to be determined, for example, the SPL of the stimuli should be randomly altered over a range of sound levels that is larger than the range of level variation caused by shifting the frequency (Langemann & Klump, 1992).

Localization of Signals

Different signal sources in the real world often can be distinguished by their position in space. Knowing the spatial position of a sound source can save one's life if the source is a predator. In communication in a cocktail party situation, masking of signals from one source by sounds from other sources can be reduced by binaural processing, which may make communication possible (e.g., in speech-on-speech masking; Bronkhorst, 2000; Darwin, 2008). Animal studies have investigated the mechanisms underlying sound localization. These studies have focused mostly on localization in the horizontal plane (azimuth localization) that is based on ITDs and ILDs (Grothe et al., 2010). Studies on azimuth localization typically use one of the following three paradigms: (a) behavioral pointing responses toward the source, (b) discrimination between different sources with only one of these sources presenting a stimulus (often being referred to as absolute localization), and (c) detection of a change in the location of a source (often being referred to as relative localization).

Pointing responses have used the natural visual orientation behavior that helps project the source of an acoustic signal on the fovea (i.e., the retinal area) providing the best visual acuity. In cats (*Felis catus*; Populin & Yin, 1998) and monkeys (*Macaca mulatta*; Populin, 2006), the accuracy of saccades of the eyes toward the sound source has been used to evaluate localization. In the barn owl, a prime model for studying sound localization, head saccades replace eye saccades (in the owl, the eyes cannot be moved, thus no eye saccades are possible) and have been evaluated to estimate localization accuracy (Knudsen, Blasdel, & Konishi, 1979). The localization error found in owls for open-loop localization (i.e., the stimulus stopped before the beginning of the saccade) in the horizontal plane was about 2 degrees for sound sources in the frontal range and it deteriorated to 11 degrees in the lateral range. For closed-loop localization (i.e., the stimulus is presented during the orienting response) the performance is improved, especially for sound sources at lateral positions. A pointing response with open-loop stimulus presentation is probably the most straightforward method to determine the precision and accuracy of absolute localization.

Absolute localization tasks often have used a paradigm that asks the animal to indicate which of two sources has presented a sound by choosing one of two response alternatives (e.g., move right if the source was on the right side and move left if the source was on the left side). However, if the potential signal sources are visible or other visual landmarks are available to the animal, this task may be solved by relating the position of a visual landmark to the perceived location of the acoustic sound source rather than evaluating the location alone by auditory cues (Feinkohl, Borzeszkowski, & Klump, 2016). Thus, this task would be a bimodal auditory/visual relative localization task. An absolute task based on choosing response alternatives should avoid presenting cues from other sensory modalities. For example, for measuring the accuracy in absolute localization, single sounds should be presented from one of multiple source positions and the subject should indicate the position of the active source by pointing to it.

Relative sound localization tasks measure the acuity of sound localization. Typically, after presentation of signals from one location, the location of the sound source is changed and the subjects need to indicate perceiving the change (e.g., by a "go" response). This task has been named the *minimum audible angle* (MAA) task, because it requires detecting the minimum angular change (Mills, 1958). Studies of the MAA often have found that subjects are better able to discriminate differences between sound source positions than indicating the absolute position of a sound source (Feinkohl et al., 2016). MAA tasks are, however, prone to the subjects using other cues related to the location of the sound sources than primary spatial cues such as ITD and ILD. This can be the case if the reference location in an experiment is kept constant and characteristics of the sound field created by this source can be learned. Countermeasures to prevent the subjects from using other cues are careful calibration and equalization of amplitude and phase spectra, as well as randomization of unwanted cues (e.g., as achieved by randomly varying the level to prevent subjects from using level as a cue). If each trial presents a different reference location before the change, this approach may also prevent subjects from using cues other than primary spatial cues. In studies with varying reference locations, a lower auditory spatial acuity (i.e., a larger discrimination angle) has been observed than in localization tasks in which only single sounds were presented (Feinkohl et al., 2016). Auditory memory may also affect the measured acuity in an MAA task. In the

European starling (*Sturnus vulgaris*; Feinkohl & Klump, 2013), the number of reference stimuli in an MAA task affects spatial acuity; presenting only one reference sound before the change results in a larger MAA than the MAA determined when presenting five reference sounds.

So far, this section has focused on the behavioral studies of azimuth localization in the horizontal plane, which is mainly achieved by exploiting interaural time and intensity differences. Localization in elevation (vertical plane) must be because of other cues, at least if it is performed in the sagittal midplane of an animal. In such a condition spectral cues are mainly used. The transfer function that results from the outer ear structure (e.g., the pinna) and body reflections creates spectral notches with a dip at a frequency that is typical for a specific position in space for each species (cat; Rice, May, Spirou, & Young, 1992; mouse [*Mus musculus*]; Lauer, Slee, & May, 2011). These spectral notches can be used to infer the elevation of a sound source as well as serve to reduce front–back errors in sound localization (cat; Tollin, Ruhland, & Yin, 2013; mouse; Lauer et al., 2011). Although birds lack pinnae, they also show spectral peaks and notches that vary with elevation of the sound source (Schnyder, Vanderelst, Bartenstein, Firzlaff, & Luksch, 2014). In the barn owl, a specialization in the representation of binaural cues is found (Keller et al., 1998). Unlike in a typical mammal, in which ITD and ILD determine the localization of sound sources in azimuth, in the barn owl ITD only reflects the azimuth and ILD reflects elevation (Moiseff, 1989).

Another dimension in sound source localization that is only little explored, is the perception of the distance of the source (the angle of sound incidence is not sufficient to pinpoint the location of the source). Studies of transmission of bird song, for example, have indicated that a number of features of the sound change proportionately with increasing distance from the source. Not only does the level change with increasing distance because of the geometric spread of sound energy and the excess attenuation produced by the environment through which the sound is transmitted, the temporal structure of the sound also is degraded by the splatter of echoes that reaches the receiver (Naguib & Wiley, 2001; Wiley & Richards, 1978). Humans and animals have been shown to be able to infer the distance of a sound source independent of the sound level on the basis of spectral and temporal degradation (e.g., Bronkhorst & Houtgast, 1999; Naguib et al., 2000).

Auditory Scene Analysis

In the natural environment (and not only at cocktail parties), listeners are regularly faced with multiple acoustic sources which makes parsing the signals from the different sources for analysis more demanding. The task of auditory scene analysis not only is solved by human listeners, but it also plays a role in the evolution of animal communication (Bee & Micheyl, 2008). There are some general principles (also known as the concept of Gestalt). Many of these principles, rooted in the laws of physics, make the world more predictable and can be used to group signals that originate from one source and segregate these signals from those originating from other sources (Bregman, 1990; Kubovy & Van Valkenburg, 2001). Sounds that are comprised of perceptually grouped components have been termed *auditory objects* or *auditory streams*.

Bregman (1990) identified two types of mechanisms in auditory scene analysis and the formation of auditory streams: (a) primitive mechanisms and (b) schema-based mechanisms. Another distinction in auditory scene analysis is between (a) bottom–up mechanisms and (b) top–down mechanisms. Primitive auditory streaming mechanisms generally are considered to be bottom–up mechanisms that automatically group components on the basis of the cues provided. Examples for bottom–up simultaneous grouping are the tonal components in a harmonic complex that are perceived together as one complex tone. Common transients in sounds (e.g., common onset or offset) also provide a potent primitive grouping cue. These grouping features owe their suitability to the physical processes of sound generation by the sender that, as a byproduct, generate the useful cues (e.g., our vocal cords produce a stack of tones with harmonic frequencies that also have a common onset and offset). Schema-based auditory grouping mechanisms often rely on top–down processing and these mechanisms may involve templates. An example of a schema-based mechanism is the phenomenon of perceptual restoration (Petkov & Sutter, 2011). In this paradigm subjects perceive a complete stimulus although parts of the stimulus are completely masked (i.e., missing). If a communication signal is interrupted by a loud noise burst (i.e., the noise burst replaces part of the signal), then humans (e.g., Samuel, 1996) and animal subjects (e.g., Seeba & Klump, 2009) perceive the communication signal as continuing through the noise burst without interruption. For complex signals such as speech or bird song elements, perceptual restoration is better if subjects are familiar with the sound suggesting that they can involve a template stored in memory in the restoration.

Not only must simultaneous sounds be grouped or segregated, but more typically sequences of sounds in communication must be attributed to a specific source. For example, if we want to comprehend a sentence when many speakers are active at the same time, we need to bind together the sequentially produced words. Common features of the sounds produced over time, such as the pitch of the voice because of the size of the larynx and the vocal cords, support the grouping of sequential sounds. In human psychophysics, a classical stimulus paradigm using ABA tone triplets has been investigated (van Noorden, 1975). Perception of a sequential series of ABA- tone triplets (the letters "A" and "B" standing for tones of a specific frequency, and "-" denoting a silent interval) very much depends on the degree of separation of the A and B tone frequencies and the temporal proximity of the signals. A series of ABA- triplets is perceived either as a galloping rhythm if the A and B tones are processed in one auditory stream, or as two separate tone series (A separate from B), each being perceived as having an isochronous rhythm. By training European starlings to differentially respond to an isochronous rhythm and a galloping rhythm (MacDougall-Shackleton et al., 1998; see Figure 2.5), it was demonstrated that these birds perceived the ABA- tone series in a similar way as one or two streams as humans do. A large separation of A and B tone frequencies and a rapid presentation rate of the tones promotes stream segregation. The neuronal mechanism underlying the segregation of streams likely relies on suppression that results in separate populations of neurons representing the different streams. The dependency of the streaming percept on tone frequency and temporal proximity of the signals parallels the suppression between A and B tones in the neuronal response (Bee & Klump, 2004, 2005). Thus, a separate representation of the streams by distinct neuron populations is a necessary prerequisite of streaming and is sufficient, if the neuron populations are activated in an alternation fashion. However, if the different neuron populations are activated simultaneously, no stream segregation occurs (e.g., Elhilali, Xiang, Shamma, & Simon, 2009). The suppressive mechanisms that may lead to stream segregation operate already at the cochlear nucleus, that is, at the bottom of the auditory pathway (Pressnitzer, Sayles, Micheyl, & Winter, 2008), indicating that this type of streaming relies on a primitive mechanism. Stream segregation can be supported by a large number of cues and not only by pitch cues—any salient cue can be used to segregate sources (B. C. Moore & Gockel, 2012).

Processing of signal components in streams affects the ability to analyze the signals. In contrast to subjective measures based, for example, on reporting the type of rhythm that is perceived, objective measures of stream segregation either rely on the perceptual analysis of a sound feature that is more salient within a stream or on the perceptual analysis of a feature that is more salient if streams are segregated (Micheyl & Oxenham, 2010). For example, the relative timing of A and B tones in the ABA- triplets can be more accurately determined in humans (Dolležal, Brechmann, Klump, & Deike, 2014) and in birds (Itatani & Klump, 2014; see Figure 2.5) if the A and B tones are processed within the same stream rather than being segregated into different streams. Neurons in the bird primary auditory cortical area exhibit a sensitivity for detecting a time shift between A and B tones and show a similar relation of the sensitivity to the frequency difference between that tones as was found for behavioral observation of detecting the shift (Itatani & Klump, 2014). An example for an improved ability to analyze signals if streams are separated is provided by the informational masking effect. In informational masking, the discrimination between features of a signal is impaired by distracting sounds that are processed in the same stream as the signal of interest

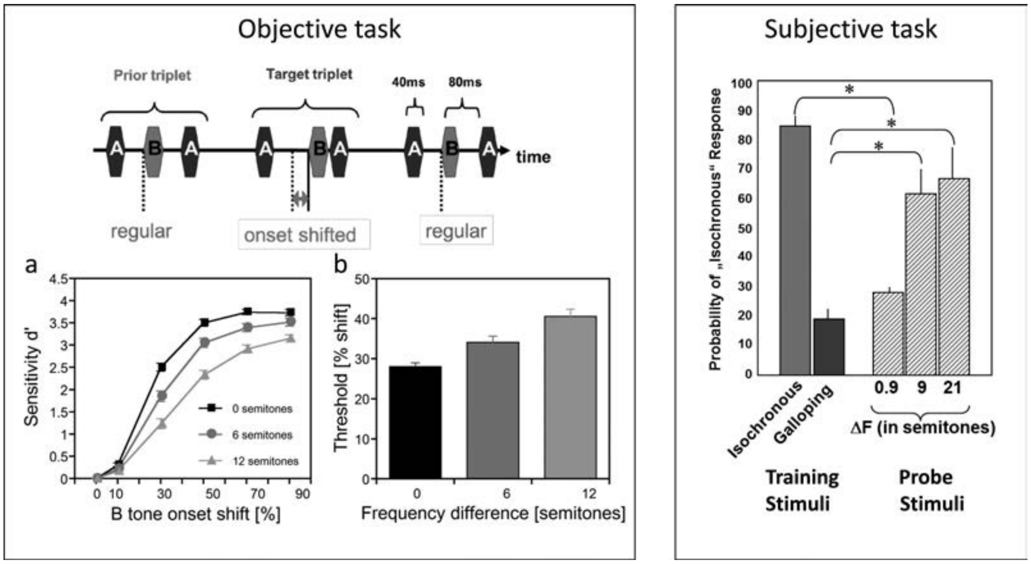

FIGURE 2.5. Objective and subjective behavioral measures of auditory stream segregation in the European starling. In the objective task, birds reported a time shift of the middle tone in a series of tone triplets (A and B represent tones of different frequency). Sensitivity for time shift detection was increased if the frequency difference between A and B tones was decreased, indicating that perceiving a time shift was more difficult comparing the timing of the tones between streams than within streams (graph a; Itatani & Klump, 2014). Time-shift detection thresholds increased accordingly (graph b). In the subjective task (MacDougall-Shackleton, Hulse, Gentner, & White, 1998), birds were trained to report the perception of isochronous rhythms and galloping rhythms of a series of tones of one frequency by pecking alternate keys. When birds had learned the task, their subjective percept was tested by presenting unrewarded probe triplet signals (with A and B tones in a triplet similar to that shown for the objective task) and registering whether they responded by pecking the "isochronous" key or the "galloping" key. For a small frequency difference between A and B tones the birds responded as if presented only with tones of one frequency in a galloping rhythm whereas for larger frequency differences between A and B tones the birds responded as if being presented only with tones of one frequency in an isochronous rhythm. $^*p < 0.05$.

(although no masking occurs in the inner ear itself). If the frequency or the level of a signal needs to be discriminated from that of a reference signal, distracting sounds that are presented intermittently to the signals being discriminated and that vary in the feature being relevant for the discrimination can considerably decrease the perceptual sensitivity (Watson, 2005). If the signals are processed in different streams from the distractors, these exert no informational masking. Such a release from informational masking with stream segregation has been demonstrated in human subjects (Winkler et al., 2003) and in Mongolian gerbils (*Meriones unguiculatus*; Dolležal et al., 2013). Parsing of signals into streams can also be affected by attentional processes. In human subjects, instruction will affect the likelihood that a certain set of stimulus parameters will result in perception of segregated or integrated streams. It is conceivable that such processes indicative of top-down mechanisms also occur in animals.

CONCLUSION

As has been demonstrated by many examples in this chapter, comparative studies on hearing and communication can provide for a deeper understanding of the mechanisms underlying human auditory perception. Although studies in human subjects generally rely on psychophysical testing and noninvasive electrophysiological or imaging methods (e.g., functional magnetic resonance imaging, electroencephalography, or magnetoencephalography), studies in animal models offer an additional invasive approach to observing the neuronal processing of sounds on the cellular level. Experiments involving psychophysical methods for studying the animals can serve to relate human and animal perception and, thus, provide the major link between the interpretation of neuronal responses on the cellular level and the gross measures of neuronal activity provided by noninvasive imaging and electrophysiology. An identical metric based on signal-detection theory allows for connecting the different experimental approaches. Although most of the experiments draw conclusions on the processing of acoustic signals on the basis of correlational evidence (e.g., demonstrate a neural correlate of perception), comparative studies in animal models in some cases even allow for directly manipulating the processing mechanism and, thus, establishing a causal relation between neuronal response patterns and perception.

Finally, comparative studies can take advantage of the specializations that animals have developed during evolution. Studying a specialist for sound localization, such as the barn owl, will reveal the general function of sensitive processing mechanisms much more clearly than the investigation of an animal that has not been subjected to such an evolutionary optimization. Furthermore, by comparing the processing mechanism and their perceptual consequences across a range of different animal species we will be able to identify the essentials in a mechanism required for solving a perceptual task. In these ways, comparative studies enable us to reach a level of understanding of hearing and communication that goes beyond what we can learn from investigating only human subjects.

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CHAPTER 3

COMPARATIVE VISUAL PERCEPTION: AN OVERVIEW

Olga F. Lazareva

> I'm sorry Frank, I think you missed it.
> Queen to bishop three, bishop takes
> queen, knight takes bishop, mate.
> —HAL 9000, in Stanley Kubrick, *2001: A Space Odyssey*

> One of Igor's former masters had *made* a tick-tock man, all levers and gearwheels and cranks and clockwork. Instead of a brain, it had a long tape punched with holes. Instead of a heart, it had a big spring. Provided everything in the kitchen was very carefully positioned, the thing could sweep the floor and make a passable cup of tea. If everything *wasn't* carefully positioned, or if the ticking, clicking thing hit an unexpected bump, then it'd strip the plaster off the walls and make a furious cup of cat.
> —Terry Pratchett, *Thief of Time*

Although computer programs capable of closely matching the most able human chess players are now commonplace, Terry Pratchett's joke still rings true: We are quite far from constructing a robot that can perform the simplest, mundane tasks that most people do effortlessly every day. Why is it that the artificial systems are so good at chess, a task that humans view as exceedingly difficult, but they are quite poor at simply perceiving and manipulating objects?

The answer, of course, is that visual perception is computationally much more complex than chess. Recovering information about the three-dimensional (3D) world from a two-dimensional (2D) projection on the retina is an inherently ambiguous process as multiple versions of the 3D environment can correspond to the same 2D retinal projection (Figure 3.1; Marr, 1982; Palmer, 1999). It is this lack of unique solution that makes visual perception so complex, and the construction of freely moving robots so challenging.

Still, we know that the human visual system manages to solve this problem with a remarkable speed and precision. How is this possible? It appears that our visual system interprets the 2D retinal input using many hypotheses about the environment and the viewing conditions (e.g., that the source of light is located above the object; Palmer, 1999). Thus, visual perception is an inferential process during which the visual system deduces the most likely 3D arrangement that has produced a given 2D retinal image. Are these assumptions unique to human visual perception? Or are they used by all reasonably complex visual systems? In this chapter, I will review how different visual systems accomplish the same basic tasks, such as dealing with resolution–sensitivity tradeoff (see Chapter 1, this volume) providing effective spatial vision and color vision, and recovering information about constant object properties despite the changes in the ambient light, distance to the object from the viewer, or angle at which the object is perceived.

FIRST CHALLENGE: CAPTURING LIGHT OR PROVIDING GOOD RESOLUTION?

Vision begins with a capture of a photon that is absorbed by a visual pigment. An effective receptor

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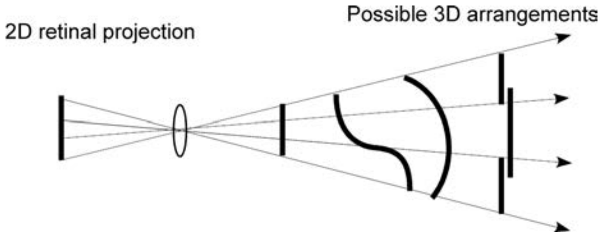

FIGURE 3.1. An illustration of vision as an ill-defined problem. The same two-dimensional projection on the retina can correspond to an infinite number of three-dimensional arrangements, making it challenging to establish the correspondence between retinal projection and the objects in the environment.

needs to reliably capture photons to produce a dependable image; therefore, such a receptor needs to be large, particularly in low-light conditions. Conversely, a quality image needs to possess fine details, which necessitates smaller and more densely packed receptors (Land & Nilsson, 2002). Because of this resolution–sensitivity trade-off, most eyes are adapted to provide a good, detailed image during the day but not at night, or vice versa.

In invertebrates, animals adapted to low light often have large eyes and large pupils allowing more light to reach photoreceptors. Most of the dim-light invertebrates, however, possess a superposition compound eye (cf. Figure 3.2) designed to enhance sensitivity by sacrificing resolution. Finally, many nocturnal and deep-sea invertebrates have larger photoreceptors, again enhancing sensitivity at a cost of resolution (Warrant, 2006).

Despite dramatic differences in design, single-chamber eyes of vertebrates living in dim-light conditions possess many similar adaptations. Nocturnal animals generally have larger eyes with larger pupils in comparison to closely related diurnal species (Lisney, Iwaniuk, Bandet, & Wylie, 2012). Often, these animals have additional adaptations for improving photon capture such as a *tapetum lucidum* or a reflective light collector (Braekevelt, 1990; Kreysing et al., 2012; Land & Nilsson, 2002). These structures return the light focused by the lens back to the retina allowing for a second chance to detect photons. In contrast to invertebrates, the nocturnal vertebrate eyes have retinal receptors of the same physical size as the diurnal eyes; however, retinal ganglion cells in dim-light adapted eyes receive input from a larger number of photoreceptors than in daylight-adapted eyes, increasing the effective size of the receptor rather than its physical size and leading to a corresponding loss of resolution (Orlowski, Harmening, & Wagner, 2012; Wagner, Fröhlich, Negishi, & Collin, 1998).

Some animals, however, need to possess a good sensitivity and a good resolution in a wide variety of light conditions. This is particularly true for many fish species. In the ocean, the amount of light decreases rapidly with depth; in rivers and lakes the water transparency (and, consequently, the amount of light passing through water) changes dramatically with seasons. Instead of adapting their eyes to high-light conditions and sacrificing their low-light vision (or vice versa), fish have retinal receptors that move in response to light. In photopic conditions, cones contract and rods elongate, placing outer segments of cones out for light capture and hiding rods in the shielding pigment. In scotopic conditions, the receptors move in opposite directions, allowing rods to capture light first. This remarkable ability is widespread among fish and amphibians, and is thought to be present in some birds (Burnside, 2001; Cahill & Besharse, 1995), but is completely absent in mammals.

SECOND CHALLENGE: FORMING AN IMAGE

The simplest form of vision, termed *spatial vision*, requires an ability to compare the amount of light coming from different directions. Without it, an organism can respond to the amount of light or dark but cannot form even a crude image of its surroundings. Development of better, more refined spatial vision is thought to be a main driving force behind the evolution of the eye (Land & Nilsson, 2002; Nilsson, 2013). This idea is further confirmed by experimental evidence indicating that some species are much better at discriminating monochrome images typical for their environment than images possessing unnatural spatial properties (David, Vinje, & Gallant, 2004; Párraga, Troscianko, & Tolhurst, 2000). What are the properties of the visual system, then, that are necessary for an effective spatial vision?

Spatial vision is commonly described in terms of spatial acuity or spatial resolution, the minimum

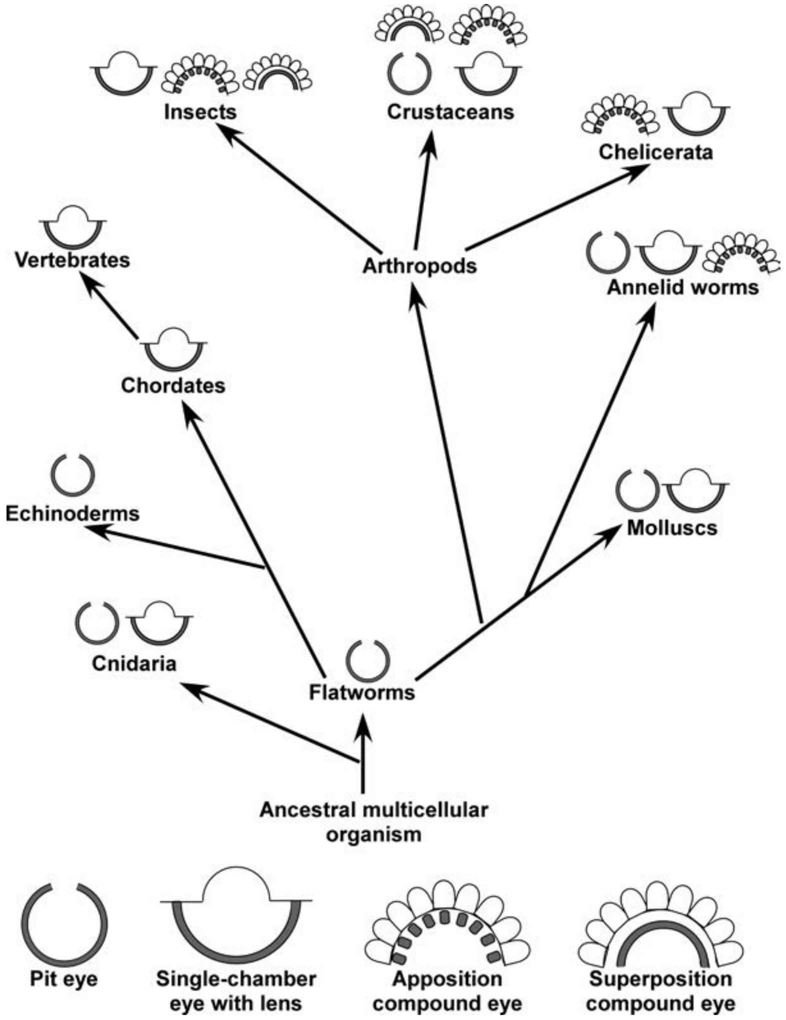

FIGURE 3.2. A simplified diagram showing evolutionary relationships between major taxa of multicellular animals and the major types of eyes. Shaded areas indicate location of photoreceptors. Several relatively rare eye types are not included (e.g., single-chamber mirror eye of the scallop Pecten). From *Animal Eyes* (p. 13), by M. F. Land and D.-E. Nilsson, 2002, New York, NY: Oxford University Press. Copyright 2002 by Oxford University Press. Reprinted with permission.

separation that is necessary for perceiving two objects in a scene as separate entities. It is commonly measured as *visual angle* (degrees, radians, or minutes of arc) where lower visual angle means better spatial acuity and vice versa. I now review two major factors affecting spatial acuity: eye optics and neural organization of the retina.

Eye Optics and Spatial Vision

The simplest eye, or an *eyespot*, consists of photoreceptors interspersed with nonsensory screening pigments that are located directly under skin (e.g., eyespots of hydromedusae jellyfish [*Leuckartiara octona]*; Singla, 1974). These medusae migrate to the surface at dusk and return back to deeper waters at dawn; they also respond to rapid changes in light intensity by contracting their body and tentacles in an attempt to move away. In other words, eyespots allow an organism to respond to changes in light intensity by initiating a certain class of behaviors. They do not, however, provide means for comparing the intensity of light coming from different directions and thus are not capable of spatial vision. Similar organs exist in many other invertebrates (see Nilsson, 2013, for a review).

At the most basic level, spatial vision requires some form of shielding so that different parts of retina receive different amount of light from different directions, together with a nervous system capable of comparing intensities of light registered by different photoreceptors (Land & Nilsson, 2002). Pit eyes and cup eyes (Figure 3.2) achieve this goal by placing photoreceptors into a cavity and using a change in pupil diameter to regulate the amount of light and the resolution (e.g., a cephalopod mollusk [*Nautilus]*; Land & Nilsson, 2002). However, the lack of a lens leads to an unsurmountable trade-off between sensitivity and resolution: Opening the pupil provides more light but results in a rapid loss of acuity, whereas closing it improves resolution but leads to a very dim image. Still, a cephalopod mollusk swimming in a water tank appears to use proximal and distal visual cues to find an exit, suggesting that its visual ability, however imprecise, is sufficient for navigation (Crook & Basil, 2013).

As Figure 3.2 illustrates, eye evolution is a complex affair, with many closely related groups possessing dramatically different types of eyes. This complexity led theorists to propose that, although the photopigment molecule is common to all light-sensitive organisms, the photoreceptors and the eyes have evolved independently in several groups of animals (Land & Nilsson, 2002; Nilsson, 2013). Single-chamber eyes and compound eyes represent two fundamentally different solutions to a problem of spatial vision; both are capable of maintaining a variety of complex behaviors, from navigation and pattern discrimination to categorization and object recognition (Lazareva, Shimizu, & Wasserman, 2012; see also Chapters 5, 6, and 22, this volume).

In a single-chamber eye, the image is formed by a lens located in front of the photoreceptors; the lens allows the eye to capture more photons while converging them on a single point of the retina.[1] Note that not all lenses perform equally well; the interested reader should refer to Land (2012) for a detailed treatment of lens evolution. A single-chamber eye with a lens is found in all vertebrates as well as in some insects, spiders, and cephalopod molluscs.

In contrast, a compound eye is formed by joining together a large number of small eyes. In an apposition compound eye, each individual unit, or *ommatidium*, produces an inverted image on a portion of retina devoted exclusively to this ommatidium; thus, an overall image is a mosaic composed of the images produced by individual ommatidia. In a superposition compound eye a single, noninverted image is projected in the vicinity of the unbroken, single-sheet retina, with each individual ommatidium redirecting light to form a single light beam (see Land & Nilsson, 2002, for more details). Finally, some compound eyes use neural superposition: These eyes are anatomically similar to apposition eyes, but instead of using separate retinal units they combine the signals from receptors pointing to the same region in space, which increases their sensitivity. Compound eyes are common in arthropods, but are also found in some annelid worms and echinoderms (Nilsson & Kelber, 2007).

Generally, compound eyes have a relatively low sensitivity and acuity in comparison to single-chamber eyes as their small size reduces the number of captured photons and makes the image susceptible to diffraction, a process of image distortion that occurs when light waves encounter a narrow opening (Land & Nilsson, 2002). Still, some compound eyes appear to deliver spatial acuity comparable to that of single-chambered eyes of a similar size (cf. Figure 3.3).

Retinal Organization and Spatial Vision

Spatial vision can be further sharpened at the retinal level by increasing the density of photoreceptors in some retinal areas and/or by increasing the density of cells processing photoreceptor signals, such as retinal ganglion cells in vertebrate retinas. Visual systems that combine the signals produced by multiple photoreceptors increase sensitivity but reduce visual acuity; thus, these adaptations are more common among nocturnal than diurnal species.

The number and the location of areas of an increased photoreceptor density are often determined by ecological factors in an organism's environment. For example, an organism moving forward in a

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[1] Instead of a lens, pit eye can be improved by introducing curved reflective surfaces, or mirrors, underlying the retina. Because this type of eye is relatively uncommon, it is not considered here (see Land & Nilsson, 2002, for more details). Somewhat more commonly, mirrors are used in conjunction with the lenses to increase sensitivity, particularly in nocturnal eyes.

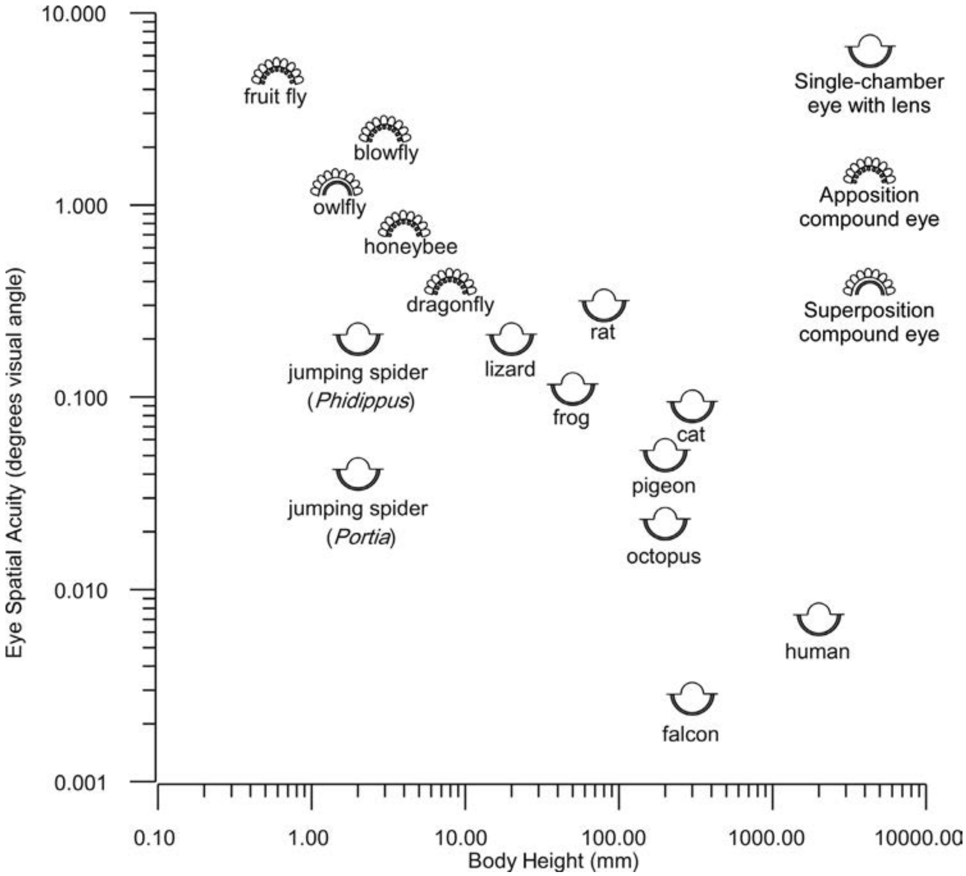

FIGURE 3.3. Log-transformed spatial acuity of different types of eyes expressed as minimum interreceptor angle plotted against log-transformed body height. Note that most single-chamber eyes provide better visual acuity than compound eyes, even after taking body height in consideration. From *How Animals See the World: Comparative Behavior, Biology, and Evolution of Vision* (p. 135) by O. F. Lazareva, T. Shimizu, and E. A. Wasserman, New York, NY: Oxford University Press. Copyright 2012 by Oxford University Press. Adapted with permission.

densely vegetated area will experience faster moving objects at the sides and slower moving objects in front, a pattern of apparent motion termed *optic flow* (Gibson, 1950). Because the objects located to the sides may be moving so fast as to be blurred, it makes sense to have a lower density of receptors in these areas as they are not likely to provide enough detailed information to support a high-resolution vision. Consequently, apposition eyes of flying insects often exhibit a higher density of ommatidia and a correspondingly higher visual acuity in the frontal area (Figure 3.4a). In contrast, eyes of animals living in flat environments such as water striders (*Gerridae*) have a horizontal strip of high resolution enabling them to most clearly see the area around the horizon (Figure 3.4b). Finally, hunters such as dragonflies (*Aeshnidae*) have a fronto-dorsal area of high acuity that improves their ability to detect a prey against the sky (Figure 3.4c). Similar adaptation exists in the eyes of insect species that actively pursue their mates: The fronto-dorsal high-acuity strip is present in eyes of male (but not female) hoverflies (*Syrphidae*) and mayflies (*Ephemeroptera*).

Despite dramatic differences in the design of invertebrate compound eyes and vertebrate single-chamber eyes, many vertebrates living in open, featureless habitats also possess a horizontal strip with an increased photoreceptor density and a corresponding increase in visual acuity, or a *visual streak* (sharks [*Chondrichtyes*], Collin, 2012; sea snakes [*Hydrophiidae* and *Elapidae*], Hart, Coimbra, Collin, & Westhoff, 2012; tinamou [*Nothoprocta perdicaria*], Krabichler, Vega-Zuniga,

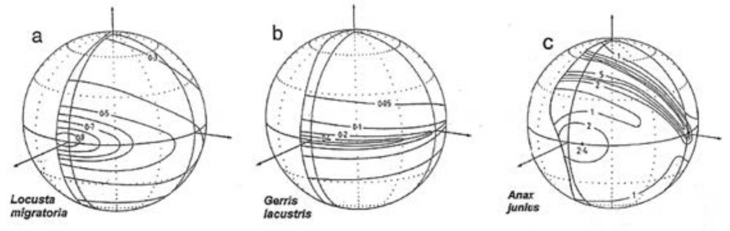

FIGURE 3.4. Distribution of density of ommaditia in representative apposition insect eyes that reflects ecological variations in eye design. Each contour represents an equal number of ommatidial axes per square degree. Higher numbers represent higher ommatidial density and, consequently, higher acuity. (a) A typical flying insect, the locust, shows higher resolution in front of the eye and lower resolution to the sides, indicating adaptation to motion-induced blur. (b) A “flatland” insect living on the surface film of water, a water strider, has the area of the highest acuity around the equator of the eye, indicating increased acuity to the area right above the horizon. (c) A typical hunter, a dragonfly, has a weak acute zone in front of the eye and a highly acute band toward the back of an eye, indicating an adaptation for detecting potential prey against the sky. From *Animal Eyes* (pp. 146–147), by M. F. Land and D.-E. Nilsson, 2002, New York, NY: Oxford University Press. Copyright 2002 by Oxford University Press. Adapted with permission.

Morales, Luksch, & Marín, 2015; penguins [*Spheniscidae*], Coimbra, Nolan, Collin, & Hart, 2012; owls [*Strigiformes*], Lisney et al., 2012; harbor seal [*Phoca vitulina*], Hanke, Hanke, Scholtyssek, & Dehnhardt, 2009; black rhinoceros [*Diceros bicornis*], Pettigrew & Manger, 2008; dogs and wolf [*Canis lupus*], Peichlcu, 1992). Single-chamber eyes of cephalopod molluscs (e.g., *Octopus*) also appear to have a horizontal strip of longer and thinner receptor cells that may be equivalent to a visual streak in vertebrates (Budelmann, 1995). Finally, some waterfowl (*Anatidae*) have an oblique, rather than a horizontal visual streak; this oblique position is thought to enhance detection of aerial predators in addition to allowing higher resolution along the horizon line (Fernández-Juricic, 2012; Fernández-Juricic et al., 2011; Lisney et al., 2013).

Many vertebrate eyes have at least one additional concentric area of increased photoreceptor density accompanied by an increased retinal ganglion cell density called *area centralis*. The area centralis is found in most mammal eyes, except for primates, as well as in fish, reptiles, and some birds (cartilaginous fish [*Chondrichthyes*], Collin, 2012; bony fish [*Osteichthyes*], Ben-Simon, Ben-Shahar, Vasserman, Ben-Tov, & Segev, 2012; tinamou [*Nothoprocta perdicaria*], Krabichler et al., 2015; waterfowl [*Anatidae*], Lisney et al., 2013; passerine birds [*Passeriformes*], Dolan & Fernández-Juricic, 2010; pinnipeds [*Pinnipedia*], Hanke et al., 2009; black rhinoceros [*Diceros bicornis*], Pettigrew & Manger, 2008; dogs and wolf [*Canis lupus*], Peichlcu, 1992). Although a single area centralis is the most common retinal adaptation in species that do not have a fovea, several species have an additional area centralis located laterally. The second area centralis is most frequently found in fish, water snakes, and aquatic mammals, and is thought to be an adaptation for either detecting prey and predators approaching from above or viewing objects in air and in water (Hart et al., 2012; Litherland & Collin, 2008; Mass & Supin, 1995). However, a second area centralis has recently been described in a terrestrial mammal, a black rhinoceros, where its function is less clear (Pettigrew & Manger, 2008).

Unlike a shallow area centralis, a *fovea* is a pit-like cavity densely packed with cones and retinal ganglion cells. Placing receptors into a pit is thought to reduce light scattering, provide better image magnification, and enable directional focus in comparison to a simple area centralis (Harkness & Bennet-Clark, 1978). Among mammals, only primate eyes have a single, centrally located fovea (Bowmaker, 2012). In contrast, a single fovea is present in many other vertebrate groups including birds (Coimbra, Collin, & Hart, 2014; Fernández-Juricic, 2012), some bony fish (Collin, Lloyd, & Wagner, 2000), and some lizards (Barbour et al., 2002; Röll, 2001). Although primates possess a shallow, bowl-like fovea, raptors and many other diurnal birds have a deep, pit-like, fovea with steep walls; these deep foveas are believed to function similarly to a telephoto lens magnifying a retinal image (Harkness & Bennet-Clark, 1978; Hodos, 2012).

In addition to a centrally located fovea, some birds have a second, dorsal fovea; this arrangement is thought to provide high acuity in a frontal field in addition to a lateral field (Fite & Rosenfield-Wessels, 1975; Gaffney & Hodos, 2003; Querubin, Lee, Provis, & O'Brien, 2009). Although a second fovea is frequently present in raptors and other birds hunting highly mobile prey (e.g., kingfishers [*Alcedinidae*], Moroney & Pettigrew, 1987), it also appears in nonhunting birds such as pigeons (*Columba livia*) and quails (*Coturnix japonica*, Budnik, Mpodozis, Varela, & Maturana, 1984). Double foveas have been reported in only one other group of vertebrates, *Anolis* lizards (Fite & Lister, 1981). These lizards hunt by sitting in one location for a period of time and scanning the surrounding environment for small prey.

Single-chamber eyes of jumping spiders (*Salticidae*) represent an interesting case as none of their eight individual eyes appear to have an area of increased visual acuity, possibly because of small size (Harland, Li, & Jackson, 2012). Instead, the individual eyes serve different functions: Six smaller, immobile secondary eyes located laterally provide a broader, lower-resolution visual field that detects moving objects and directs principal eyes toward a source of movement, whereas two large principal eyes possess a complex, four-layer retina, with the first layer containing densely packed, narrow receptors providing impressively high spatial resolution (cf. Figure 3.3).

THIRD CHALLENGE: SEEING THE WORLD IN COLOR

Color perception is one of the most interesting psychological aspects of vision (see Chapter 1, this volume), as physical objects and lights are not "colored" per se; instead, color is perceived because of interactions between the visual system and the physical properties of light (Palmer, 1999; Purves & Lotto, 2011). At a minimum, color vision requires at least two types of photoreceptors differentially sensitive to the wavelength of light; an animal with a single photoreceptor type, by definition, lacks color vision (*monochromaticity*). However, the presence of two or more such receptors, or cones, does not, by itself, demonstrate color vision, as it is possible that each cone simply initiates a specific behavior (Jacobs, 2012; Neumeyer, 2012). Such wavelength-specific behaviors were demonstrated in many animals including flatworm planarians whose simple eyespot clearly cannot support true color vision (Paskin, Jellies, Bacher, & Beane, 2014). Thus, color vision also requires a comparison of the output of different photoreceptors by visual system (Figure 3.5), and ideally should be demonstrated through behavioral experiments. Unfortunately, only a handful of species have been used in such behavioral experiments, making it difficult to make definite conclusions about the presence or absence of color vision in many groups despite the wealth of anatomical information about their visual system.

Although color vision has undoubtedly evolved independently in multiple taxa, the photosensitive protein called *opsin* is shared by nearly all species (Gehring, 2014). Vertebrates and invertebrates possess four major, independently evolved, opsin classes distinguished by their spectral sensitivity: UV, blue, green, and red (Pichaud, Briscoe, & Desplan, 1999). In vertebrates opsins are further differentiated into cone-specific and rod-specific opsins. The rod pigment rhodopsin is extremely sensitive to light which makes it well-suited for scotopic vision, but it is not involved in color perception.

With the exception of placental mammals, all terrestrial vertebrates have double cones in addition to single cones (Bowmaker, 2012). Double cones are more long-wave sensitive than single cones and are thought to be involved in movement detection in turtles and birds, although their function in other vertebrate groups may be different.

Some invertebrates appear to also possess a separate scotopic, low-light system and a photopic, color-based system, distinguished by the type of projections

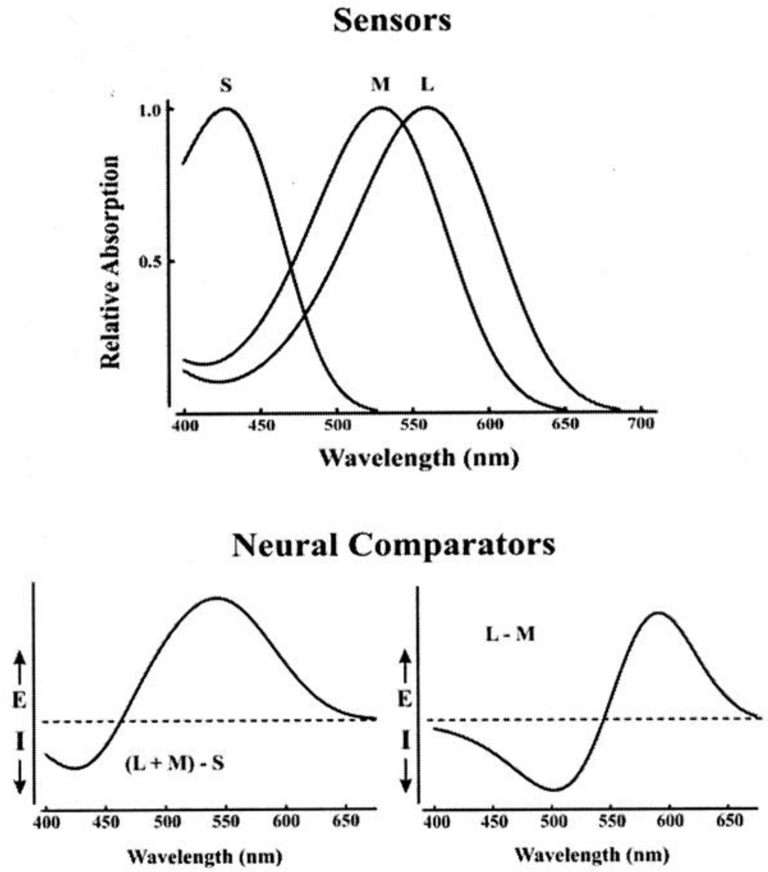

FIGURE 3.5. A schematic illustration of two mechanisms required to support color vision, tuned spectral sensors and neural comparators. Top: Spectral sensitivity of three cones found in human eye, conventionally designated as S, M, and L. Bottom: Neural comparators combining the outputs of the three cones through excitatory/inhibitory interactions (letters E and I indicate excitation and inhibition, respectively). In case of a single comparator, an evaluation of activation of two photoreceptor classes yields a single dimension of color vision (dichromatic vision). A second comparator adds another dimension to color vision, producing trichromatic vision. Finally, adding another photopigment (top) with an additional neural comparator element (bottom) will lead to tetrachromatic vision. From "The Evolution of Vertebrate Color Vision," by G. H. Jacobs, 2012, *Advances in Experimental Medicine and Biology, 739*, p. 158. Copyright 2012 by Landes Bioscience and Springer. Reprinted with permission.

from the photoreceptors (e.g., short visual fibers and long visual fibers in the *Drosophila* retina; Pichaud et al., 1999). However, other nocturnal insects appear to maintain ability to discriminate colors even under low-light conditions demonstrating scotopic color vision (Kelber, Balkenius, & Warrant, 2002).

In addition to different types of opsins, color vision can be further fine-tuned by using oil droplets that are present in all major classes of vertebrate animals except for bony fish and placental mammals. Colored oil droplets contain high concentrations of carotenoids and may function as filters that broaden or narrow spectral sensitivity of an individual receptor, at least in theory (Bowmaker, 2012; Bowmaker, Heath, Wilkie, & Hunt, 1997; Jacobs, 2012). Unfortunately, no behavioral evidence is currently available to demonstrate improved color discrimination in presence of color droplets. In contrast, pale or transparent oil droplets present in amphibians are thought to function as microlenses enhancing photon capture and possibly improving acuity, although behavioral evidence supporting this idea is again unavailable. Finally, individual ommatidia of some compound eyes contain screening pigments that can narrow or broaden the sensitivity of photoreceptors (Kelber, 2006).

Despite this staggering variety in low-level mechanics of color vision, there are two building principles that appear to be universal for all visual systems with a well-developed ability to discriminate colors. First, theoretical calculations show that three or four types of wavelength-sensitive photoreceptors are sufficient to sample the entire spectrum of visible light (Barlow, 1982; see also Jacobs, 2012). In other words, there is little or no advantage in having more than four cones but there is a clear energetic cost to maintain additional photoreceptors together with appropriate neural comparators. Supporting this argument, all vertebrate animals possess four or fewer cone types while demonstrating an exquisite sensitivity to spectral information, reliably discriminating colors differing by as little as 1 nm in certain parts of the spectrum (Neumeyer, 2012). Similarly, most invertebrates have four or fewer spectrally sensitive photoreceptors; although some insects like dragonflies, flies, and butterflies have five or even six photoreceptors, some of these receptors have very wide spectral sensitivity suggesting that they might not be involved in color vision per se (Briscoe & Chittka, 2001; Kelber, 2006).

The second building principle that appears to be necessary for finely tuned color vision is a presence of a spectrally opponent processing stage during which two cones with a different spectral sensitivity converge on a single neural cell that compares their output. Initially discovered in fish, spectrally opponent cells are now found in a wide variety of vertebrate and invertebrate species and are believed to be a necessary requirement for successful color vision (Jacobs, 2014; Kelber, 2006). These cells often occur in the retina, but can be also present at later stages of visual processing (e.g., Maturana & Varela, 1982; Yazulla & Granda, 1973).

Mantis shrimp (order *Stomatopoda*) represent a rather interesting exception from both of the principles described previously. Some mantis shrimp have 12 different photoreceptor types with very narrow sensitivity curves to represent the spectral range covered by four receptors in most other animals. Surprisingly, mantis shrimp are unable to discriminate colors that differ by 12 nm or less (Thoen, How, Chiou, & Marshall, 2014); in other words, the extremely high number of photoreceptors is coupled with the very poor ability to discriminate colors. It appears that the visual system of mantis shrimp does not use spectrally opponent processing; instead, each photoreceptor generates an independent signal enabling recognition of colors but not their discrimination. Mantis shrimp therefore appear to be an exception that proves the rule: Overabundance of color receptors in absence of spectral opponency provides poor color vision.

FOURTH CHALLENGE: SEEING CONSTANCY IN THE CHANGING WORLD

Many vision scientists have pointed out that vision is not a simple veridical reflection of a reality; instead, it is an active process of reconstruction, inference, and prediction that interprets signals from photoreceptors and transforms them into perceptions of objects in space (Marr, 1982; Palmer, 1999). Perceptual constancies provide excellent supporting evidence for this proposition: Even though information received by photoreceptors changes with the lightning conditions as well as with the angle and the distance from the object, we perceive these objects as having the same shape (shape constancy), size (size constancy), lightness (lightness constancy), and color (color constancy). Perceptual constancies are clearly essential for any successful visual system: Vision would not be of much use if learning to recognize a predator in bright daylight did not help identify the same predator under an overcast sky. Again, the human visual system deals with this problem by attempting to differentiate the properties arising from viewing conditions from those belonging to the "true" image. Remarkably, many other visual systems appear to operate under the same principles, although in most cases we do not yet know whether these behavioral commonalities are accompanied by neurobiological similarities.

Color Constancy

Subjectively, objects tend to have approximately the same color when illumination changes: Grass is perceived as green in daylight when main illumination is white and at dusk when main illumination is red. Physically, however, the wavelength properties of light received by the retina depend on the reflective properties of that surface and the spectral properties of the illuminating light. To arrive at *color constancy*, a constant perception of object color, the visual system automatically adjusts perception of surface color on the basis of perceived properties of illumination: If all objects in the scene have a similar chromatic property (e.g., red tint), then it is likely to be discounted to infer the object's true color (Foster, 2011). The authomaticity of color constancy gives rise to optic illusions such as the cube illusion, where a change in background color leads to a change in perceived color of a surface (Lotto, Purves, & Nundy, 2002).

The most straightforward way to behaviorally demonstrate color constancy is to train an organism to select a colored stimulus under one type of illumination and then change the properties of illuminating light during testing. Color constancy is shown when an organism continues to correctly select the trained stimulus despite the changes in the chromatic properties of illumination. Vertebrates (goldfish [*Carassius auratus*], toad [*Bufo bufo*], cat [*Felis catus*], rhesus monkey [*Macaca mulatta*]) and invertebrates (honeybee [*Apis mellifera*], swallowtail butterfly [*Papilio Xuthus*], moths [*Sphingidae*]) have demonstrated color constancy in this procedure suggesting that it may be a common property of color vision (Balkenius & Kelber, 2004; Dörr & Neumeyer, 1996; Dzhafarli, Maksimov, Kezeli, & Antelidze, 1991; Gnyubkin, Kondrashov, & Orlov, 1975; Kinoshita & Arikawa, 2000; Neumeyer, 1981; Tritsch, 1993).

Color constancy can be also demonstrated via simultaneous *color contrast*, a phenomenon in which the color of a surrounding area affects the perceived color of a central area: For example, a gray area appears yellow when surrounded by blue and blue when surrounded by yellow. In a typical color contrast experiment, an animal is trained to select a certain color out of several alternatives when these colors are presented on a black or grey background. In the test, the same colors are presented on a differently colored background and a change in choice pattern is interpreted as an indicative of simultaneous color contrast. Again, vertebrates (goldfish [*Carassius auratus*], chimpanzee [*Pan troglodytes*]) and invertebrates (swallowtail butterfly [*Papilio Xuthus*]) showed simultaneous color contrast (Dörr & Neumeyer, 1997; Grether, 1942; Kinoshita, Takahashi, & Arikawa, 2008; Neumeyer, 1981). Physiologically, simultaneous color contrast is thought to be based on *double color opponent cells* that respond to the difference in wavelength between the center and the surround of their receptive field. These cells are present in the primary visual cortex of primates (Shapley & Hawken, 2011), lateral geniculate nucleus of cats (Pearlman & Daw, 1970), and in the retina of bony fish (Shimbo, Toyoda, Kondo, & Kujiraoka, 2000), but they are yet to be found in other species.

Successive color contrast, or afterimages, is another indication of color constancy. This type of color contrast is present when prolonged exposure to a colored image results in a temporary perception of a complementary hue (e.g., a green after exposure to a red) after the disappearance of that image. This type of color contrast has been behaviorally demonstrated in honeybees (Neumeyer, 1981) and pigeons (Lea, Earle, & Ryan, 1999; Williams, 1974).

Lightness Constancy

Similarly to color constancy, *lightness constancy* is an ability to perceive an achromatic surface as having the same lightness regardless of the differences in illuminating light. Lightness constancy is believed to be achieved by adaptation (i.e., becoming less sensitive in bright light and more sensitive in dim light) as well as by an automatic adjustment of perceived lightness on the basis of ambient illumination (Palmer, 1999). Like color constancy, light constancy underlies some well-known illusions (e.g., corrugated plaid illusion; Adelson, 2000), and produces simultaneous brightness contrast where the perceived lightness of the center is affected by the lightness of its surround. Simultaneous brightness contrast has been demonstrated in swallowtail butterflies (Michiyo, Yuki, & Kentaro, 2012), pigeons (Hodos & Leibowitz, 1978), rhesus monkeys

(Davis, Masters, & Tjomsland, 1965), and chimpanzees (Grether, 1942).

Size and Shape Constancy

Size constancy refers to an ability to perceive the intrinsic size or shape of an object even though the size and the shape of its retinal projection varies with the distance and the viewpoint angle from the object to the observer (Palmer, 1999). Although there are several potential explanations for how the human visual system accomplishes size and shape constancy, all of them imply that the visual system infers the true size and shape of the object using distance and perspective cues. Several well-known size illusions such as the Ponzo illusion and Ebbinghaus illusion have been demonstrated in redtail splitfins (*Xenotoca eiseni*), pigeons, chicken, rhesus monkeys, and chimpanzees (Fujita, 1997; Fujita, Blough, & Blough, 1991; Nakamura, Watanabe, & Fujita, 2008, 2014; Sovrano, Albertazzi, & Rosa Salva, 2015; see also Chapter 8, this volume), suggesting that size constancy may be present in nonhuman animals.

Size constancy can be also tested directly by training an animal to select a larger of the two targets presented at one distance and then moving the larger target farther away during the test. Animals that do not display size constancy should lose the ability to perform the discrimination when the larger target subtends the same visual angle as a smaller target. Instead, bony fish, frogs (*Rana pipiens*), and ducklings (*Anas platyrhynchos*) have continued to select the larger target demonstrating that size constancy is present in most major groups of vertebrate animals (Douglas, Eva, & Guttridge, 1988; Ingle & Cook, 1977; Pastore, 1958; Schuster, Rossel, Schmidtmann, Jäger, & Poralla, 2004). It remains to be seen whether size or shape constancy is also present in invertebrates (although, see Maldonado & Rodriguez, 1972).

Interestingly, some experimental research suggests that pigeons are strongly affected by changes in the size of the discriminative stimuli (Peissig, Kirkpatrick, Young, Wasserman, & Biederman, 2006). In addition, pigeons and chickens showed a reverse Ebbinghaus illusion, again indicating a somewhat unusual approach to size constancy (Nakamura et al., 2008, 2014), whereas baboons showed no evidence of being affected by the Ebbinghaus illusion (Parron & Fagot, 2007). However, in all of those cases the discriminative stimuli were 2D drawings displayed on a computer monitor. In contrast, the successful evidence for size and shape constancy comes from the experiments using real-world, 3D objects as discriminative stimuli. It is therefore possible that the nature of discriminative stimuli and task rather than the visual abilities per se are responsible for these differences (see Sovrano et al., 2015, for a similar argument).

FIFTH CHALLENGE: SEEING THE WORLD IN DEPTH

Depth perception is a classic case of an ill-defined problem in visual perception: In principle, an infinite number of 3D configurations can produce the same 2D retinal projections (cf. Figure 3.1; Gibson, 1950; Marr, 1982; Palmer, 1999). To cope with this problem, the visual system makes a number of assumptions about the likely arrangement of 3D objects given a specific 2D input. Readers interested in a detailed overview of depth-processing cues in human vision should consult Palmer (1999); here, we will only review the cues that have been reasonably well studied in non-human animals.

Stereopsis

Stereopsis, or the ability to perceive depth on the basis of the disparate retinal information obtained from the two eyes, occurs when animals' eyes have overlapping visual fields. As Figure 3.6 illustrates, because the eyes are positioned in slightly different locations, retinal projections of the objects in the overlapping portion of the visual fields will be somewhat different. This lateral displacement allows the visual system to derive information about the "true" location of the objects in depth (Palmer, 1999). In local stereopsis, only small areas of visual display are used for comparison, whereas global stereopsis involves comparison and processing over a large area of retina. Global and local stereopsis are mediated by different brain areas in humans, suggesting that the two processes depend on somewhat different mechanisms (Fortin, Ptito, Faubert, & Ptito, 2002; A. Ptito, Zatorre, Larson, & Tosoni, 1991).

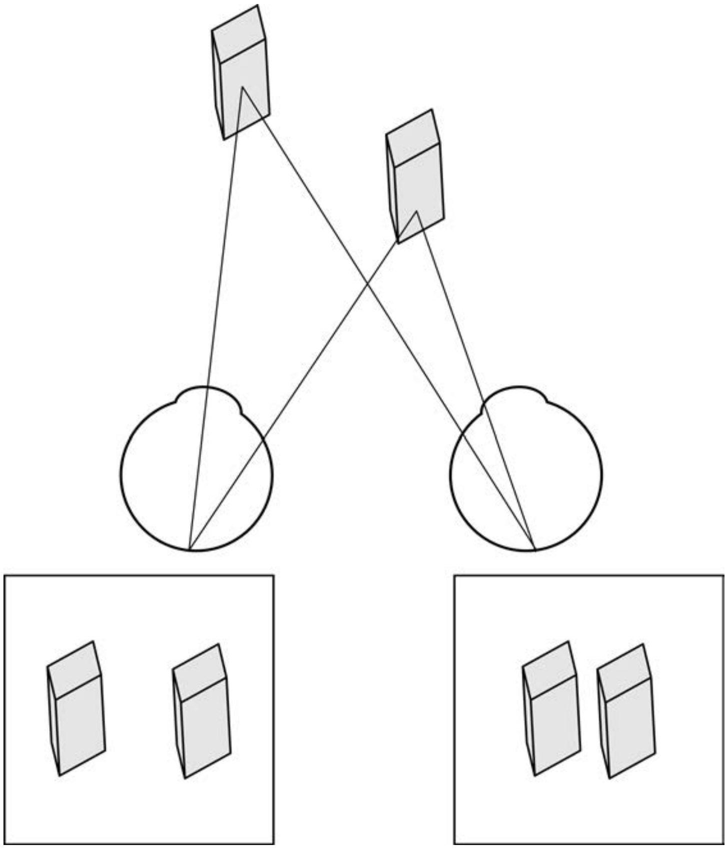

FIGURE 3.6. A schematic demonstration of binocular disparity. Because the two eyes are offset by a few centimeters, they will receive slightly different retinal information when viewing the same scene.

The simplest, though not the most convincing demonstration of stereopsis, is to compare an animal's ability to judge distances when only one eye is open and when both eyes are available; a demonstration of higher accuracy in the binocular viewing condition suggests the use of binocular cues (praying mantis [*Stagmatoptera biocellata*], Maldonado & Rodriguez, 1972; toad, Collett, 1977; pigeon [*Columba livia*], Watanabe, Hodos, & Bessette, 1984; meercat [*Suricata suricatta*], Moran, Timney, Sorensen, & Desrochers, 1983; horse [*Equus ferus caballus*], Timney & Keil, 1999). Unfortunately, finding no difference between the binocular and monocular conditions does not necessarily imply that a species lacks stereopsis; instead, it is possible that other depth perception cues such as motion parallax are used more heavily in the monocular condition to compensate for a lack of binocular information (Ashida, 1972). In addition, this behavioral approach does not distinguish between global and local stereopsis.

A more convincing demonstration of stereopsis uses stereograms, in which two images viewed separately by the left and the right eye give a rise to a different, illusory display. In addition to the simple stereograms, vision researchers frequently use random-dot stereograms composed of thousands of small dots; when viewed binocularly, these stereograms produce a convincing perception of depth in human observers (Julesz, 1964). Random-dot stereograms provide a better demonstration of stereopsis because they remove all monocular depth perception cues as well as eliminate possible influences of familiarity of the images on depth perception; in addition, they also allow distinguishing between global and local stereopsis as the ability to perceive depth in random-dot stereograms requires processing over large portions of retina.

Global stereopsis using random-dot stereograms have been shown in a very few vertebrate species (barn owl [*Tuto alba*], van der Willigen, Frost, & Wagner, 1998; cat [*Felis catus*], M. Ptito, Lepore, & Guillemot, 1991; horse [*Equus ferus caballus*], Timney & Keil, 1999; rhesus monkeys [*Macaca mulatta*], Cao & Schiller, 2002; squirrel monkeys [*Saimiri sciureus*], Livingstone, Nori, Freeman, & Hubel, 1995). A lack of evidence for stereopsis in birds is particularly interesting because even birds with laterally placed eyes have a considerable area of binocular overlap in a frontal visual field. Yet, with the exception of owls, there is little evidence to support global stereopsis in birds on either behavioral or neuronal level; it is, in fact, possible that binocular vision in most birds plays a minor role and is mostly used for specialized functions such as control of bill placement during pecking or chick feeding (Martin, 2009). Interestingly, rats have recently been reported to use binocular vision primarily for detection of overhead stimuli instead of judgment of distances to the objects located on the same plane as the animal (Wallace et al., 2013). This converging evidence suggests that the extensive use of stereopsis in depth perception may be less widespread in vertebrate animals than previously believed.

Motion Parallax

Motion parallax involves comparing retinal images over time as we move our heads or simply move through the environment. Because visual field becomes larger as the distance from retina increases, the objects that are located closer to an observer stay in the visual field for shorter periods of time than the objects located farther away. Thus, the relative motion can be used to judge the position of these objects in depth. Unlike stereopsis, motion parallax is a monocular depth cue that does not require binocular integration.

Behaviorally, motion parallax has been demonstrated in many insects (e.g., praying mantis [*Tenodera sinensis*], Kral, 1998; locust [*Shistocerca Americana*], Sobel, 1990; dragonfly [*Anisoptera*], Olberg, Worthington, Fox, Bessette, & Loosemore, 2005, and many others) and crabs (*Brachyura*, Barnes, Johnson, Horseman, & Macauley, 2002; Hemmi & Zeil, 2003). Surprisingly, only a few vertebrate species have been used in behavioral studies demonstrating motion parallax (barn owl [*Tuto alba*], van der Willigen, Frost, & Wagner, 2002; gerbils, Ellard, Goodale, & Timney, 1984; Goodale, Ellard, & Booth, 1990; rat, Legg & Lambert, 1990; rhesus monkeys, Cao & Schiller, 2002). Given its potential importance in depth perception, especially for species with limited use of stereopsis (Kral, 2003; Martin, 2009), motion parallax deserves more attention from comparative psychologists.

Other Monocular Depth Cues

In addition to motion parallax, a number of pictorial depth cues can be used to judge depth in static, monocularly viewed images (Figure 3.7). Because the size of elements in naturally occurring textures, such as pebbles on a beach, decreases with the distance, it can be used to judge the distance to the different parts of texture (*texture gradient*). Relatedly, objects spaced closely together are perceived to be farther from the observer than the objects located farther away (*density*); and, larger objects are perceived to be closer to the observer than smaller objects (*relative size*). Because parallel lines in a 3D environment project on a 2D retinal image as lines converging toward a single point on a horizon line, such converging lines can be used to induce perception of depth in a 2D image (*linear perspective*). Objects that partially block another object are perceived as being closer to observer (*occlusion* or *interposition*). Finally, *shadows* cast by the objects also induce depth perception in a 2D image.

Unfortunately, behavioral evidence for the use of these cues in nonhuman animals is quite scarce. For example, only horses (*Equus ferus caballus*), baboons (*Papio papio*), and chimpanzees (*Pan troglodytes*) have been shown to be affected by linear perspective cues (Barbet & Fagot, 2007; Imura, Tomonaga, & Yagi, 2008; Timney & Keil, 1996; see also Chapter 8, this volume). A single cephalopod species, a cuttlefish (*Sepia officinalis*), has been shown to respond to changes in texture density (Josef et al., 2014), but the use of other monocular depth cues in single-chamber eyes of invertebrates remains largely unexplored. Although it is commonly believed that compound eyes support poor depth perception because of their small size and low resolution, recent research suggests that some invertebrates with compound eyes such as fiddler crabs (*Uca vomeris*) may

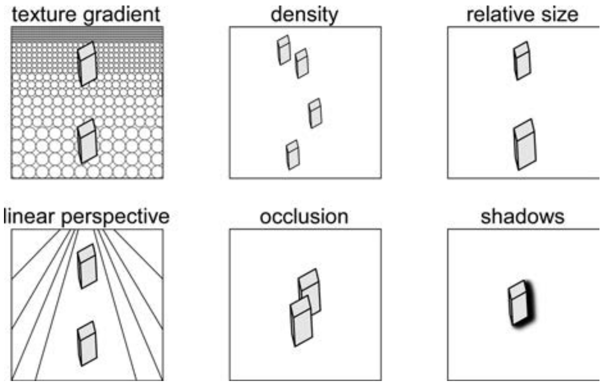

FIGURE 3.7. **Examples of several pictorial depth perception cues that have been studied in nonhuman animals. A perception of depth can be induced by a systematic change in the size of texture elements (texture gradient), a presence of parallel lines converging on a single point (linear perspective), a systematic change in a perceived distance between closely located objects (density), a larger size of objects located nearby in comparison to more distant objects (relative size), a blocking of a more distant object by an object located closer to an observer (occlusion), or by the presence of shadows or variations in shading of a surface of an object (shadows and shading).**

be using unique cues to evaluate distance, such as retinal elevation with respect to the ground (Collett, 2003; Hemmi & Zeil, 2003). Whether other species with compound eyes also use similar cues to evaluate distance is currently unknown.

The evidence for the use of monocular depth perception cues in pigeons (*Columba livia*), the most extensively studied bird species, remains mixed. On one hand, pigeons appear to be unaffected by linear perspective cues (Cerella, 1977; Nagasaka, Lazareva, & Wasserman, 2007); on the other, they are sensitive to Ponzo illusion which is presumably mediated by linear perspective (Fujita et al., 1991; see also Chapter 8, this volume). Multiple studies have demonstrated that pigeons appear not to recognize occluded objects in 2D displays (Sekuler, Lee, & Shettleworth, 1996; Ushitani & Fujita, 2005), presumably because of the failure to separate an object from an occluder (DiPietro, Wasserman, & Young, 2002; Lazareva, Wasserman, & Biederman, 2007). Yet, Cavoto and Cook (2006) reported that pigeons can use occlusion, together with relative size and relative density, to extract information about relative location of the objects. In short, any conclusions about the generality of monocular depth cues in nonhuman vision must await further comparative research.

CONCLUSION

Do all reasonably complex visual systems use a similar set of assumptions to derive a correspondence between a two-dimensional projection on the retina and three-dimensional objects in the environment? Despite the remarkable progress, we still have more questions than answers. Comparative psychologists and anatomists have convincingly demonstrated that basic principles of spatial vision and color vision seem to be remarkably similar across multiple taxa, despite dramatic differences in eye structure and mechanics of neural processing. Possibly because of the complex and time-consuming nature of behavioral experimentation, the evidence for similarity at more advanced levels of visual processing (e.g., perceptual constancies or depth perception) is still quite scarce. Yet, this knowledge is essential for our ability to understand the basic principles of constructing a successful visual system or to appreciate how the properties of a visual system change as a result of its adaptation to a specific environment. Such knowledge can only be acquired if comparative psychologists begin to use species as a tool, selecting a species because it possesses a specific type of visual system rather than because it is easy to work with in laboratory settings (Hulse, 2006; Shettleworth, 1993). Some recent work has provided promising examples of such experimentation (e.g., Brokovich et al., 2010; Qadri, Romero, & Cook, 2014); undoubtedly, future research will bring us even closer to understanding how different visual systems operate in a complex world.

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CHAPTER 4

CHEMORECEPTION

Alicia Mathis and Adam L. Crane

The recognition that each species occupies its own perceptual world (Von Uexküll, 1934/1957) has been central to the development of the fields of animal behavior and comparative psychology (Dyer & Brockmann, 1996). It is easy for humans to assume that nonhuman animals perceive the world as we do, and scientists must be careful to avoid this bias (Dethier, 1969).

Few other sensory mechanisms better fit Von Uexküll's (1934/1957) conception of "invisible worlds" than *chemoreception*. The ability to assess the immediate environment and respond appropriately to opportunities (e.g., prey or mates) and threats (e.g., predators and parasites) profoundly affects an organism's survival and reproductive success. Understanding chemosensory behavior requires piecing together clues from anatomy, neurophysiology, genetics, and behavior.

Information about the environment is readily available in the form of the airborne or waterborne chemicals that surround all organisms. Chemical cues have an advantage over visual cues because they are available in habitats that are not well lit or that have visual obstructions, or the emitter of the cues, such as a predator, is quiet and visually cryptic. In comparison to vocalizations, chemical cues can be relatively low-cost in terms of energetics (Alberts, 1992). Unlike tactile cues, they can be detected without requiring close proximity. It is therefore not surprising that most species of animals have developed rich chemosensory abilities that are specialized for their unique environmental challenges.

In this chapter, we first review the specialized terminology that is used in descriptions of behavior involved in communication via chemical cues. Unfortunately, there is disagreement among researchers over precise definitions of some terms, potentially leading to confusion. Until more standard usage is agreed on, authors are advised to specify their definitions of technical terms.

Second, we provide an overview of the anatomical features that are used in chemoreception in a range of invertebrate and vertebrate taxa. Note that many other aspects of biology influence chemosensory behavior, including genetics (Nei, Niimura, & Nozawa, 2008), biochemistry (Wyatt, 2014b), energetics (Palouzier-Paulignan et al., 2012), neurophysiology (Gabor, Phan, Clipperton-Allen, Kavaliers, & Choleris, 2012), and development (Bertin et al., 2016), and we recommend the aforementioned references as introductions to those topics. We chose to focus on anatomy because chemosensory postures are often directly associated with anatomical specializations.

Third, we describe the behavioral bioassay methodologies that are most commonly used for studies of chemoreception. Behavioral assays are frequently the most straightforward way of determining whether a chemical cue is present and detected, and changes in behavior frequently reveal functional consequences of chemoreception. Fourth, we give examples of how chemoreception plays an important role in the major functional categories of animal behavior: orientation and homing, kin-associated behavior, competition-related behavior,

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sexual behavior, foraging, predation avoidance, and parasite–host interactions. Although we focus on behavioral responses to chemical stimuli, note that responses can also include adjustments to physiology, morphology, development, and the timing of their life-history switches (e.g., Lecoq et al., 2009; Petrusek, Tollrian, Schwenk, Haas, & Laforsch, 2009; Relyea, 2007).

Fifth, because chemoreception is a sensory modality that is particularly vulnerable to environmental pollutants, we briefly discuss how toxins in the environment can impair chemoreception. We conclude the chapter by pointing to some directions for future research in this dynamic field.

DEFINITIONS

Chemical messengers that are external to the body are known as *semiochemicals*. Operationally, semiochemicals are defined as being produced by one individual (the sender) and causing a change in behavior, development, or physiology of another individual (the receiver). The specific subdivisions that make up semiochemicals are the subject of some debate (Dicke & Sabelis, 1988), but some functional categories, if not their precise definitions, are generally accepted. The primary subdivision is based on whether chemical signals transmit messages between individuals in the same (usually *pheromones*, but see the following) or different (*allelochemicals*) species.

Restrictions to the usage of the term pheromone have been suggested by some authors, although these have not been universally accepted. For within-species semiochemicals, Wyatt (2014a) recommended that chemicals that are involved in individual or group (kin or colony) recognition be classified as *signature mixes* because these chemicals require learning, whereas pheromones in his view should be species wide. Some experts (e.g., Wisenden, 2015) also require that pheromones be the result of natural selection favoring the sender because of the communication benefit, and that only such chemicals should be called *signals*. For example, if a male locates a female by following an unmodified urine scent, the urine is simply an environmental *cue*, but if selection has favored a modification to the urine because of its effectiveness at attracting males, it would be a pheromone and a signal. Although this distinction clearly has heuristic benefits, it can be challenging from an operational standpoint because it limits use of these terms to cases where benefits to the sender have been clearly demonstrated or else invites adaptive storytelling (Gould & Lewontin, 1979). This restrictive definition is also awkward when a semiochemical has multiple functions.

Allelochemicals usually are subdivided by whether the sender (*allomone*) or the receiver (*kairomone*) of the chemical obtains a potential fitness benefit. Although this distinction could also require problematic assumptions, the putative benefits to the sender and receiver are usually clear-cut. Most allomones benefit the sender (but not the receiver) by repelling predators or attracting prey. Kairomones include chemicals released by prey that attract predators or parasites/parasitoids or chemicals released by predators that warn prey of nearby danger; although the receiver benefits from detection of these cues, the sender clearly does not. If the sender and the receiver of the chemical benefit, the chemical is classified as a *synomone* (e.g., Wyatt, 2014a). The most common examples of synomones are chemicals released by plants during plant–animal interactions, such as chemicals that attract pollinators (Müller-Schwarze, 2006). However, interspecific territorial markers could fall into this category as well.

ANATOMY OF CHEMORECEPTION

Chemoreceptor neurons are located in the epithelium and are frequently, but not always, localized in the nasal cavity and mouth. The membranes of the cells typically contain receptor proteins that bind with environmental chemicals, initiating an electrical stimulus that travels through the axon either directly to the brain (*olfaction*) or to a peripheral neuron (*gustation* or taste; Wyatt, 2014a, 2014b).

Although there are some similarities, vertebrate and invertebrate chemoreceptors appear to have evolved independently (Touhara & Vosshall, 2009). Therefore, the terms *smell* and *taste* are not directly parallel in the two groups. Moreover, because of the large diversity of invertebrates, there is correspondingly large variation in chemoreceptors. In some taxa, chemoreceptors appear to belong to a single class, with no clear distinction between taste and smell, whereas two classes of receptors are evident in groups including arthropods, crustaceans, and nematodes (Krieger & Breer, 1999). In general, invertebrate chemoreceptors are contained within hollow hair-like structures (*sensilla*; see Figure 4.1A) that extend through the cuticle. Olfactory and taste receptors are generally distinguished by the structure of the sensilla, the receptor proteins that are present, and the types of chemicals that are detected (Reinhard, 2010). Location of invertebrate chemoreceptors is highly variable, including the antennae, tentacles, mouthparts, legs, wing margins, ovipositors, and feet (Reinhard, 2010).

In vertebrates, olfactory and gustatory senses also differ in that they are interpreted by different areas of the brain—the olfactory lobe for smell and other areas for taste (e.g., fish: Yoshimoto et al., 1998; humans: Kobayakawa et al., 2005). Like most other vertebrate sensory organs, the olfactory, vomerolfactory, and gustatory senses are connected to the brain via cranial nerves. Two cranial nerves connect the olfactory/vomerolfactory senses—the *olfactory nerve* and the lesser known *terminal nerve*, which is anterior to the olfactory nerve (Wirsig & Getchell, 1986). Taste is mediated by three cranial nerves—the *facial*, the *glossopharyngeal*, and the *vagus nerves* (Cranial Nerve X; Hara, 1994).

In most vertebrates, taste buds are localized in the mouth and pharynx, but in fish they also can

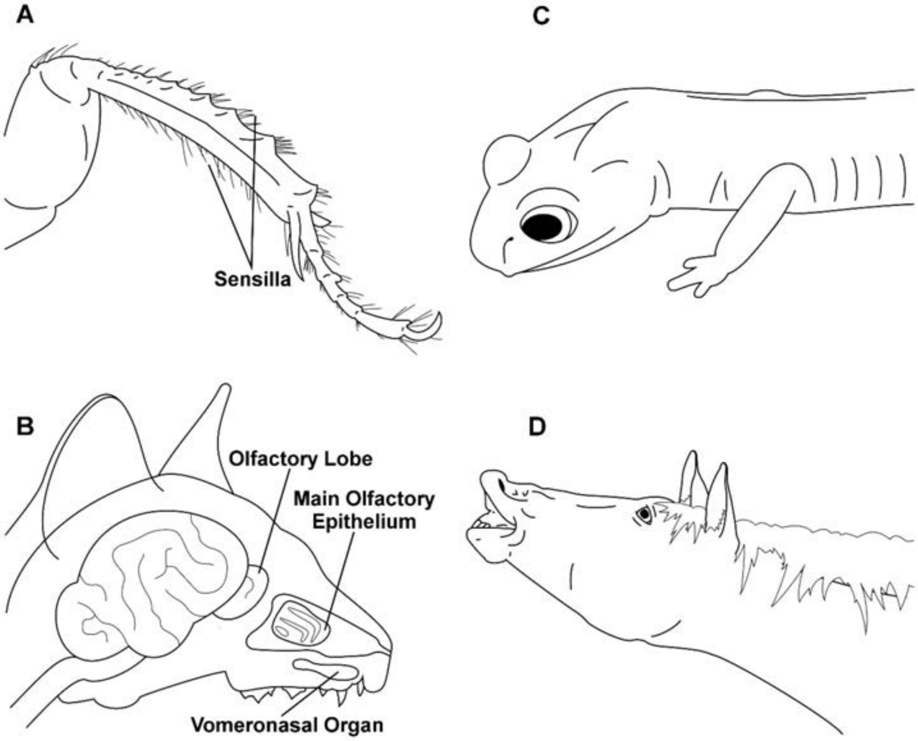

FIGURE 4.1. Some anatomical structures and behaviors associated with chemoreception. (A) The leg of a beetle (*Coleoptera*) with sensory hairs (sensilla) that contain chemoreceptors. (B) Sagittal view of the head (without mandible) of a domestic cat (*Felis catus*) showing the vomeronasal organ and the main olfactory region in the nasal cavity and the olfactory lobe of the brain. (C) Nose-tapping behavior by a terrestrial salamander (*Plethodontidae*). Salamanders in this family have grooves that connect the exterior nares to the upper lip. Both males and females collect waterborne chemicals by tapping the cirri on the tip of the lip to the substrate; chemicals are taken by capillary action to the vomeronasal organ. (D) A male domestic horse (*Equus ferus caballus*) exhibiting a Flehmen response, in which the upper lip is curled and the horse breathes with the nostrils closed; this behavior facilitates exposure of the vomeronasal opening to pheromones from females.

occur on the entire body surface, including the face, lips, and gills, as well as on barbels of catfish (*Siluriformes*: Kasumyan & Døving, 2003). Taste receptors are bundled together to form taste buds, which typically cover the surface of papillae (Butler & Hodos, 2005). The number and type of taste buds vary among taxa and among individuals, with fish generally having the most and birds the least (Butler & Hodos, 2005). Although taste receptors are generally accepted to be specialized for detection and assessment of food, they also could be involved in detection of other chemicals (e.g., from predators), particularly for aquatic species. Some species, most notably fish, have an additional class of chemosensory receptors—*solitary chemosensory cells*—that are similar to taste receptors but are different in their appearance (they are not bundled together), function (e.g., primarily for predator detection), and developmental timing (occur earlier; Kotrschal, Krautgartner, & Hansenm 1997).

In most tetrapods, with the likely exception of birds (Roper, 1999), the olfactory system is subdivided into the main olfactory system and an accessory system called *vomerolfaction*, whose receptors are located in the vomeronasal organ (VNO; see Figure 4.1B). Although there is some overlap between the two systems, it appears that the VNO is specialized for detection of chemicals of heavier molecular weight (usually waterborne), whereas the main olfactory system is specialized for detection of airborne chemicals (Baxi, Dorries, & Eisthen, 2006; Wyatt, 2014a). Although the VNO was originally hypothesized to function solely in detection of pheromones (many of which are of high molecular weight), the current data do not support this hypothesis: Many chemicals that are not pheromones (from prey, predators, etc.) are also detected by the VNO (Baxi et al., 2006). In amphibians and reptiles, the VNO is connected to the mouth via palatal holes, with the VNO and main olfactory organ in a common chamber in amphibians but completely separated from the main olfactory organ in reptiles (Müller-Schwarze, 2006). Some salamanders (*Plethodontidae*) have cirri that lead from the lip to the nose and function like capillary tubes, collecting water-borne chemicals from the substrate (Dawley & Bass, 1989), and cues are detected by tapping the cirri on the substrate (Figure 4.1C). Snakes and some lizards collect cues via tongue-flicking and deliver them to the VNO through the palatal openings (e.g., Burghardt, 1967). In mammals, the VNO is accessed through the nares, with the organ located at the base of the nasal septum (Døving & Trotier, 1998). Some ungulates (hooved mammals) and felids (cats) collect urine-borne pheromones on their tongues through licking and through a lip-curling behavior called *flehmen* (Figure 4.1D) to assist in delivery of chemicals to the VNO. Whether humans have a functional vomeronasal system is debated (e.g., Hohenbrink, Mundy, Zimmermann, & Radespiel, 2013; Meredith, 2001).

BEHAVIOR

In this chapter, we focus on the behavioral outcomes of chemoreception across a wide range of taxa and ecological contexts. Examples were chosen to highlight either findings of theoretical and conceptual interest or because they illustrate methods that are either standard in the field or that offer creative solutions to methodological problems.

Common Methods for Chemosensory Behavioral Assays

Choice designs (Figure 4.2A–E) are a major category of behavioral bioassays (Mason, Chivers, Mathis, & Blaustein, 1998). In these designs, animals have an option to freely choose to move toward (preference or attraction) or away (avoidance) from experimental stimuli. Most choice designs use simple mazes with neutral starting points and arms or side compartments that contain different stimuli (see Volume 1, Chapter 6, this handbook). When using choice designs, it is important to control for position bias, either by randomizing the assignment of chemical cues to each arm or compartment of the maze in each trial or by evaluating choices in the absence of stimuli. The spatial orientation of the maze may need to be shifted if stimuli outside the maze (e.g., lighting, visual landmarks, sounds, other smells) could influence the choices of animals (see Chapter 21, this volume).

In many cases, exposure to chemical cues influences behaviors other than simple attraction or avoidance. In such instances, researchers typically

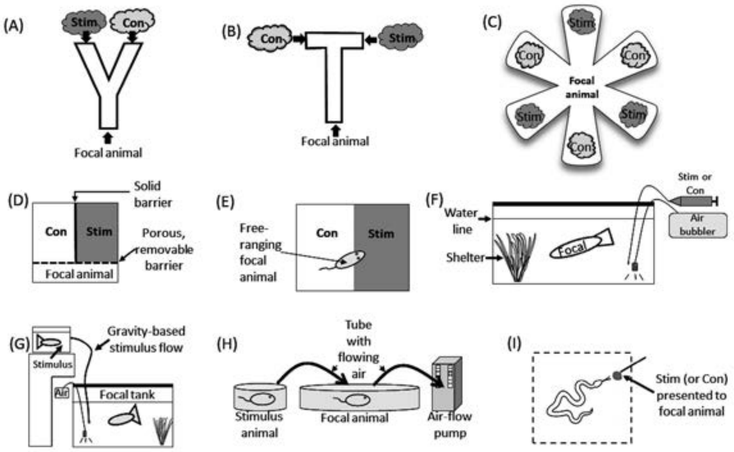

FIGURE 4.2. Common methodological approaches to the experimental study of chemoreception. (A–E) Simple mazes or arenas are frequently used to test for attraction or avoidance to test target stimuli or controls that are introduced simultaneously. (F–I) Different stimuli can also be introduced to the focal animal's testing chamber in separate trials. Stimuli can be introduced into the water for aquatic species either via a syringe (F) or through gravity-fed tubes (G). Airborne chemicals can be introduced into the air of terrestrial chambers by using air-flow pumps to move stimuli through the testing chamber (H). Stimuli also can be held directly in front of the focal animal (I). Stim = stimuli; con = control.

test whether animals behave differently in the presence of different categories of stimuli. The cues can be introduced and allowed to disperse throughout the arena via diffusion through substrates (air or water; see Figure 4.2F) or they may be actively transported from the source of the scent (usually a stimulus animal) by water flow (Figure 4.2G), wind tunnels, or air pumps (Figure 4.2H). Scents can also be added to testing chambers by adding items that have been marked by the stimulus of interest, including bedding material, articles such as cotton balls that have been rubbed over scent glands or other parts of stimulus animals, or paper towels that have been kept in the home cage of the stimulus area. Because it may take variable amounts of time for focal animals to locate the new stimulus in their chamber, which contributes to the variability of the responses, some studies introduce the stimulus directly in front of the animal using cotton swabs (Figure 4.2I) or other stimulus introduction devices. Examples of behavioral responses include sensory behaviors (sniffing, tongue-flicking, licking), activity levels, behavioral postures (aggressive, submissive, alert), shelter use, and group spacing.

Hypotheses about whether chemoreception plays a role in assessment of stimuli can also be tested by interfering with chemoreceptory structures and seeing whether behavior differs in comparison to control individuals with functional structures. For example, as early as the late 19th century, researchers showed that removal of the antennae in a number of insect species impaired their ability to detect or assess chemical information (reviewed in Glaser, 1927). For vertebrates, cuts to the olfactory nerve (e.g., Zuri & Halpern, 2003), use of mechanical plugs to block the external nares (e.g., Kats, 1988; Vrieze et al., 2010), and applications of zinc sulfate (e.g., McBride, Slotnick, & Margolis, 2003) to the olfactory epithelium have also been effective techniques. The latter two methods have the advantage of inducing only reversible or short-term anosmia.

Studies in natural habitats are important but are challenging and require creative research designs. Attraction and avoidance can be tested in some animals by monitoring trapping success of traps marked with various stimuli that are placed within natural areas where focal species are known to occur. Trapping studies have been successful in terrestrial and aquatic habitats (e.g., Wisenden, Pohlman, & Watkin, 2001). Observing behavioral responses of free-ranging animals to introduced chemical scents without using traps requires that scents are strategically placed in specific locations where focal individuals are likely to encounter them, such as in very high density areas, known nesting or roosting sites, within or around known individual territories, or in areas where animals have been trained to expect food rewards (e.g., Sündermann, Scheumann, & Zimmermann, 2008). Behavior can be recorded via video or field cameras left at scent stations, and animal presence can be determined by examining substrates around stations for footprints; these techniques can be problematic because statistical independence of data may require that individuals can be identified.

Another field technique for testing chemoreception is to locate focal individuals and introduce stimuli directly in front of the animal via a stimulus introduction device. For example, Anson and Dickman (2013) located semiarboreal Australian ring-tail possums (*Pseudocheirus peregrinus*) with a spotlight at night, and then used a 2 m pole to expose individuals to a cloth that was soaked in fecal cues from predators. Resampling the same individuals was avoided because focal possums were not sampled within the home range of any previously tested individual. In an aquatic habitat, alarm chemicals were introduced to individual stream fish (darters [*Etheostoma caeruleum*]) using an injection apparatus (a syringe connected to plastic tubing which was tied to a PVC frame), with each new trial beginning at least 3 m upstream from the last trial, a distance greater than darters moved between trials (Crane, Woods, & Mathis, 2009). An additional challenge of releasing cues in aquatic habitats is that unseen currents can deflect flow of the introduced stimulus. One way to solve this problem is by mixing experimental and control cues with food coloring so that the observer can confirm that the plume of the cue reaches the focal animal before beginning to record behavioral observations (Crane, Woods, & Mathis, 2009). Because chemical cues move with currents, each trial should be conducted up-wind or upstream from the previous trial if other potential focal animals are nearby.

Function

Orientation and homing. In most species, individuals need to locate home sites or other specific places containing food, mates, or seasonal habitats (e.g., breeding or overwintering areas; see Chapter 22, this volume). Although orientation in some taxa is primarily by visual landmarks or geomagnetic cues, others possess exceptional olfactory abilities that allow them to orient on the basis of detection of specific chemical cues.

A straightforward form of orientation on the basis of olfactory cues is the chemical trails laid on the substrate by many terrestrial invertebrates. In ants (reviewed in Morgan, 2009), there is considerable interspecific variation in the source (various glands and the hind gut) and chemistry of trail pheromones, suggesting that trail-laying has evolved multiple times in this group. Substrate chemical trails can also be laid by some flying insects, including some stingless bees (*Hymenoptera*, *Apidae*, and *Meliponini*), with successful foragers laying intermittent chemical trails on vegetation between the food site and the nest site. Recognition of trail pheromones is not entirely innate because choice of trails can be influenced by odors within the nest (Reichle, Jarau, Aguilar, & Ayasse, 2010). In some cases, pheromone trails can provide directional information. For example, in intertidal zones, sea slugs (*Onchidium verruculatum*) emerge from rock crevices to forage at low tide and then retrace their mucus trails back to their home crevices as the tide rises. When positioned on their trails in the wrong direction, they re-orient toward the origin of the trail (McFarlane, 1981). Although orientation by use of trails can be effective, a downside is that predators can use the trails to locate prey (e.g., Webb & Shine, 1993).

Homing—returning to a home area following displacement to an unfamiliar area—can also occur without the utilization of trails. Use of olfactory cues has been shown to be critical for determining homeward direction in some species (e.g., giant garden snails [*Limax maximus*]: Gelperin, 1974) and not in others (e.g., wood mice [*Apodemus sylvaticus*]: Benhamou, 2001). There is considerable evidence for the use of olfactory cues in orientation of homing pigeons, (reviewed in Wallraff, 2015), although there is still some debate over the exact role that olfaction plays (Phillips & Jorge, 2014). Chemical cues can be used to guide large-scale movements, a phenomenon that has been best studied in fish. A classic example is the Pacific salmon (*Oncorhynchus* spp.), where larvae learn the odor of their natal sites via *olfactory imprinting*, and then, as adults in the open ocean, recognize and follow these odors to return to their natal spawning sites (Dittman & Quinn, 1996). Lampreys (*Petromyzon marinus*) use odor cues in returning to their home spawning sites in tributaries (Vrieze et al., 2010).

Some species use chemical cues for locating aggregation sites. An Antarctic tick (*Ixodes uriae*) forms large aggregations under rocks around penguin rookeries. When penguins arrive at the rookeries, ticks leave these sites and attach to the penguins, but return to the aggregation sites after the penguin's breeding season. Ticks apparently locate aggregation sites via attraction to chemicals found in conspecific excretory products that collect beneath the aggregations (Benoit et al., 2008). Neonatal snakes might have only a few weeks to move long distances from parturition sites to communal dens for overwintering. In Y-maze tests, neonatal rattlesnakes (*Crotalus horridus*) followed scent trails from conspecifics more often than blank control marks, indicating that they may use scent trails to locate dens (Brown & MacLean, 1983).

Kin recognition. Distinguishing between kin and nonkin can facilitate cooperation among kin and reduce competition, cannibalism, and inbreeding. Social insects are well known to use chemical cues to distinguish between nestmates and nonnestmates (e.g., S. J. Martin, Vitikainen, Helanterä, & Drijfhout, 2008). Although the frequency varies among vertebrate taxa, olfactory-based kin recognition has been reported in all major vertebrate taxa (fish, amphibians, reptiles, birds, and mammals, including humans; Hepper, 2011). However, chemosensory recognition of kin has been reported only rarely in reptiles, which may be because of their generally low levels of sociality or because the potential for kin recognition in this group has been understudied.

Mechanisms involved in kin recognition range from learning olfactory phenotypes of close kin and then comparing the scents of others to the learned scent (*phenotype matching*), to comparing the phenotype of self to others (*self-referencing*), to innate recognition of scents associated with shared genes, such as loci associated with the major histocompatibility complex (overview in Breed, 2014). In vertebrates, use of olfactory cues in kin recognition has been particularly well studied among amphibians (Mason et al., 1998) and mammals, including humans (Weisfeld, Czilli, Phillips, Gall, & Lichtman, 2003). Parent–offspring recognition via chemosensory cues has been extensively studied in numerous species of mammals, where mothers associate with their young for extended postnatal periods (reviewed in Halpin, 1990).

Competitive interactions. When individuals, reproductive pairs, or groups sequester resources within defended areas (territories), advertisement of ownership is frequently via pheromonal markings (see Volume 1, Chapter 41, this handbook). In general, territorial advertisement via chemical cues is rare in aquatic species, presumably because advertisement pheromones would rapidly become diluted and disperse in the water. In terrestrial ectotherms, some species of salamanders (e.g., genus *Plethodon*) aggressively defend territories (interstitial spaces under rocks and logs) and advertise ownership using chemical cues deposited on substrates or fecal pellets. These cues can provide signal receivers with information about sex, body size, diet, parasite load, and familiarity (neighbor vs. stranger; e.g., Dalton & Mathis, 2014; Jaeger, 1981). Territoriality is common in many lizard species, but territorial markers serving as signals to competitors have only been reported in a few taxa, whereas scent marks serving as advertisement of males to potential mates may be more common (J. Martín & López, 2014).

Pheromonal signals appear to be extremely common in advertisement of mammal territories. Individual secretions might be multifunctional, such as when a pheromone serves to "warn" competitors and to attract members of the opposite sex. Mammalian scent marks can be present in saliva, urine, or feces or they can be produced by a wide variety of integumental skin glands, most of which are derived from sudoriferous (sweat) or sebaceous glands. As with salamanders, some mammal scent marks can provide information on traits such as sex, size, diet, reproductive condition, and social status (Ferkin, 2015). Marking over scent deposits of other individuals is a common behavior in mammals. For example, in wild banded mongooses (*Mungos mungo*) adults were more likely to overmark the scents of same-sex individuals, and the most recent scent was more important than that of the bottom scent in determining the response to the marking (Jordan et al., 2011). There is substantial interspecific variation in patterns of territorial scent marks. Common patterns include locating scent marks primarily at peripheral margins of territories, at contact zones between adjacent territories, at central locations within territories, at particularly active sites, or at sporadic locations over the entire territory (Müller-Schwarze, 2006).

Chemical information can also help determine the outcomes of dominance interactions outside of territoriality. For example, dominant spiny lobsters frequently release urine in interactions with subordinates, and individuals that release urine are more successful in aggressive encounters (Shabani, Kamio, & Derby, 2009). Scent marks by dominants can also play a role in supressing reproduction of subordinates in species ranging from eusocial insects (e.g., honeybees [*Apis mellifera*]: Moritz, Simon, & Crewe, 2000) to primates (e.g., tamarins and marmosets [family *Callitrichidae*]: Beehner & Lu, 2013).

Sexual interactions. Many species use pheromones during different aspects of sexual behavior. Chemical stimuli can be used for locating potential mates and in simply distinguishing between juveniles versus adults or males versus females (e.g., Thomas, 2011). In addition, when females mate only once during a reproductive season, chemical cues can also be used by males to discriminate between mated and unmated females; females can be chemically marked as "mated" by males during courtship, with the ejaculate, with mating plugs, or following copulation. In some mammal species—including rodents, ungulates, and primates—chemical cues from either males of females can lead to synchronization of female oestrous cycles (Dehnhard, 2011); synchronization can be particularly important when reproduction is seasonal.

Mate assessment. Sexual pheromones can also provide information useful in assessment of mate quality (see Volume 1, Chapter 37, this handbook). Most studies have focused on female assessment of males, but male assessment of females occurs in some species. Assessment pheromones can indicate benefits to opposite-sex receivers that are either direct (indicators of fertility or resources) or indirect (indicators of good genes, genetic compatibility, or Fisherian "sexy son" effects: Johansson & Jones, 2007). These types of sex pheromones occur in many invertebrates (particularly insects) and in all major vertebrate taxa.

In some species, *courtship pheromones* are delivered directly to the female by the male, resulting in increased receptivity by the female. These "aphrodisiac" pheromones are relatively common in arthropods (e.g., the spider *Pholcus beijingensis*: Xiao, Zhang, & Li, 2010), but appear less common in vertebrates. One exception appears to be amphibians, particularly salamanders (*Caudata*; Arnold & Houck, 1982). For example, in some species of aquatic newts (*Salamandridae*), males deliver courtship pheromones to females either by wafting chemicals released into the water toward females via tail fanning or by rubbing their cheek glands directly on the females' nares. In some terrestrial salamanders (*Plethodontidae*), males deliver courtship pheromones directly to the female, either by "slapping" his submandibular gland on her nares or by abrading her skin with his premaxillary teeth and then rubbing his mandibular gland over the "wound," which has the effect of injecting the pheromone directly into her skin capillaries.

Sneaker pheromones. Pheromone mimicry can allow individuals to "sneak" into areas where they normally would be prohibited. For example, foreign workers would normally be reproductively supressed in hives of South African honeybees of *Apis mellifera scutellata*, but individuals of another subspecies (*A. m. capensis*) can become reproductive "social parasites" by mimicking the pheromones of the queen of the host nest (Wossler, 2002). Subordinate sneaker males sometimes use mimicry of female pheromones and gain access to females near a dominant male. For example, nesting male black gobies (*Gobius niger*) react with aggressive behavior in response to ejaculate from other parental males but not toward the ejaculate of sneaker males, indicating either mimicry of the scent of females or chemical crypticity (Locatello, Mazzoldi, & Rasotto, 2002). Similarly, some males in populations of garter snakes (*Thamnophis sirtalis*) exhibit female mimicry by releasing a female-like pheromone; the pheromone apparently gains them access to females by confusing the "normal" males (Mason & Crews, 1985).

Foraging. Because prey are often difficult to detect visually, predators that can detect prey via chemical cues are often favored by selection. Predators take advantage of chemical information released by prey in a wide array of circumstances.

Herbivory and pollination. There are widespread examples of use of chemosensory cues in foraging by herbivores, particularly in insects (van Loon, 1996). Many flies, for example, have taste buds on their feet and extend their proboscises when they step on sugar-containing substrates (Duerr & Quinn, 1982). Some insects, such as grasshoppers (*Romalea microptera*) use airborne chemical cues to locate their preferred plant foods (Helms et al., 2003). In a particularly intriguing example, sea slugs (*Elysia tuca*) find seaweed using waterborne chemicals; the cholorphyll from the seaweed is integrated into the tissues of the sea slug and provides ongoing energy to the predator through photosynthesis. In another interesting twist, the seaweed produces a toxin that deters most predators, but the sea slugs are immune to it (Rasher et al., 2015). Vertebrates can also use odors to detect some food plants. Fruit bats (*Artibeus watsoni* and *Vampyressa pusilla*), for instance, detect hanging fruits using olfaction in combination with echolocation (Korine & Kalko, 2005), illustrating that much of animal sensory behavior is *multimodal.*

Many flowering plants release scents that attract foragers, particularly when visual cues are limited, such as during nighttime blooming (e.g., tobacco plants, *Nicotiana* spp., that are pollinated by hawkmoths of the Family *Sphingidae*; Raguso, Levin, Foose, Holmberg, & McDade, 2003). Such scents are attractive because they promise a food reward to recipients. However, some plants, such as orchids (family *Orchidaceae*), produce odors that attract pollinators in the absence of a food reward because they mimic sex pheromones of the pollinator species (Schiestl, 2005).

Prey kairomones, trail following, and eavesdropping. Most animals emit chemicals (kairomones) that are costly to the sender because they become public information that is available to nontarget individuals (see Chapter 19, this volume), such as predators (see Volume 1, Chapter 40, this handbook). Many prey kairomones are general metabolites, such as amino acids, which can be either volatile or nonvolatile (review in Müller-Schwarze, 2006). However, more specialized chemicals can also be used. For example, queen snakes (*Regina septemvittata*) feed almost exclusively on freshly molted crayfish (*Cambaridae*), which are vulnerable for a few hours while their exoskeletons are relatively soft; snakes are strongly aroused by the molting hormone ecdysone and only feed on crayfish when ecdysone is present (Jackrel & Reinert, 2011). In some taxa, individuals can locate or identify prey on the basis of cues left by foraging conspecifics; for example, timber rattlesnakes (*Crotalus horridus*) can use cues from successfully foraging conspecifics to select ambush sites (Clark, 2007), and weanling rats (*Rattus norvegicus*) are attracted to chemicals deposited in foraging areas by adults (Galef & Heiber, 1976).

Predators can also intercept chemical signals that are released by prey during communication; this behavior is often referred to as *eavesdropping*. In insects, individuals in many taxa produce a wide variety of sex and alarm pheromones that provide locational cues to predators and parasitoids (Stowe, Turlings, Loughrin, Lewis, & Tumlinson, 1995). Mice (*Mus domesticus*) mark territories with pheromones and mammalian predators (*Felis catus, Vulpes vulpes, Canis lupus dingo*) are attracted to their scent marks (Hughes, Price, & Banks, 2010). Eavesdropping is also potentially widespread among vertebrates.

Although many species rely on chemical cues to trail their prey, venomous predators that strike and release prey have a particular challenge because they must locate the same prey individuals twice. For example, following the strike and release of a mouse, rattlesnakes (*Crotalus viridis*) can distinguish between trails laid by envenomated and nonenvenomated mice (*Mus musculus*; Lavín-Murcio & Kardong, 1995) and can also use chemical information about the prey that is gathered during the strike (Melcer & Chiszar, 1989).

Predation avoidance. Use of chemical information by prey can lead to increased probability of survival (see Volume 1, Chapter 40, this handbook). These cues can be kairomones, alarm cues, or, surprisingly, chemicals that attract predators. Chemical defenses (toxins, venoms, etc.) are also widespread, but we will not cover these in this chapter because their effects are largely physiological.

Predator kairomones. Detection of predator kairomones is common in invertebrates and vertebrates and in terrestrial and aquatic habitats (see Apfelbach, Blanchard, Blanchard, Hayes, & McGregor, 2005; Kats & Dill, 1998). Typical behavioral responses are hiding, reduced activity, reduced feeding and reproductive activities, increased grouping behavior, increased chemosensory or other detection behavior, alarm signaling, and defensive postures (Kats & Dill, 1998). The recent diet of predators can affect their chemical signatures, providing additional information for assessment of predation risk (e.g., spiders: Persons, Walker, Rypstra, & Marshall, 2001; fish: Mathis & Smith, 1993).

Chemoreception of predator kairomones can be remarkably sophisticated in some species. A strong concentration of kairomones could indicate that predators are either nearby or numerous. In laboratory assays, experienced minnows (*Pimephales promelas*) could determine whether a given concentration of kairomones reflected proximity and density of predators (*Esox Lucius*; Ferrari, Messier, & Chivers, 2006).

Chemical alarm cues. When exposed to predators, individuals of some species emit chemical alarm cues that are recognized by conspecifics (and sometimes heterospecifics) and elicit antipredator responses. Behavioral responses can take a number of forms. For example, aphids (*Aphididae* spp.) that are threatened by predators produce droplets at the tips of their cornicles (abdominal tubes) that repel nearby conspecifics from the site for up to 60 min. In contrast, in social insects, such as ants and bees, alarm pheromones function to attract conspecifics for group defense (Blum, 1985). Other examples of voluntarily released compounds that indicate risk to conspecifics include the secretions released by distressed annelid worms (e.g., Ressler, Cialdini, Ghoca, & Kleist, 1968) and terrestrial plethodontid salamanders (e.g., Mathis & Lancaster, 1998). Some aquatic species release *disturbance cues* that appear to be a pulse release of urinary ammonia that elicits a vigilance response in receivers (Kiesecker et al., 1999). Similar urine-borne "stress" chemicals have also been reported for some mammals (Boissy, Terlouw, & Le Neindre, 1998).

In many aquatic vertebrate and invertebrate species, injuries to prey result in release of chemicals that lead to alarm responses by nearby conspecifics (see Ferrari, Wisenden, & Chivers, 2010). This phenomenon was first described by Von Frisch (1941) as *schreckstoff* (shock substance). Clearly, receivers benefit by being alerted to the presence of potential danger, but the primary function of the substance from the standpoint of the sender is not clear. Potential benefits to the sender of alarm cues might include direct benefits accrued through distracting the predator or indirect benefits through warning kin (Smith, 1999). Alternatively, senders could benefit via nonalarm functions such as healing of wounds caused by the injury (Chivers et al., 2007). Another potential nonalarm benefit of injury-released chemicals is attraction of secondary predators. Some prey fish produce an alarm chemical that attracts secondary predators that can interfere with the predation event, resulting in increased probability of survival of the prey (Chivers, Brown, & Smith, 1996; Mathis, Chivers, & Smith, 1995). A similar strategy also functions in some plant species that release chemicals called *herbivore-induced plant volatiles* when attacked by herbivores; these chemicals attract carnivores that prey on the herbivores and reduce loss of plant biomass (Dicke, 2009).

Some species can recognize alarm cues produced by members of other species, particularly when there is close taxonomic similarity (Gibson & Mathis, 2006) or if species are syntopic and experience predation by similar predators (Crane, Lampe, & Mathis, 2013). Such responses can be innate or learned.

Chemical crypsis. There is compelling evidence that a variety of prey species are capable of chemical crypsis—a mechanism that has allows prey to "blend in" with the chemical background of their environment (reviewed by Ruxton, 2009). Prey can become chemically cryptic by either minimizing the chemical cues they produce or by sequestering chemical cues in their diets to modify their odor to match their background chemical signature, allowing them to go undetected or be misidentified by their predators. For example, cod predators (*Cephalopholis* spp.) of a coralivorous reef fish (*Oxymonacanthus longirostris*) distinguished between the odor of the prey fish and the odor of the background coral only when the fish diet did not match the coral species (Brooker, Munday, Chivers, & Jones, 2015).

In addition to chemical crypsis by prey, predators also may be capable of altering their chemical signatures so that they go undetected by prey. This chemical cheating can take the form of simply supressing identifying chemical cues or by expressing cues that mislead their prey (Lambardi, Dani, Turillazzi, & Boomsma, 2007; Longhurst, Baker, & Howse, 1979). In one study, male moths of four species consistently flew toward predatory spiders (*Mastophora hutchinsoni*) from downwind, suggesting that the spider mimicked the sex pheromones of the moths (Gemeno, Yeargan, & Haynes, 2000). Gas chromatography-electroantennography revealed that the chemical components of the spider volatiles matched those of the sex pheromone of its primary prey species, the bristly cutworm moth (*Lacinipolia renigera*).

Parasite–host interactions. In the natural environment, animals often face a variety of parasite species, some of which can cause major negative effects, including death. Therefore, host species with strategies that minimize their chance of infection should be favored by selection (Moore, 2002).

Individuals can potentially avoid parasites by detecting them from a distance via chemical cues. For example, a soil nematode (*Caenorhabditis elegans*) can distinguish between bacteria that are prey versus bacteria that are pathogens; in that species, genetic tests indicated that two specific neurons are required for parasite detection and that bacteria must contain a specific peptide (serrawettin W2) to be identified as parasitic (Pradel et al., 2007). Individuals can also benefit by avoiding areas where parasites are present. Larval treefrogs (*Hyla versicolor*) face potential infection from parasitic trematodes that use snails as an intermediate host, and females laid fewer eggs in pools containing infected snails (Kiesecker & Skelly, 2000).

Parasite avoidance is a particular problem during social behaviors, including mating and territorial defense, which can facilitate parasite transmission (Loehle, 1997; Altizer et al., 2003). In some species, chemical cues can be used to distinguish between conspecifics with and without parasites, so that parasitized conspecifics can be avoided. For example, female terrestrial salamanders (*Plethodon angusticlavius*) spent more time near territorial markers from males with lower loads of mite (*Hannemania eltoni*) parasites compared to males with higher parasite loads (Maksimowich & Mathis, 2001). Moreover, nonparasitized males performed more threat postures in response to substrate markings from parasitized conspecific males (Dalton & Mathis, 2014). Similarly, female mice (*Mus musculus*) used urinary odors to identify males that were parasitized by a gastrointestinal nematode (*Heligmosomoides polygyrus*), even though there were no obvious signs of sickness (Kavaliers, Choleris, Ågmo, & Pfaff, 2004). Interestingly, females lacking the genes for oxytocin and estrogen-receptors were impaired in their recognition of the odors of infected individuals (Kavaliers et al., 2004).

Many parasites have also evolved chemosensory capabilities for finding their target hosts (see Lewis, Jones, Gross, & Nordlund, 1976). Pea crabs (*Dissodactylus primitivus*) are ectoparasites that cut and ingest the quills of their sea urchin hosts, frequently exhibiting host-switching; individuals are more attracted to olfactory cues of their host-urchin species than to nonhost urchins that share the same habitat (De Bruyn, De Ridder, Rigaud, & David, 2011). Similarly, black-legged ticks (*Ixodes scapularis*) are attracted to markings made by the tarsal and interdigital glands of white-tailed deer, leading to tick aggregations along deer trails (Carroll, Mills, & Schmidtmann, 1996).

A special category of parasites called *parasitoids* inserts their eggs into hosts; the parasitoid larvae eventually consume the host from inside its body. These parasitoids are well known for sophisticated use of chemical information in host searching (see by Fatouros, Dicke, Mumm, Meiners, & Hilker, 2008). Parasitoid wasps (suborder *Apocrita*), for example, attack the younger life stages (eggs, larva, pupa) of other insects, such as butterflies, as hosts. Instead of locating these inconspicuous life stages directly, some tiny wasps (~1 mm in length; *Trichogramma brassicae*) use chemical cues to locate a mated female butterfly, ride on her body as she travels to egg-laying sites, and then parasitize her freshly laid eggs (Fatouros, Huigens, van Loon, Dicke, & Hilker, 2005). Wasps showed a preference for the chemical odor of mated females, with wasps recognizing a specific odor (an "antiaphrodisiac") that is passed from males to females during mating that functions in making mated females less attractive to other males (Fatouros et al., 2005). However, the source of chemical cues used by parasitoids varies widely among species. Nonvolatile odors specific to the host and volatile odors from ingested plant material are used by a parasitic wasp (*Microplitis croceipes*) to locate their hosts, larvae of moths (*Heliothis zea*; Lewis & Tumlinson, 1988). In contrast, other parasitoids use cues from injured plants to find their hosts; for example, one parasitoid wasp (*Chrysonotomyia ruforum*) is attracted to a volatile terpene that is released by Scotch pine (*Pinus sylvestris*) when its host (larval sawflies [*Diprion pini*]) oviposits on the plant (Hilker, Kobs, Varama, & Schrank, 2002).

IMPAIRMENT OF CHEMORECEPTION

Because olfactory receptors of animals are exposed to the air or water surrounding them, environmental pollutants such as sulfur-containing volatiles, surfactants, acids, pesticides, and heavy metals can damage these receptors, physiologically and morphologically (Halpern, 1982; Tierney et al., 2010). For example, short-term exposure to zinc sulfate, a toxic industrial pollutant, caused lesions on the peripheral olfactory receptor sheets of neonatal rats (*Rattus norvegicus*; Stewart, Greer, & Teicher, 1983), which exhibited impaired, odor-directed behavior toward their mothers. After 5 days, control pups exhibited widespread and high levels of olfactory-bulb activity, but treated pups showed almost no such activity. Loss of olfactory acuity and associated morphological damage, including ulcers and sinonasal cancers, have also been reported for humans exposed to environmental toxins (Sunderman, 2001).

Fish frequently are model organisms for toxicological research, and olfactory impairment has been the subject of many of these studies. The most common bioassay used by toxicologists has been to determine whether the chemical in question is avoided (Tierney et al., 2010). However, analyses of other variables, such as diminished antipredator responses, are becoming more frequent. For example, when eggs of a larval marine fish (*Amphiprion percula*) were raised at increased levels of CO_2 (and consequently lower pH), newly-hatched larvae actually became attracted to the smell of predators (Dixson, Munday, & Jones, 2010). No abnormalities in olfactory morphology were observed in this study, suggesting that these environmental changes either disrupted the transfer of chemosensory signals across the olfactory epithelium or within the neurosensory system (Dixson et al., 2010).

CONCLUSION AND FUTURE DIRECTIONS

Animals live in a multimodal sensory world, gaining information via visual, chemical, auditory, and other cues. The extent to which specific cues are used varies among taxa and also may be situation dependent. For the chemosensory modality, collection of information is by olfactory and taste receptors and sometimes by other receptors, such as solitary chemosensory cells. Functionally, chemosensory cues can mediate virtually every aspect of animals' lives. Chemical information helps animals orient within their habitats and to return "home" following displacement. It is used by predators to locate potential food and determine whether it is nutritious and palatable, and by parasites/parasitoids to detect their hosts. Prey animals can use chemical cues to detect predators and in some cases can use either the concentration or chemical constituency of cues to determine the level of threat posed (e.g., size, closeness, diet of predator). Chemical cues often mediate social behavior by providing information concerning identification of kin and assessment of potential competitors, and by being used to attract, stimulate, or assess potential mating partners. Because a variety of environmental pollutants can impair chemosensory systems, pollutants can be a major contributor to species decline, and these damaging effects should be considered when conservation decisions are made.

Fascinating examples of chemoreception are widespread, but some taxa have been largely unexplored. Although arthropods and mollusks have received substantial study, many other invertebrate taxa need more attention. Among vertebrates, species that are flamboyant in their use of visual or auditory modalities, such as birds, adult frogs, and marine mammals, have been understudied with respect to chemosensory systems. Even among major taxa that have been the subject of considerable study, the trend is that only a few species of any one group are studied in any detail. To understand many aspects of the evolution of chemical communication requires in-depth knowledge of the sensory biology of many species within the group. For example, mapping of behavioral characters on well-supported phylogenies can provide useful insights into the evolutionary history of chemosensory biology (Ord & Martins, 2010), but data from a variety of species are needed for this method to be successful.

Additional studies of the development of chemoreception, including effects of experience, would be useful for questions concerning biological constraints, ecological function and evolution. In a few taxa, it has been shown that chemoreception by embryos can influence postnatal/posthatching behavior. Some taxa respond appropriately to at least some chemical cues innately (without experience), whereas learning is important in recognition of other cues. What accounts for the differences among taxa and why is learning required for some cues but not for others? To what extent are responses to chemical cues able to be modified by experience? What role does chemosensory-based learning via operant or classical conditioning play in behavior? Energetics likely place constraints on chemoreception abilities, but costs are poorly understood. For example, do offspring from mothers in good condition develop chemoreception abilities earlier or more effectively than offspring from energetically stressed mothers?

For some functional categories, possible contributions of chemoreception have been ignored because the more easily observed roles of auditory and visual cues have been assumed to be sufficient explanations. For example, the classic elaborate reproductive behavior of sticklebacks (*Gasterosteus aculeatus*) was described by Tinburgen in the early 1950s, but the first documentation that chemical cues also play a role did not occur until 40 years later (Waas & Colgan, 1992). The importance of one sensory modality does not rule out involvement of others, and chemosensory involvement is frequently overlooked because of its “invisible” nature (e.g., Von Uexküll, 1934/1957). Even many well-studied behaviors need to be re-examined in the light of potential chemosensory involvement.

Because the sensory world of animals is multimodal, more study on cue integration and the context-dependency of specific cue usage is necessary. When multiple cues are used, are there additive effects, with each modality providing additional useful information? Are there synergistic effects, with information from one modality enhancing the operation of another? Are there hierarchical effects, with one modality used preferentially and the other as a “back-up”? What happens when different modalities yield conflicting information? Are different modalities operating preferentially under different circumstances, such as visual cues during the day and chemical cues at night, or chemical cues for mate location and auditory cues for mate assessment?

Researchers should incorporate the role of chemical information in emerging conceptual areas of study in ethology and comparative psychology. For example, work on animal personality (*behavioral syndromes*) should consider whether chemosensory phenotypes are correlated with other behavioral types. Studies of *social networks* (the link between individual and group behavior) should determine the importance of information exchange via chemical cues. More research is needed about the uncertainty associated with chemical information (e.g., because of lack of experience, conflicting information, or possible cue crypsis). Does the source of the information—individual experience versus social—alter behavioral responses?

In addition to filling taxonomic gaps and addressing current and emerging conceptual problems, there is a pressing need to examine the challenges to chemosensory behavior imposed by the rapidly changing environment, particularly in light of global species extinctions. To address all of these issues, comparative psychologists and ethologists must build on our rich history of conceptual, theoretical, and methodological innovations.

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Chapter 5

PERCEPTUAL AND FUNCTIONAL CATEGORIZATION IN ANIMALS

Ulrike Aust

Categorization is not an exclusively human trait but can been found everywhere throughout the animal kingdom. This suggests that sorting similar stimuli into classes is an ability that represents an evolutionary adaptation of considerable value to almost any kinds of organisms. However, the level of abstraction at which an animal solves a particular categorization task and the underlying perceptual and cognitive mechanisms have often been found difficult to identify. Categorization may be based just on simple rote learning or, alternatively, on the formation of equivalence classes based on the abstraction of perceptual or functional similarities among class members. The most cognitively demanding types of equivalence formation require the recognition of abstract relations among stimuli or even among relations. Not surprisingly, relational categorizations have been convincingly shown only in a handful of nonhuman species so far. This chapter addresses two levels of categorization for which evidence frequently has been found in a wide range of animals: perceptual and functional categories.

CATEGORIZATION: DEFINITION, SIGNIFICANCE, AND LEVELS OF ABSTRACTNESS

Categorization is commonly regarded as a process of determining what things "belong together," and a category is therefore a class of stimuli that cohere (Zentall, Galizio, & Critchfied, 2002).

What Is Categorization?

In its broadest sense, a subject can be said to categorize when it treats a set of objects or events as equivalent and responds to them in the same (or a similar) manner. To do so, it has to detect recurrences (i.e., constancies across time and space) in the environment despite variations in the appearance of the objects it encounters (Herrnstein, 1984; Zentall, Wasserman, Lazareva, Thompson, & Rattermann, 2008). Categorization thus requires a subject to find points of contact between previous situations and the current context (Medin, 1989; Zayan & Vauclair, 1998). This, in turn, requires abstraction—the ability to combine experiences from a number of situations to detect common features—and leads to generalization—the ability to group two or more stimuli on the basis of the similarities they have and despite the perceived differences between or among them.

But the ability to generalize is only one side of the coin. The second component of categorization is discrimination—the ability to distinguish between or among individual stimuli. With regard to between-category discrimination, this means that a subject must be able to distinguish between members and nonmembers of a particular class (or between members of one class and members of another class). Yet, categorization also requires within-class discrimination, that is, the ability to distinguish between the individual members of the same class, despite the perceived similarities between or among them. In other words, failure

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to discriminate disqualifies similar (or identical) response behavior toward members of the same class from reflecting categorization. To put it concisely, categorization requires (a) generalization across class members, (b) discrimination between class members and nonmembers, and (c) discrimination among class members.

The Functions of Categorization

The benefit of categorization is cognitive economy, arising from the fact that it enables an organism to partition the multitude of environmental stimuli into smaller classes (Medin, 1989). Categorization can therefore be seen as an economical principle which considerably reduces the amount of cognitive demand by simplifying the complex and changing environment. In other words, categorization serves the organization of knowledge and is thus an evolutionary adaptation that makes the external world more manageable. It thereby allows a subject to deal efficiently with and react appropriately to the events and objects it encounters. To be precise, the ability to categorize yields a dual benefit: It solves the information bottleneck problem and it enables inference.

First, animal sensory systems encounter bottlenecks whenever information has to be passed on from one processing stage to the next (see Chapters 3 and 6, this volume). This starts already at the level of the sensory organs where the flood of incoming information about the environment exceeds by far the receptive capacities of the sensory system and must thus be selectively filtered and thereby reduced. But still, more information is transmitted to the nervous system than to which the motor system can possibly respond. The solution to the bottleneck problem at this level is provided by categorization as the mechanism by which irrelevant information is omitted and critical information is condensed in the service of building more general classes of objects (see Rosch, 1978; Zayan & Vauclair, 1998).

Second, if every encountered object was perceived as unique, a subject would have to explore them all individually to gain knowledge about features and functions and to decide how to respond. This may be not only time-consuming but also potentially dangerous or even fatal. However, objects of the same category tend to share certain features and functions and, therefore, it will usually make sense to react to them in a similar way. If an animal recognizes a novel object as member of a familiar class it can apply to this item its knowledge about the category that it has acquired already during previous encounters with other members of that class (Huber, 2000; Medin, 1989; Zayan & Vauclair, 1998; Zentall et al., 2008). In other words, further (invisible) features can be inferred as soon as class membership of an object has been recognized by means of its perceptual features because categorization provides access to large quantities of information about that type of objects, including their function(s) and expectations concerning their (future) behavior as well as knowledge about how to appropriately respond to them. Categorization thus saves the animal the need to explore every novel object through trial and error (and thus the costs and risks associated with this type of learning) by providing it with the possibility of making predictions on the basis of partial information (Medin, 1989; Zentall et al., 2008; see also Chapter 29, this volume).

Levels of Categorization

There have been numerous efforts to systematize categorization. The framework on which the remainder of this chapter will be based combines and modifies some of the most commonly used classification systems, as, for example, those suggested by Herrnstein (1990); Urcuioli (2001); Wasserman (1995); Zayan and Vauclair (1998); Zentall et al. (2002, 2008); and Zentall, Wasserman, and Urcuioli (2014). Generally, what these systems have in common with the one presented here is that they put forward several categorization levels of increasing complexity and abstractness.

Fundamentally, categorization on the basis of *rote learning* has to be distinguished from classification types that involve the formation of *equivalence classes*. In rote learning, every single item gets associated with a reinforcer but this does not, by itself, establish any relationship among class members. A famous example of this type of learning was provided by Vaughan and Greene (1984), who showed that pigeons *(Columba livia)* could learn to correctly classify

160 pictures showing complex random squiggles, each of which had arbitrarily been assigned to the positive or the negative class. By contrast, the formation of equivalence classes always entails some kind of relation among the stimuli belonging to a category. As a consequence, members of equivalence classes become interchangeable (see, e.g., Zentall et al., 2014). Several levels of equivalence classes can be distinguished, which differ from one another with respect to the nature and abstractness of the relationships among category members (Table 5.1).

Perceptual categories. Instances of perceptual categories have some physical properties in common and are therefore characterized by perceptual coherence, or, to put it in more mundane terms, they "look alike" (see, e.g., Herrnstein, 1990; Zentall et al., 2002, 2008, 2014). For example, there are many different types of flowers and likewise, there are many different types of dogs. Nevertheless, individual flowers will resemble each other more strongly than they will resemble dogs. Category judgments are thus based on physical similarity, with members of the same category being perceptually more similar to each other than to members of other categories. Because the number of possible class members is potentially unlimited, such categories are often referred to as *open-ended categories*.

Associative categories. In contrast to perceptual categories, members of associative categories become equivalent not because of physical similarity but by virtue of a common association, and they develop through experience. To this end, diverse experiences are combined into a category on the basis of similar meaning (Zentall et al., 2014; see also Chapter 15, this volume), which is referred to as *functional similarity*. So far, there largely is agreement among the various categorization classification systems. However, they differ in the degree to which they distinguish between two basic types of stimuli that may become associated and/or in the emphasis they place on one or the other (see, Aust, Apfalter, & Huber, 2005; Lea, 1984; Huber, 2010; Zentall et al., 2002, 2008, 2014); namely, the stimuli to be associated may be either arbitrary (i.e., share no obvious common function outside the experimental context) or may indeed be related by such a common function.

Equivalence among arbitrary stimuli. This type of category is what many researchers have in mind when they talk of "acquired equivalence classes" (e.g., Urcuioli, 2001, 2013; Zentall et al., 2014). It consists of stimuli that are associated with a common event or outcome (e.g., a food reward or a light). Importantly, the stimuli that get associated are not only perceptually arbitrary (meaning that they are not related by physical similarity) but also functionally arbitrary (in the sense that they lack a common function outside the experimental context). Category membership is established solely through training and experience gained during an experiment, and the common consequence within

TABLE 5.1

Levels of Categorization

		Level	Relation among category members
high ← abstractness → low	Formation of equivalence classes	Categories based on rote-learning	
		Perceptual categories	Physical similarity
		Associative categories	
		Acquired equivalence classes	Common consequence (in experiment)
		Functional categories	Common function (outside experiment)
		Relational categories	Logic
		First-order relationships	
		Second-order relationships	
		Analogies	

Note. This chapter covers only evidence coming from the perceptual and the functional levels of categorization.

this context is the only relation among class members and therefore the only potential basis for generalization: Class extension is possible only through the mediating effects of particular, individual stimuli. In a conditioned discrimination task, for example, equivalence between a sample stimulus A and a sample stimulus B may be established only if they require choice of the same comparison stimulus. Whether such equivalence has indeed emerged can be evaluated by subsequently reassigning one sample stimulus, for example, (A) to a novel comparison stimulus and then testing if choice of the novel comparison stimulus is spontaneously transferred to the other sample stimulus (B).

Functional categories. By contrast, members of functional categories are related to one another by a particular function that is reinforced but not established by common consequences in an experiment. More specifically, this function is an abstract feature shared by a set of stimuli that is of biological importance to an animal independent of common reinforcement of these stimuli in an experiment. This means that the stimuli that get associated are perceptually arbitrary but, unlike in acquired equivalence classes, are functionally similar (in the sense that they share a common function outside the experimental context). Famous examples of functional categories are *food*, *tool*, and *familiarity*. In contrast to acquired equivalence classes, members of such classes can become associated with each other and with a certain common response already prior to their presentation in an experiment. What is still to be learned in the experiment then is to emit a *different response* to such stimuli than the one learned in the natural context (e.g., to press a lever in the presence of a food stimulus rather than trying to consume it or to peck a key in the presence of a familiar conspecific stimulus rather than to engage in social behavior). Functional similarity in the form of an abstract feature of biological significance makes the extension of such categories independent from any associations among particular, individual instances and thereby is a faster and more encompassing process than could ever be at work in acquired equivalence classes with their “one-by-one mode” of adding further stimuli to a category. This is the reason why I have placed functional categories more toward the “high level” end in the hierarchy of categories than acquired equivalence classes (see Table 5.1). Importantly, however, this does not mean that acquired equivalence classes necessarily represent a lower level of abstractness regarding the relation among class members than do functional categories.

A final point worth noting is that an obvious common function may, in practice, not always be shared by all members of a functional category but rather may apply only to a subset. An example is the concept of *familiarity*. Familiarity is an abstract feature that allows correct classification of exemplars that bear no physical similarity. But it may be difficult to imagine cases in which familiarity, as such, will serve a particular biological function. Rather, subclasses of familiar items, like conspecifics (or, even more specifically, friends, partners, or enemies) will be characterized by such a function. Thus, if one defines *function* as a very specific purpose, familiarity, in general, may not always meet the criteria of a functional category. But if one applies an extended definition in the sense of a general functional relevance, as will be done in this chapter, familiarity would indeed be an example of a functional category (see, Stephan, Wilkinson, & Huber, 2013).

Relational categories. Categories at this level are characterized not by perceptual or functional similarity but by a logical relationship either among category members or among relations (see Chapter 17, this volume). *First-order relationships* are abstract relations between two or more stimuli, meaning that one stimulus is categorized relative to another. Famous examples of such categories that have frequently been investigated also in animals, mainly birds (e.g., pigeons, parrots [*Psittacus erithacus*]) and primates (e.g., baboons [*Papio papio*]), are same/different (e.g., Gibson & Wasserman, 2003; Pepperberg, 1987; Wasserman, 1995; Wasserman & Castro, 2012; Wasserman, Fagot, & Young, 2001; Wright & Katz, 2006; Young & Wasserman, 1997) and symmetric/asymmetric (e.g., Huber, Aust, Michelbach, Ölzant, Loidolt, & Nowotny, 1999). *Second-order relationships* are relations among relations. For example, a subject may have to determine if the relationships between the components of two stimulus pairs are the same or different. *Analogical reasoning,* finally, is defined as the ability to judge the equivalence of relationships between two sets of stimuli at a level that extends beyond sameness and difference (see Pearce, 2008). Typical analogical reasoning tasks are found, for example, in intelligence tests for humans where they have to solve problems like “As cat is to kitten, so dog is to what?” Evidence of categorization at the two most abstract levels (second-order relationships and analogical reasoning) is scarce (and usually shaky) in nonhumans and, for the most part, restricted to language trained primates (e.g., Gillan, Premack, & Woodruff, 1981; Premack, 1983).

Concepts. The topic of concepts has given rise to a lot of confusion and misunderstanding. The core of the problem lies in the lack of a common currency or terminology, which makes the concept a key notion for which there is no generally accepted definition, as Zentall and his colleagues (2008) aptly put it. On the one hand, it has become common practice in some research traditions to consider perceptual feature learning and transfer of the resulting discriminations to novel category instances a sufficient criterion for concept formation (see, Lazareva & Wasserman, 2008; Wasserman, Kiedinger, & Bhatt, 1988; Zentall et al., 2002, 2008, 2014). As a consequence, the term has been used more or less synonymously with categorization beyond the level of individual exemplars (i.e., for all kinds of equivalence classes including the ones on the basis of perceptual similarity). On the other hand, we find concept definitions that emphasize the importance of human language, either by expecting verbal expression of a rule, or by assuming that the investigation of concepts is justified only on condition that there is a sense of concept that applies to humans as well as to nonlinguistic animals (Chater & Heyes, 1994). Others, like Geach (1957), even claimed that conceptualization requires the ability of an organism to discuss its own concepts. This goes even beyond the claim for verbal expression as the subject should be able to manipulate its concepts mentally. Thus, although some concept definitions have been so broad that they encompassed almost all types of categorizations, others have been so narrow that conceptualization could hardly be achieved by any nonhuman animal.

In the absence of a consensus definition, it is evident that concepts provide a slippery foundation for experimental analysis. Today, however, two criteria are accepted by many authors to define concept formation. These are rapid and spontaneous generalization over class members and an ability to classify objects on the basis of some functional similarity or abstract (logical) relationship (i.e., independent of physical resemblance; see Lea, 1984; Zayan & Vauclair, 1998). Lea (1984) suggested two behavioral indicators to recognize conceptualization. *Clumping* refers to the idea that once a concept has been formed, it should be more difficult to learn a new task in which different responses are required to different instances of the concept (and the same response to instances of different concepts) than a task in which the same response is required to all instances of one concept and different responses to all instances of different concepts. *Instance-to-category generalization* means that if something is learned about one instance of a concept, it should spontaneously transfer to other instances. In combination, these two criteria seem appropriate for indicating concept formation. It should be taken into account, however, that in practice, it may be difficult to distinguish between clumping and instance-to-category generalization occurring as a consequence of mere stimulus generalization or of true categorization (with the latter including not only generalization among class members and discrimination between classes, but also discrimination within classes).

If we adopt a definition of concept in terms of categorization independent of physical similarity and accept clumping and instance-to-category generalization as behavioral indicators of conceptualization, then which levels of categorization reflect concept formation? Neither rote learning nor perceptual categorization fulfill these requirements and categorizations at these levels should not be called concepts. Within the level of associative categories the subtype of acquired equivalence among arbitrary stimuli is a bit tricky. On the one hand, such categories meet the claim for classification of stimuli regardless of their physical appearance, and numerous experiments have also shown evidence of clumping and instance-to-category generalization. On the other hand, rapid and spontaneous generalization to novel instances does not occur at this level, as further stimuli can be added to a category only one-by-one (i.e., by an association between a particular novel and one or more familiar stimuli being established). We may therefore best describe acquired equivalence classes of arbitrary stimuli as preconcepts, for they meet some but not all the requirements of true concepts and are restricted to categories defined by functions that do not exceed the level of recognizing common reinforcement contingencies in an experiment (see Aust et al., 2005). By contrast, functional categories clearly meet all criteria of concepts in the previous sense, and so do relational categories. Therefore, the term *concept* will be applied only to categorization performances at these levels.

Distinguishing between different levels of categorization. At first sight, it appears that the previous system provides a clear and simple basis for distinguishing between the different levels at which an animal may make category judgments. On closer inspection, however, it becomes obvious that unambiguously assigning a certain categorization task to one particular level may, in practice, be difficult. The reasons for this are twofold.

Fuzzy boundaries. First, although the distinction between the various levels of categorization is quite clear cut in theory, there are sometimes no such strict dividing lines in practice. At the level of rote learning, for example, according to the definition given previously, each category member is individually associated with the reinforcer, but no associations among category members are established. In practice, however, such relations, mediated by the common contingencies of reinforcement, may well emerge as training of an animal proceeds. Thereby, categorization by rote seamlessly shifts into categorization by acquired equivalence among arbitrary stimuli. Such transitions can best be shown in reversal experiments. For instance, in a classical experiment, Vaughan (1988) trained pigeons to discriminate between two sets of tree slides. The individual stimuli had arbitrarily been assigned to the positive and the negative set so that the only feature to distinguish between the two classes were the contingencies of reinforcement (reward or nonreward). Such categories are called pseudocategories because their members are not related by any similarity principle (or "rule") that sets them apart from the members of the opposite category. Instead, between-class similarities are just as strong as within-class similarities. Therefore, the previous task constituted a quite demanding example of rote learning. Nevertheless, the pigeons learned the discrimination, at which point they were subjected to a series of discrimination reversals in which the previously positive stimulus set became negative and the previously negative stimulus set became positive. The pigeons indeed reversed their responding to all stimuli of each set appropriately after the first few trials. Most important, however, they were able to do so only after dozens of reversals. This suggests that, initially, the members of each set got individually associated with the contingencies of reinforcement but not with each other. Such secondary categorical relations among class members obviously emerged only in the course of extensive reversal training—indicating that the pigeons eventually considered each tree slide as belonging to a common set (i.e., had learned arbitrary stimulus equivalences). Hence, the birds showed evidence of rote learning according to the previous definition in the first part of the experiment (initial discrimination) but shifted to the level of acquired equivalence of arbitrary stimuli (i.e., the formation of interstimulus associations because of a common outcome) in the second part (reversal learning).

Parallel strategies. Second, the mechanism by which an animal accomplishes a certain categorization task is not always evident. For example, a subject's classification behavior may well correlate with a conceptual rule intended by the experimenter. However, there is no guarantee that the animal has indeed used that rule for solving the task. Instead, it may have relied on another, simpler, rule that paralleled the conceptual one (Lea, 1984). Rather than recognizing any abstract properties shared by the members of the respective category, the animal may just have extracted some simple perceptual invariants that inadvertently correlated with the concept. If, for example, a subject is required to sort items into the categories "food" and "nonfood," it may, indeed, do so on the basis of edibility (i.e., according to function). If, however, the presented food (or the nonfood) objects also share, by accident, some salient perceptual feature (e.g., all being soft), the animal may just as well categorize them according to physical similarity. In short, it may rely either on the perceptual or on the functional aspects of a category if both redundantly predict class membership and there is evidence that both sources of information may even be used simultaneously and may thus interfere (see Castro, Wasserman, Fagot, & Maugard, 2015).

Similarly, an animal may extract and use in parallel item-specific information (corresponding to the level of rote learning) and category-specific information (corresponding to the formation of an equivalence class). In Aust and Huber (2001), for example, pigeons trained to sort photographs according to the presence or absence of humans were found to rely on idiosyncratic features of individual stimuli and target specific features typical of human figures (see section on the modified feature model). Likewise, some categorization tasks may be solved by means of either perceptual or relational features. For example, in experiments that investigated the presence of an abstract same/different rule in pigeons and baboons by training them to indicate whether the 16 icons of an array were identical or different it was revealed, on closer inspection, that the animals solved the task by means of display variability (i.e., a merely perceptual feature that paralleled the intended same/different rule; Wasserman, 1995; Wasserman et al., 2001; Young & Wasserman, 1997). Furthermore, there is evidence that perceptual and relational information may interact in a subject's category decisions (see Chapter 17, this volume). In Gibson and Wasserman (2003) pigeons were also taught to discriminate arrays of 16 identical items from displays of 16 different ones. This time, however, the "same" arrays were created from one set of items (A) and the "different" arrays from another set of items (B). On test, the birds were presented with reversed arrays, meaning that same arrays were created with items of set B and different arrays were created with items of set A. The pigeons performed below chance with these arrays, which suggested control by perceptual features. However, they performed significantly above chance with arrays composed of novel icons (neither set A nor set B), which indicated control by relational features. The results thus provided evidence that animals can learn and use in parallel perceptual stimulus properties and abstract features when both are relevant discriminative cues.

The difficulties that may be encountered in practice when it comes to identifying the level at which an animal performs in a particular categorization task have led some authors to suggest that there may be no chasm but a continuum from perceptual to conceptual processing (see, Castro et al., 2015). For example, Goldstone and Barsalou (1998) stated that "concepts usually stem from perception, and active vestiges of these perceptual origins exist for the vast majority of concepts" (p. 232). As a consequence, claims have been raised to abandon the categorical distinction between perceptually and conceptually defined categories (e.g., Barsalou, 2008; Goldstone, 2004; Goldstone & Barsalou, 1998; Tomlinson & Love, 2006; see also Castro et al., 2015). However, I take a different view. Although it may be indisputably difficult to disentangle particular categorization *strategies* in practice, the theoretical distinction between *types* of categories is quite obvious (if the latter are properly and clearly defined) and should be maintained to provide a clear framework to which one can refer when analyzing and interpreting the results of a particular categorization experiment. The greatest effort should be invested, however, in devising categorization tasks that allow for clearly distinguishing between perceptual and more abstract properties, ideally by providing only one or the other type of information. But as this may sometimes be difficult to achieve in practice, experimental designs should, at least, be devised in a way that allows for post-hoc analysis of the used strategies, for example, by putting different types of cues into conflict (as was done in the studies by Aust & Huber, 2001; Gibson & Wasserman, 2003).

As a final point, I would like to stress that the hierarchy of categories as suggested in this chapter is not undisputed in the scientific community. I suspect, however, that much of this disagreement is rooted in different terminologies rather than in substantive differences regarding the basic characteristics of the various types of categories (see, Zentall et al., 2002, 2008, 2014). To some authors, relational categories, for example, cover a full range from perceptually related identity to analogies, whereas in the present chapter it is used only for categories whose members share an abstract relation. Also, an explicit distinction between acquired equivalence classes of arbitrary stimuli and functional categories within the level of associative categories is not always made and/or it is claimed that the critical feature of associative categories be generalization of learning about one member of the category to other members. The latter, however, means that the associative level would cover also categorizations on the basis of perceptual similarity or on abstract (logical) relations, whereas the present classification system places them between these two. In short, there is considerable room for differences of opinion concerning the classification and characterization of categories. The classification system put forward in this chapter is thus only one among several ones that take somewhat diverging views on particular terms and conceptions but are equally valid.

PERCEPTUAL CATEGORIES

Perceptual similarity guides category judgments made by animals just as it guides the speaking of humans, most of whose language categories (e.g., houses, tables, trees) are indeed defined by means of perceptual properties that are shared by category members and set these apart from nonmembers (see Zentall et al., 2008).

Evidence in Animals

It is also well established that a wide variety of animal species can learn to perform categorizations at this level, including fish, various bird taxa, numerous mammal species (particularly primates), and even some invertebrates. Providing a comprehensive survey would by far go beyond the scope of this chapter, which demands that the present overview be selective with just a few examples being given to illustrate the generality and widespread distribution of animals' perceptual categorization abilities (for reviews see, Bovet & Vauclair, 2000; Fagot, 2000; Jitsumori & Delius, 2001; Mareschal, Quinn, & Lea, 2010; Pearce, 2008; Zentall et al., 2002, 2008, 2014).

Among birds, chicks (*Gallus gallus*, for example) have been shown to categorize objects on the basis of perceptual features like color, shape, and size (Fontanari, Rugani, Regolin, & Vallortigara, 2011). But above all, pigeons have been found able to discriminate a wide variety of categories, among them people, trees, bodies of water, pigeons, fish, flowers, chairs, cars, houses, cats, and dogs (e.g., Aust & Braunöder, 2015; Aust & Huber, 2001, 2002, 2003; Bhatt, Wasserman, Reynolds, & Knauss, 1988; Ghosh, Lea, & Noury, 2004; Goto, Lea, Wills, & Milton, 2011; Herrnstein, 1979, 1985; Herrnstein & de Villiers, 1980; Herrnstein & Loveland, 1964; Lazareva, Soto, & Wasserman, 2010; Lazareva, Vecera, & Wasserman, 2006; Lea, De Filippo, Dakin, & Meier, 2013; Matsukawa, Inoue, & Jitsumori, 2004; Nicholls, Ryan, Bryant, & Lea, 2011; Wasserman et al., 1988; Watanabe, 1992; for reviews, see, Huber, 2001; Huber & Aust, 2011; Zentall et al., 2008). Some of the previous categories involve items that may well be part of a pigeon's natural environment so that it is not too surprising that these birds were found able to deal with them. However, several experiments have shown that pigeons can also learn to routinely sort completely unfamiliar stimuli like fish (Herrnstein & de Villiers, 1980). Two interesting examples shall further illustrate this (see Chapter 6, this volume). Watanabe, Sakamoto, and Wakita (1995) trained pigeons to discriminate between color slides of paintings by Monet and by Picasso. Subsequently, the birds showed transfer not only to novel pictures by these painters but also to pictures by other artists with a similar painting style. For example, they generalized from paintings by Monet to paintings by Cezanne and Renoir and from paintings by Picasso to paintings by Braque and Matisse. This indicated that the birds were obviously able to abstract some perceptual features that characterized (and distinguished) impressionist and cubist painting styles. In a later study (Watanabe, 2010), pigeons also learned to discriminate between "good/beautiful" and "bad/ugly" paintings by children (with the pictures being assigned to these categories by the experimenter according to prior ratings by human adults) and subsequently showed transfer also to novel instances of these classes. Further tests indicated that the pigeons used color and pattern cues to solve the task.

Impressive perceptual categorization abilities have also been found in primates. Some studies have shown that several macaque species (*Macaca spp.*) can learn to sort pictures according to the presence or absence of people or monkeys (e.g., D'Amato & Van Sant, 1988; Schrier & Brady, 1987), although their respective categories were probably more inclusive than, and not entirely congruent with, the ones built by humans. For example, a slice of watermelon or a flamingo were misclassified as humans, presumably because their reddish color resembled human skin. Furthermore, rhesus macaques (*Macaca mulatta*) learned to discriminate between pictures of trees and nontrees and between pictures of fish and nonfish (Vogels, 1999). Sands, Lincoln, and Wright (1982) showed that rhesus macaques perceived perceptual coherence of pictures showing different instances of fruit. In the same study evidence was found for them perceiving human and monkey faces as similar (see Chapter 7, this volume) and, likewise, trees and flowers, as pictures of these categories were clustered together (i.e., monkeys responded to them in a similar way). Roberts and Mazmanian (1988) trained pigeons, squirrel monkeys (*Saimiri sciureus*) and humans (*Homo sapiens*) to make discriminations at different levels of abstractness, namely, with pictures of kingfishers versus other birds, birds versus other animals, and animals versus nonanimals. The results suggested that the pigeons as well as the monkeys were probably not able to rely on conceptual information to solve the tasks but were largely restricted to the use of perceptual features. These findings are widely consistent with those of a similar study with a gorilla (*Gorilla gorilla*) that was trained at three levels of abstraction with sets of photographs showing instances of a wide variety of natural categories (Vonk & MacDonald, 2002).

Models of Perceptual Categorization

Exemplar, feature, and prototype models. Today, essentially three major types of probabilistic models of categorization compete, and it has not been possible yet to capture the multitude of different results under one single theoretical framework. It seems that each model is able to explain part of the data and, despite their different basic assumptions, it is sometimes difficult to distinguish among the three explanatory accounts. *Exemplar models* postulate that every instance (or exemplar) encountered is remembered, as well as the category to which it belongs, and novel instances are then assigned to the category of the stored exemplar to which it bears the highest degree of perceptual similarity. *Feature models* purport that class-specific aspects are extracted from individual exemplars and are then combined to form a feature list, consisting of the relative frequencies of those features. Novel stimuli are assigned to the class whose feature list matches best the featural description of the stimulus to be classified. Finally, *prototype models* assume that categorization is accomplished by the abstraction of a summary representation of a category that corresponds to the average, or central, tendency of all exemplars that have been experienced. Classification of novel exemplars is supposed to be based on their similarity to the prototype. For a review of the different models see Huber and Aust (2011).

A categorization theory on the basis of a modified feature model. Huber and Aust (2011) proposed a *modified feature theory* of categorization (MFT). Although it was put forward to explain perceptual categorization in pigeons, it may in fact be applicable to a wide range of species. As do all modern versions of feature theory, the MFT postulates flexibility in feature creation and selection. But, in addition, it acknowledges that (a) animals may switch between features even within a particular task—an aspect that is often underrated or completely disregarded by other feature theories, and (b) animals' category decisions may be based on various features from different dimensions and levels of complexity. In the following sections, examples for these two claims of the MFT are provided.

Item- and category-specific information. Traditional feature theories assume that, although item-specific information may also be acquired, it is the abstraction of category-specific features that is critical for categorization. By contrast, the MFT holds that the balance of the two will depend on a multitude of factors, including, for example, category structure and procedural details. For instance, Aust and Huber (2001) trained pigeons to discriminate between color photographs with humans (P) and without humans (NP). Classification was found to be controlled by item- and category-specific features, but only in birds, which were reinforced on P pictures was category-specific information given precedence over item-specific information when the two were brought into conflict. (This was achieved, for instance, by pasting novel human figures on familiar NP backgrounds.)

Another example was provided by Loidolt, Aust, Meran, and Huber (2003), who trained pigeons to discriminate between individual male human faces, half of which were (randomly) defined as positive and the others as negative. This phase was followed by training that required the same birds to discriminate between male and female faces (i.e., by means of category-specific information). This latter phase also involved the presentation of the male faces shown in the first task, to determine whether the pigeons would retain the previously formed associations (on the basis of item-specific aspects) in spite of the subsequent category training. Results indicated that the pigeons learned both tasks, which suggested that they could use either type of information—item- or category-specific—depending on the requirements of the task. Furthermore, category-specific information had precedence over item-specific information, as the birds assigned the male faces from the first task according to sex in the second task. Most important, they did so even when this required changing a stimulus's associative value (e.g., if a particular face belonged to the negative class in the first task but, to that bird, male faces constituted the positive class in the second task).

Lower- and higher-level features. An animal may furthermore rely on some simple physical dimensions (like intensity or color) in one task but make use of a polymorphous class rule (some "higher" feature) in another. The latter means that identification of a class member is not accomplished just by means of some single feature, but by applying a more complex response rule, which integrates a collection of differently weighted target features that contribute to classification in an additive way. The use of such a polymorphous class rule was shown by Aust and Huber (2002) in a study on pigeons that were trained to classify photographs according to the presence or absence of humans. It was revealed that properties related to target size and internal structure played a particularly important role, and so did the presence of items of apparel. Furthermore, some parts of the human figure (like arms and heads) made good class predictors whereas others (like legs or skin color) did not.

Cook, Wright, and Drachman (2013), by contrast, found evidence of pigeons reducing the categorical stimulus space to a few visual features when they were trained to categorize line drawings of birds and mammals. In particular, the results suggested that they segregated and primarily used the principal axis of orientation of the depicted animal figures.

Similarly, pigeons learned to discriminate between pictures of male and female human faces by using overall intensity (male faces tended to be darker than female faces; Huber, Troje, Loidolt, Aust, & Grass, 2000; Troje, Huber, Loidolt, Aust, & Fieder, 1999). When they were deprived of this cue (by equalizing the intensity of the faces), they turned to color information (male faces contained, on average, a larger proportion of red, whereas female faces contained larger proportions of green and blue) and, if deprived of this cue as well, they relied on patterns of shading. This suggests that the birds were able to accomplish the male–female discrimination by attending exactly to those feature dimensions that, at each stage of the experiment, most accurately divided the two classes.

Local and global features. As a final example of flexible feature use, the issue of local versus global processing is considered. There is evidence that the human visual system tends to prioritize more highly the global level of perceptual analysis, meaning that we perceive objects as integrated wholes rather than (or prior to) collections of independent component parts (e.g., Fagot & Tomonaga, 1999; Goto, Wills, & Lea, 2004; Navon, 1977). Experiments with other (nonhuman) primates like baboons (Deruelle & Fagot, 1998; Fagot &

Deruelle, 1997), capuchin monkeys (*Cebus apella*; Spinozzi, De Lillo, & Truppa, 2003), cotton- top tamarins (*Saguinus oedipus*; Neiworth, Gleichman, Olinick, & Lamp, 2006), and chimpanzees (*Pan troglodytes*; Fagot & Tomonaga, 1999) yielded either no reliable preference for either processing level or (with the exception of cotton-top tamarins that were rather globally biased) revealed a local advantage. Among birds, pigeons have repeatedly shown a local bias (see, Cerella, 1980) that has become known as the *local precedence effect* (e.g., Cavoto & Cook, 2001; Cook, 1992; Gibson, Wasserman, Gosselin, & Schyns, 2005). Recently, a local preference has also been found in domestic chicks (Chiandetti, Pecchia, Patt, & Vallortigara, 2014; see also Chapters 8 and 9, this volume).

Table 5.2 summarizes the findings of some selected key studies on local and global processing in various species, and Figure 5.1 compares the results of experiments on the preferred processing styles of pigeons, chicks, cotton-top tamarins, and humans. It has to be considered, however, that direct comparisons between species are usually difficult because of variations in the testing procedures

TABLE 5.2

Comparison of Various Species Regarding Their Preferred Processing Style (Local or Global)

Species	Study	Stimuli	Basic procedure	Result (preference)
Pigeon	Cerella (1980)	scrambled line drawings (cartoon figures)	go/no-go	local
	Kirkpatrick-Steger et al. (1998)	scrambled line drawings (objects)	4AFC	local + global
	Aust and Huber (2003)	scrambled photographs (humans)	go/no-go	local + global
	Cavoto and Cook (2001)	hierarchical (letters)	4AFC	local
	Goto et al. (2004)	hierarchical (complex geometric figures)	go/no-go	global
	Lazareva et al. (2006)	intact/scrambled/blurred photographs (trees, flowers, chairs, cars)	4AFC	local + global[a]
	Stobbe et al. (2012)	tiles (pattered squares building strings)	2AFC	local + global/ intermediate
	Aust and Braunöder (2015)	intact/scrambled/blurred photographs (trees)	2AFC	local
Chick	Chiandetti et al. (2014)	hierarchical (circle/square)	2AFC	local
Kea	Stobbe et al. (2012)	tiles (pattered squares building strings)	2AFC	local
Cotton top tamarin	Neiworth et al. (2006)	hierarchical (circle/square)	go/no-go	global/local + global[b]
Tufted capuchin monkey	Spinozzi et al. (2003)	hierarchical (circle/square/ rhombus/letter X)	MTS	local
Baboon	Deruelle and Fagot (1998); Fagot and Deruelle (1997)	hierarchical (circle/square)	visual search task	local
Chimpanzee	Fagot and Tomonaga (1999)	hierarchical (circle/square)	visual search task	local/local + global[b]
Human (adults)	Deruelle and Fagot (1998); Fagot and Deruelle (1997); Fagot and Tomonaga (1999)	hierarchical (circle/square)	visual search task	global
	Goto et al. (2004)	hierarchical (complex geometric figures)	go/no-go	global
	Neiworth et al. (2006)	hierarchical (circle/square)	2AFC	global
Human (children)	Neiworth et al. (2006)	hierarchical (circle/square)	2AFC	global/local + global[b]

Note. 2/4 AFC = two/four alternative forced-choice procedure; MTS = matching-to-sample procedure.

[a] Depending on stimulus category. [b] Depending on density of local elements.

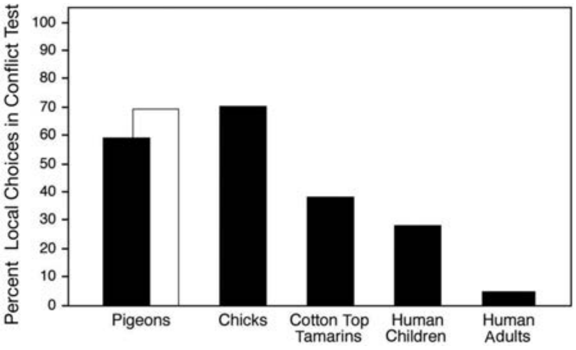

FIGURE 5.1. Comparison of pigeons (*n* = 4; Cavoto & Cook, 2001), domestic chicks (*n* = 142; Chiandetti et al., 2014), cotton top tamarins (*n* = 8; Neiworth et al., 2006), human children (*n* = 12; Neiworth et al., 2006), and human adults (*n* = 35; Neiworth et al., 2006) as percentage choices according to the local level in a conflict test with hierarchical stimuli. The white bar represents the pigeon results obtained when the data of the only bird that showed no preference for either processing style were excluded (i.e., *n* = 3). Means were taken across subjects.

(e.g., go/no-go, visual search tasks, matching-to sample, two or four alternative forced-choice procedures), the measured parameters (e.g., choice accuracy, choice preferences, response times, numbers of sessions to reach criterion), and stimuli (e.g., scrambled/blurred photographs or line drawings, hierarchical stimuli). The situation is further complicated by the fact that, in some species, the preferred processing level has occasionally been found to depend on specifics of the presented stimuli: Most of the studies cited previously used so-called "hierarchical stimuli," that is, large (global) stimuli that consist of a number of small identical (local) elements, like a letter made up of small letters. Training an animal to discriminate hierarchical stimuli that differ either at the local or at the global level allows for identifying the preferred processing style. Particularly informative in this respect are conflict tests that involve stimuli providing inconsistent information at the local and at the global level (like a T letter made up of small S letters). Interestingly, some studies using hierarchical patterns have found that the preferred processing level depended on specifics of the presented stimuli. For instance, human children as well as adult tamarins showed a global bias with dense displays (i.e., with stimuli consisting of many local elements) but use of local and global properties with sparse displays (i.e., with stimuli consisting of few local elements; Neiworth et al., 2006). Chimpanzees, by contrast, showed an advantage for processing the local shape in the low-density condition but showed no advantage in the high-density condition (Fagot & Tomonaga, 1999).

Because of all these difficulties, Figure 5.1 presents only results from studies that are roughly comparable, at least (i.e., they all used hierarchical stimuli and involved a conflict test). But still, several simplifications and restrictions regarding the selection of the presented data had to be made in the service of clarity and comparability: Means were taken across the two different density conditions under which tamarins and humans were tested, as this aspect was not assessed in the studies with pigeons and chicks. Furthermore, the chicks were also tested monocularly, but, to provide comparability with the other species, the Figure 5.1 shows only the data obtained under binocular viewing conditions.

In a recent study we found further support for pigeons using local features as their preferred source of information when making category judgments (Aust & Braunöder, 2015). Pigeons were trained to discriminate between color photographs of natural scenes that were characterized by either the presence (S+) or the absence (S−) of one or more trees. The birds were assigned to three different groups (intact, scrambled, blurred) that were trained with different versions of the stimuli. The intact group was presented with the original pictures, the scrambled group with scrambled versions of the same pictures, and the blurred group with blurred versions (Figure 5.2A). The idea was that scrambling would destroy configural information (intact local but degraded global information) whereas blurring would destroy the fine details of the images (intact global but degraded local information). Only the pictures shown to the intact group provided intact local and global information, so that the pigeons could use either or both to solve the discrimination. After training, the subjects were tested for transfer to the other two (i.e., previously untrained) presentation modes. Interestingly, the blurred group needed longer to learn the training task than the other two groups (Figure 5.2B). This

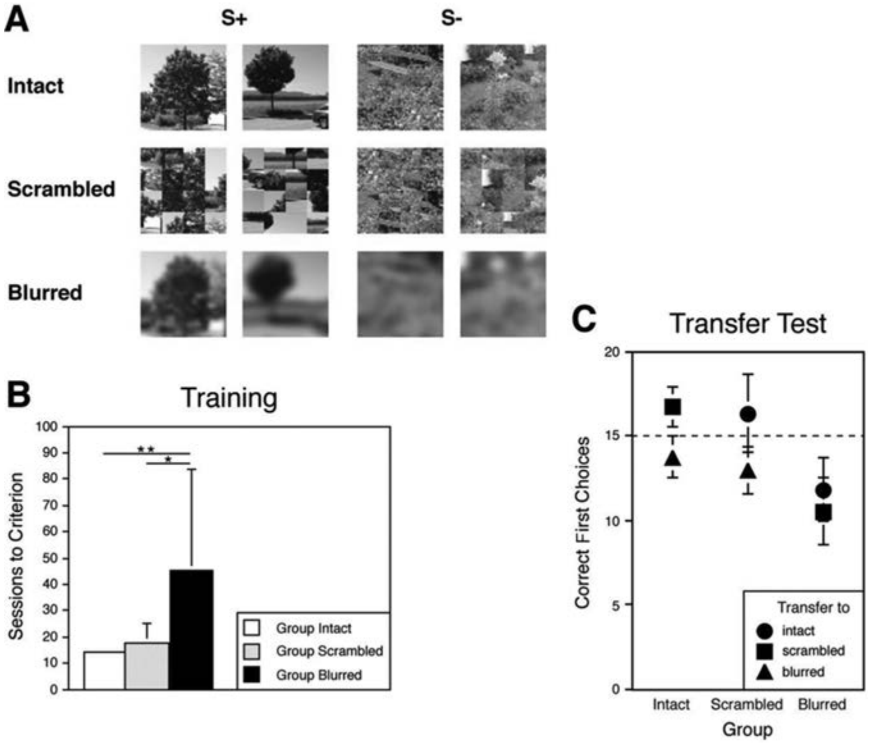

FIGURE 5.2. (A) Examples of positive (S+) and negative (S−) intact, scrambled, and blurred stimuli. (B) Number of training sessions required by the pigeons of the three groups (intact, scrambled, and blurred) to achieve the criterion of mastery (significant performance in a binomial test in 8 out of 10 successive sessions). Means (± SD) were taken across subjects. (C) Performance in the test for transfer to the two untrained modes as correct first choices out of 20. Means (± SD) were taken across subjects. The dashed line denotes the limit of significance. Adapted from "Transfer Between Local and Global Processing Levels by Pigeons (*Columba livia*) and Humans (*Homo sapiens*) in Exemplar- and Rule-Based Categorization Tasks," by A. Aust and E. Braunöder, E., 2015, *Journal of Comparative Psychology, 129,* pp. 6, 8, & 11. Copyright 2014 by the American Psychological Association. * $p < .05$; ** $p < .001$.

suggested that the loss of fine details constituted a disadvantage and was thus an indication of the importance of local information. Furthermore, we found good transfer from intact to scrambled pictures and vice versa, whereas generalization from intact and scrambled to blurred stimuli was poor, as was transfer from blurred to intact and scrambled stimuli (Figure 5.2C).

We interpreted these results in terms of a *transfer barrier*—caused by the lack of intact local information in blurred stimuli—that hampered or even prevented transfer from and to this type of picture. Most important, the blurred group could not even recognize intact versions of their training stimuli although these (like the blurred training stimuli they eventually learned to discriminate) provided intact global information. This suggests that the blurred group did not use global information but, like the other two groups, focused on local cues. However, degradation of local information in blurred stimuli made acquisition of the training task difficult and severely impeded transfer to the other presentation modes. By contrast, transfer between intact and scrambled pictures was possible because both types of stimuli contained intact local information. Together, the findings suggested a local processing strategy which was not abandoned even when local information was largely destroyed (blurred group) and thus provided a much worse basis for categorization than global information (which was intact). The study therefore supported the idea that local processing prevails in pigeons' visual categorization. However, there is reason to doubt the general validity of this claim. Some examples may illustrate this.

Kirkpatrick-Steger, Wasserman, and Biederman (1998) trained pigeons to discriminate four line drawings of human-made objects (watering can, desk lamp, sailboat, iron), with each object becoming associated with one of four response buttons. Subsequent tests with modified versions of the training stimuli (including the deletion of various local elements as well as different types of object scrambling) revealed that the spatial organization of the constituting elements was a major contributor to picture recognition, but that the individual elements were also important, with different individuals showing control by different subsets of local elements.

Similarly, Lazareva et al. (2006) trained pigeons first to associate members of the categories flowers, people, cars, and chairs with different response buttons and then tested them with scrambled and blurred versions of the stimuli. Whereas scrambling impaired the categorization of flowers and people, it had no effect on cars and chairs. By contrast, blurring did not affect the categorization of flowers or people but impaired the discrimination of cars and, to a lesser extent, chairs. This indicated that pigeons' discrimination of cars and chairs depended on local features and their discrimination of flowers and people more on global features. As a possible explanation for this dissociation between natural and artificial stimuli regarding processing style, the authors suggested that the natural categories they used may have been less perceptually diverse in respect to the overall shape of the target figure, compared to the artificial categories. So, the pigeons may have relied on the (relatively uniform) overall shape of the target objects when discriminating people and flowers, but not when discriminating cars and chairs. In short, the results suggested that pigeons' choice of processing style may, among other factors, depend on some perceptual specifics of the target objects to be identified.

Another example for the importance of local and global features comes from an experiment by Huber et al. (2000). In that study, pigeons were first trained to discriminate between pictures of male and female faces and were then subjected to two filter tests that examined the effects of presenting blurred pictures as well as block images. Blurred pictures were obtained by means of Gaussian filters that replaced the intensity and color of each single pixel by the weighted average of its neighborhood. Block images were created by means of mosaic filters that replaced the intensity and color of all pixels within a certain area by the average intensity and color of this region. Neither type of manipulation substantially affected performance, which pointed to the robustness of the birds' categorization abilities against losses in either local or global cues and was thus evidence for the flexible use of both sources of information even within the same task.

Also some results obtained by Aust and Huber (2003) suggested an equally important role for local and global cues. After being trained to categorize color photographs according to the presence (S+) or absence (S−) of human figures, pigeons were tested with distorted pictures of humans, meaning that their constituent parts were not in their proper spatial arrangement. Performance on these stimuli was decreased as compared to pictures of humans whose configuration was intact, however, it exceeded the level of responding found for pictures without humans. This indicated that, on the one hand, the birds must have recognized that the parts of the depicted targets were not in their proper spatial location, but on the other hand they also recognized that the distorted versions contained the same elements as the intact originals. The results thus suggested an important role for both componential features and their spatial organization.

Troje and Aust (2013) first trained pigeons to discriminate a left facing from a right facing point-light figure in apparent motion (i.e., seemingly walking to the left or to the right; Figure 5.3A). The birds were then tested with stimuli showing apparently backward moving walkers (which provided a conflict between local and global cues to direction) as well as with scrambled walkers in apparent motion (which destroyed the global configuration of the stimuli). Although the majority of the birds was found to rely on local motion as a cue to direction (with movement of the feet being of particular

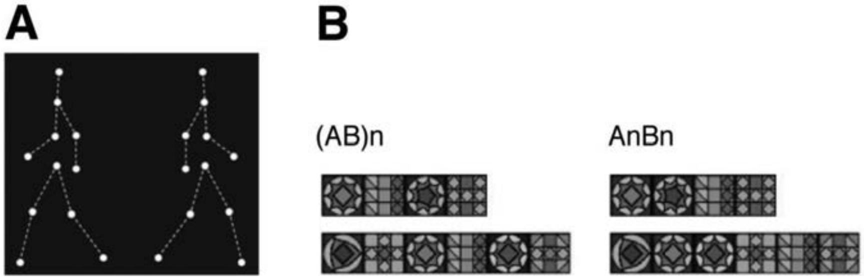

FIGURE 5.3. (A) Example of a left facing and a right facing biological point light walker. The dotted lines were not shown to the pigeons and are provided here only to illustrate the articulated shape of the displays. From "What Do You Mean With 'Direction'? Local and Global Cues to Biological Motion Perception in Pigeons," by N. F. Troje and U. Aust, 2013, *Vision Research, 79,* p. 49. Copyright 2013 by Elsevier. Adapted with permission. (B) Examples of training stimuli used in an artificial grammar learning task with pigeons and keas. From "Visual Artificial Grammar Learning: Comparative Research on Humans, Kea (*Nestor notabilis*) and Pigeons (*Columba livia*)," by N. Stobbe, G. Westphal-Fitch, U. Aust, and T. W. Fitch, 2012, *Philosophical Transactions of the Royal Society: Series B, Biological Sciences, 367,* p. 1997. Copyright 2012 by the Royal Society Publishing. Adapted with permission.

importance), some individuals preferred global, configural information, and each bird had a clear preference for one or the other strategy.

Another example comes from an artificial grammar learning experiment in which pigeons and keas (*Nestor notabilis*) had to discriminate between strings of complex square elements, called tiles (Stobbe, Westphal-Fitch, Aust, & Fitch, 2012; Figure 5.3B). There were two types of tiles (A and B) that differed regarding the prevailing colors and shapes of the constituting elements. Each stimulus consisted of a number of A and B tiles that were arranged according to one of two different rules (or grammars). $(AB)^n$ strings were composed of alternating A and B tiles whereas in (A^nB^n) strings A and B tiles built two separate clusters (i.e., from left to right, a stimulus consisted of a number of A tiles followed by a number of B tiles). For half of the birds, the $(AB)^n$ strings were the positive stimuli and the (A^nB^n) strings were the negative ones, whereas contingencies were reversed for the other half. When the subjects had acquired the discrimination they were tested with a number of transfer stimuli, including, for example, extensions (i.e., stimuli containing more tiles than the training patterns), reversals (i.e., training stimuli in which the order of A and B tiles was reversed), permutations (i.e., strings with novel combinations of A and B tiles), and foils (i.e., strings in which one element was removed from the grammatical stimuli so that the construction rules underlying the training task were violated). The most cognitively demanding way to categorize these stimuli was the application of a logical solution, which would have required the birds to understand the underlying grammar rules (see Volume 1, Chapter 14, this handbook). However, analysis of the results clearly showed that none of the subjects was able to grasp the abstract rule intended by the experimenters. Instead, all birds relied, without exception, on perceptual information. The important point for the present discussion is that the perceptual strategies that could potentially be used included both local ones that required reliance on certain substrings (e.g., attending only to the first or the last few tiles of a string) and global ones that required attention to overall stimulus properties concerning the transition structure between the tiles (i.e., the birds had to focus on visual homogeneity or heterogeneity of the stimuli). Post-hoc analyses revealed that the keas used one or (at most) two local strategies that varied among individuals, whereas individual pigeons adopted an idiosyncratic mix of several local and global strategies as well as of strategies lying somewhere between local and global (Ravignani, Westphal-Fitch, Aust, Schlumpp, & Fitch, 2015). Some pigeons even seemed to prefer an intermediate strategy to a mixture of clearly local and global ones.

The ability of pigeons to process either type of information is reflected also by an interesting lateralization in the brain (see Volume 1, Chapter 27, this handbook). Yamazaki, Aust, Huber, Hausmann, and Güntürkün (2007) trained pigeons to categorize photographs according to the presence or absence of humans and then tested them binocularly or monocularly (left or right eye) for hemispheric specialization in the solution of the task. The results revealed that the left hemisphere concentrated mainly on the local cues of the images, whereas the right hemisphere relied more on configuration.

Taken together, the available evidence strongly suggests that ascribing a general local precedence to pigeons is not just an over-simplification but completely unjustified. Rather, pigeons may, like other species, use either level of processing (or both) and flexibly shift between parts and wholes even within a task (see Table 5.2). The previous examples show that the occasional demonstration of a preference for the local processing level in these birds neither means that such an effect will occur in every task and with every experimental set-up, nor that local and global processing will necessarily be exhibited to the exclusion of the other. Which strategy an individual—be it a pigeon, a kea, or a primate—will apply in a certain situation seems to depend on the specifics of the task (like feature salience, configural organization, or viewing distance), as well as on attentional and motivational factors and on the properties of the investigated species' visual system (Cook, 2001; see also Aust & Braunöder, 2015; Goto et al., 2004; Watanabe, 2011; Chapter 3, this volume).

FUNCTIONAL CATEGORIES

The ability to sort objects into classes on the basis of an abstract feature seems, not too surprisingly, to be less widespread among nonhuman species than the ability to categorize stimuli by means of physical similarity. Nevertheless, there is also solid evidence for categorizations at least at the medium levels of abstractness (i.e., at the associative level and even at the level of first-order relationships). Regarding associative learning, particularly the ability to form equivalence classes of arbitrary stimuli has been found quite frequently in numerous nonhuman species (for reviews see Urcuioli, 2013; Zentall et al., 2014), but there is evidence also of functional categorizations (i.e., category judgments made on the basis of a common biological function) in a variety of taxa.

Evidence in Animals

Two of the most frequently studied functional concepts have been *food* and *tool*, with respective evidence coming mainly from primate species. For example, baboons (*Papio anubis*) trained to discriminate between one food object (apple) and one nonfood-object (padlock) showed subsequent transfer to novel instances of these two classes (Bovet & Vauclair, 1998). Similarly, chimpanzees could sort various objects into the categories food and tool and could transfer this discrimination to novel items (Savage-Rumbaugh, Rumbaugh, Smith, & Lawson, 1980). Some individuals succeeded even when the real objects were then replaced with lexigrams that they had previously learned to associate with specific food and tool items. A similar result was obtained by Tanaka (1997) who found that a chimpanzee trained to categorize stimuli into the classes *food*, *tools*, and *containers* could then correctly match lexigrams that corresponded to the functional categories. Indeed, the results suggested that the use of lexigrams rather than pictures might even have improved categorization on the basis of function. Tanaka (1995) reported that chimpanzees spontaneously grouped objects that had been used together in their previous manipulative experience (e.g., bottles and their caps), and sometimes they also grouped familiar versus novel objects. Indeed, a large part of the work in the area of functional categories has been done with regard to the concept of familiarity, which will therefore be discussed in detail in the next section.

Interesting with respect to Tanaka's work on object grouping are also studies on chimpanzees' spontaneous class grouping behavior which focused on the construction of precursory logico-mathematical operations such as classifying.

For example, 5-year-old chimpanzees have been shown to spontaneously categorize objects into two classes at a level comparable to that beginning to develop in human infants by the age of 18 months (see Potì, Langer, Savage-Rumbaugh, & Brakke, 1999; Spinozzi, 1996; Spinozzi, Natale, Langer, & Brakke, 1999; Tomasello & Call, 1997). Furthermore, chimpanzees could systematically combine their manipulations into routines (including reproduction of the same manipulations and planned actions that anticipated subsequent manipulations) to generate class-consistent categories of objects (Spinozzi & Langer, 1999).

The Familiarity Concept as an Example of a Functional Category

Among the various categories that an animal may possibly establish, classes defined by familiarity have recently received considerable attention. Knowledge of previously encountered external entities—be it conspecifics, heterospecifics or objects—is beneficial as it allows fast and appropriate behavioral responses, and there is evidence from a wide range of species that the functional importance of familiar individuals or objects may indeed control an animals' discriminative behavior (Wilkinson, Specht, & Huber, 2010).

Conspecific recognition. The ability to discriminate between familiar conspecifics and strangers is critically important especially for socially living animals, including species that form loosely structured social groups that have pronounced territorial behavior, like pigeons (Vriends, 1988; Wilkinson et al., 2010). Occasionally, even nongroup-living animals like lizards (*Amphibolurus muricatus*) or orangutans (*Pongo pygmaeus*) have been found to distinguish between familiar and unfamiliar members of their species (Hanazuka, Shimahara, Tokuda, & Midorikawa, 2013; Van Dyk & Evans, 2007; see also Stephan et al. 2013; Vonk & Hamilton, 2014; Wilkinson et al., 2010). It has been argued that such an ability is important for territorial animals as it enables them to minimize the costs of resource defense by adapting their aggressive behaviors to the different levels of threat emanating from different intruders (Van Dyk & Evans, 2007; see also Volume 1, Chapter 41, this handbook).

Evidence of conspecific recognition on the basis of visual information comes from several studies with birds. Chickens, for instance, have been shown to aggregate more with familiar conspecifics than with strangers, and to choose flockmates rather than unfamiliar conspecifics as feeding companions, but this latter preference disappeared when photographs instead of real birds were used (Bradshaw, 1992; Dawkins, 1996). Further investigations confirmed that hens can discriminate between familiar and unfamiliar conspecifics in real-life situations, but not when presented as 2D stimuli (Bradshaw & Dawkins, 1993). However, pictures present only an impoverished version of the depicted items (see Chapter 6, this volume, for a review on picture-object recognition).

Nevertheless, a study with pigeons has shown that these birds are able to categorize pictures of conspecifics according to familiarity and are thus able to perceive a correspondence between photographs of pigeons and the real animals (Wilkinson et al., 2010). Pigeons were presented in a two-alternative forced-choice procedure with photographs that showed familiar and unfamiliar conspecifics (Figure 5.4A). In each trial they were presented a picture of a familiar and an unfamiliar pigeon and were rewarded for pecking at the former. Subsequently, the birds were tested for transfer to pictures of novel familiar and unfamiliar conspecifics. Two of the six pigeons tested were indeed able to correctly classify pictures of aviary mates which they had not seen as photographic stimuli before as familiar and pictures of entirely unknown birds as unfamiliar (Figure 5.4B: George and Judith). By contrast, all birds in a control group that had no real-life experience with any of the depicted pigeons failed. As there were no consistent visual features among familiar and/or unfamiliar conspecifics, the birds could not rely on perceptual information. The results therefore suggested that the successful subjects must have responded on the basis of an abstract functional concept.

Further tests revealed the importance of contact and interaction with the real birds for recognizing them as familiar in pictures (in the sense that they recognized them as birds with whom they had previously interacted). When the two pigeons that

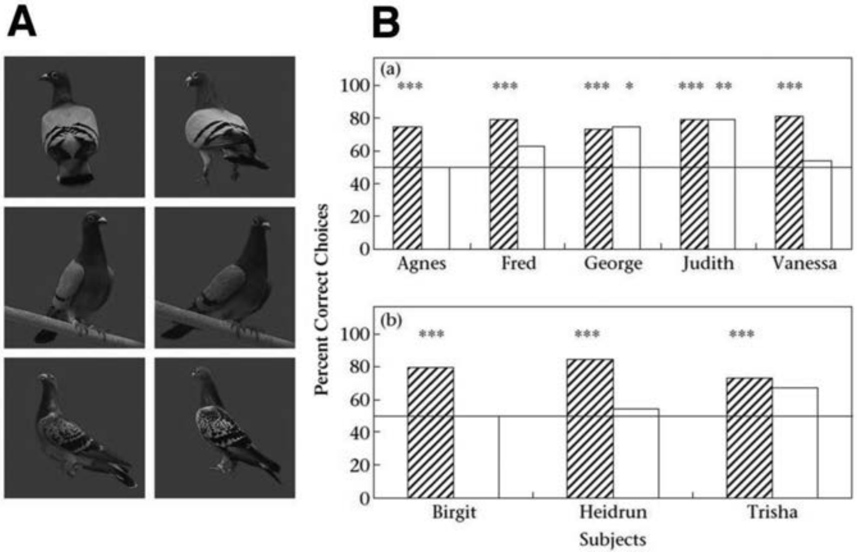

FIGURE 5.4. (A) Examples of stimuli showing familiar (left column) and unfamiliar conspecifics (right column). (B) Percentage of correct choices in the test for transfer to pictures of novel familiar and unfamiliar conspecifics for (a) the experimental birds and (b) the control birds. White bars: performance in test trials; striped bars: performance in intermixed training trials. The solid line represents chance level (50%). From "Pigeons Can Discriminate Group Mates From Strangers Using the Concept of Familiarity," by A. Wilkinson, H. L. Specht, and L. Huber, 2010, *Animal Behavior, 80*, pp. 111 & 113. Copyright 2010 by The Association for the Study of Animal Behaviour. Reprinted with permission. * P < .05; ** P < .001.

had passed the first transfer test were presented with photographs of semifamiliar conspecifics with which they had only visual contact (i.e., they were living in a different aviary) they were unable to categorize them as familiar. But when an unfamiliar pigeon was introduced into their aviary, they could recognize it as familiar in pictures after an exposure of only 24 hrs. Wilkinson et al. (2010) argued that this suggests a flexible recognition system that rapidly adapts to novel instances of the stimulus class. The finding that semifamiliar conspecifics were not recognized as familiar in pictures was explained in terms of biological relevance: As the aviary of the semifamiliar birds was detached from that of the experimental subjects, the latter could not mate or fight or interact in any other direct way with the former so the semifamiliar pigeons had no functional importance to them.

Most evidence of conspecific recognition comes, however, from studies with primates. For example, an oddity paradigm was used to investigate if capuchin monkeys can judge the in-group/out-group status of conspecifics depicted in photographs (Pokorny & de Waal, 2009a, 2009b). Namely, the monkeys had to indicate which picture (out of four) showed an individual that did not belong to the same social group as the others. All subjects learned the task and performed significantly in a subsequent transfer test. In a simultaneous discrimination procedure three long-tailed macaques (*Macaca fascicularis*) correctly identified in transfer trials novel views of group members after training on a minimum of examples, and one subject could even match pictures of different face views as well as face views with other body parts of the same familiar group members (Dasser, 1987). More recently, similar results were obtained for chimpanzees that were found able to match pictures of a group mate's face and pictures of their behinds (de Waal & Pokorny, 2008). Vonk and Hamilton (2014) tested orangutans (*Pongo abelii*) and a gorilla by simultaneously presenting them with a photograph of a familiar and an unfamiliar conspecific in each trial and rewarding them for selecting the picture of the familiar individual. The apes quickly learned this discrimination and some of them were also able to transfer it to novel pictures of familiar and unfamiliar individuals, thus showing evidence of categorizing photographs of conspecifics on the basis of familiarity.

There is evidence that conspecific recognition may occur even at a finer level than that of functional subclasses like familiar versus unfamiliar, namely, at the level of the individual. Individual recognition is not a trivial task, as it requires identification of a unique set of features (see Tricarico, Borrelli, Gherardi, & Fiorito, 2011). Nevertheless, such an ability has been found not only in animals with complex nervous systems or advanced cognitive traits, like various fish, bird, and mammal species, such as sheep (*Ovis aries*; K. M. Kendrick, da Costa, Leigh, Hinton, & Peirce, 2001), heifers (*Bos taurus*; Coulon, Deputte, Heyman, & Baudoin, 2009) and dogs (*Canis familiaris*; Huber, Racca, Scaf, Virányi, & Range, 2013), but also in some invertebrates, including, insects (*Polistes fuscatus*; Tibbetts, 2002), crustaceans (*Neogonodactylus spp.*; Cronin, Caldwell, & Marshall, 2006), and octopuses (*Octopus vulgaris*; Tricarico et al., 2011; for a review, see Tibbetts & Dale, 2007).

Heterospecific recognition. Evidence for the recognition of familiar and unfamiliar individuals among heterospecifics (i.e., individuals of a species other than the one of the perceiver) is still scarce and comes mainly from studies on predator recognition and the recognition of humans by animals in urban areas or in captive situations (e.g., Bogale, Aoyama, & Sugita, 2011; Ferrari, Messier, & Chivers, 2008; Levey et al., 2009; Munksgaard, De Passillé, Rushen, Thodberg, & Jensen, 1997; Racca, et al., 2010; Slobodchikoff, Kiriazis, Fischer, & Creef, 1991; Stephan, Wilkinson, & Huber, 2012; Stone, 2010; Taylor & Davis, 1998).

Stephan et al. (2012) investigated pigeons' ability to recognize pictures of familiar human faces. After the birds had learned to respond to photographs of objects on the basis of familiarity in a two-alternative forced choice procedure (see section on object recognition) they were tested for generalization of that concept to human faces (Figure 5.5). To this

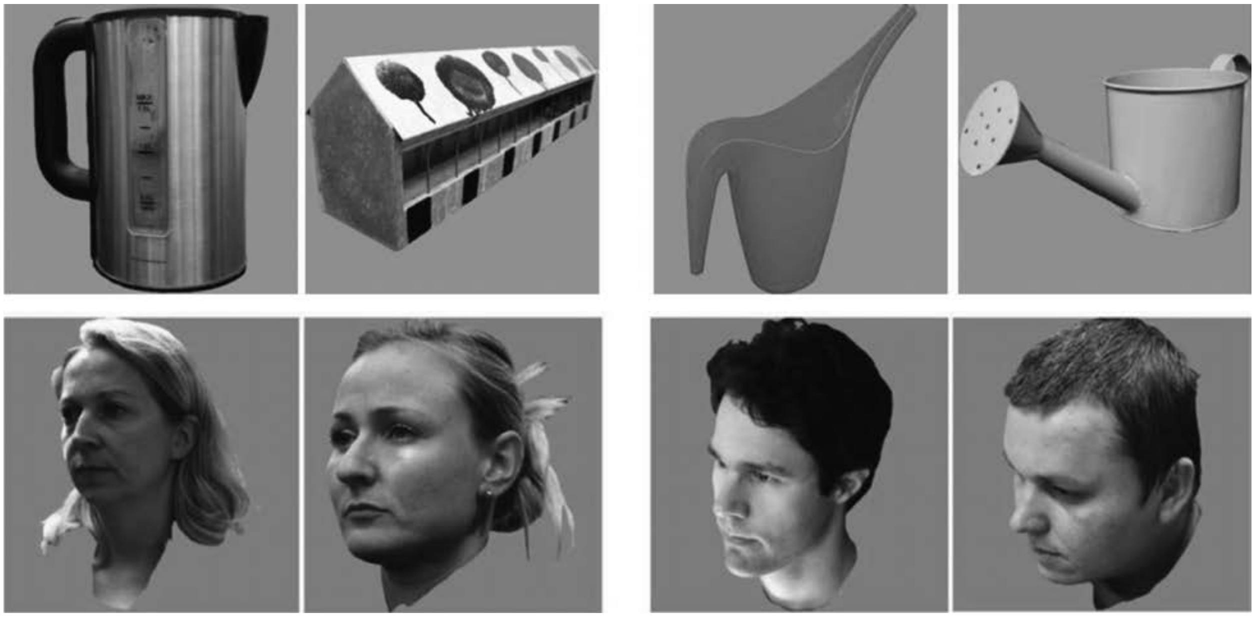

FIGURE 5.5. Examples of stimuli shown during the acquisition phase (top row: objects) and during the test (bottom row: human faces). The right stimulus of each pair was familiar, the left stimulus was unfamiliar. From "Have We Met Before? Pigeons Recognise Familiar Human Faces," by C. Stephan, A. Wilkinson, and L. Huber, 2012, *Avian Biology Research*, *5*, p. 77. Copyright 2012 by Science Reviews 2000 Ltd. Adapted with permission.

end, photographs of familiar and unfamiliar human heads were taken. On test trials, the pigeons had to choose between one familiar and one unfamiliar human face presented simultaneously. Indeed, half of the birds, at least, successfully categorized the pictures of human faces according to familiarity, whereas all birds in a control group for which all depicted humans were unfamiliar failed. The results thus showed that a discrimination according to familiarity that was acquired with one type of stimulus (i.e., objects) could be extended to a novel type of stimulus (i.e., human faces) that were perceptually very different and with whose 3D referents the birds had learned to interact in a different way. The experiment therefore demonstrated the generality and thus the high level of abstractness of the underlying response rule.

But how may such an advanced form of categorization in a bird species be explained that is not particularly known for its high abstractive abilities? Stephan et al. (2012) suggested that, in contrast to corvids, for instance, pigeons are probably not genetically predisposed to show such high-level cognitive skills. Instead, the extensive exposure to humans as ecologically relevant heterospecifics may have promoted cross-specific recognition that may manifest in the formation of a familiarity concept as was found in the study just described. This is in line with the so-called pre-exposure hypothesis proposed by Lee, Lee, Choe, and Jablonski (2011) according to which species living in human environments should rapidly learn to discriminate among humans, as they represent potentially relevant stimuli. Indeed, recognition of individuals beyond species borders has been found in real-life situations in a number of urban birds, including pigeons that were reported to discriminate and remember humans on the basis of their previous experience with them. For example, feral pigeons were found to selectively avoid humans that had previously behaved in a hostile manner (like chasing) during foraging (Belguermi et al., 2011). In a similar vein, Dittrich, Adam, Ünver, and Güntürkün (2010) reported that pigeons displayed reduced levels of activity on the entrance of their usual feeders when the latter were wearing masks, indicating that they could recognize humans on the basis of facial cues. Some studies also suggested a facilitating effect of clothing or acoustic cues on pigeons' recognition of humans (Belguermi et al., 2011; Sliwa, Duhamel, Pascalis, & Wirth, 2011; Wascher, Szipl, Boeckle, & Wilkinson, 2012).

In recent years, the study of dogs' recognition of familiar humans versus unfamiliar ones has attracted increasing attention. The reason for this may be that, among all animals, dogs probably have the closest relationship to humans (see Volume 1, Chapters 16 and 33, this handbook) and are thus supposed to have a great deal of experience in discriminating them and sorting them into subclasses (like familiar people versus strangers). Indeed, there is growing evidence of dogs discriminating pictures of human faces on the basis of familiarity. For example, Racca et al. (2010) reported that dogs looked longer at pictures of novel human (and dog) faces than of familiar ones. In contrast, Somppi, Törnqvist, Hänninen, Krause, and Vainio (2012), using eye tracking, found that dogs looked longer at familiar than at novel human (and dog) faces. Additionally, Somppi, Törnqvist, Hänninen, Krause, and Vainio (2014) found that familiar eyes and faces produced more fixations than those of strangers. The reasons for these inconsistent looking tendencies are not clear, but in any case, all three studies showed that dogs can detect the difference between familiar and novel human faces. Pitteri, Mongillo, Carnier, Marinelli, and Huber (2014) reported that dogs successfully distinguished between pictures of isolated parts of the face of their owner and pictures of the same parts of the face of a stranger. In all the studies cited, however, it was unclear whether the dogs recognized the human faces individually or categorically (i.e., just as familiar versus unfamiliar). Such a distinction was possible in a study by Huber et al. (2013) where dogs were trained to discriminate between familiar human faces, first presented in the form of real faces and then in the form of pictures. The results indicated that the dogs were basically able to distinguish between familiar human faces, even under difficult conditions, as provided by static 2D representations. Evidence of heterospecific discrimination at the individual level comes also from other mammal species like sheep that were shown to discriminate between the faces of individual dogs, humans, and goats (da Costa, Leigh, Man, & Kendrick, 2004; Davis, Norris, & Taylor, 1998; K. M. Kendrick et al., 2001).

Object recognition. It is reasonable to expect that familiarity would be a useful discriminative feature not only in the context of an animal's social life, but it may be advantageous in the categorization of any external object that has the potential to be relevant to a subject because of its inherent function. However, evidence of the classification of inanimate objects on the basis of familiarity is still scarce and experiments dedicated to this question have often yielded inconsistent or inconclusive results (for reviews see Stephan et al., 2013; Wilkinson et al., 2010); however, research by Kartteke, De Souza Silva, Huston, and Dere (2006) showed rats' (*Rattus norvegicus*) recognition of objects in consideration of where and when they had previously seen them (for a review, see Eacott & Easton, 2010).

In pigeons, research has largely been focused on the discrimination of familiar and unfamiliar landscapes, as such tasks were thought to be relevant to these birds' highly developed homing abilities. For example, Wilkie, Willson, and Kardal (1989) and D. F. Kendrick (1992) found evidence of familiarity effects in pigeons' categorization of landscapes, but the results of both studies were difficult to interpret because important controls were missing. Macphail and Reilly (1989) found that pigeons could discriminate between pictures of complex familiar and unfamiliar objects. However, the study was mainly aimed at examining short-term memory and did not allow for any conclusions regarding the ability to infer familiarity on the basis of previous experiences with real objects when pictures of the latter were presented.

By contrast, more recent studies have, indeed, yielded conclusive evidence of pigeons being able to classify pictures of inanimate objects from their everyday life on the basis of familiarity. Wilkinson et al. (2010) reported that the familiarity concept in pigeons' recognition of conspecifics could be extended also to objects. To examine whether the two birds that had shown evidence of such a concept had only learned specifically about conspecifics, they were presented with photographs of familiar objects that were highly salient to the pigeons (water dispenser and food trough) and with unfamiliar ones that were entirely unknown (Wellington boots and spade). The rationale was that the use of pictures of familiar objects that were functionally important to the birds should promote categorization, similarly to the previous test with familiar (as opposed to semifamiliar) conspecifics. Indeed, one of the subjects, at least, discriminated significantly between the pictures of familiar and unfamiliar objects, which suggested a broad understanding of familiarity in that bird that was not restricted to conspecifics.

In a follow-up study, Stephan et al. (2013) found that pigeons were able to use a categorical rule of familiarity to classify photographs of objects of their environment, but only if they had experience with the real-world referents of the depicted items. This suggests that the pigeons transferred their real-life experience with the objects to the pictures. The impact of additional functional properties of the objects was then assessed by separately analyzing responding to objects that were considered functionally relevant to the birds (like a trough or a nesting box) and those that were not (like a watering can or a helmet). Indeed, birds that were rewarded for choosing familiar objects showed a significant preference for relevant objects, and birds that were rewarded for choosing unfamiliar objects made significantly more errors on relevant than on irrelevant familiar objects. No such effects were found for the control birds that lacked real-life experience with any of the presented items. The results thus provided further support for the notion of functional relevance promoting the formation of a familiarity concept in pigeons (Wilkinson et al., 2010).

Among mammals, discrimination between pictures of familiar and unfamiliar objects has been found in dogs. Racca et al. (2010) reported that dogs looked longer at pictures of novel objects than at pictures of familiar ones. Similar to the work on pictures of human faces described earlier, the opposite tendency was found by Somppi et al. (2012) with dogs looking longer at pictures showing familiar than at pictures showing novel letters or toys.

In summary, the available evidence suggests an ability to form categories on the basis of familiarity in a wide range of species, and such categorizations can be made in the context of conspecific or heterospecific recognition, or both. Furthermore, some animals also seem able to sort inanimate objects on the basis of familiarity. The ability of some species to transfer a familiarity concept acquired with one type of stimulus (e.g., conspecifics) to a completely different type of stimulus (e.g., objects) is suggestive of a broad and highly abstract category.

CONCLUSION

The critical advantage of categorization is that it provides great efficiency to learning. It is therefore not surprising that this ability is not exclusive to humans but has parallels in nonhuman animals. The present chapter has provided evidence of categorization at various levels of complexity in a wide range of species. However, to appropriately judge and interpret the performance of an animal in a particular categorization task, it is mandatory to have at hand a reasonable theoretical framework to refer to. Therefore, an overview of the different levels of categorization has been provided here, with particular focus on the notions of functional categories and concepts, for which there still exist no consensus definitions among the various research traditions. An effort has been made to carefully distinguish functional categories not only from the perceptual and relational levels of categorization, but also from associative classes that consist of arbitrary stimuli. Furthermore, a definition of concepts was advocated that excludes category judgments made on the basis of physical similarity but restricts conceptualization to more abstract forms of categorization.

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CHAPTER 6

OBJECT AND PICTURE PERCEPTION

Shigeru Watanabe and Ulrike Aust

As a result of natural selection, animals as well as humans are equipped with the ability to navigate in an ever-changing environment. This requires them not only to *perceive* objects but also to *recognize* them. Object perception and recognition are thus inseparably linked processes that allow a subject to make sense of its environment.

OBJECT PERCEPTION AND RECOGNITION

Prior to discussing in more detail the mechanisms that mediate perception and recognition and considering how the two are related it may, however, be useful to provide definitions of these terms as they will be used in the chapter.

Disentangling Perception and Recognition

Perception, in general, can be understood as the process "by which information acquired via the sense organs is transformed into experiences of objects, events, sounds, tastes, etc." (Roth, 1986, p. 81). *Visual perception* in particular (to which this chapter will be restricted) refers to the processing of information contained in visible light, or, more precisely, it can be understood as "the process of acquiring knowledge about environmental objects or events by extracting information from the light they omit or reflect" (S. E. Palmer, 1999, p. 5). *Object recognition* (which requires preceding object perception) is the process of determining that one has already seen a particular object before, no matter if one also knows what it is (for reviews see Kirkpatrick, 2001; Soto & Wasserman, 2014).

Bottom-Up and Top-Down Processing

Object perception and recognition are not passive receipts of signals from the environment but cognitive activities. As one looks around, one immediately sees a number of meaningful objects in a three-dimensional space. But how can such experiences emerge from the incomplete light pattern that strikes the retina of the eye? How does a perceiving human or animal know, for example, which regions of a scene are part of the same object? To provide appropriate, well-structured percepts of objects and thus the ability to recognize them, vision requires a variety of filtering, organization, and interpretation processes (see Chapter 9, this volume).

Overall, there are two types (or "directions") of stimulus transformation involved in the achievement of this goal that usually work together (see Bernstein, 2010; Hubel & Wiesel, 1979). As will be outlined in the next section of this chapter, visual information is filtered and reduced all along its path from the eye to the brain, where these bits and pieces are then transformed into structured percepts of complex three-dimensional (3D) objects through the processes involved in perceptual organization. To this end, some basic features of a stimulus (*low-level information*) are separately analyzed first and are then recombined to create the perceptual experience of an object (*higher-level information*). Such features, for example, may be lines, edges, corners, shapes, orientation in space, color, or motion, to which certain cells (feature detectors) selectively respond (like the "bug detectors" in the frog's [*Rana pipiens*] eye; see the following section). Regarding

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edge properties, theories of object recognition in mammals have traditionally relied mainly on nonaccidental statistics like symmetry, collinearity, curvilinearity, and codetermination to recover the correct 3D information from two-dimensional (2D) projection patterns. More recently, studies with pigeons have revealed that nonmammalian visual systems are also biased to recognize objects from nonaccidental statistics (Gibson, Lazareva, Gosselin, Schyns, & Wasserman, 2007; Lazareva, Wasserman, & Biederman, 2008; Nielsen & Rainer, 2007). The transformation of low-level into higher-level information is called *bottom-up processing*. The resulting high-level percepts, however, will hardly ever involve a comprehensive representation of all (or even just most) low-level features potentially provided by an external object. For example, the mentioned bug detectors will lead to an extremely simplified (though efficient) representation of prey objects by frogs. Similarly, so-called key features have a privileged role in the recognition of predators (or other animals). For instance, Beránková, Veselý, Sýkorová, and Fuchs (2014) provided evidence for the importance of yellow eyes in the recognition of sparrowhawks (*Accipiter nisus*) by great tits (*Parus major*). It should, however, be noted that (unlike the frog example) the tits were found to have a more inclusive percept of sparrowhawks with more than just one single feature being necessary to prompt recognition. As another example, it was shown in a recent study that red-backed shrikes' (*Lanius collurio*) recognition of the Eurasian jay (*Garrulus glandarius*), a common nest predator, relies not only on colors but on other surface features as well (Němec et al., 2015): The shrikes attacked a stuffed dummy (feathered surface) more often than a plush dummy (hairy surface), which, in turn, elicited more attacks than a silicone dummy (glossy surface).

Furthermore, object perception and recognition are shaped also by a subject's expectations (one may also say, by its "readiness" to perceive a stimulus in a certain way; see Chapters 1 and 9, this volume). Expectancy, which results from previously acquired knowledge and depends on a number of selective mechanisms like learning, memory, expertise (familiarity), attention, motivation, and the context in which a stimulus appears, can bias recognition toward one or another interpretation of the same sensory input. Such *top-down processing* helps humans (and animals) to recognize objects by making inferences. It is responsible for the fact that visual percepts (other than the mere 2D patterns of light on the retina from which they are derived) may be ambiguous, instable, or even fallacious (illustrated by psychophysical phenomena like multistable figures or optical illusions; see Chapter 8, this volume). Also, they are the reason why the ease with which an object is recognized depends, among other factors, on the context in which it appears. It has been shown, for instance, that appropriate context (e.g., a loaf of bread in a kitchen scene) facilitates object recognition in humans, whereas inappropriate context (e.g., a bass drum in the same scene), hinders it (T. E. Palmer, 1975). Also, increases in visual search response time were found when a target object was embedded into an array of randomly arranged objects relative to when the latter were shown in their proper spatial arrangement (see S. E. Palmer, 1999; see also Chapter 9, this volume). Goujon and Fagot (2013) showed a similar contextual cueing effect in baboons (*Papio papio*), with shorter reaction times occurring if the configuration of a number of distractors predicted the location of an embedded target than if distractor configuration was nonpredictive of target location. Comparable results have been obtained for pigeons that showed robust contextual cueing when they had to peck a target that could appear in one of four locations if the picture background was predictive of target location (Wasserman, Teng, & Castro, 2014).

Generally, it has been shown that animals may be highly flexible regarding feature creation and selection (Cook, 2001; Huber & Aust, 2012; see also Aust & Braunöder, 2015; Watanabe, 2011). Some of the factors that are responsible for this flexibility, like the specifics of the animal's visual system, affect bottom-up processing, whereas others, like attentional or motivational factors, the history of reinforcement, or stimulus properties like feature salience or configural organization, affect top-down processing. Pigeons, for example, are able to use various features from different domains and levels of complexity (for reviews, see Huber & Aust, 2012; see also Chapter 5, this volume). Depending on the specifics of the task, their recognition of objects may be based, for instance, on local or global features, on isolated stimulus components, or on more configural ones, and they may rely on "simple" physical dimensions (e.g., intensity or color) or on a compound of various properties (i.e., on some higher feature).

Object Perception

Abstraction. The perceptual systems of animals (including humans) are confronted with the so-called *bottleneck problem*, which results from the fact that the sensory system transmits more information to the nervous system than can possibly be responded to by the motor system (see Chapter 3, this volume). There are thus specific filters that eliminate irrelevant and condense essential information, a process called abstraction. Indeed, abstraction is a very basic perceptual ability. Already at the level of the sensory organs there are mechanisms that selectively filter the incoming visual information (see Chapters 1 and 9, this volume). A famous example is the receptive fields of frogs that specifically respond to small, dark, moving (i.e., bug-like) objects (Lettvin, Maturana, McCulloch, & Pitts, 1959). Similarly, toads (*Bufo bufo*) distinguish moving objects by means of figural features, with the combination of object size and movement direction signaling prey, nonprey, enemies, or potential partners (Ewert, 1970). Thus, the stimuli that are passed on to the brain have already undergone substantial steps of abstraction and information reduction. The higher cognitive processes then bear on the results of these transformations and further abstractions take place at each of these levels. Abstraction thus solves the bottleneck problem by filtering and channeling the flood of information with which an organism is continuously confronted.

Perceptual organization. Considering that the information that eventually reaches the brain not only draws on an incomplete 2D light pattern that stimulates the eye, but has already been filtered and transformed in many ways, one has to ask how all these bits and pieces of information eventually lead to structured percepts of meaningful 3D objects. The process that enables this is perceptual organization, a concept that originated with the Gestalt psychologists early in the 20th century. The ultimate goal of perceptual organization is to determine which parts of the visual information belong together (i.e., build separate objects). Among the most important processes involved in reaching this goal are grouping, region segmentation, texture segregation, parsing, and figure/background segregation (see Goldstein, 2013; S. E. Palmer, 1999, for reviews).

Interpretation. Subjectively, object perception seems to be a simple and effortless process, but this is only because it happens outside conscious awareness (Goldstein, 2013). Also, one might be tempted to assume that, because our percepts of objects are accurate in the sense that, for the most part, they enable us to interact with the environment in an appropriate way, they are indeed consistent with the actual objects. However, psychophysical phenomena like optical illusions clearly show that perception is not veridical (see S. E. Palmer, 1999, for a discussion). Interestingly, it has been found that also many nonhuman animals fall victim to various visual illusions. For example, Nakamura, Fujita, Ushitani, and Miyata (2006) showed that pigeons (*Columba livia*) perceive the Müller-Lyer illusion (a horizontal line with outward-pointing brackets looks shorter than the same line with inward-pointing brackets). Pepperberg, Vicinay, and Cavanagh (2008) found evidence of that illusion in Alex, a Grey parrot (*Psittacus erithacus*). Alex could identify the bigger or smaller of two objects by reporting its color or matter using a vocal label. If the objects did not differ in size he stated "none." When Alex was presented with Müller-Lyer figures in which the central lines were of contrasting colors and was asked which color was bigger or smaller, his answers strongly suggested that his visual system processed the illusion in much the same way as that of humans. Fujita, Blough, and Blough (1991) investigated if pigeons, rhesus macaques (*Macaca mulatta*) and chimpanzees (*Pan troglodytes*) can see the Ponzo illusion (the same bar appears different in length, depending on its position within converging lines). Indeed, all three species perceived the illusion, but it was stronger in the pigeons than in the primates. Also, pigeons and bantams (*Gallus gallus domesticus*) have been found sensitive to the Zöllner illusion, however, in the opposite direction as humans (i.e., parallel lines with series of short crosshatches appear to converge upward to humans, whereas they appear to converge downward to pigeons and bantams; Watanabe, Nakamura, & Fujita, 2011, 2013). Similarly, pigeons and bantams were shown to perceive a reversed Ebbinghaus-Titchener illusion (humans perceive a disc surrounded by smaller discs as larger, and a disc surrounded by larger discs as smaller, whereas the birds perceived a disc as larger when surrounded by large discs and as smaller when surrounded by small discs; Nakamura, Watanabe, & Fujita, 2008, 2014). The authors explained this reversal in the birds' perception of the illusion relative to humans in terms of assimilation effects (meaning that target and distractor discs were assimilated to each other in size). Interestingly, chicks were found to perceive that illusion in the same way as humans (Rosa Salva, Rugani, Cavazzana, Regolin, & Vallortigara, 2013), which suggests differences among bird species in the perceptual processes that underlie such illusory perceptions. Recently, evidence of the perception of a (nonreversed) Ebbinghaus-Titchener illusion has been shown even in fish (*Xenotoca eiseni*; Sovrano, Albertazzi, & Rosa Salva, 2015). An example of susceptibility to optical illusions in nonhuman primates was provided by Barbet and Fagot (2002), who showed that baboons are sensitive to the corridor illusion (a consequence of the ability of the visual system to perceive size constancy: an object in the background of a picture appears larger than the same object presented in the foreground). Finally, a number of mammal and bird species as well as insects have been found to perceive illusory contours (perceived boundaries without physical differences between shape and background; Sáry et al., 2008; see Nieder, 2002, 2012 for reviews). For example, such an ability has recently been shown in a Grey parrot (Pepperberg & Nakayama, 2016). After being trained to identify 3D shapes (1-, 2-, 4-, 6-cornered regular polygons) the bird demonstrated that he could correctly identify Kanizsa figures (configurations in which pac-man-shaped inducers are aligned in the visual field such that the edges form a shape and thereby trigger the percept of an illusory contour).

The important point for our considerations is that the existence of illusions (in humans as well as in animals) is clear evidence of object perception being not veridical, but an interpretative process. The visual system thus works on hypothetical models of the environment rather than directly on the physical information available in the stimulation of the eye. The advantage of such models is that they allow a subject to make predictions and to plan for the future (S. E. Palmer, 1999). The latter, however, requires that objects are not only perceived, but also recognized.

Object Recognition

We have considered object perception as a process of abstraction and interpretation in the service of making the flood of sensory input manageable. Economy then goes even further at the level of object recognition because dealing with the environment in an efficient and appropriate way also requires organizing the percepts of objects and the knowledge about them in a parsimonious but nevertheless informative way.

Object recognition can be established at different levels of generality and thus involves different degrees of information reduction. *Object identification* refers to a specific familiar object and may therefore be seen as a special case of object recognition. Animals are confronted with the problem that most objects they encounter will not recur in exactly the same way. Due to extrinsic factors like light conditions, perspective, or context they may appear quite different at different occasions. However, treating the same object as something new at every encounter would be highly inefficient (e.g., in landmark or social recognition). The most basic level of object recognition is therefore characterized by the ability to determine that a particular object encountered in one situation is the same as the one encountered in another situation (see Chapter 3, this volume). Establishing object identity thus requires focusing on the intrinsic properties of an object (like its shape or texture) and at the same time disregarding extrinsic factors that may modify the appearance of the former. But even if an animal is able to recognize particular objects encountered at different occasions as being the same (see Chapter 26, this volume), it would still get overwhelmed by the multitude of stimulus information if it perceived every object as unique. Thus, a further step of information reduction is required. *Object categorization* is the mechanism of abstracting from objects and building more general classes. At this level of generality recognizing an object means recognizing it as something (e.g., as a tree, a person, or an enemy). The enormous advantage of categorization is not only its parsimony in terms of required memory capacities but also that it allows individuals to apply knowledge that was previously acquired during encounters with objects of the same class to the new object. This will, in most cases, be a very efficient shortcut (compared to exploring every new object individually) because objects of the same category tend to have many properties, functions, and behaviors in common. Thus, the ability to categorize allows a subject to make predictions on the basis of partial information. The categorization of objects is covered in Chapter 5 of this volume.

RELATIONSHIP BETWEEN OBJECTS AND PICTURES

Picture-object recognition refers to the ability of a subject to see some correspondence between an object and a pictorial representation of that object. It is a special case of object recognition insofar as it requires the comparison and matching of two different types of representations (that of the picture and that of the real object) which refer to the same entity in the environment. Usually, one thinks of picture-object recognition as the ability to understand the representational nature of pictures. But as will see, this is only one of several possible ways in which correspondence between objects and pictures may be established. Indeed, recognizing that an object in a 2D image represents a 3D object in the real world is a cognitively demanding task and may therefore be a limited case rarely found in nonhuman species.

The Problem of Picture-Object Recognition

Pictures are some of the most frequently used types of stimuli in studies on animal perception, learning, and cognition. However, the question of whether and, if so, at what level of abstraction, animals recognize the correspondence between pictorial images and their real-world referents has, for a long time, been widely disregarded or, at least, not been investigated in a systematic way. The reasons for this neglect were probably twofold.

The double nature of pictures. First, it was because of the tacit (and, from today's perspective, somewhat naive) assumption that animals will interpret pictures in a human-like way, that is, as 2D representations of real 3D objects. However, not even in humans is recognition of the representational nature of pictorial images as straightforward as one might think; it has been found to depend on experience with this type of stimuli (DeLoache, 1995, 2000; Deregowski, 1989; Deregowski, Muldrow, & Muldrow, 1972; R. J. Miller, 1973; Slater, Morrison, & Rose, 1984; Tomasello, 1999; Tomasello, Call, & Gluckman, 1997). All the more, a state of uncertainty holds for animals, considering that the ability to understand the representational aspect of pictures is not trivial. Pictures have a concrete and an abstract nature, meaning that they are objects themselves, but they also stand for something other than themselves. Thus, recognizing pictures as representations of the real world requires the achievement of a dual representation: The subject must, on the one hand, represent pictures as real entities and, on the other hand, appreciate their abstract relations to their referents (De Loache, 1995, 2000; Ittelson, 1996; see also Aust & Huber, 2010).

Picture-object recognition versus categorization. Second, it has mistakenly been assumed that evidence of an animal's ability to categorize pictures automatically implies that it will also understand what the pictures show. This is, however, by no means obvious. The problem at its extreme is that it is impossible to access other beings' subjective experiences when they are confronted with pictures. But what may potentially be revealed is whether they are able to recognize some correspondence between real objects and pictures of them and, if evidence of picture-object recognition is indeed found, to make an educated guess on the mechanism that underlies this ability (Delius, Emmerton, Hörster, Jäger, &

Ostheim, 2000). Conclusive experiments on the question of picture-object recognition require, however, appropriate methodology that takes into account the fact that pictures are just modified and impoverished versions of the entities of the real world they portray.

Pictures are abstractions. Pictures are always simplifications, meaning that they misrepresent or completely lack numerous features of their real-world referents that may, however, be important for proper recognition. Above all, pictures provide no 3D information, although they may contain some indirect depth cues. For example, there is evidence that object shading leads to three-dimensional perception in pigeons and starlings (*Sturnus vulgaris*) and thereby creates highly salient features for shape processing (Cook, Qadri, Kieres, & Commons-Miller, 2012; Qadri, Romero, & Cook, 2014). In a similar vein, a recent study found that cuttlefish *(Sepia officinalis)* were responsive to a depth illusion created by a visual cue involving a texture gradient that (to humans) resembled an illusionary crevasse (Josef et al., 2014).

Also, pictures normally lack motion, auditory, and olfactory cues. This impoverishment compared to real objects has to do with the two-dimensionality of pictures as well as with technical shortcomings, such as poor luminance and chromatic replication or flicker. Moreover, picture generation and presentation technology is adjusted to the specifics of the human visual system (Bovet & Vauclair, 2000; Delius et al., 2000) and, consequently, pictures often lack or misrepresent some critical features of animal vision. For example, the tetrachromatic, or maybe even pentachromatic, visual system of pigeons and other birds (see Chapters 1 and 3, this volume) probably enables them to differentiate color qualities that humans cannot perceive and that are, thus, not accounted for in the generation of pictures that are made by and for humans (Bowmaker, 1977; Bowmaker, Heath, Wilkie, & Hunt, 1997; Delius et al., 2000, Emmerton & Delhis, 1980; Varela, Palacios, & Goldsmith, 1993). For all these reasons pictures will, without doubt, appear quite different to animals from real objects, with the extent and nature of this difference depending on experience, picture quality and the specifics of the visual system of the species under investigation.

Levels of Picture-Object Recognition

There are basically three levels at which an animal may recognize the relation between an object and its picture, and clearly distinguishing between them is an indispensable prerequisite for interpreting data in experiments that involve the presentation of pictorial stimuli. These levels differ in the type of information extracted from pictures (and from their real-world counterparts) as well as in the complexity and abstractness of the perceived relation between pictures and their 3D referents (see, Aust & Huber, 2006, 2010).

Perceptual level. The first and minimal step for perceiving picture-object correspondence requires an animal to discriminate one or more visual features of the picture and recognizing them in the real object (or vice versa). Positive transfer from pictures to objects (or vice versa) would then be mediated by simple invariant 2D characteristics that are present in the object and the picture. Picture-object recognition at the perceptual level could, for instance, be based on the extraction of some conspicuous shapes or textures that are present in real objects and their pictures. Processing pictorial images at this level does, however, not require recognition of the real 3D object in the picture and is, of course, totally different from a perception of pictures as representations of the real world.

Associative level. At a level half way between simple feature learning and true representational insight regarding abstractness and cognitive demand, an animal may come to associate individual parts of an object through real-life experience. The resulting object representation (or at least a similar one) may then be activated not only in the presence of the real object, but also when the subject is exposed to a picture of the object (Aust & Huber, 2010): An animal that has experience with a particular object may acquire knowledge not only about one or few features (or parts) of that object, but also about the spatial relationships among these parts and may then be able to transfer this knowledge to pictures. Still, such ability would not necessarily involve an understanding of the representational nature of pictures, but would clearly go beyond the recognition of simple individual 2D features. For example, recognizing picture-object correspondence at this level should enable a subject to correctly classify test pictures that provide visual information that is complementary to the one that was present in the training pictures by calling up a representation of the whole (real) object that includes all parts of the object and their relationships. Such an experiment will be discussed in more detail following.

Abstract level. Gain of true representational insight is the most advanced mechanism of picture-object recognition. It makes considerable demands on a subject's cognitive abilities because it requires an understanding of the abstract relation between an object and its picture: The animal must understand that the picture shows a particular object but is not the object. In other words, recognition must transcend the level of perceptual 2D features and associations, although, at the same time, the picture must not be mistaken for its real-world referent. Picture-object confusion can, for instance, be inferred (and representational insight thus excluded) if a subject shows adapted behavior in the presence of a picture (i.e., it reacts to the picture as if it was the real object, e.g., by grasping for a depicted object).

It may be worth noting that other authors have suggested different classification systems to describe the various mechanisms by which an animal may process pictures. For example, Fagot, Martin-Malivel, and Dépy (2000) have put forward the following three levels of pictorial processing: (a) confusion (the animal treats pictures as if they were real exemplars of their referent), (b) independence (the animal makes no connection between the picture and its content despite their sharing common features), and (c) equivalence (the picture is "read" as being a symbolic and iconic representation of its referent). Although this classification system and one used in this chapter have some conceptions in common (e.g., confusion and equivalence) they are, overall, based on and focused on slightly different aspects of picture-object recognition and are thus not well comparable. The experimental evidence on picture-object recognition that will be reviewed in the following sections will be evaluated with reference to the classification system put forward by the authors of this chapter.

Methods of Investigating Picture-Object Recognition

Adapted behavior. Display of the same behavior in the presence of a picture as would be expected to occur in the presence of the real object is a likely sign of picture-object confusion and thereby rules out the possibility of a subject seeing no correspondence between picture and object at all. If, for example, an animal exhibits social behavior with pictures of conspecifics, fear with threatening stimuli, or predator behaviors or grabbing movements with pictures of food it is very likely that it mistakes the picture for the real object. This means that, on the one hand, the animal obviously sees the similarities between objects and pictures of them, but, on the other hand, does not understand the representational nature of pictures. Adapted reactions to still and motion pictures are indeed a widespread phenomenon in the animal kingdom (for a review, see Bovet & Vauclair, 2000). Among primates, such responses were displayed to significant stimuli photographs (showing things like prey, predators, or conspecifics) by marmosets (*Callithrix jacchus*), macaques (e.g., *Macaca fascicularis*), and chimpanzees. Other mammals, like sheep (*Ovis aries*), showed adapted behaviors in the presence of pictures of conspecifics, and more recently, adapted behavior was shown in cattle (*Bos taurus*; Coulon, Baudoin, Heyman, & Deputte, 2011). But such responses are not exclusive to mammals. They have been found also in fish (e.g., guppies [*Poecilia reticulata*], sticklebacks [*Gasterosteus aculeatus*]), birds (e.g., pigeons, fowls [*Gallus gallus spadecius*]), reptiles (e.g., lizards [Anolis *nebulosus*]), and even in some invertebrates (e.g., jumping spiders [*Maevia inclemens*]; see Bovet & Vauclair, 2000, for a review).

In addition to observing an animal's behavior in the presence of pictures, it may also be explicitly tested whether or not it is able to tell pictures and objects apart. For example, Watanabe (1993, 1997) trained pigeons to discriminate either objects from photographs or pictures and objects of one category from pictures and objects of a different category. The fact that the birds subsequently showed transfer to novel exemplars in both tasks is evidence that they could not only discriminate the two categories, but that they could also distinguish between true objects and pictures.

Picture-object transfer. The most common method of investigating an animal's ability to recognize some correspondence between objects and pictures has been to test it for transfer from one presentation mode to the other. One possibility is to train the subject to discriminate between pictures of two categories and then present it with the real objects. In case of picture-object recognition the discrimination previously learned with the pictures should spontaneously be transferred to the objects. Alternatively, the subject may be trained with real objects and then be tested for transfer to pictures of them. Again, the discrimination should be transferred without further training in case of picture-object recognition. Most studies on picture-object transfer in animals have been conducted with birds, especially pigeons. Evidence comes, however, also from primates like rhesus monkeys, baboons, and chimpanzees (for reviews see Bovet & Vauclair, 2000, Fagot, 2000). Recently, such ability was even found in bumblebees (*Bombus impatiens*) that showed transfer learning from artificial flowers to photographs (Thompson & Plowright, 2014).

Very rarely, however, have experiments that applied one of these methods (investigation of adapted behavior or picture-object transfer) allowed researchers to determine the mechanism by which transfer was accomplished. The problem with most traditional approaches was that the pictures contained some of the same perceptual information as the real objects they portrayed. As a consequence, it was almost impossible to tell whether transfer occurred on a merely perceptual basis (by means of simple 2D features) or was because of a more abstract recognition process (by transferring knowledge about the relationships among object parts to pictures or maybe even by appreciating the pictures' representational content). It is surprising that only few attempts have been made to pinpoint the exact mechanism underlying picture-object recognition in animals. One exception was provided by Wilkinson, Mueller-Paul, and Huber (2013) who investigated picture-object recognition in the red-footed tortoise (*Chelonoidis carbonaria*). After being trained to discriminate between food and nonfood objects on a touch screen, the tortoises showed transfer to color photographs of those objects. The nature of this correspondence was then investigated by presenting the subjects with a choice between the real food object and a photograph of it. The fact that the tortoises showed no preference for the one or the other suggested picture-object confusion and argued against recognition at a more abstract level. Another approach that also allowed for some conclusions on the nature of the associations formed between objects and pictures was used in a study that used border collies (*Canis familiaris*) as subjects (Kaminski, Tempelmann, Call, & Tomasello, 2009). The dogs' task was to infer the intended referent of a human's communicative act via iconic signs that were either replicas or photographs. Whereas the dogs were highly successful in using replicas to fetch the desired item, they performed less well with the photographs. It is thus evident that the photographs were more difficult for the dogs than the replicas, suggesting that the photographs' representational content was not recognized, although some correspondence was obviously seen (still, two subjects were above chance from the beginning).

Another example of an experimental design that allowed for disentangling the different mechanisms of picture-object recognition was provided by Dasser (1987), who showed that macaques (*Macaca fascicularis*) could match pictures of different body parts of the same familiar group members. Similarly, de Waal and Pokorny (2008) found that chimpanzees were able to match a picture of a group-mate's face and a picture of their behinds. However, they were unable to do so when the presented body parts belonged to an unfamiliar conspecific. This suggested a recognition mechanism beyond feature matching because the latter should be equally effective with pictures of familiar and unfamiliar conspecifics (see also Vonk & Hamilton, 2014; the issue of familiarity concepts is covered in Chapter 5, this volume.)

The complementary information procedure. In Aust and Huber (2006, 2010), pigeons were tested for picture-object recognition with an experimental design that followed a similar logic as the one applied by Dasser (1987). Unlike most traditional approaches, the complementary information procedure (CIP) allows researchers to clearly distinguish between perceptual and abstract mechanisms of picture-object recognition. The basic idea is to train a subject on pictures of incomplete objects and then test it for transfer to pictures of the previously missing parts. Such transfer cannot be based on the recognition of any simple, item-specific 2D features for the following reasons. First, the training and the test stimuli are complementary regarding their informational content (i.e., they show different object parts) so that transfer from training to test pictures cannot be based on any features that are depicted in both. Second, test stimuli do not show the missing parts of exactly the objects depicted in the training stimuli, but of different objects of the same category. This rules out the possibility of transfer being guided by item-specific simple features that are found in different parts of the same object. For example, complementary parts of the same object may be equal (or at least similar) in brightness, color, or texture. Third, the use of spurious features inherent in all or most parts of an object is also controlled for by the presentation of nonrepresentative stimuli (i.e., no true object parts but arbitrary patches) that are derived from the same objects as the representative test stimuli (i.e., the ones that show true, complementary parts). If recognition indeed occurs at a level beyond the perceptual one, transfer should be better to representative than to nonrepresentative parts.

The CIP was first applied and tested in an experiment with pigeons (Aust & Huber, 2006; see Figure 6.1). Subjects were divided into two groups: the no hands group and the no heads group. The stimuli were color photographs, half of which showed one or more people (class P), whereas the others showed something else, but never contained any humans (class NP). In the no hands group, the human figures depicted in class P were devoid of hands; in the no heads group, they were devoid of heads. The pictures of class NP were the same for both groups. During training, the birds of both groups had to learn the discrimination between a set of class P and an equally large set of class NP stimuli. For all birds, the class P stimuli were the positive ones, and the class NP stimuli were the negative ones. The subjects were then tested with three types of stimuli. Stimuli of the first type (seen part [SP]) showed that part of the body which had been present in the training stimuli of the respective group, but not in those of the other group (i.e., hands for the no heads group and heads for the no hands group). Those stimuli served mainly as a control. Stimuli of the second type (unseen part [UP]) showed that part of the body which had not been present in the training stimuli (i.e., hands for the no hands group and heads for the no heads group). The third type (skin [SK]) showed arbitrary and therefore nonrepresentative patches of human skin. These were the same for both groups. The rationale was that if the birds recognized the pictures as representations of real humans, they should show transfer to seen parts, and, most important, to unseen parts, but should reject the arbitrary skin patches. Indeed, the pigeons responded significantly less to SK than to SP and UP stimuli, whereas there was no difference in responding to SP and UP stimuli.

This result suggested picture-object recognition at a level beyond simple feature discrimination as the only obvious way in which the pigeons could distinguish between pictures of previously unseen true parts and nonrepresentative skin patches was that they had learned about human figures and their parts through experience with real humans and were able to transfer this knowledge to pictures of humans. This conclusion was further substantiated in a follow-up test where pigeons were shown versions of the UP stimuli in which the shape of the depicted human parts was destroyed. This means that they were no longer representative, whereas everything else in the picture remained unaltered. Indeed, destroying the shapes of the unseen parts led to significant performance decrements, with response rates dropping to the level found for arbitrary skin patches in the previous test. This showed that the pigeons did not just respond, for example, to any irrelevant background cues or to the presence of skin in general.

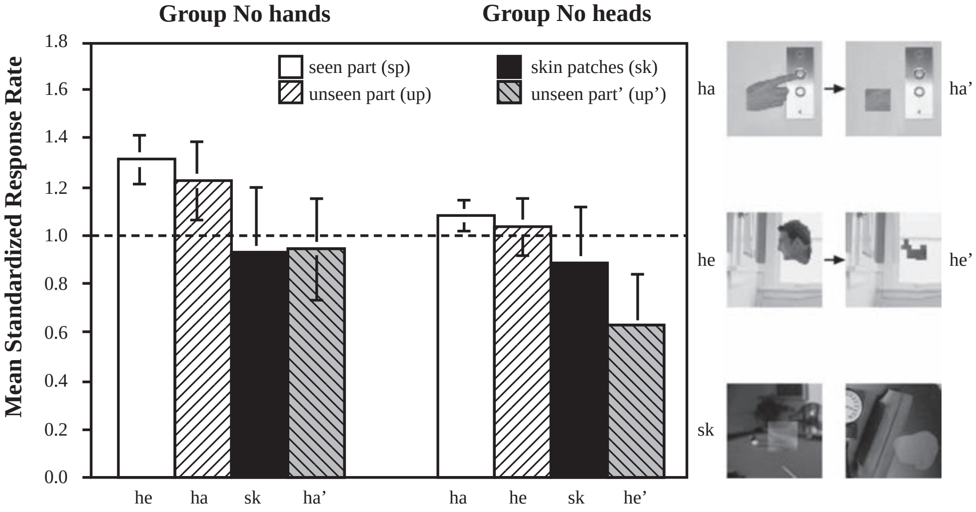

FIGURE 6.1. Results of the test for picture-object recognition (sp, up, sk) and of the follow-up test (up’), including examples of the individual types of test stimuli. Peck rates to previously seen (sp) and unseen (up) parts exceeded those to arbitrarily shaped skin patches (sk) and to unseen parts with arbitrary shapes (up’). Performance is shown separately for the two groups as mean standardized response rates (± SD). Means were taken across the birds of each group. The dashed line indicates the average response level. ha, he = hands and heads stimuli shown in the picture-object-recognition test; ha’, he’ = modified hands and heads stimuli shown in the follow-up test. Reprinted from “Picture-Object Recognition in Pigeons: Evidence of Representational Insight in a Visual Categorization Task Using a Complementary Information Procedure,” by U. Aust and L. Huber, 2006, *Journal of Experimental Psychology: Animal Behavior Processes, 32,* p. 192. Copyright 2006 by the American Psychological Association.

To make testing even more stringent, the basic experiment was then replicated also with birds whose visual experience with humans was systematically restricted (Aust & Huber, 2010; Figure 6.2). Namely, they had never seen human heads. To this end, a group of pigeons were raised, kept, and tested in a special aviary, which prevented them from seeing anything outside, and no human heads in particular. These pigeons were trained to discriminate between pictures of headless humans and pictures without humans and were subsequently presented with the same test stimuli as were used in the previous experiment (seen parts, which were pictures of hands; unseen parts, which were pictures of heads, and arbitrary skin patches). The birds’ performance was compared to that of another group of pigeons that were raised under visually unrestricted but otherwise identical conditions. The results showed that the visually unrestricted pigeons showed a significant preference for the UP over the SK stimuli, whereas no such preference occurred in the restricted pigeons. The most straightforward way to interpret this group difference was to assume that experience with real heads enabled the unrestricted pigeons to recognize the depicted heads as parts of human figures. For the restricted pigeons, by contrast, the UP stimuli showed just arbitrary patches because these birds had never experienced live human heads. The findings were thus consistent with the notion of picture-object recognition being achieved at the associative level or maybe even by means of representational insight. If the pigeons had just relied on the discrimination of some simple perceptual features, visual experience should not have been critical for classification and performance of the visually restricted and unrestricted birds should not have differed.

Apart from showing picture-object recognition in pigeons at a level beyond feature discrimination, the experiments just described demonstrated that the CIP indeed provides a powerful means for testing such ability in animals. Nevertheless, the CIP is limited by the fact that it does not allow for a clear distinction between recognition at the associative

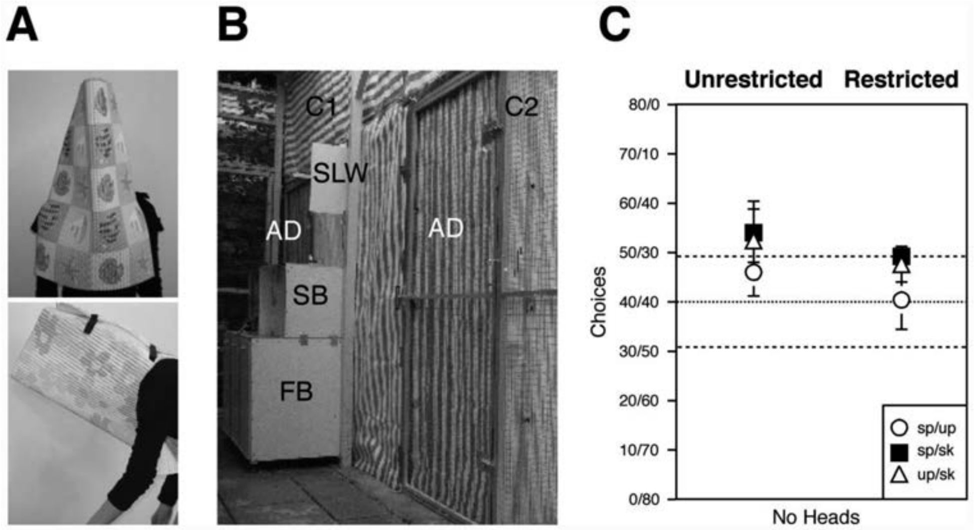

FIGURE 6.2. (A) Photographs of a person wearing a special mask to prevent the birds that were kept and tested under visually restricted conditions from sight of human heads. (B) Photograph of the aviary and the testing apparatus of the visually restricted birds. The aviary was divided into two compartments to which an outdoor Skinner box was attached. The box could be accessed from either side so that the pigeons could be let in from one compartment and released into the other after they had done their daily sessions. This prevented individual birds from monopolizing access to the box and from entering more than once per day. AD = Aviary door; C1/2 = aviary compartments; FB = Feeder box; SB = Skinner box; SLW = Sliding window. (C) Results of the Picture-Object Recognition Test as numbers of trials (± SD) out of 80, in which the birds chose seen parts in preference to unseen parts (sp/up), seen parts in preference to skin patches (sp/sk), and unseen parts in preference to skin patches (up/sk). The dashed lines indicate the limits of significance in a two-tailed binomial test ($\alpha = 0.025$); the dotted line at 40/40 marks the level of equal numbers of choices of the two compared stimulus types. From "Representational Insight in Pigeons: Comparing Subjects With and Without Real-Life Experience," by U. Aust and L. Huber, 2009, *Animal Cognition, 13,* pp. 210, 214. Copyright 2009 by Springer-Verlag. Adapted with permission.

level and true representational insight (and, to our knowledge, there are also no other studies so far that have clearly distinguished between these two mechanisms). Indeed, transfer to representative complementary parts and poorer (or lacking) transfer to nonrepresentative ones is compatible with both accounts. At the associative level, the test pictures of previously missing parts may call up a representation that includes also the complementary training parts because of an association between training and test parts that was built through experience with real (complete) objects. The activation of this representation will then elicit a similar response behavior toward the test stimulus as exhibited toward the training pictures. Nonrepresentative stimuli, by contrast, will not call up such a representation (and would thus not trigger a respective response) because they do not occur in real humans and have thus not been associated with any true human parts (encountered in real humans and shown in the training pictures). Alternatively, transfer to representative, but not to nonrepresentative complementary parts, may be based on the subjects' recognizing the object parts depicted in the training as well as in the representative test stimuli as representations of real human parts, whereas they would "know" that the nonrepresentative stimuli do not show any meaningful parts. But in any case, such a results pattern can be achieved only if the subjects are able to transfer some knowledge acquired through real-life experience with objects to pictures and if they can do so at a level beyond the discrimination of simple features. The CIP is therefore an appropriate tool to distinguish between the perceptual level and more abstract mechanisms of picture-object recognition and thereby represents an improvement compared to most traditional methods of investigating such abilities in nonhuman species.

PERCEPTION OF PAINTING AND ART

Painting or visual art started as a way to represent real objects. However, painting art is not a simple transfer of a 3D object on a 2D canvas, but is a transformation through the inner process of the painter/artist.

Discrimination of Painting and Art by Animals

Paintings have two properties, namely discriminative stimulus property and reinforcing property. We can discriminate painting styles of different artists and enjoy preferred paintings. In the sections that follow, we describe the discriminative stimulus property of paintings to nonhuman animals.

Painting and the real world. We can easily identify objects in paintings by impressionists, but the relation between paintings and objects is vague in abstract paintings. Cook, Wright, and Drachman (2013) successfully trained pigeons to discriminate between monochromatic drawings of birds and mammals obtained from animal books, but they found that pigeons were not able to discriminate between the outlines of birds and mammals. Bumblebees are able to discriminate between pictures of different artificial flowers, and they generalized a learned preference for one artificial flower to its silhouette, but this generalization was also not transferred to outline images (Thompson & Plowright, 2014). Itakura (1994) reported recognition of line drawings in one chimpanzee but Close and Call (2015) suggested difficulty in recognizing black and white line drawing in chimpanzees. In addition, contour completion of line drawings is not easy for apes (Martin-Malivel, 2011). Humans are able to identify outline drawings, and some cave drawings are outline drawings, but nonhuman animals have difficulty recognizing objects depicted in outline drawings.

A cartoon is visual art in which some aspects of the object are neglected and others are exaggerated. In this sense, a cartoon shares some aspects with cubist and abstract paintings. Cerella (1980) taught pigeons to recognize the cartoon character Charlie Brown and then tested them with scrambled pictures of Charlie Brown, in which the head, trunk, and legs were connected but randomly arranged. The birds did not show any decrease in responding to the scrambled versions. In contrast, after pigeons were taught to discriminate between photographs of two individual pigeons, scrambling these photos did disrupt their ability to recognize the individual birds in each photo (Watanabe & Ito, 1991). Photographs have a strong relation to reality, but a cartoon does not. Watanabe (2001a) examined the ability of pigeons to discriminate between two types of objects, humans and pigeons, shown in two types of medium, photographs and cartoons. Scrambling the images depressed the response and had the greatest effect on the response to photos of pigeons and the smallest effect on the response to cartoons of humans. The object and the medium had a significant effect on the response rate. Therefore, the effects of scrambling depend on the type of object and the type of medium, and the suppression of responses is greater for real and familiar objects.

Visual category. There is a lot of discussion about the similarity and dissimilarity between human and animal visual category formation. For example, the human definition of a triangle is a rule that can be described verbally. In contrast, pigeons have to establish nonverbal definition-like rules of a triangle through behavioral experience alone. Comparing the pigeons' patterns of response to novel triangles after training with multiple exemplars and after training with a single exemplar suggests that exposure to multiple exemplars may be essential to the formation of an artificial geometrical category on the basis of a definition-like rule (Watanabe, 1991; see also Chapter 17, this volume).

Behaviorally, a *category* is defined as a generalization within a stimulus class and discrimination between classes (see Chapter 5, this volume). Herrnstein and Loveland (1964) were the first to find evidence for a complex visual category in pigeons. Since then, researchers have uncovered a long list of natural and artificial categories formed by pigeons (e.g., Herrnstein, Vaughan, Mumford, & Kosslyn, 1989; Lea & Harrison, 1978; Lea & Ryan, 1990; Wasserman, Kiedinger, & Bhatt, 1988; Watanabe, 1988; Watanabe, Sakamoto, & Wakita, 1995). A basic procedure to test the formation of a visual category in pigeons is training with multiple exemplars, followed by testing with stimuli never seen during the discriminative training.

Painting style discrimination. Painting style can be considered a visual category. Each artist has his/her own style and there is similarity or consistency within a style. When we see paintings by Picasso and Monet, we can say which is Picasso and which is Monet with some accuracy even if we have never seen these particular paintings before. However, this ability is not necessarily innate. Gardner (1970) suggested that the ability to recognize painting styles develops around adolescence. Experiencing art education seems especially helpful in understanding abstract paintings (Cela-Conde, Marty, Munar, Nadal, & Burges, 2002). These results suggest that humans require experience to form categorical schemata of complex visual stimuli.

The ability of birds to discriminate between different paintings has been reported in pigeons (Watanabe, 2001b; Watanabe et al., 1995) and Java sparrows (Ikkatai & Watanabe, 2011). In the earliest study (Watanabe et al. 1995), eight pigeons were trained to discriminate between Picasso and Monet paintings using 10 paintings from each artist. The birds required six to 24 sessions (20 trials of 25 s presentation for each artist) to reach the criterion for discrimination. The pigeons were then tested with novel Picasso and Monet paintings that were not included in the discriminative training, and paintings by Renoir, Cezanne, Braque, Matisse, and Delacroix. The pigeons showed generalization not only from trained Monet (or Picasso) paintings to new Monet (or Picasso) paintings, but also from Monet to Renoir and Cezanne, and from Picasso to Braque and Matisse. This indicates that the pigeons had formed categories of impressionism and cubism. However, if the birds could not discriminate among paintings within a given category, their discriminative behavior would reflect confusion rather than a category. To clarify this point, a new group of pigeons was trained on pseudocategory discrimination, in which 10 Picasso and 10 Monet paintings were shuffled and divided into two stimulus groups. Both groups of stimuli contained Monet and Picasso. The birds were able to learn this discrimination task, suggesting that the birds could not only discriminate each painting but also could discriminate among the paintings on the basis of a category of the painting style. A follow-up study demonstrated a similar category-like discrimination between van Gogh and Chagall in pigeons (Watanabe, 2001b). In Picasso versus Monet and van Gogh versus Chagall discrimination tasks, the subjects maintained their ability to discriminate in a gray-scale test, indicating that color cues were not crucial for the discrimination. In addition, the birds were able to maintain this discriminative ability even when mosaic or out-of-focus processing was carried out on the original paintings.

Pigeons were also able to discriminate Western (impressionist) paintings from Japanese paintings (Watanabe, 2011). Technically speaking, and in a narrow sense, Japanese paintings use colored glue, and the diameter of the molecules of the glue color is larger than that of the glue color used in other countries. More broadly, different features characterize Japanese paintings: in contrast to Western impressionists' paintings, they are not representative like photographs, and they do not use shadows or dark colors. Although Japanese paintings influenced the impressionists, it is easy for humans to discriminate paintings by impressionists from Japanese paintings. Watanabe (2011) selected 10 Western paintings and 10 Japanese paintings and trained eight pigeons to learn to discriminate between the two styles. This took 12 to 36 sessions (20 trials of 25 s presentation for each style). During testing, the discrimination generalized to novel Western paintings (again by impressionists) and Japanese paintings that had not been presented during the discriminative training. Watanabe and Ikkatai (2011) also confirmed discrimination between Western and Japanese paintings and generalization to novel paintings by Java sparrows, suggesting a cross-species generality of painting style discrimination in birds.

Paintings are human-made stimuli, but birds can use their ability of developed visual cognition to perform these discrimination tasks. However, birds and humans may use different strategies to accomplish painting discrimination. Several experiments have demonstrated a dominance of local elemental cues in complex visual discrimination in pigeons (Aust & Braunöder; 2015; Cavoto & Cook, 2001; Cook, Riley, & Brown, 1992; Legge, Spetch, & Batty, 2009; Greene, 1983). Aust and Huber (2001) analyzed the ability of pigeons to discriminate between human images using scrambled pictures. The images were divided into small square elements that were randomly distributed over the whole area of the image. Although scrambling at this extreme level resulted in a reduction in discrimination, the discrimination behavior of some pigeons, at least, was still significant. Watanabe (2011) used a similar division and random rearrangement technique to analyze the role of elemental cues in painting discrimination in pigeons. If pigeons attend to local elemental cues, transfer from the original painting to a scrambled one, and from a scrambled painting to the original, should be the same. One group of pigeons was trained on discrimination between Japanese paintings and Western paintings and tested with their scrambled images, whereas the other group was trained on discrimination between scrambled Japanese paintings and scrambled Western paintings and tested with the original paintings. The pigeons showed bidirectional transfer: from the original to the scrambled painting and vice versa (see Figure 6.3). This suggests that the birds used local cues in both discrimination tasks (see Chapter 5, this volume).

In addition to being able to discriminate between different styles of paintings, humans can also discriminate between different painting mediums, for example, watercolor and pastel. Watanabe (2010) trained pigeons to discriminate between watercolor paintings and pastel paintings created by school children. The pigeons had to discriminate among the paintings on the basis of the difference in painting medium. They succeeded in learning this task. Moreover, in generalization tests with new paintings, the pigeons clearly discriminated watercolor from pastel. However, discrimination of gray-scale test stimuli was lower, and the mosaic processing of the paintings affected the discrimination task. Thus, color and fine cues are important for watercolor versus pastel discrimination.

Most rodents do not have a developed visual system and have been considered olfactory animals. It was reported that mice used visual cues for social

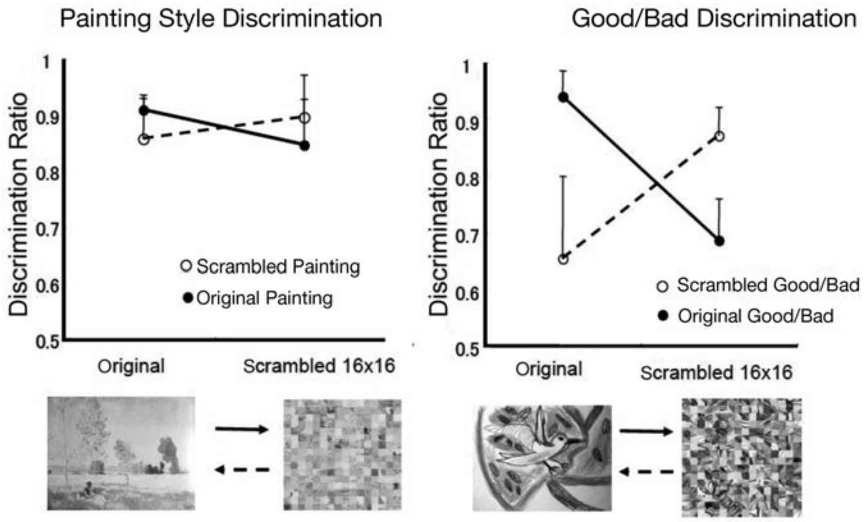

FIGURE 6.3. Bidirectional transfer between original and scrambled painting. Pigeons showed the transfer in painting style discrimination (left) but not in good/bad discrimination, suggesting they used different strategies for different tasks. From *Emotions of Animals and Humans: Comparative Perspectives* (p. 150), by S. Watanabe and S. Kuczaj, 2012, Tokyo, Japan: Springer. Copyright 2012 by Springer. Copyright 2012 by Springer Japan. Reprinted with permission.

cognition (Langford et al., 2006), suggesting the possibility of higher visual cognition in rodents. Watanabe (2013) selected 10 paintings by Mondrian and 10 paintings by Kandinsky and trained mice to discriminate between paintings by these artists. First, preference between the two types of paintings was examined by time spent at the paintings displayed on iPods. Then, conditioned-place-preference-like conditioning was carried out to train mice to discriminate between the two types of paintings. In this training, the mice were injected with morphine and confined in a compartment with one particular type of painting (e.g., a Kandinsky painting). The next day, they were injected with saline and restricted in another compartment with the other type of painting (e.g., a Mondrian painting). After such conditioning, the mice stayed longer at the compartment with the painting associated with the morphine injection. They also showed generalization of the conditioned preference for paintings never shown during the conditioning. Therefore, they had the ability to discriminate Kandinsky paintings from Mondrian paintings. A similar result of discrimination between paintings by Renoir and Picasso was obtained. Mice in another group underwent conditioned place preference training with two sets of paintings. One set contained five paintings by Picasso and five paintings by Renoir, and the other set contained another five paintings by Picasso and another five paintings by Renoir. Morphine was injected in association with one set for 10 mice and with the other set for the remaining 10 mice. The subjects demonstrated successful conditioning, similar to the results of the pseudocategory discrimination in pigeons (Watanabe et al., 1995), suggesting that the mice could not only discriminate each painting but also could discriminate among the paintings on the basis of a category of the painting style.

Watanabe (2013) also trained four mice on simultaneous discrimination of a pair of paintings by Kandinsky and Renoir in an operant chamber equipped with a touch screen. After reaching the criterion of the discrimination task, the subjects were trained on a new pair of paintings by Kandinsky and Mondrian. Four mice were trained on four different pairs of these paintings successively. The mice required 31.5 sessions (20 trials per session) on average to learn the first task. To learn the fourth task, the mice needed just two to four sessions. The mean correct response ratio in the first session of the second task was 0.74 (range, 0.55–0.85) and that in the first session of the fourth task was 0.79 (range, 0.70–0.85). Thus, the mice were able to discriminate between paintings from the two artists and transfer the discrimination to novel stimuli, suggesting category-like discrimination of painting style.

Discrimination of good and bad paintings. Criteria of beauty may depend on age, culture, and individual preferences. However, we may have a common sense of beauty for relatively less-sophisticated paintings, such as those drawn by schoolchildren. There should be some common, perceptually lower level features in these "beautiful" paintings. If so, nonhuman animals probably could learn the human category of beauty as a discriminative stimulus category on the basis of perceptual similarity.

To examine this, Watanabe (2010) used pictures made by children in an elementary school as stimuli in a set of experiments. To identify good and bad paintings, Watanabe used evaluations of these paintings by an elementary school art teacher and by ordinary adults. Four pigeons were trained to discriminate 10 good paintings from 10 bad paintings. The birds learned the discrimination task in about 20 sessions (20 trials of 25 s presentation for each category). Then they received a generalization test with novel paintings that had again been judged as good or bad by ordinary people. The birds maintained their discrimination in the test. Thus, it would be fair to say that they had acquired the category of good versus bad. When the paintings were presented in gray scale, good/bad discrimination was considerably disrupted, suggesting that color was important for discrimination of beauty. When the paintings were presented after mosaic processing, discrimination was disrupted depending on the level of processing, suggesting that the spatial pattern was also important for discrimination of beauty. Thus, color and spatial pattern play an important role in the discrimination of good from bad paintings.

Humans and pigeons may use different strategies for discrimination, even though these strategies result in similar discriminative performances. As described earlier, pigeons displayed successful bidirectional transfer between original and scrambled stimuli in the case of Western versus Japanese painting style (Watanabe, 2011). Watanabe (2011) also examined bidirectional transfer between original paintings and their scrambled counterparts with the good and bad paintings. The pigeons could not maintain their discrimination when tested with the scrambled paintings. The pigeons also learned to discriminate scrambled good paintings from scrambled bad paintings, but they did not discriminate the original paintings. There was no transfer between the original and scrambled stimuli. Local elemental cues were not crucial for the discrimination of good versus bad paintings. Thus, pigeons used different strategies for good versus bad discrimination and painting style discrimination (see Figure 6.3).

Reinforcing Properties of Painting and Art

We can discriminate painting styles and feel pleasure when viewing a beautiful picture. One particular aspect of perception of art is its reinforcing effect (see Watanabe, 2014 for review). Gordon (1951) indicated that modern paintings are much more extreme or more radical than traditional paintings in context and technique, and so may be more difficult to appreciate their beauty. But even though beauty is a socially constructed category, there seem to be certain common reinforcing properties of beauty that exist at a basic level. In the framework of behaviorism, Berlyne (1971) proposed a new experimental aesthetic in which he introduced four methods of investigation: verbal judgment, psychophysics, statistical analysis, and measurement of exploratory behavior. The last method can be applied to nonhuman animals as well as to humans, because it measures behavior. According to Berlyne, beauty is sensory reinforcement; hence, aesthetics is the study of reinforcers. Behavioral theories of sensory reinforcement have skipped analyses of the subjective experience of pleasure. There is, however, some correlation between behavioral measures and verbal reports in humans. Berlyne (1972) showed line drawings to human subjects and performed a factor analysis of verbal reports and looking time. He found a correlation of 0.82 between the complexity-uncertainty (curiosity) score and looking time, and a correlation of 0.40 between the hedonic value score and looking time. We are not able to obtain subjective reports from animals, but the time spent looking at them might reflect the two aspects of curiosity and hedonic value.

Sensory reinforcement by complex visual stimuli. Many studies have demonstrated that sensory stimulation has a reinforcing effect (Kish, 1966). The classic example is the 1964 experiment by Berlyne, Salapatek, Gelman, and Zener, in which a rat pressed a lever to light a lamp for 1 s, whereas a yoked control rat received the same amount of lighting with the same timing without having to press a lever. The increment of the operant (lever press) clearly depended on the contingency between operant (lever press) and reinforcer (lighting). Monkeys also show preference for particular fractal images over other fractal images as measured by choice and also by gazing time (Takebayashi & Funahashi, 2009). Rensch (1957, 1958) compared preference for visual patterns in several species and reported that capuchin monkeys, meerkats, and crows prefer regular patterns to irregular ones. Later, Anderson, Kuwahata, Kuroshima, Leighty, and Fujita (2005) confirmed similar preferences in capuchin and squirrel monkeys.

Biologically relevant visual stimuli often have reinforcing value; for example, an image of a conspecific has reinforcing value for Java sparrows (Watanabe, 2002), rooks (Bird & Emery, 2008), and macaques (Schwartz & Rosenblum, 1980). Furthermore, a particular behavior displayed by a conspecific can have a reinforcing effect, such as agonistic behaviors for chimpanzees (Bloomsmit, Keeling, & Lambeth, 1990) and gorillas (Maloney, Leighty, Kuhar, & Bettinger, 2011), social behaviors for bonnet monkeys (Andrews & Rosenblum, 1993), and behaviors of males during the breeding season for male Japanese monkeys (Mizuno, 1997). Deaner, Khera, and Platt (2005) found that male rhesus macaques preferred to watch female perinea and faces of high-status monkeys, indicating the reinforcing value of sex-related visual information in monkeys. Watanabe, Shinozuka, and Kikusui (2016) examined sensory reinforcement of three different videos of conspecific behavior, namely sniffing, copulation, and fighting, in mice using a box that consisted of a central compartment and two side compartments. In each side compartment there was an iPod showing a video, and time spent in each compartment was measured. Mice preferred the copulation video to the sniffing video, the fighting video to the sniffing video, and the fighting video to the copulation video. Thus the video of fighting had the strongest reinforcing value. An individual's observation of fighting among conspecifics may provide information to the individual on the dominant/subordinate relationships within the group. Jays (Paz-y-Miño, Bond, Kamil, & Balda, 2004) and cichlid fish (Grosenick, Clement, & Fernald, 2007) can use such information to infer their relative status (see Chapter 18, this volume).

Several studies have demonstrated the reinforcing effect of non–biologically relevant visual stimuli in primates. Humphrey (1972) trained monkeys to press a button to see a Walt Disney film and observed that the monkeys preferred the continuous story to the looped film. F. A. Wilson and Goldman-Rakic (1994) measured the gaze of rhesus monkeys as they viewed faces, colored pictures obtained from magazines, and colored patterns and found that the monkeys spent more time looking at the faces than the colored patterns, and more time looking at the pictures than the colored patterns.

Sensory reinforcement by painting and art. Mammals are originally nocturnal animals, and rodents are typical nonvisual animals. In contrast, most birds are diurnal and have highly developed visual cognition. Ikkatai and Watanabe (2011) examined the reinforcing property of paintings in the Java sparrow. The procedure was similar to the mouse experiment described previously. In a long experimental chamber, two computer monitors displayed two of three different styles of paintings, Japanese, impressionist, or cubist, and another monitor displayed a gray-scale pattern. Considerable individual differences were observed, but five of seven birds preferred cubist to impressionist paintings, three preferred Japanese to cubist paintings, two preferred cubist to Japanese paintings, and six did not show a preference between the impressionist and Japanese categories.

Watanabe (2013) measured the reinforcing property of paintings by Mondrian and Kandinsky for mice using a similar apparatus to that used for the analysis of preference for the videos. Both artists are classified as abstract painters, but their styles are different. Mondrian is a minimalist who demonstrates elemental aspects of pictures, such as line or color, whereas Kandinsky is an expressionist who conveys his inner images or consciousness. Watanabe (2013) selected 10 paintings by Mondrian and 10 paintings by Kandinsky and loaded them on two iPods. One iPod displayed paintings by Kandinsky and the other displayed paintings by Mondrian in a random series, and the two iPods were placed at the ends of two chambers of an apparatus. The time spent of mice in each chamber was measured. Only one of 22 mice showed a statistically significant preference for Kandinsky, and the others did not show a consistently longer time spent at a particular artist. This preference test with paintings by Renoir and Picasso was carried out but again mice did not show preference for a particular artist (see Figure 6.4). Thus, the reinforcing effect of paintings was very rare in mice. As described previously, mice can discriminate among paintings by different artists, but they do not have preferences.

Evolutionary origins of the reinforcing property of art stimuli. Even though the reinforcing property of art is based on a human standard, we can find a lot of beauty in nonhuman animals. If nonhuman animals can perceive beauty, beauty in the human sense should have evolutionary origins (see Watanabe, 2014, for review). One traditional evolutionary approach, called evolutionary aesthetics (see Grammer, Fink, Møller, & Thornhill, 2003; Thornhill, 1998; Voland & Grammer, 2003), explains aesthetics as the result of natural selection. According to this theory, the origin of human aesthetics is in part an innate affiliation to plant and animal habitats (E. O. Wilson, 1983). Our ancestors had to find protective and safe habitats, select suitable food, and avoid dangerous animals. This evolutionary history has resulted in preferences for particular landscapes. In fact, landscape preference tests have revealed that humans prefer a savanna-like environment similar to the one

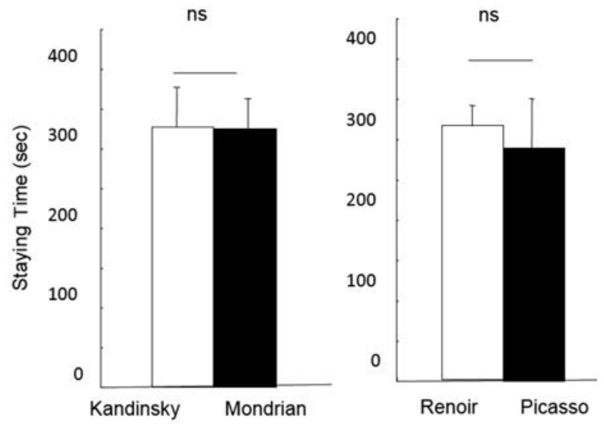

FIGURE 6.4. Mice did not show preference for particular paintings. From "Preference for and Discrimination of Paintings by Mice," by S. Watanabe, 2013, *PLOS ONE*, *86*, p. e65335. Copyright 2013 by Shigeru Watanabe. Reprinted with permission.

where our ancestors lived (Balling & Falk, 1982). As Kahneman (2003) and other cognitive scientists pointed out we have fast intuitional judgment and slower judgment on the basis of reasoning. Aesthetic judgment is fast one (Winkielman & Cacioppo, 2001) and moral judgments also have fast evaluation (moral intuition; Haidt, 2001). Hence, Kaplan (1992) argued that quick, automatic decisions in environmental choice resulted in our environmental aesthetics. Another theory of natural selection is the camouflage theory (Cott, 1940; Thayer, 1909), which was first proposed by Wallece (1889). He examined the color patterns of butterflies and found that cryptic colors could form a camouflage in some situations. A developer of military camouflage, Thayer (1909) described every pattern and coloration in animals as camouflage to conceal them from predators or prey. Even male peacock feathers can act as camouflage, and the pink feathers of the flamingo are also camouflage at sunrise and sunset.

Darwin's explanation of beauty in animals was based on sexual selection. He assumed that there is a "sense of beauty" in females, but Morgan criticized this idea as too anthropomorphic (Morgan, 1896). Modern evolutionary biology considers a beautiful morphological feature such as the feathers of a male peacock as a "signal" or "fitness indicator" of the signal sender. Such beauty may be the result of a health condition, such as a lack of parasites or high immune-system activity. Although different animals may use different honest signals (see Volume 1, Chapter 30, this handbook), there are some common cross-species features in honest signals, for example, the symmetry of the body as a signal of good health. This may be the reason why some animals look beautiful to humans.

Items constructed by animals may also have the same function as the honest signal; for example, male bowerbirds construct complex bowers and decorate them with many colorful materials to attract females (see Madden, 2007; see also Volume 1, Chapter 37, this handbook). They even "paint" using chewed plants (Hicks, Larned, & Borgia, 2013). Male great bowerbirds (*Chlamydera nuchalis*) make courts with gray and white objects that increase in size with distance from the avenue entrance (Endler, Endler, & Doerr, 2010). This arrangement creates a false perception of size and distance. When a researcher disrupts this size-distance gradient, the males reconstruct their gradients again, with little difference from the original structure. Such complex architecture among bowerbirds can be an honest signal of the health condition (Doucet & Montgomery, 2003), the motor skills (G. F. Miller, 2000), the social rank (Madden, 2002), or a large brain (Day, Westcott, & Olster, 2005; Madden, 2001) of these male birds.

Understanding the signal or message contained within a piece of art is the key to understanding the origin of our art. Dutton (2009) wrote that the best way for a man to demonstrate his resources to a woman is by giving her expensive and useless things, for example flowers and diamonds. It is time-consuming to make such gifts. Dutton also pointed out that the global warming period after the end of the last ice age gave our ancestors free time for nonadaptive activities, such as painting and chatting. Such free time made it possible to produce nonadaptive and useless objects, or art. A communicative society could evaluate the value of such useless products. We can say that beauty is preferred by the opposite sex because it is an honest signal of good genes, higher ability, wealthy resources, and so forth, but the truth may be just the reverse—that is, beauty may be a verbal expression or explanation of our preference for an honest signal.

CONCLUSION

Just like in humans, the mechanisms of object perception and recognition in animals have been shaped by the necessity to efficiently deal with the environment. In bottom-up processing, various steps of filtering and abstraction reduce and thus make more manageable the flood of incoming sensory information and top-down processing allows a subject to make inferences on the basis of interpretations resulting from expectations, that, in turn, arise from prior experience and knowledge. Many animals are even able to recognize some correspondence between objects and their pictures, which constitutes a special case of object recognition. The underlying mechanisms can be manifold, ranging from picture-object confusion and the discrimination of simple 2D features to true representational insight. There is furthermore evidence that nonhuman animals can discriminate painting style, painting medium, and painting quality (good or bad) in pictorial stimuli. Thus, humans and nonhuman animals, particularly birds, share the ability to visually discriminate paintings, even though they may use different strategies of discrimination. Humans and birds developed different fine visual brains through a different evolutionary history. Most of the mammals do not have a well-developed visual brain, because they appeared on the earth as nocturnal animals and the primates acquired sophisticated visual brain including color vision. They used their already well-developed telencephalon (originally olfactory brain) to process visual information. On the other hand, the birds started their lives as diurnal animals and kept their midbrain (optic tectum) for visual information processing. Thus, even though there is a convergence of higher visual cognition in humans and birds, humans and birds use different brain structures suggesting different algorithm. Such different algorithm of visual information processing constraints their visual discrimination strategy.

In contrast, the reinforcing property of art paintings is rather hard to observe in nonhuman animals, although at the present time there is insufficient data to make a firm conclusion. Art paintings are human-made stimuli and beauty is a homocentric idea. However, our sense of beauty does have an evolutionary origin; hence, human preferences and animal preferences can sometimes overlap, although this is not always the case. Discriminative and reinforcing properties are two basic properties of art. In auditory art, many nonhuman animals can discriminate music, but only a few species show a preference for types of music (see Watanabe, 2012, for a review). These observations are similar to the observations concerning visual arts as described in this chapter.

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Chapter 7

FACE PERCEPTION AND PROCESSING IN NONHUMAN PRIMATES

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Humans live in a very complex social environment. Human social groups are relatively big compared to many other animals and relations between individuals change dynamically across time, yet humans still manage to communicate effectively with other people on a daily basis. In such a challenging environment, however, humans usually have little trouble communicating with others. Faces play an important role in social interactions by providing a great amount of information about individual identity, age, sex, attentional state, and emotional state, among others (for reviews, see V. Bruce & Young, 1998; Tsao & Livingstone, 2008). Humans constantly and regularly monitor others' faces to retrieve such information and adjust our behaviors accordingly. Because of the previously mentioned importance of faces, the perception of faces appears to involve specialized processes at the perceptual, neurobiological, and cognitive levels (V. Bruce & Young, 1986).

How did humans acquire such a sophisticated ability to extract information from faces? Human cognitive abilities are the products of millions of years of evolution, just as with the human body and human society. Comparative studies across species can provide important perspectives for addressing this question. In the last couple of decades an expanding number of studies have explored face perception and processing in nonhuman species. In this chapter, we focus on and review studies on nonhuman primates, as these species are phylogenetically close to humans and thus can provide many insights into the evolution of face processing ability in humans. We acknowledge, however, many interesting and related findings in studies of nonprimate species. We start our review by covering studies which explored if faces are special stimuli as such they quickly capture attention from nonhuman primates. We then move to review what information nonhuman primates could extract from faces. We specifically focus on species recognition, individual recognition, emotional expression recognition, and gaze recognition. Finally, we cover studies addressing the underlying mechanisms how nonhuman primates perceive faces.

DO FACES CAPTURE ATTENTION IN NONHUMAN PRIMATES?

Humans quickly and almost automatically shift and pay attention to faces. For example, a face in a scene is detected immediately, suggesting rapid detection and quick attentional shift toward faces (Fletcher-Watson, Findlay, Leekam, & Benson, 2008; Treisman & Gelade, 1980; Wolfe, 1994). When a search display contains only facial stimuli and observers are required to find a specific face among others, the subjects did not show a pop-out effect (Tong & Nakayama, 1999). By contrast, when a face appears among nonface objects (e.g., cars, houses, etc.), it is detected without any effort.

In nonhuman primates, similar quick attention shifts toward faces have been reported. Kano and colleagues (Kano, Call, & Tomonaga, 2012; Kano & Tomonaga, 2010) applied an eye-tracking method to humans and four ape species: chimpanzees

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(*Pan troglodytes*), bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla*), and orangutans (*Pongo abelii*). These studies directly evaluated the subjects' attention shift through their looking behavior toward various scenes, especially those including faces. All tested species were presented with photographs containing images of conspecifics and heterospecifics. The authors found considerably similar viewing patterns across the five species. The subjects looked longer at the animal figures than at background and, among the animal figures, the subjects focused on the face region for longer than other parts of the body. Furthermore, the face region was detected at first sight by the subjects. Using a similar paradigm, Shepherd, Steckenfinger, Hasson, and Ghazanfar (2010) compared the gaze behavior of humans and long-tailed macaques (*Macaca fascicularis*) as they viewed movie clips. They reported significant intersubject and interspecies gaze correlations, suggesting that both species looked at animals and people, especially at their faces in a similar manner. In a series of experiments with a visual search paradigm, Tomonaga and Imura (2015) reported that chimpanzees searched for a face as efficiently as humans. Additional testing showed that a front-view face was more readily detected than a face in profile, suggesting the important role of eye-to-eye contact. These studies nicely illustrated how faces attract attention in nonhuman primates.

WHAT DO THEY EXTRACT FROM FACES?

Earlier, we briefly reviewed studies showing that nonhuman primates pay attention to faces in much the same way as humans do. But what information do they extract from faces? Like humans, most other primate species form social groups and regularly interact with other group members. Many species also establish a social rank hierarchy (de Waal & Tyack, 2003). In such a complex social environment, it would be advantageous for animals to extract social information from other individuals to function smoothly within the group.

Species Recognition

As identifying one's own species is clearly essential, species have evolved a variety of behavioral mechanisms for recognizing their own species. Although hybrid individuals occur in some primate populations in the wild (e.g., baboons: Nagel, 1973; Sugawara, 1979; macaques: Groves, 1980; Watanabe & Matsumura, 1991), wild hybrids are relatively rare and more likely to occur in places where artificial disturbance of the environment is suspected. More typically, primate species in the wild have established reproductive isolation. Yoshikubo (1987) proposed that primate individuals actively chose to mate only with conspecifics because of a psychological preference for conspecifics, through psychological reproductive isolation mechanisms.

To explore the existence of such mechanisms, Fujita and colleagues (Fujita, 1987, 1993; Fujita & Watanabe, 1995; Fujita, Watanabe, Widarto, & Suryobroto, 1997) tested several macaque species and measured their visual preferences among photographs of conspecifics and other species, using a sensory reinforcement procedure. In this procedure, subjects were allowed to choose various photographs of scenes by pressing buttons or levers (Fujita & Matsuzawa, 1986). In general, the subjects showed visual preferences for conspecifics over heterospecifics. Furthermore, monkeys preferred photographs containing the faces compared with those featuring other body parts, suggesting the importance of the face in visual preference for conspecifics (Fujita, 1993).

More recent studies reported that nonhuman primates form a concept of species that integrates faces and voices. Martin-Malivel and Fagot (2001a) tested cross-modal representation in Guinea baboons (*Papio papio*), an Old World monkey species. These authors trained subjects to discriminate between human and baboon vocalizations. Then they introduced in probe trials either human or baboon photos as a brief prime before the stimulus vocalization. The results showed that presentation of photographs of faces of the matching species shortened the response time in one of the two baboons. Adachi and colleagues (Adachi, Kuwahata, Fujita, Tomonaga, & Matsuzawa, 2006, 2009) tested whether infant Japanese macaques in their first year of life have a cross-modal representation of species. Using an expectancy violation procedure, they presented monkeys with a photograph of either a monkey or a human face after playing a vocalization of one of those species. In general, the infant monkeys looked at the photographs longer when voice and face mismatched than when they matched. This suggests that they were expecting to see a face of the species they had just heard, and so were surprised when they saw the mismatched face. These studies provide evidence that nonhuman primates not only discriminate and prefer conspecific faces, but actually recognize their own species from their faces at a conceptual level (see Chapter 5, this volume).

Individual Recognition

Most researchers agree that for highly social species the ability to keep track of conspecifics and their social relationships is critical for survival (Cheney & Seyfarth, 1990; Jolly, 1966; see also Volume 1, Chapter 43, this handbook). Recognizing other individuals plays a fundamental role in mental tracking of the social environment. Whether and how nonhuman primates recognize faces has been studied in comparative cognitive science for decades. This section focuses on studies exploring individual recognition (for the underlying perceptual system, see the section How Do They Perceive Faces?).

Matsuzawa (1991) tested if a chimpanzee, Ai, recognized familiar conspecifics and human individuals from pictures of their faces, using a symbolic matching-to-sample procedure. Ai was able to learn the pairings of faces and the corresponding names of the individuals, irrespective of stimulus species. However, her discrimination performance was better for conspecifics. A similar own-species advantage in face discrimination has also been reported in other primate species. Pascalis and Bachevalier (1998), for example, tested humans and rhesus monkeys using a visual paired-comparison task. This task indexes the relative interest in a pair of visual stimuli consisting of one novel item and one familiar item viewed during a prior familiarization phase (Pascalis, de Haan, & Nelson, 2002). The results demonstrated that human participants showed novelty preference for human faces but not for monkey faces, and vice versa for the monkeys. Dufour, Pascalis, and Petit (2006) used the same method with Tonkean macaques (*Macaca tonkeana*), and capuchin monkeys (*Cebus apella*) and obtained similar results. These findings suggest that (a) the ability to discriminate faces is relatively widespread in the primate lineage, and (b) similar to humans, nonhuman primates have better individual recognition of conspecific than heterospecific faces.

Although the ability to discriminate faces plays an important role in extracting individual identity from faces, the question remains if animals actually recognize individuals from the faces in photographs. Potentially, they might rely simply on the perceptual similarities to solve this task, without actually recognizing the individuals in the photographs (see Chapter 5, this volume). Some studies attempted to overcome this by focusing on viewpoint invariance for face discriminations (Parr, Winslow, Hopkins, & de Waal, 2000; Pokorny & de Waal, 2009; Rosenfeld & Van Hoesen, 1979). However, an advantage for familiar faces over unfamiliar faces in identity discrimination across different viewpoints, commonly found in human face identification, has not been observed. The subjects in these studies, therefore, may not recognize identity of faces in photographs. Boysen and Berntson (1989) evaluated the ability of a chimpanzee to recognize photographs of conspecifics, using heart rate as a measure. The heart rate of the chimpanzee was recorded before, during, and after viewing photographs of familiar and unfamiliar individuals. The subject displayed a differential pattern of heart-rate response to the stimuli even without prior experience with the photographs. The results suggest that the chimpanzee was able to recognize photographs of individual conspecifics and that heart rate change reflected the nature of established social relationships between chimpanzees. However, it is still unclear if nonhuman primates recognize faces in the photographs at a level of familiarity or of identity.

Hashiya and Kojima (2001) and Kojima, Izumi, and Ceugniet (2003) overcame the problems by testing chimpanzees' multimodal individual recognition, integrating faces and voices. They successfully trained a chimpanzee to match vocalizations of familiar individuals to the visual images of the individuals and they found that the subject's matching performance rapidly transferred to other stimulus individuals who were not presented during the training. This suggests that chimpanzees recognized the faces in photographs as a real representation of the individuals and understood the parings of faces and voices on the basis of common identity. Similarly, Adachi and Fujita (2007) tested squirrel monkeys (*Saimiri sciureus*) with a modified delayed matching-to-sample procedure. Briefly, in the training phase, subjects were trained to discriminate visual stimuli in a delayed matching-to-sample task. They were then tested on trials in which during a delay they heard a voice that either matched (congruent condition) or mismatched (incongruent condition) the visual sample stimulus, before making a choice. The authors hypothesized that if monkeys recognize individuals on the basis of the faces and voices, presentation of mismatching voices during the delay interval should interfere with their memory of the visual stimulus. The subjects did show poorer performance in the incongruent condition than the congruent condition, as predicted. Finally, Adachi and Hampton (2011) reported that rhesus monkeys also form cross-modal representations of familiar individuals. These studies demonstrated that nonhuman primates not only discriminate faces in photographs, but actually recognize individuals by faces in photographs.

Emotional Expression Recognition

Humans communicate their emotional states to others via multiple cues. Facial expression is one of the most salient and powerful cues for humans. Our species has a large repertoire of facial expressions, and it is also known that some basic expressions are common across cultures (Ekman, Sorenson, & Friesen, 1969). Because facial expressions are formed by the mimetic facial musculature, which is a product of evolution, basic human expressions are widely shared across the animal kingdom, although there are also some expressions unique to humans (Darwin, Ekman, & Prodger, 1998). Nonhuman primates in particular possess a broad repertoire of facial expressions involving the lips and eyes, which are similar to human expressions (Andrew, 1963; Ghazanfar, Nielsen, & Logothetis, 2006; Hadidian, 1980; Maestripieri & Wallen, 1997; Preuschoft & van Hooff, 1995; Smith, 1999).

Do nonhuman primates understand others' emotional expressions and adjust their behaviors accordingly? Cook and Mineka (1989) reported that macaques acquire the fear of toy snakes and crocodiles after observing videos of conspecifics reacting fearfully to them (see Volume 1, Chapter 39, this handbook). More recently, Morimoto and Fujita (2011, 2012) reported that tufted capuchin monkeys recognize objects as elicitors of others' expressions. Observer monkeys witnessed another individual (demonstrator) reacting either positively or negatively to the contents of one of two containers and were then allowed to choose one of the containers. The observer preferred the container that evoked positive expressions in the demonstrator and avoided the container that evoked negative expressions. This result suggests that the monkeys appropriately linked the emotional valence of others' expressions to specific containers.

Regarding facial expressions, experiments have shown that chimpanzees can accurately discriminate photographic expressions (Parr, 2003; Parr, Hopkins, & de Waal, 1998). Some macaque monkeys can also learn to categorize expressions of monkeys and humans (Dittrich, 1990; Kanazawa, 1996) although they need a considerable amount of training. However, discriminating facial expressions in a visual discrimination task does not necessarily mean that the meaning of the expressions is understood. To date few studies have addressed this question. Miller and colleagues (Miller, Caul, & Mirsky, 1967; Miller, Murphy, & Mirsky, 1959), for example, demonstrated the ability of rhesus monkeys to communicate affective information with facial expressions. The experiment involved two monkeys: a stimulus monkey and a subject monkey. In the setup, the monkeys received an electric shock after a conditioned stimulus (CS), but the shock could be avoided by pressing a lever. The stimulus monkey had visual access to the CS but no access to the lever, whereas the subject monkey had access to the lever but no visual access to the CS. Instead, the subject monkey had a visual access to the stimulus monkey, via a television monitor. The subject was able to use the facial cues given by the stimulus monkeys to successfully avoid the shock. Rhesus monkeys, therefore, can use the facial expressions of other individuals as a cue to predict and avoid an aversive event. This is one step beyond simple discrimination of facial expressions described previously. It is, however, still not clear whether the subject monkey perceived the other's facial expressions as an emotional signal or as a simple visual cue (see Chapter 34, this volume).

Parr (2001) overcame this problem by examining chimpanzees' responses to emotional stimuli. The subject chimpanzees were required to use facial expressions to categorize emotional video scenes (i.e., favorite food and objects, and veterinarian procedures) according to their positive and negative valence (Figure 7.1). With no prior training, subjects spontaneously matched the emotional videos to conspecific facial expressions according to their shared emotional meaning. This result demonstrates that chimpanzees recognize conspecifics' facial expressions as emotional signals. Further comparative studies are necessary to understand the degree to which such emotional recognition is shared across nonhuman primates.

Gaze Recognition

Humans have great sensitivity to others' eyes and are good at acquiring information about others' attentional state through the eyes. Humans not only understand where other individuals look but also make inferences about their thoughts and intentions (see Chapter 32, this volume). This aspect of face processing may be particularly well developed in humans because of the unique morphology of our eyes which have a widely exposed white sclera surrounding the darker colored iris, making it easy to discern the direction in which they are looking (Kobayashi & Kohshima, 1997).

Eye-tracking studies have revealed that apes and monkeys show strong interests in the eye region when viewing images of conspecifics faces (Gothard, Erickson, & Amaral, 2004; Kano et al., 2012; Kano & Tomonaga, 2010; Keating & Keating, 1982; Nahm, Perret, Amaral, & Albright, 1997), as has been observed in humans. There are also reports of nonhuman primates being highly sensitive to whether they are being looked at or whether another's gaze is directed away from them (Keating & Keating, 1982; Sato & Nakamura, 2001; Tomonaga & Imura, 2010); this is true even when the direct gaze were only made by eyes, with the head directed away from the subject (Perrett & Mistlin, 1990; but also see Tomonaga & Imura, 2010). Because direct gaze is often associated with predation and with the likelihood that an individual will approach or engage the observer, it has been adaptive for animals to evolve sensitivity to direct gaze from others.

There are a plenty of studies examined if nonhuman primates have sensitivity to the gaze direction of other individual as well (see Chapter 32, this volume). One of the best studied phenomena is

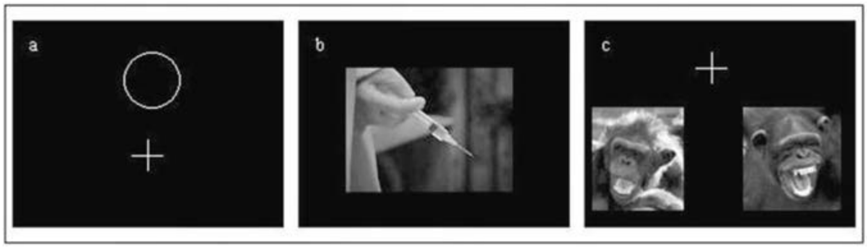

FIGURE 7.1. Experimental procedure of Parr (2001). From left to right these panels illustrate (A) the orienting stimulus and the cross-shaped cursor; (B) the digitized video stimulus presentation showing an example from the DART category; and (C) the two comparison facial expressions, one of which conveys a similar emotional valence as that depicted in the video (e.g., positive or negative). In this example, the correct response is to move the cursor to contact the negative facial expression, scream face, on the right. The nonmatching example shows a play face on the left. From "Cognitive and Physiological Markers of Emotional Awareness in Chimpanzees (*Pan troglodytes*)," by L. A. Parr, 2001, *Animal Cognition*, 4, p. 226. Copyright 2001 by Springer-Verlag. Reprinted with permission.

gaze following reflex, by which an individual almost automatically shifts its attention in the same direction as others after seeing their gaze directions. This gaze-following reflex is considered to be an important precursor to more complex social abilities, such as perspective taking and theory of mind (Baron-Cohen, 1997). So far majority of the studies demonstrated that such automatic gaze-following reflex exists in nonhuman primates (Anderson & Mitchell, 1999; Emery, Lorincz, Perrett, Oram, & Baker, 1997; Ferrari, Kohler, Fogassi, & Gallese, 2000; Tomasello, Call, & Hare, 1998; but also see Tomonaga, 2007).

A remaining question is if nonhuman primates actually recognize and understand where the other individual looking at, connecting to perception taking through others' gaze. However, behavioral tests initially failed to find this evidence in nonhuman primates. Povinelli and Eddy (1996), for example, trained chimpanzees to request food from one of the two experimenters. In each condition, one experimenter could see the subject but the other could not (e.g., facing the other way, the face occluded by a bucket, eyes closed). The subjects selectively requested from the experimenter who could see the subject only in the most basic condition—one experimenter faced the subject whereas the other had her back turned. This indicates that chimpanzees do not have strong sensitivities of state of eyes. Kaminski, Call, and Tomasello (2004) further explored this issue in three ape species—chimpanzees, orangutans, and bonobos—by systematically controlling the experimenter's face and body orientation as well as the state of the eyes. The subjects were trained to poke through one of the holes of the Plexiglas panel to request the container located in front of the hole before the experiment. The occurrences of the requesting behaviors were modulated by of the experimenter's face and body orientation but not by the state of eyes, suggesting that apes have sensitivities to face and body orientation but not to the state of eyes. Similarly, other studies, using object-choice procedures have demonstrated the limited extent of nonhuman primates' sensitivity toward gaze direction. In this procedure, typically, subjects are presented with multiple containers, only one of which contains food. By following a social cue given by an experimenter (e.g., looking, orienting his/her head, pointing toward the container), subjects can obtain the food. Nonhuman primates tested in this paradigm, which is a cooperative situation, showed poor performance when cue consisted of eye-gaze only: chimpanzees (Call, Agnetta, & Tomasello, 2000; Call, Hare, & Tomasello, 1998), rhesus monkeys (Anderson, Montant, & Schmitt, 1996), and capuchin monkeys (Anderson, Sallaberry, & Barbier, 1995; Vick & Anderson, 2000).

In contrast, there are more consistent findings from studies that used a competitive paradigm. Flombaum and Santos (2005) demonstrated that rhesus monkeys selectively stole food items from an experimenter who was not able to see the food even when the only cue was provided by the experimenter's eyes. Additionally, Hare and colleagues (Hare, 2001; Hare, Addessi, Call, Tomasello, & Visalberghi, 2003; Hare, Call, Agnetta, & Tomasello, 2000) found that subordinate chimpanzees but not capuchin monkeys took a dominant individual's perspective into account and went preferentially for food that only they and not the dominant could see.

The seemingly inconsistent patterns of results from the two different types of paradigms have been discussed from a socioecological perspective. Hare (2001) proposed the competitive cognition hypothesis, which predicts that chimpanzees will demonstrate the greatest skill or motivation in competitive rather than cooperative tasks, because of their relatively competitive social structure (see also Tomasello, Call, & Hare, 2003). Hare and Tomasello (2004) conducted a series of four experiments in which chimpanzees were given two cognitive tasks, an object choice task and a discrimination task, in the context of either cooperation or competition. In both tasks chimpanzees performed more skillfully when competing than when cooperating, as predicted. More recently, Hattori and colleagues proposed other potential causes of inconsistent results in the two paradigms from a different perspective. First, in the cooperative task, the subject has to respond to attentional states of a cooperative trainer, who will reward the subject with food, which is an unusual situation in the subjects' daily life. Second, the tasks may require subjects not only to take into account an experimenter's attentional state but also to direct it toward the hidden food (double requirements in their cognitive load; Hattori, Kuroshima, & Fujita, 2010). To explore these ideas, Hattori et al. (2010) modified the cooperative paradigm to reduce the cognitive load for the double requirements. In their task, food is not hidden in a container but held directly by the experimenter. The capuchin monkeys in this study changed their behaviors appropriately on the basis of the experimenter's attentional variations, including eye gaze. Furthermore, Hattori, Tomonaga, and Fujita (2011) tested chimpanzees' on a similar task and found that chimpanzees would adjust their begging behaviors on the basis of the experimenter's attentional variations. In this study, they directly compared two requesting situations: an unnatural setup in which food was put on a table, which is similar to the most previous tasks, and a more natural situation in which chimpanzees requested food held by an experimenter. Importantly, chimpanzees did not change their begging behaviors in the former condition, supporting the authors' hypothesis. Future studies need to explore how the two factors proposed by Hare and Hattori might interact in gaze recognition in nonhuman primates.

HOW DO THEY PERCEIVE FACES?

Even though humans encounter hundreds and thousands of people in their lives, they rarely have trouble discriminating faces, especially those belonging to their own race (Bahrick, Bahrick, & Wittlinger, 1975). As a visual discrimination, this is actually very challenging because all faces share the basic features arranged in the same configuration such that eyes are located above a nose and mouth (the first-order relationships), which is important for discrimination faces from nonfaces, and because the range of morphological variations of each feature in a face is rather small. So what do we rely on to accomplish such a challenging task?

Configural Processing and the Face Inversion Effect

Humans focus on configurations of facial features, including subtle differences in the relative placement of the eyes, nose, and mouth (the second-order relationships; Diamond & Carey, 1986; Farah, Wilson, Drain, & Tanaka, 1998; Searcy & Bartlett, 1996). Over the years, evidence has accumulated supporting the assumption that configural information is explicitly represented as precise spatial relationship among facial features (Diamond & Carey, 1986; Freiwald, Tsao, & Livingstone, 2009; Leder & Bruce, 2000; Rakover & Teucher, 1997) or implicitly, as a combination of input from neurons selective for complex features (Perrett & Oram, 1993). However, the face discrimination is known to be disrupted when faces are displayed up-side down, a phenomenon known as the face inversion effect (FIE; Yin, 1969).

To explore the primate origins of our sophisticated face perception, many studies have addressed the question of whether such configural processing is shared with nonhumans. The FIE in particular has been widely tested. Most studies on humans' evolutionary closest relatives, chimpanzees (*Pan troglodytes*), have consistently demonstrated FIE, which is stronger for familiar than unfamiliar faces (Dahl, Rasch, Tomonaga, & Adachi, 2013b; Parr, Dove, & Hopkins, 1998; Parr & Heintz, 2006; Tomonaga, 1999, 2006).

However, behavioral findings from other primate species are rather inconsistent (Table 7.1). Some studies show superior perception of upright faces in monkeys (cotton-top tamarins [*Saguinus Oedipus*]; Neiworth, Hassett, & Sylvester, 2007), squirrel monkeys (Nakata & Osada, 2012; Phelps & Roberts, 1994), pigtail macaques (*Macaca nemestrina*; Overman & Doty, 1982), Japanese macaques (*Macaca fuscata*; Tomonaga, 1994), and rhesus monkeys (*Macaca mulatta*; Gothard, Brooks, & Peterson, 2009; Parr, Winslow, & Hopkins, 1999). However, in other studies no difference in accuracy between inverted and upright faces was found (cotton-top tamarins: Weiss, Kralik, & Hauser, 2001; long-tailed macaques: C. Bruce, 1982; Dittrich, 1990; rhesus monkeys: Gothard et al., 2004; Rosenfeld & Van Hoesen, 1979; Guinea baboons: Martin-Malivel & Fagot, 2001b).

The inconsistency in these findings may arise from various sources. For example, many studies used experimental paradigms that are not ideally

TABLE 7.1

Summary of the Findings on Face Perceptual Systems

	Ape	Old World monkey	New World monkey
Face inversion effect	Chimpanzee: Y	Japanese macaque: Y Pigtail macaque: Y Rhesus macaque: M Guinea baboons: N Long-tailed macaque: N	Squirrel monkey: Y Tufted capuchin monkey: Y Cotton-top tamarin: M
Laterality effect	Chimpanzee: M	Rhesus macaque: M	
Perceptual narrowing	Chimpanzee: Y	Japanese macaque: Y	

Note. Potential confounds and reasons for the negative or mixed results are discussed in text. Y = positive result(s); N = negative result(s); M = inconsistent result(s).

suited for testing FIE: Matching-to-sample tasks were designed so that a cue photograph was presented upright and match-distractor photograph pairs were presented in the inverted orientation (or vice-versa; Parr, Dove, & Hopkins, 1998; Parr et al., 1999; Tomonaga, 1999; Weldon, Taubert, Smith, & Parr, 2013). In a visual-paired-comparison task, two identical images of an upright face were followed by the same face in combination with a different face, both inverted (Gothard et al., 2009). With these paradigms, an effect automatically reflects the combination of a general view-dependency known from view-based object recognition (Logothetis, Pauls, Bülthoff, & Poggio, 1994) and FIE. It is nearly impossible to disentangle these two factors and separate the effect solely because of face-specific processing. In many studies there is no temporal separation between the cue and the match-distractor photograph pair (Overman & Doty, 1982; Parr et al., 2000; Weldon, Taubert, Smith, & Parr, 2013). In this paradigm, subjects could use a photograph-based matching strategy rather than configural processing mechanisms, or a combination of both. Stimulus material is not well-controlled in terms of low-level properties and irrelevant features, such as background (Gothard et al., 2004; Tomonaga, 1994) or external facial cues (Weiss et al., 2001; Weldon et al., 2013). With these stimuli, individuals are easily discriminated on the basis of external cues such as the hair-line given the high degree of variance among individuals (Weldon et al., 2013).

The question remains why similar paradigms revealed FIE in chimpanzees (Parr, Dove, & Hopkins, 1998) but not monkeys (Parr et al., 1999). The plausible answer is that monkeys took advantage of these paradigms and used a strategy that does not rely on the face-processing system (Martin-Malivel, Mangini, Fagot, & Biederman, 2006). The fact that chimpanzees showed FIE despite the deficient paradigm may indicate that configural processing mechanisms were more stable and dominant, able to at least partially overshadow other factors, compared to other tested species. However, this does not necessarily indicate that monkeys do not process faces in the same way as humans. More recently, accumulating evidence from scientifically valid assessments indicates that FIE exists in nonhuman primates and that FIE reflects configural processing of facial features (Adachi, Chou, & Hampton, 2009; Dahl, Logothetis, Bülthoff, & Wallraven, 2010; Dahl, Logothetis, & Hoffman, 2007; Dahl et al., 2013b; Dahl, Wallraven, Bülthoff, & Logothetis, 2009; Pokorny & de Waal, 2009; Pokorny, Webb, & de Waal, 2011).

For example, Adachi, Chou, and Hampton (2009) focused on the *Thatcher effect*, and tested whether rhesus monkeys experience this effect. To illustrate this effect, Figure 7.2 presents two inverted photographs of the same person. Although both photographs seem identical, turning them upright reveals a striking difference between them. This phenomenon is called the Thatcher effect

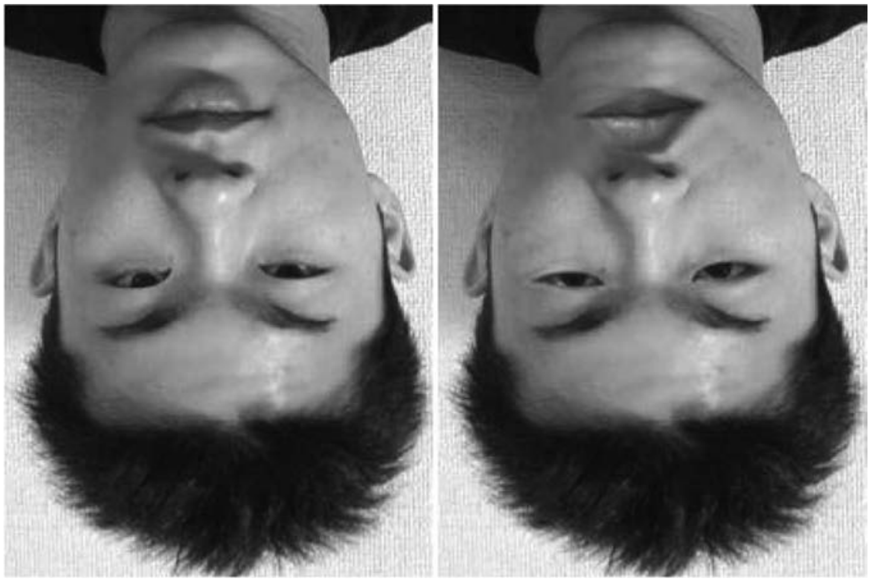

FIGURE 7.2. Example of the Thatcher effect. The face on the left is unaltered, whereas the face on the right has been "thatcherized" by inverting the mouth and eyes relative to the rest of the face. Thatcherization is most obvious when faces are viewed upright, as opposed to viewed inverted (as shown). From "Thatcher Effect in Monkeys Demonstrates Conservation of Face Perception Across Primates," by I. Adachi, D. P. Chou, and R. R. Hampton, 2009, *Current Biology, 19*, p. 1271. Copyright 2009 by Elsevier Inc. Reprinted with permission.

because it was first demonstrated with an image of the face of Margaret Thatcher (Thompson, 1980). The images differ in the relations among features: The orientation of the eyes and mouth is altered in the thatcherized face. The fact that we can more easily detect manipulation of the configuration of features in upright faces demonstrates our configural processing of faces in upright faces but not inverted faces. Adachi, Chou, and Hampton (2009) used a habituation–dishabituation paradigm to test the Thatcher effect in rhesus monkeys. In the habituation phase of each test, they repeatedly presented a conspecific's face either upright or inverted. The dishabituation phase followed, in which the original and the thatcherized face of the habituated face were presented in the same orientation used as in the habituation phase. In both orientations, monkeys showed habituation to the face in the habituation phase but showed recovery of looking time toward the thatcherized face only in the upright orientation in the dishabituation phase. Importantly, this habituation–dishabituation paradigm (a) does not train monkeys to discriminate faces, (b) presents faces in the same orientation between habituation phase and dishabituation phases, and (c) presents images sequentially so that there is no way for the subject to apply photograph-based matching techniques. This result, therefore, clearly demonstrated that monkeys are more highly sensitive to manipulation of configural relationships of face features in upright faces than in inverted faces. These recent findings with valid methodologies further support the existence of FIE in all species tested. Therefore, the lack of FIE in previous studies cannot be interpreted as evidence for differences in configural processing of faces in those species; instead, the negative findings are due to a mixture and interaction of uncontrolled factors and methodological limitations. Further studies are needed to revisit FIE in comparative cognitive approaches, using these better tasks.

Laterality Effect for Face Perception in Nonhuman Primates

In humans, the right hemisphere is known to dominate in discriminating faces (Berlucchi, Heron, Hyman, Rizzolatti, & Umiltà, 1971; Geffen, Bradshaw, & Wallace, 1971). Evidence includes faster (Broman, 1978) and more accurate (Ellis, 1975; Hilliard, 1973) identification of faces presented to the left than to the right visual field. Studies with lateral brain-damaged patients showed selective functional impairments in face processing (Bouvier & Engel, 2006; Levy, Trevarthen, & Sperry, 1972; Sergent & Signoret, 1992); neuroimaging studies showed stronger activation in the right than the left hemisphere (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Golarai et al., 2007; Grill-Spector, Knouf, & Kanwisher, 2004; Ishai, Ungerleider, & Haxby, 2000) or only activation in the right hemisphere (Campanella et al., 2001; D. Morris, Moaveni, & Lo, 2007; Rotshtein, Vuilleumier, Winston, Driver, & Dolan, 2007).

In nonhuman primates, the evidence for lateralization in face processing is rather mixed (see Volume 1, Chapter 27, this handbook). Early work using single-cell recordings revealed clear evidence for asymmetrically right-hemispheric representations of face-selective neurons in the superior temporal sulcus of the monkey brain (Perrett et al., 1988). However, fMRI in awake and anesthetized macaques showed lateralized response characteristics, but not predominantly in the right hemisphere (Ku, Tolias, Logothetis, & Goense, 2011). Although some studies suggest a human-like brain architecture (Tsao, Moeller, & Freiwald, 2008) by showing right-hemispheric face patches from visual area 4 to rostral temporal cortex (Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003), others show equivalently pronounced face patches in the two hemispheres (Bell et al., 2011; Popivanov, Jastorff, Vanduffel, & Vogels, 2012). A PET study in chimpanzees showed no right hemispheric lateralization when comparing face and object activations. However, a general patch of activation was found in the right ventral temporal sulcus (Parr, Hecht, Barks, Preuss, & Votaw, 2009), which resulted from comparisons of faces or objects against a resting period. This is suggestive, but not compelling enough to claim face-selective patches. Patches in the face-versus-resting condition can arise from feature dimensions similar to those of objects and not selectively from faces.

Several behavioral studies have also focused on this issue, but again the results are not consistent. Overman and Doty (1982) presented so-called chimeric faces (i.e., a face where one side is vertically flipped to the other side) to humans and macaques and found an advantage for processing for left-chimeric faces in humans, but not macaques. Striking behavioral evidence for brain asymmetries in monkeys comes from split-brain studies (Hamilton & Vermeire, 1988), albeit there are also unsuccessful attempts (Hamilton, 1977, 1983). FIE has been shown involving the right hemisphere (Vermeire & Hamilton, 1998), indicating that monkeys process faces configurally in the right hemisphere. Further, split-brain monkeys showed advantages in learning and remembering facial discriminations in the right hemisphere (Vermeire, Hamilton, & Erdmann, 1998).

In chimpanzees, chimeric faces of happy and neutral expressions were easier to discriminate when the happy half fell into the left visual field (R. Morris & Hopkins, 1993). Plotnik, Nelson, and de Waal (2003), however, failed to demonstrate left visual field advantage in chimpanzees with a matching-to-sample paradigm (no temporal delay between cue and match-distractor pair). In their study, chimpanzees were extensively trained on matching chimeric faces (including a chimeric face as cue) before the actual test condition, which included an original face followed by the left and right chimera. This training might lead to idiosyncratic response strategies to successfully differentiate between the two chimeric faces of one individual resulting in unbiased responses in the testing phase.

More recently Dahl, Rasch, Tomonaga, and Adachi (2013c) tackled this question using improved methods. They did not train their chimpanzees with chimeric faces before the test condition, and investigated discriminating of chimeric faces of chimpanzees and humans, that is, the combination of either left or right sides of a face vertically flipped and merged into a whole face (Figure 7.3). They found that the left-chimeric face was chosen more often than the right-chimeric face as being closer to the original face, reflecting an advantage for the right side of the brain in processing faces. Moreover, they

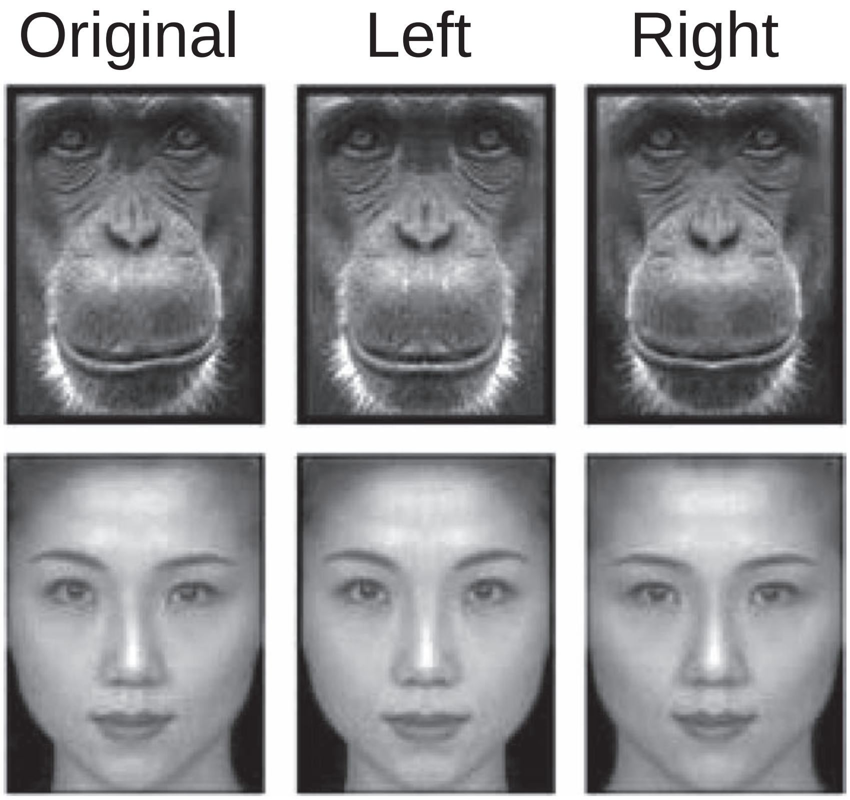

FIGURE 7.3. **Example stimuli of original and chimeric chimpanzee and human faces used in the study by Dahl et al. (2013b). In addition to the original picture, for each individual two chimeric faces (left-chimeric and right-chimeric faces) were generated. The two sides (left and right) for the chimeric faces were extracted by cutting the original face in the vertical dimension. The cutting line was placed through the tip of the nose and the mid-intereye distance.**

found a modulation by age of the subjects, suggesting that exposure history with a particular category shapes the right-hemispheric neural correlate to a configural/holistic processing strategy (Figure 7.4).

Taken together, findings support the view that nonhuman primates, similar to humans, process faces predominantly in the right hemisphere of the brain. However, in a broader perspective, it is still far from clear whether human and nonhuman primate brains show similarities in the distribution of face selectivity. The factors underlying the inconsistent results in previous studies remain largely elusive.

Development of Face Perception in Nonhuman Primates

In humans, newborns are already equipped with a system that allows them to pay attention to face-like patterns (Fantz, 1963; Turati, Simion, Milani, & Umiltà, 2002). Being helped by the mechanism of automatic attentional bias toward face-like

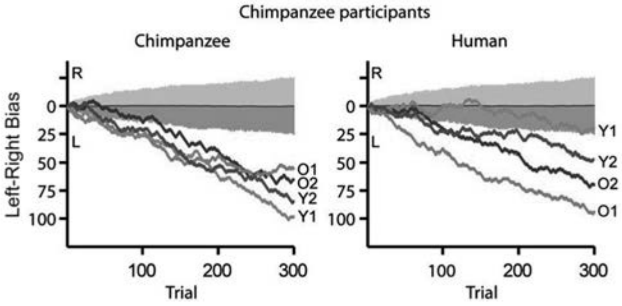

FIGURE 7.4. **Main results of Dahl et al. (2013b), showing a left-chimeric face bias for chimpanzee participants. Colored lines indicate the participants' responses plotted as a cumulative function of left–right decisions (*x*-axis) over time/trials (*y*-axis). The light red bar distribution around the zero line shows an iterative randomization procedure of left–right decisions indicating the significance level of 5%.**

configuration, infants start to get exposed to more faces in their environment, which they can start process more efficiently by tuning their perceptual system (Morton & Johnson, 1991). At around 4 months of age human infants start to process configural information of faces (the first order and second order relationships; Turati, Sangrigoli, Ruely, & Schonen, 2004). Infants at 6 to 9 months of age drastically tune their perceptual system to discriminate faces precisely (Pascalis et al., 2002). At 6 months, human infants can discriminate faces of different races and even different species as well as those from their own race. However, after 9 months of age, infants are less able to discriminate faces to which they are not frequently exposed (e.g., other races and other species). This quick tuning is called *perceptual narrowing*, which refers a rapid modification of our perceptual systems to better process stimuli that are frequently encountered during the early stage of development (Pascalis et al., 2005; see also Chapter 9, this volume).

To date, only a small number of studies have focused on the development of face perception in nonhuman primates. Myowa-Yamakoshi and colleagues (Myowa-Yamakoshi, Yamaguchi, Tomonaga, Tanaka, & Matsuzawa, 2005; Tomonaga et al., 2004) reported that chimpanzees recognize their mother's face within a month of birth, although the underlying mechanisms are not clear. Myowa-Yamakoshi and Tomonaga (2001) presented a male infant gibbon (*Hylobates agilis*) with simple drawings, and used a preferential tracking procedure from 15 to 22 days after birth. The infant showed clear preference for a schematic face, but this response depended on the whole configuration of the stimulus. A similar result was obtained in pigtail macaque infants (Lutz, Lockard, Gunderson, & Grant, 1998). Kuwahata, Adachi, Fujita, Tomonaga, and Matsuzawa (2004) explored one step further and reported developmental changes in infant macaque monkeys' face preference. Those authors reported that (a) infant monkeys preferred schematic faces to other stimuli, and (b) spatial configuration was the important factor during the first month, with feature details becoming important later. This suggests that their preference when tested was affected by the shape of the components and the overall configuration. As the developmental change and the contribution of both facial aspects are similar to those in human infants, it may suggest that primates share common cognitive processes in early schematic face recognition.

Sugita (2008) manipulated rearing conditions of Japanese monkeys, not possible for human infants, and provided not only evidence of similar development in the monkeys, but also important implications for mechanisms of human face perception. He showed that, even without exposure to faces, monkeys displayed a preference for human and monkey faces, but soon after they had been exposed to one face class the perceptual system selectively tuned toward that class resulting in difficulty in discriminating the nonexposed face class (Sugita, 2008). This finding demonstrates the existence of an early attentional bias toward face-like features even without any exposure to faces, and perceptual narrowing in monkeys. Further, Sugita's results indicate the existence of an experience-independent ability for face processing as well as an apparent sensitive period during which a broad but flexible face prototype develops into a concrete one for efficient processing of familiar faces.

By contrast, individuals with lifelong intense exposure to faces know more about faces than newborns know. Representations change qualitatively with experience (Diamond & Carey, 1986; Johnson & Mervis, 1997). It has been shown that extensive training is sufficient to develop the ability to discriminate an object class for which no innate representation was present. For example, dog experts classify dogs equally fast at subordinate and basic levels (Johnson & Mervis, 1997; Tanaka & Taylor, 1991). Conceptually, an ability process one class of faces more efficiently than another with only a little amount of experience (in the first years of life) provides evidence for an early component, although such an ability following extensive exposure over a lifetime provides evidence for a late component in the development of face processing. In naturalistic conditions, however, it is challenging to disentangle these two components because individuals are exposed to the same class of faces in early and late phases of their lives (e.g., conspecifics, own race). The other-species effect, in which a species shows better discrimination abilities for conspecific faces than for nonconspecific faces (Dahl et al., 2009; Martin-Malivel & Okada, 2007), leaves the relative contribution of early and late components unanswered; the effect might be due to an early tuning toward conspecific face morphology, extensive exposure to conspecific faces, or both.

To attempt to disentangle developmental components in face recognition, Dahl, Rasch, Tomonaga, and Adachi (2013a) investigated chimpanzees of varying ages with lifelong exposure to humans at differing levels of experience. First, they found an advantage in discriminating chimpanzee faces compared to human faces in young chimpanzees, reflecting a predominant contribution of an early component that drives the perceptual system toward the conspecific faces. Second, they found an advantage for human faces compared to chimpanzee faces in old chimpanzees, reflecting predominance of a later component that shaped the perceptual system toward the human faces.

CONCLUSION

Faces are one of the most salient and important stimulus classes for humans. We extract a rich amount of social information from faces especially of conspecifics, including individual identity, age, gender, emotional state, and attentional state. To explore the evolutionary origins of human face processing, a rapidly growing number of studies have explored face processing in nonhuman primates. In this chapter, we reviewed what other primates extract from faces, specifically focusing on individual identity, emotional state, and attentional state; how they perceive faces; and how perceptual mechanisms are tuned through development. Apes and macaques have been studied in the greatest detail and, in general, studies have revealed many shared features of face processing. Nonhuman primates show similar face-selective responses in their behavior and in their brain as humans do. This suggests that the basic features of our face perceptual mechanisms already existed in our common ancestors, dating back to more than 20 million years ago.

However, some studies have reported apparent species differences in face perception, especially between chimpanzees and rhesus monkeys, and have tried to explain species differences in terms of the structure of their societies. For example, Parr (2011) proposed that species living in fission-fusion societies require more cognitive abilities to represent individual identity, which could potentially explain why humans and chimpanzees are more similar in their face perception compared to macaques, which live in large social groups characterized by strict, linear dominance hierarchies. This hypothesis is attractive and provides a valuable framework for comparative approaches, especially in terms of which species need to be tested. However, it has also been argued that apparent species difference might be a result of methodological confounds (Adachi, Chou, & Hampton, 2009; Dahl et al., 2013b) as previously discussed. It is important therefore that future studies use appropriate methods (e.g., experimental design and stimulus control) to revisit the possibility of such species among primates.

Even though a growing number of studies explore face processing in nonhuman primates, the majority of these studies have tested apes and macaque monkeys; very few have explored the question in New World monkeys. A small number of behavioral studies suggest that some New World monkey species show similar aspects in their face processing, but neural specialization for faces has not been investigated at all. Future studies are needed to explore face processing in New World monkeys, to better map out potential similarities and differences across primate species.

Expanding the comparative approach on nonprimate species is also important. However, currently there are relatively few studies focusing on nonprimate species and they limited to only a few species. For example, Kendrick and colleagues (Tate, Fischer, Leigh, & Kendrick, 2006) have conducted a series of studies in sheep (*Ovis aries*) and reported that their face processing closely resembles that of humans and monkeys including brain lateralization. Dog (*Canis familiaris*) is another species relatively well studied in this field. For example, dogs have cross-modal representation of their owners (Adachi, Kuwahata, & Fujita, 2006), can recognize human expressions (Buttelmann & Tomasello, 2013), and follow their owner's head orientation and eye position to find a reward (Hare & Tomasello, 2005). Although those studies on sheep and dogs make a valuable contribution to the literature, they provide neither a comprehensive assessment of face processing nor taxonomic coverage to enable us to create a solid theoretical model for the evolution of face perception and processing. Future research on nonprimate species is needed to answer the many open questions regarding mammalian face processing and its evolutionary relationship to face processing in primates.

Last but not least, we need more empirical studies about what information nonhuman primates extract from faces. In this chapter, we have reviewed literature suggesting that primates extract individual identity, emotional states, and attentional states from their faces. In addition to the information reviewed in the chapter, some studies have explored other kinds of information such as gender recognition (Itakura, 1992; Koba & Izumi, 2006; Paukner, Huntsberry, & Suomi, 2010) and kin recognition (Parr & de Waal, 1999). In general, nonhuman primates appear to extract such information in a manner similar to humans. However, it is far from clear how and to what degree they extract such information. Further studies are needed to understand to what degree they recognize the category in question, as well as the underlying mechanisms.

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CHAPTER 8

COMPARATIVE VISUAL ILLUSIONS: EVOLUTIONARY, CROSS-CULTURAL, AND DEVELOPMENTAL PERSPECTIVES

Kazuo Fujita, Noriyuki Nakamura, Sota Watanabe, and Tomokazu Ushitani

Visual illusions are not only an enjoyable phenomenon but also an excellent material to know how the human perceptual system functions. They exemplify how it actually works, like an enlarging lens. This is why so many psychologists have been fascinated by this intriguing phenomenon and why visual artists have created various, impressively beautiful, illusory figures.

Although studies of visual illusions are pleasing in themselves, we believe that the studies can be more fruitful if they incorporate a comparative stance. Studying visual illusions from a comparative perspective has several advantages. The first is genetic understanding of visual illusions, in other words, to shed light how visual illusions come to appear. The timescale of such genetic processes include learning, development, and evolution.

The second is to know the adaptive significance of visual illusions. This may be done by comparing agents living in different niches or lifestyles to analyze the relationship of these factors with presence and/or strength of the illusions in question.

The third is that we are able to know in detail the effects of experience by controlling it in nonhuman agents, as exemplified by the classic study by Held and Hein (1963), which gave kittens experience of observing moving stripes. Although the visual experience was the same, the kitten that observed the motion not contingent on its own movement resulted in a permanent damage of its motion perception.

The fourth is that we are able to look for the neural substrate of the illusions in question in a detailed fashion by a method not applicable to humans. Although several noninvasive techniques such as fMRI and near-infrared spectroscopy have been created, some of the invasive methods, particularly newly devised ones such as optogenetics, are powerful ways to identify the responsible neural structures and their functions in detail.

These four points lead us to the last and the most important point, which is to establish a grand theory of visual illusions that accounts for not only phenomenological aspects of various illusions but also evolutionary and developmental histories, learning, and neural backgrounds of them. So many different parameters are supposed to contribute visual illusions, and comparative studies may answer otherwise unidentifiable questions, which ones are fundamental and which are subsidiary for the particular illusion.

In this chapter, we first discuss studies of visual illusions in nonhuman animals. Classical studies have shown that many nonhuman animals perceive various illusions just as humans perceive them. But in more recent systematic comparative studies, considerable across-species differences have been found in perceiving several illusory figures (see Table 8.1). Next, we discuss studies of visual illusions across cultures and developmental stages. Although this area has a long history, the obtained results have been too diverse to allow us to draw a firm conclusion. Finally, we summarize the knowledge accumulated so far.

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TABLE 8.1

Summary of Studies of Visual Illusions in Nonhuman Animals

	Illusory figure	Müller-Lyer	Müller-Lyer reversed	Müller-Lyer reversed	Ponzo	Ponzo (var. dot)	Ebbinghaus-Titchener circles	Zöllner	Jastrow	Horizontal-vertical (Surface size)	Horizontal-vertical (Line length)	Oppel-Kundt	Breadth of rectangles	Orbison	Corridor	Rotating Snake
		Figure 1e	**Figure 1i**	**Figure 1j**	**Figure 1k**	**Figure 3c**	**Figure 1g**	**Figure 1f**	**Figure 1a**	**Figure 1b (left)**	**Figure 1b (right)**	**Figure 1c**	**Figure 1d**	**Figure 1h**	**Figure 1l**	
Mammals	Chimpanzee				Fujita (1997) [+]	Fujita (1997) [+]									Imura, et al. (2008) [+]	
	Rhesus macaque	Tudusciuc & Nieder (2010) [+]	*Tudusciuc & Nieder (2010)* [−]		Fujita (1997) [+]	*Fujita (1997)* [−]		Agrillo et al. (2014) [+]		Dominguez (1954) [+]	Dominguez (1954) [+]		Dominguez (1954) [+]		Fujita (1996) [+] Bayne&Davis (1983) [+]	
	Stumpailed macaque												Harris (1968) [+]			
	Pigtail macaque															
	Guinea baboon						*Parron & Fagot (2007)* [−]								Barbet&Fagot (2002) [+]	
	Anubis baboon							Benhar & Samuel (1982) [+] ^{b}								
	Sooty mangabey									Dominguez (1954) [+]	Dominguez (1954) [+]		Dominguez (1954) [+]			
	White-throated capuchin monkey									Dominguez (1954) [+]	Dominguez (1954) [+]		Dominguez (1954) [+]			
	Tufted capuchin monkey	Suganuma et al. (2007) [+−]														
	Horse														Timney & Keil(1996) [+]	
	Bottlenosed dolphin						Murayama et al. (2012) [+]									
	Cat															Bååth et al. (2014) [+] ^{b}
	Guinea pig						Dücker (1966) [+]	Dücker (1966) [+]								

Birds	Pigeon	Malott, et al. (1967) [+−]	*Nakamura et al. (2006)* [−]	*Nakamura et al. (2009) [−]*	Fujita et al. (1991) [+]		**Nakamura et al. (2008)** [R]	**Watanabe et al. (2011)** [R]								
		Nakamura et al. (2006) [+]			Fujita et al. (1993) [+]											
	Ring dove	Warden & Baar (1929) [+]														
	Domestic chicken	Winslow (1933) [+]					**Nakamura et al. (2014)** [R]	Dücker (1966) [+]	Révész (1924) [+]	Révész (1924) [+]	Winslow (1933) [+]	Winslow (1933) [+]	Winslow (1933) [+]			
							Rosa Salva et al. (2013) [+] (chick) [a]	**Watanabe et al. (2013)** [R]								
	African grey parrot	Pepperberg et al. (2008) [+]														
	Budgerigar	Watanabe et al. (2014) [+]														
	Starling						Dücker (1966) [+]	Dücker (1966) [+]						Dücker (1966) [+]		
	Avadavat						Dücker (1966) [+]	Dücker (1966) [+]						Dücker (1966) [+]		
	Mistle thrush							Dücker (1966) [+]								
	Great bowerbird														Kelly & Endler (2012) [+]	
Fish	Crucian carp						Dücker (1966) [+]	Dücker (1966) [+]						Dücker (1966) [+]		
	Redtail splitfin						Sovrano et al. (2015) [+]									
	Guppy															Gori et al. (2014) [+] [b]
	Zebrafish															Gori et al. (2014) [+] [b]

Note. Studies listed in bold showed reversed illusion, whereas studies listed in italics showed no illusion. [+] = positive; [−] = negative; [R] = reversed positive

[a] Imprinting procedure. [b] Direction of illusion is unidentified.

COMPARISON ACROSS SPECIES

Visual illusions received much attention by comparative psychologists in the first half of the 20th century. In the sections that follow, we review important findings.

Early Studies

Many early studies focused on birds, probably because of their dependence on vision. One of the oldest was Révész (1924) on the Jastrow illusion (Figure 8.1a), for which a curved band placed inside another curved band looks larger than the other (like two bananas). After training domestic hens (*Gallus gallus*) to choose the smaller of two otherwise identical shapes, he tested them with a pair of curved bands of the same size placed in parallel. They tended to choose the one placed outside. This bias was the same as what humans make of this illusion.

The same paper reports a horizontal-vertical illusion of surface size (Figure 8.1b left), for which vertical figures look larger than horizontal ones. A hen successfully trained on the size discrimination tended to choose a horizontal rectangle rather than a vertical one of the same size. Dominguez (1954) cited Winslow's (1933) work with domestic chickens (*Gallus gallus*) who reported a horizontal-vertical illusion of line length (Figure 8.1b right), illusion of interrupted extent (Oppel-Kundt illusion; Figure 8.1c), breadth of rectangles illusion (Figure 8.1d), and Müller–Lyer illusion (Figure 8.1e).

Warden and Baar (1929) also reported perception of Müller–Lyer illusion in ring doves (*Turtur risorius*). The birds trained to choose the shorter of two horizontal lines tended to choose the lines with outward-pointing brackets over those with inward-pointing ones. Although this was consistent with human perception of the same figures, the demonstration seems unreliable because of low baseline

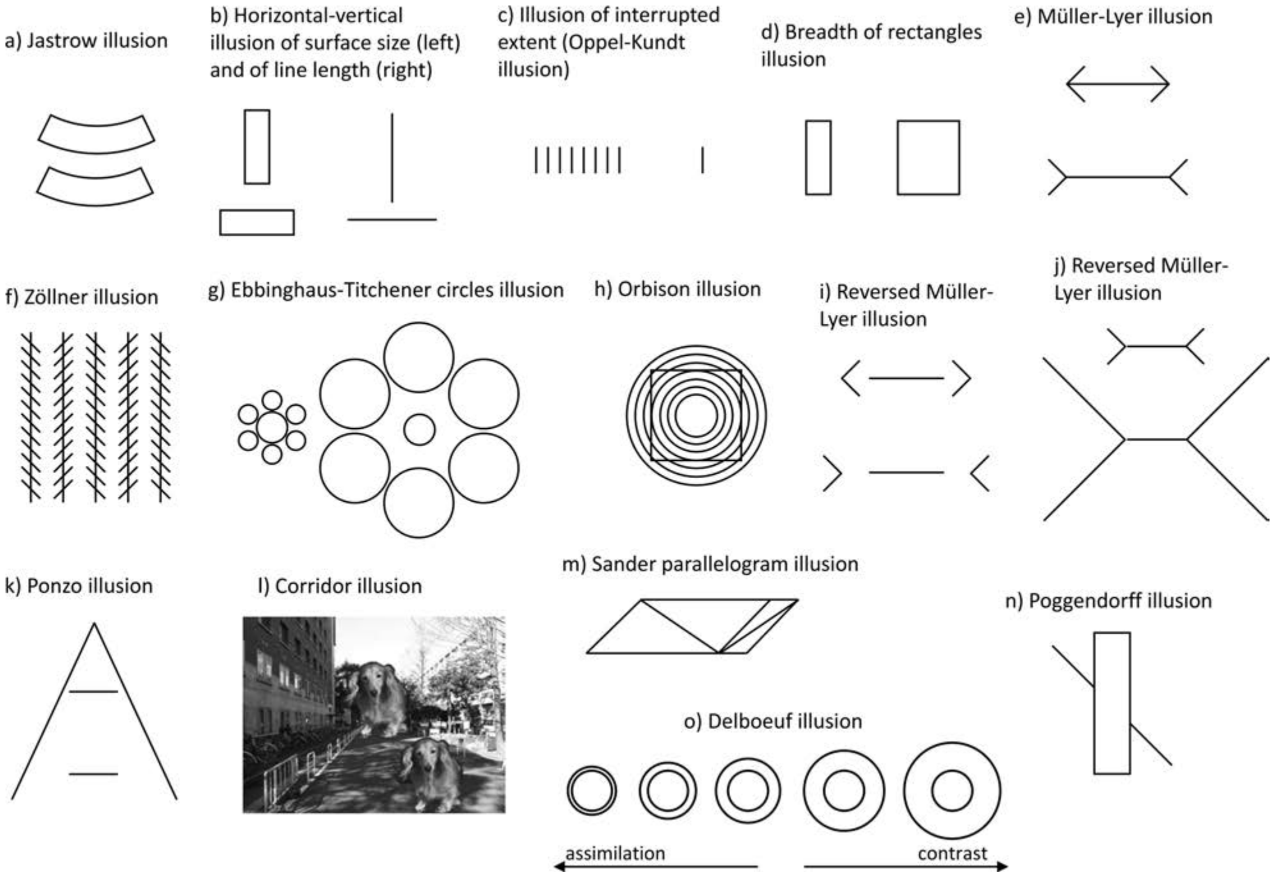
a) Jastrow illusion
b) Horizontal-vertical illusion of surface size (left) and of line length (right)
c) Illusion of interrupted extent (Oppel-Kundt illusion)
d) Breadth of rectangles illusion
e) Müller-Lyer illusion
f) Zöllner illusion
g) Ebbinghaus-Titchener circles illusion
h) Orbison illusion
i) Reversed Müller-Lyer illusion
j) Reversed Müller-Lyer illusion
k) Ponzo illusion
l) Corridor illusion
m) Sander parallelogram illusion
n) Poggendorff illusion
o) Delboeuf illusion

FIGURE 8.1. Various visual illusions.

accuracies, which was below 70% and 60% for the two birds tested.

Dücker (1966) tested several illusions in fish, birds, and mammals. He reported that crucian carp (*Carassius auratus gibclio*), a chick (*Gallus gallus*), avadavats (*Amandava amandava*), starlings (*Lamprotornis splendidus*), a mistle thrush (*Turdus viscivorus*), and Guinea pigs (*Cavia cobaya*) were susceptible to the Zöllner illusion (Figure 8.1f); crucian carp, avadavats, a starling, and a Guinea pigs to the Ebbinghaus–Titchener circles illusion (Figure 8.1g); and crucian carp, a starling and an avadavat to the Orbison illusions (a square placed on the concentric arcs looks curved; Figure 8.1h).

Dominguez (1954) demonstrated that three species of monkeys (rhesus macaques [*Macaca mulatta*], a sooty mangabey [*Cercocebus atys*], and a white-throated capuchin monkey [*Cebus capucinus*]) perceived the horizontal-vertical illusion of surface size (Figure 8.1b left), that of the length and the breadth of rectangles illusion (Figure 8.1d). The last one was also shown in stumptailed macaques (*Macaca arctoides*; Harris, 1968, cited in Davis, 1974).

As mentioned previously, these earlier demonstrations are intriguing but spotty at best and not sufficiently sophisticated to discuss factors contributing illusory perception in question and to draw out possible species differences.

More Recent Studies After the Birth of Animal Psychophysics

In the 1950s and 1960s, comparative psychologists established a new scientific area named *animal psychophysics* (Stebbins, 1970; see also Chapter 1, this volume). The fundamental technique was to train animals first to discriminate stimuli strictly on the basis of the stimulus dimension the experimenter intended to ask about and then to test the animals with systematically modified stimuli. For instance, Blough (1958) trained pigeons (*Columba livia*) to peck at one key if there was light on it and to peck at the other if there was no light. Thus the presence of light completely controlled the pigeons' pecking behavior. Then he placed the birds in total darkness and systematically modified luminance of the light on the key following a staircase method depending on the pigeons' "report." As a result, luminance of the light, which signifies the absolute threshold of light sensitivity, decreased as time passed, demonstrating dark adaptation in pigeons. Stebbins, Green, and Miller (1966) trained crab-eating macaques (*Macaca fascicularis*) and pigtailed macaques (*Macaca nemestrina*) to press a telegraph key in the presence of 1-kHz pure tone, which unpredictably started to play on monkeys' pressing another key. Thus the presence of the tone, not temporal or somatosensory stimuli, completely controlled the monkeys' responses to the report key. Then the intensity of the tone was gradually decreased to obtain the absolute threshold. This was done for 13 different frequencies to draw an auditory threshold curve.

We mention these examples because the importance of establishing a definitive stimulus dimension that controls animals' reporting behavior cannot be overstated in tests of visual illusions. Illusory figures are usually much more complex than a mere presence of a light or a tone. For example, in the Müller–Lyer illusion (Figure 8.1e) typical patterns have a pair of figures, each figure has one horizontal shaft and two brackets. Thus there are a total of six elements in the pattern. Three issues need to be carefully considered. First, researchers can ask human observers to focus on and judge two (the shafts) of the six elements verbally. However, they cannot do so with nonhuman participants. Here, a systematic training to force nonhuman participants to report the stimulus elements in question is of critical importance. Another important consideration is that the experimenter must ensure the animals are consistently reporting the elements in tests. The performance of animals can be easily disrupted by a mere presentation of novel stimuli in generalization tests. Thus, systematic approximation of the stimuli used in the training to those used in the test is also of extreme importance. A final consideration is that one must eliminate learning about the test stimuli. This is done by using either randomly reinforced probes, all-reinforced probes, or extinction probes in test trials.

Most recent demonstrations of illusory perception in nonhuman animals were careful in these points, but we find some unsatisfactory, as is discussed later in this chapter. Next, we review the main visual illusions that have been tested in more than one species of nonhuman animals.

The Müller–Lyer illusion. As preveiously noted, there are old demonstrations of the Müller–Lyer illusion in domestic chickens (Winslow, 1933) and ring doves (Warden & Baar, 1929). More recently, Malott, Malott, and Pokrzywinski (1967) tested this illusion in pigeons. Using a variable-interval schedule, they trained pigeons to peck at a specific length of a horizontal bar with two vertical short lines at both ends (like a flat H) presented on a key. In the test, the vertical short lines were replaced by inward- and outward-pointing brackets. In the generalization test under extinction, the peak of the birds' response rates shifted to longer lines for outward-pointing brackets (<—>), which was consistent with this illusion, but there was no such shift for inward-pointing ones (>—<). A strength of this study is the use of a successive, not simultaneous, discrimination task, in which a stricter stimulus control by the shaft may be established thanks to the simplicity of the display. But, as the authors discussed, pigeons might have responded on the basis of some other unidentified aspects of the stimuli, as suspected by the lack of a response shift for inward-pointing brackets. The demonstration was thus weak.

Nakamura, Fujita, Ushitani, and Miyata (2006) provided strong evidence for the Müller–Lyer illusion in pigeons. Using a successive discrimination task on the touch monitor, they trained pigeons to classify six different lengths of horizontal lines into long and short by differentially pecking at report keys located beneath the line. Then after being accustomed to the stimuli with brackets orienting the same direction at both ends (<—< and >—>, known as Judd figures), the pigeons were tested with the Müller–Lyer figures.

In test sessions, responses to report keys were nondifferentially reinforced. The pigeons showed a robust tendency to classify the target lines with inward-pointing brackets into long more often and those with outward-pointing brackets less often than the control Judd figures (Figure 8.2). Careful additional analyses rejected the use of covaried clues such as the entire length of the figures including brackets and the size of the gap between two brackets.

Watanabe, Nishimoto, Fujita, and Ishida (2014) showed that budgerigars (*Melopsittacus undulatus*) perceive this illusion too. They first trained birds to peck at the longer (or shorter) of two horizontal lines presented on the touch monitor. Next, one of the two lines, either top or bottom, was attached to brackets of the same orientation (the Judd figures). Finally the birds were tested with Müller–Lyer figures. The proportion of the choice showing the lines with brackets to be perceived longer was clearly higher for lines with inward-pointing brackets and lower for those with outward-pointing brackets.

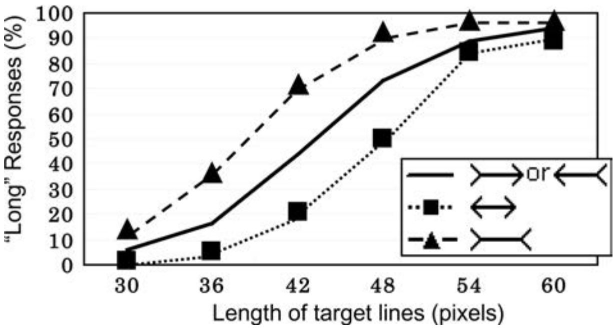

FIGURE 8.2. **Result of a Müller–Lyer test in pigeons. Reprinted from "Perception of the Standard and the Reversed Müller–Lyer Figures in Pigeons (*Columba livia*) and Humans (*Homo sapiens*)," by N. Nakamura, K. Fujita, T. Ushitani, and H. Miyata, 2006, *Journal of Comparative Psychology, 120*, p. 254. Copyright 2006 by the American Psychological Association.**

Pepperberg, Vicinay, and Cavanagh (2008) reported this illusion by an African grey parrot (*Psittacus erithacus*), Alex (see Volume 1, Chapter 31, this handbook). Alex verbally answered a question "which color is bigger/smaller?" in the presence of two adjacently placed Müller–Lyer figures having differently colored shafts. Alex's vocal answer was in general consistent with the illusion observed by humans. But the stimulus dimension that controlled Alex's responses was not completely clear. It is unfortunate that in no single condition the proportion of reports consistent with the illusion was significantly above chance because of small numbers of test trials and that such reports disappeared as the test was repeated.

Suganuma, Pessoa, Monge-Fuentes, Castro, and Tavares (2007) tested whether capuchin monkeys (*Cebus apella*) are susceptible to this illusion. They first trained monkeys to choose the longer line among the two. The training included lines with brackets but the difference in length was so large that was supposed to override any effect of the illusion. Then they were tested with the lines of the same length with brackets. The monkeys' choice was consistent with the typical Müller–Lyer illusion observed in humans. However, explicit reinforcement of the monkeys' choice of lines with inward-pointing brackets makes interpretation of the result difficult. A more serious problem is that these apparent biases may have simply resulted from the monkeys' report of overall lengths of stimuli. Thus their demonstration was not conclusive.

Tudusciuc and Nieder (2010) trained rhesus macaques (*Macaca mulatta*) in a sequential delayed matching-to-sample task of line length. The sample stimulus, either a line with or without brackets, was presented for a short duration on monkeys' grabbing a lever. The comparison stimulus presented after a delay was always an ordinary line. The correct response was to release the lever if the comparison matched the sample in length and to maintain the lever if it did not. One of the two monkeys showed a bias consistent with the illusion for inward- and outward-pointing brackets. This result was convincing. But the other monkey's bias for the outward-pointing brackets was unclear. This monkey might have reported the overall length of the stimuli.

In sum, the Müller–Lyer illusion has been clearly demonstrated in pigeons, budgerigars, and one rhesus macaque. Demonstration in other birds and monkeys remains inconclusive. This illusion is in fact difficult to test in nonhuman animals because it is too easy for them to base their responses on the overall size of stimuli. Careful control stimuli are needed.

Some variants of this illusion may be noted here. The first was discovered by Yanagisawa (1939). If one bracket is detached from the target shaft, humans judge the shaft with the outward-pointing bracket to be longer than the shaft with the inward-pointing bracket, though the effect is much weaker than the standard figures (Figure 8.1i). Nakamura et al. (2006) tested this reversed illusion in pigeons. But there was no effect of brackets in this species. Tudusciuc and Nieder (2010) also included these stimuli in their test in rhesus macaques, but no clear effect was obtained. Such species differences between humans and nonhuman animals may be due to sensitivity of the experimental procedure. But by using exactly the same procedure as pigeons, human subjects clearly perceived this reversed illusion in Nakamura et al. (2006).

Another reversed illusion has been demonstrated by Obonai (1954); the perceived length of the shaft starts to shrink as the inward-pointing brackets are extended (Figure 8.1j). Nakamura, Watanabe, and Fujita (2009) tested pigeons with variously extended brackets. Underestimation of the shaft length started for brackets of horizontal length about half of the shaft length in humans, but it never occurred in pigeons.

Whereas the standard Müller–Lyer illusion may be accounted for by assimilation of the shaft length into the inducing brackets, the two reversed illusions in humans are explained by the contrast of the shaft against the overall frame of the entire stimuli. Thus Nakamura et al. (2009) speculated that pigeons are susceptible to assimilation effect but not to contrast effect of the stimuli. Assimilation is a perceptual function to perceive a figure to be similar to adjacent ones, whereas contrast is to perceive it to be more different to others. For instance, two concentric circles of similar sizes look more similar in size to each other, whereas those of much different sizes look more different in size from each other (the Delboeuf illusion, Figure 8.1o; see T. Goto et al., 2007, for details of these effects).

The Ponzo illusion. The Ponzo illusion (Figure 8.1k) may be easier to test than the Müller–Lyer illusion in nonhuman animals because the target bars are separated from the inducing lines in typical figures. Fujita and colleagues (Fujita, 1996, 1997; Fujita, Blough, & Blough, 1991, 1993) tested pigeons and nonhuman primates with various versions of this illusion.

Their general procedure was like Nakamura et al. (2006). Unlike typical Ponzo figures, only one bar was presented at a time. Animals were trained to classify horizontal bars of six different lengths into long and short by differentially responding on the keys at the bottom of the touch-sensitive monitor. Once they acquired the discrimination, context lines were superimposed. In one presentation, the context lines were an inverted V. After the subjects showed consistent classification of bar lengths on this baseline figure with the context lines at a fixed middle location (middle context), they were tested with figures having the target bar either nearer to (low context) or farther from (high context) the apex of the inverted V (see Figure 8.3a). No differential reinforcement was used in the test trials. As a result, pigeons (Fujita, Blough, & Blough, 1993), rhesus macaques and a chimpanzee (*Pan troglodytes*; Fujita, 1997) showed a bias toward long when the target bar came closer to the apex and short when it was farther from it (Figure 8.3d). Thus, all of the three species tested perceived the typical Ponzo illusion.

Because the Ponzo illusion provides impression of depth, some researchers have suggested misapplied size constancy as a cause of this illusion (e.g., Gregory, 1963). To test this idea in nonhuman subjects, Fujita (1997) and Fujita, Blough, and Blough (1991) added to the existing context lines three additional lines converging at a point on each outer side (Figure 8.3b). However, these additional lines did not enhance the illusion compared with the single inverted V, something that was true for humans too. Thus, the Ponzo, which has been demonstrated in various species, is likely to depend on the innermost lines, not the strength of an impression of perspective.

When the inverted V context lines were replaced with a pair of short vertical lines, with the size of the gap between the target bar and the context unchanged (the Dot context condition, see Figure 8.3c), there was a considerable difference in the magnitude of the illusion in the three primate species (Fujita, 1997). Humans perceived a significantly larger illusion, about double, than in the standard one (Figure 8.3a). The magnitude of the illusion was comparable between the two types of context in chimpanzees, but surprisingly, rhesus macaques perceived no illusion at all in the Dot context condition.

Another species difference was discovered when the photos having natural perspective impression (a photo of highway) replaced the lines (Fujita, 1996), which is known as the corridor illusion

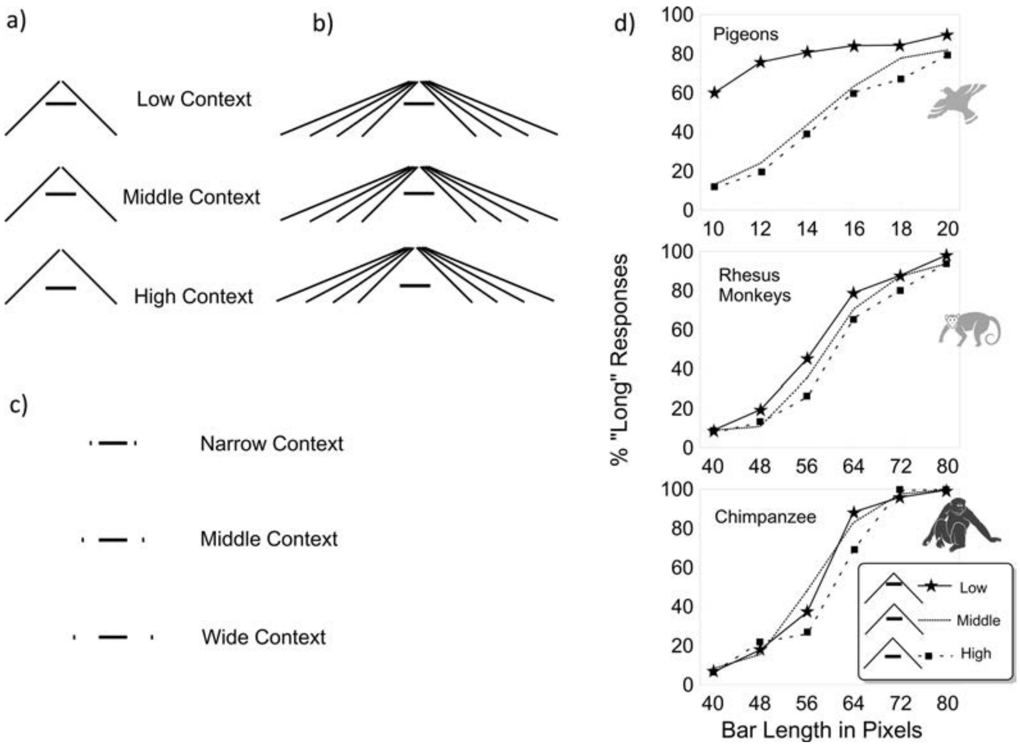

FIGURE 8.3. Figures and results of the studies on the Ponzo illusion by Fujita (1997) and Fujita et al. (1991, 1993): (a) inverted-V context; (b) perspective context; (c) dot context; and (d) results of three species.

(e.g., Figure 8.1l). Humans showed a strong illusion when a target bar was embedded in different vertical locations on the upright photo, demonstrating a typical corridor illusion, but there was no illusion when the photo was top-bottom inverted. This effect remained unchanged if the inverted V context was superimposed on the photos. That is, in humans, the effect of photographic depth impression overshadowed any effects of geometric frames. However, when the same test was administered to rhesus macaques, they perceived the illusion whenever the inverted V was superimposed, irrespective of the orientation of the photo. There was effect of photographic perspective when the photo was used without the context lines; therefore, the perspective impression has the effect to give rise to Ponzo-like illusion in rhesus macaques but the effect was so weak that it was overshadowed by the effect of the context lines superimposed.

Such effect of naturally-given perspective impression was also shown in horses (*Equus caballus*; Timney & Keil, 1996). A similar effect provided by perspective line drawings (a corridor illusion) has been obtained in Guinea baboons (*Papio papio*; Barbet & Fagot, 2002) and chimpanzees (Imura, Tomonaga, & Yagi, 2008). Imura and Tomonaga (2009) expanded their work to show that moving cast shadows, which led to a change in the impression of depth by implying vertical location of the object, affected the corridor illusion in a chimpanzee (see Chapter 9, this volume). Bayne and Davis (1983) also showed that rhesus macaques perceived the rectangle placed on a perspective line drawing as the trapezoid with the farther side longer. It is thus suspected that many species have sensitivity to pictorial depth, which leads to visual illusion explained by the misapplied size constancy, but the strength of this effect greatly varies across species.

The Ebbinghaus–Titchener circles illusion. To test their hypothesis that pigeons may be susceptible to assimilation effect but not to contrast effect, Nakamura, Watanabe, and Fujita (2008) studied the Ebbinghaus–Titchener circles illusion in pigeons. This illusion occurs as a result of contrast of the central circle against surrounding disks. They first trained the birds to classify the size of the isolated disk into large and small. Then six inducer disks were faded in around the target disk. The size of the inducer disks was fixed. After achieving reliable classification performances, the pigeons were tested with larger and smaller inducer disks in nondifferentially reinforced probe test trials. In the test trials, the pigeons' classification was shifted from that on the baseline trials. However, the shift was in the other direction from that by humans. That is, the pigeons tended to classify the target disk smaller if it was surrounded by inducers smaller than baseline and larger if surrounded by larger inducers.

Might the pigeons have responded to the inducers, not the targets? This is impossible because the inducers were constant in size in the training. Otherwise, might they have responded on any mixture of the size of the target and inducer disks? However, these factors could not account for the results actually obtained. Further, the birds' classification was intact for isolated disks. Thus it is highly unlikely that they used the size of the inducers for their classification performance. This suggests that pigeons perceive a reversed Ebbinghaus–Titchener circles illusion, probably as a result of assimilation to, not contrast with, the inducers. Thus the hypothesis by Nakamura et al. (2008) was supported. Using the same procedure, Nakamura, Watanabe, and Fujita (2014) demonstrated that bantams (*Gallus gallus*) also perceive the reversed Ebbinghaus–Titchener circles illusion.

Why do they perceive it as such? A hint may come from Morinaga (1956) and Weintraub (1979), which showed that the direction of this illusion is reversed (i.e., the target disk looks larger than it is) if we erase the distal portions of the large inducers (Figure 8.4). This suggests that the contrast effect occurs only if global information is processed. Pigeons are noted for their local-oriented vision (see Chapter 5, this volume); for instance they show local- not global-precedence effect in hierarchically organized stimuli (Cavoto & Cook, 2001; cf. Navon, 1977). They also show a pattern inferiority, not superiority, effect (Donis & Heinemann, 1993; Kelly & Cook, 2003), for which humans and chimpanzees enhance discrimination of the same figures with common additional figures that make up emergent configurations (K. Goto, Imura, &

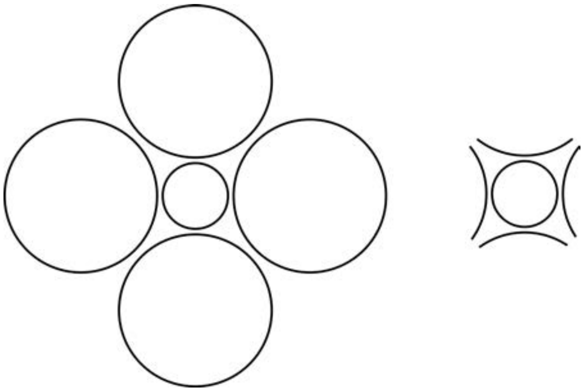

FIGURE 8.4. **A reversed Ebbinghaus–Titchener illusion.**

Tomonaga, 2012). They do not amodally complete partly occluded figures in situations humans and nonhuman primates easily do (Fujita, 2001; Fujita & Giersch, 2005; Fujita, Nakamura, Sakai, Watanabe, & Ushitani, 2012; Fujita & Ushitani, 2005; see also Chapter 9, this volume). Likewise, bantams also fail to amodally complete (Nakamura, Watanabe, Betsuyaku, & Fujita, 2010, 2011).

In support of this view, Guinea baboons have been shown not to be deceived by the Ebbinghaus–Titchener figures (Parron & Fagot, 2007); they perceive no explicit illusion on these figures. They, too, show a local-precedence effect (Fagot & Deruelle, 1997).

It is interesting that fish (Redtail splitfins [*Xenotoca eiseni*]; Sovrano, Albertazzi, & Rosa Salva, 2015) and a bottlenosed dolphin (*Tursiops truncatus*; Murayama, Usui, Takeda, Kato, & Maejima, 2012) have been shown to perceive the same illusion as humans for the Ebbinghaus–Titchener figures. Also, domestic chicks were reported to perceive this illusion as humans do, under imprinting procedures (Rosa Salva, Rugani, Cavazzana, Regolin, & Vallortigara, 2013). As previously noted, Dücker (1966) reported that crucian carp, avadavats, a starling, and a Guinea pigs perceived the Ebbinghaus–Titchener circles illusion. It is also noteworthy that young children are reported to be less likely to perceive this illusion than adults (Doherty, Campbell, Tsuji, & Phillips, 2010, but see also Yamazaki, Otsuka, Kanazawa, & Yamaguchi, 2010).

These divergent results across, and sometimes even within, species may suggest that observers are susceptible to contrast effect only if they attend to the entire stimulus displays including distant inducers. Whether an individual attends to a global or local aspect can be changed in different contexts and training history, though some species like pigeons may be more likely to be locally oriented in most situations because of their inherited characteristics.

The Zöllner illusion. Behar and Samuel (1982) tested the perception of the Zöllner illusion (Figure 8.1f) in two anubis baboons (*Papio anubis*). The baboons were given three cards. Each card had either four parallel lines or four alternatingly converging lines on it, like a letter W with top and bottom portions cut out. The task was to choose the one that had an odd orientation (i.e., oddity discrimination of orientation). In the critical test trials with two cards of parallel lines and one of alternatingly converging lines, crosshatches were superimposed on one of the parallel line stimulus so that the lines were perceived as nonparallel to human eyes. The baboons chose intact parallel lines, thus suggesting that they perceived the parallel lines with crosshatches to be nonparallel.

However, this does not necessarily mean that the baboons perceived the illusion of the same orientation as humans; the perceived false convergence may be in the other orientations. This question was investigated in three studies; Watanabe, Nakamura, and Fujita (2011) in pigeons, Watanabe, Nakamura, and Fujita (2013) in bantams, and Agrillo, Parrish, and Beran (2014) in rhesus macaques.

Watanabe et al. (2011) trained their birds to peck at a narrower (or wider) gap of two converging lines. Then, after the birds were accustomed to various crosshatches on the lines with various angles faded in (see Figure 8.5a), they received critical test trials for which parallel lines appeared with crosshatches superimposed that created a downward-converging (Figure 8.5b) or upward-converging impression (Figure 8.5c) in humans. Responses on the test trials were nondifferentially reinforced. Humans tested in exactly the same procedure with larger stimuli tended to respond as downward-converging for the former and upward-converging for the latter, as expected. However, the birds responded in a completely reversed way; they

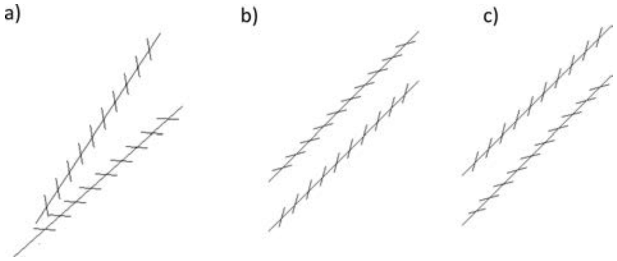

FIGURE 8.5. Figures used in the Zöllner studies of Watanabe et al. (2011, 2013).

responded as upward-converging for the stimulus shown in Figure 8.5b and downward-converging for that in Figure 8.5c. Watanabe et al. (2013) obtained the same results in bantams. Thus these two avian species commonly perceive a reversed Zöllner illusion. In contrast, rhesus macaques tested in a similar procedure of gap size discrimination in Agrillo et al. (2014) showed that this species see the illusion of the same orientation as humans.

The reason of difference between birds and primates is yet to be identified. But Watanabe et al. (2011) expanded their hypothesis of assimilation dominance in pigeons (Nakamura et al., 2008) to this orientation illusion. That is, they proposed that pigeons may perceive acute angles to contract (i.e., to be more acute), as a result of assimilation of orientations of two lines. This is based on a theory of Zöllner illusion raising the expansion of acute angles between crosshatches and target lines as the most important factor in humans (e.g., Kitaoka & Ishihara, 2000; Oyama, 1975). This expansion may be viewed as resulting from a contrast of orientations of two lines at the crossing. Therefore if pigeons perceive contraction rather than expansion of acute angles, this may lead to a reversed perception of orientation of the target lines. This might reflect a significant difference in the brain structure and resulting visual processing pathways (Butler & Hodos, 2005; Shimizu, 2009). Before further discussion, however, tests with other avian and mammalian taxa are needed to assess whether this taxonomic difference is global.

Other recent studies of interest. Several recent studies have focused on perception of illusory motion and use of naturally occurring perspective illusion in wild birds. Bååth, Seno, and Kitaoka (2014) tested domestic cats' (*Felis catus*) responses toward the snake illusion. A snake illusion is an extremely powerful one, in which humans perceive a strong impression of rotation of stationary circular "snakes" (Kitaoka, 2003). The authors showed that cats tried to "catch" the snake repeatedly on the presented figure. Gori, Agrillo, Dadda, and Bisazza (2014) trained two species of fish, guppies (*Poecilia reticulata*) and zebrafish (*Danio rerio*), to choose a rotating geometric figure over an identical stationary figure. When they were given a choice between the snake illusion figure and the corresponding control figure, which gave no impression of motion to humans, both species significantly chose the illusory rotating figure. Kanazawa, Kitaoka, and Yamaguchi (2013) showed that 6- to 8-month-old human infants also perceive this motion illusion by a preferential looking method.

Currently, it is unclear what causes this illusion. One explanation is the difference in the reaction time of neural responses induced by the contrast between areas of different color or brightness (e.g., Kitaoka, 2006). Another explanation is that transient oculomotor events including microsaccades, saccades, and blinks of the eyes may be the cause (Otero-Millan, Macknik, & Martinez-Conde, 2012). It may be useful to test various nonhuman animals that show different types of eye movements to identify what factors actually contribute to this powerful illusion.

Kelley and Endler (2012) presented an interesting case in which great bowerbirds (*Ptilonorhynchus nuchalis*) may make use of a perspective illusion to enhance reproductive success. Males of this species make bowers to attract potential mates (see Volume 1, Chapter 37, this handbook and Chapter 6, this volume). The bowers are typically an accumulation of twigs forming two sidewalls and a narrow avenue of about 60 cm between them (see Figure 8.6). Males place many stones and shells on the courts located at each end of the avenue, where they display holding a colorful object while females watch them from inside the avenue. Kelley and Endler found that stones were placed so that their size increased proportional to the distance from the bower. In fact, the gradient of the size slope positively correlated with the mating success of the males. When the researchers randomized the arrangement, males eagerly rearranged the stones

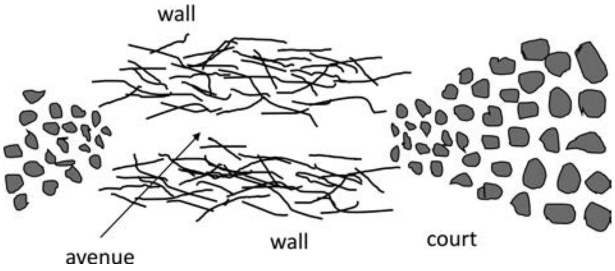

FIGURE 8.6. **A drawing of the courting bower constructed by great bowerbirds.**

so that they restored the original gradient. Kelley and Endler argued that with this arrangement the stones look more homogeneous in size. When the female watch the moving object during the male display, the apparent size of the object may change rapidly as a consequence of Ebbinghaus-like illusion. This rapid change may make the object more attractive to the female. It is unlikely that the males are aware of this effect, but natural selection should have favored the use of such illusory effect to attract potential mates.

COMPARISON ACROSS CULTURES AND AGES

Are visual illusions determined by inherited characteristics of the visual system or are they learned? The studies in various species reviewed previously may be viewed as showing the former determination. However, individuals of one species may differ in the strength of susceptibility to particular illusions. In the case of humans, studies of people from different cultures and of different ages, have suggested considerable variation within our species.

Cultural Differences

A classic study by Segall, Campbell, and Herskovits (1963) compared Müller–Lyer, Sander-parallelogram (Figure 8.1m), and two types of horizontal-vertical illusions across 15 societies. They found considerable differences in the magnitude of the illusions among societies. In general, people of European origin were more susceptible to the former two illusions whereas the tendency was reversed for the latter two. The variability for Müller–Lyer illusions was notably large; the magnitude of illusion was 20.3 % for people living in Evanston, Illinois, whereas it was 1.4% for South African, nonEuropean mine workers, and 1.7% for a group of African hunter-gatherers.

Susceptibility to the Ponzo illusion has also been shown to significantly vary across cultures (e.g., Brislin, 1974; Brislin & Keating, 1976; Leibowitz, Brislin, Perlmutrer, & Hennessy, 1969). For instance, Leibowitz et al. (1969) used a perspective photo such as a railroad as a context, as well as typical Ponzo figures. They found no difference in the magnitude of illusion for the typical Ponzo figures. In contrast, Pennsylvania students perceived an enhanced illusion with the additional photographic perspective but Guamanian students did not.

One account of such differences across human cultures is the "carpentered world" hypothesis (Segall, Campbell, & Herskovits, 1968). People in urban areas experience more straight and rectangular crossing structures than in rural environments. If we look at the corner of the apartment from outside, we see a vertical line with two outward-pointing brackets and the lines is closer than the brackets. On the other hand, if we look at the corner from inside the room, we see a vertical line with two inward-pointing brackets and the line is farther than the brackets. These two patterns apparently correspond to Müller–Lyer figures. The shaft is perceived closer than the brackets in the former, and farther in the latter. These tacitly perceived distances call the misapplied constancy scaling Gregory (1963) proposed, resulting in the under- and overestimation of the shaft in the former and the latter, respectively. Similarly, as the view of the terrain is markedly different between urban and rural areas, limited experience of clear cues for distance, like railroads, makes the illusion susceptibility of rural people much weaker than that of urban people.

Another account is based on the potential difference in the ability to extract perspective information from two-dimensional (2D) information between industrialized and nonindustrialized societies. People in the former learn how to retrieve three-dimensional information from 2D drawings through their daily contact and systematized education at school. This idea originates in the work by Hudson (1960) showing that African Bantu people recognize the pictures drawn with a perspective method differently from Westerners. In one example, a human hunter holds a spear toward an antelope, but between the spear and the animal there is small elephant drawn on a distant hill, which would be close to the spear if perspective were to be ignored. Hudson asked people which animal, the elephant or the antelope, was the hunter aiming at. Bantu people tended to answer elephant rather than the antelope. Thus the difficulty to recognize depth from 2D drawings may account for less susceptibility to illusions such as the Ponzo and the Müller–Lyer, for which perspective can contribute (see also Deregowski, 1989, for review).

However, most of these cross-cultural studies are outdated and the misapplied constancy scaling hypothesis has received little support. For instance, if two vertical lines replace horizontal lines in the inverted V context of the typical Ponzo illusion, very little illusion is perceived (Humphrey & Morgan, 1965). A texture gradient analogue of the converging context produces much weaker illusion than the Ponzo (Fineman & Carlson, 1973). A Ponzo figure drawn in the background suggesting no depth (like a vaulting horse) still produces the same amount of illusion as the regular ones (Newman & Newman, 1974). Further, as described earlier, enhancing perspective impression by increasing the number of converging lines had no facilitating effect even in humans (Fujita, 1997; Fujita et al., 1991), though photographic perspective had effects in humans and rhesus macaques (Fujita, 1996).

Although a difference in the perspective processing among cultures is unlikely to be a major factor leading to a difference in the susceptibility to visual illusions, more recent studies identified an interesting difference in recognizing pictures between Eastern and Western cultures. For instance, Masuda and Nisbett (2001) compared how Japanese and American people perceived a video clip showing an underwater scene, in which fish swam among various background objects. When they were asked to report what they saw in the video, Americans noted predominantly features of the fish, whereas Japanese focused more on the background items such as plants and rocks. Kitayama, Duffy, Kawamura, and Larsen (2003) showed such difference in attended objects in the scene may change simple judgment of the line length embedded in the square frame. In their study, participants were asked either to draw a line of the same absolute length or to draw a line of the same ratio to the frame, in the frame different in size from the sample figure. The authors found that whereas Americans more accurately completed the absolute task, Japanese people did so in the ratio task. These results show that Japanese attend more to the surroundings in such simple figures. Miyamoto, Nisbett, and Masuda (2006) suggested that such difference in the nature of attention may be constructed by culturally characteristic environments, such that Japanese scenes photographed in cities of various sizes were more ambiguous and had more elements than American scenes, which may naturally encourages attending more to contextual information. Such difference in perceptual attitudes may lead to a difference in perception for some illusory figures, which is an interesting question for future research.

de Fockert, Davidoff, Fagot, Parron, and Goldstein (2007) reported an interesting difference between UK English speakers and Himba people from northern Namibia. The authors presented two types of Ebbinghaus–Titchener circles illusion. The target was a circle for both patterns. The inducing figures were also circles for one type and diamonds for the other. For both groups of people, the magnitude of the illusion was smaller for the figures with diamond inducers. However, Himba people were more accurate in reporting the larger target circles (i.e., weaker illusion) than English speakers. Reduced susceptibility to this illusion has been shown in patients with autism spectrum disorder (Dakin & Frith, 2005), young children (Káldy & Kovács, 2003), and males compared with females (Phillips, Chapman, & Berry, 2004). Thus the authors suspect that more locally oriented tendency may cause weaker illusion on this figure.

In fact, such account of visual illusions by the strength of context dependence receives support by a more recent work. Doherty, Tsuji, and Phillips (2008) compared susceptibility to a version of Ebbinghaus–Titchener circles figure among four groups of university students and staffs: Japanese male mathematical scientists, Japanese female social scientists, UK male mathematical scientists, and UK female social scientists. Doherty et al. found that Japanese experience a stronger illusion than UK people. They also found female social scientists are more susceptible to the illusion than male mathematical scientists, though the contribution of gender and that of major field cannot be separated. Further systematic comparison is needed.

Developmental Changes

Development of susceptibility to visual illusions in human children has a long history of research but has not reached a firm conclusion. The earliest study is found in Binet (1895, cited in Kato, 2005), who found that 9-year-old children perceive a stronger Müller–Lyer illusion than 12-year-olds. In the middle of the 20th century, Piaget tested various visual illusions in children. He distinguished primary and secondary illusions (e.g., Piaget & Inhelder, 1969/2000), with the former occurring in an automatic manner and the latter requiring active perceptual activities. Hirai (1972) summarized studies on age-related changes in geometric illusions. According to him, susceptibility to the Müller–Lyer, Poggendorff (Figure 8.1n), and Delboeuf illusions generally decreases with age for children older than 4 years. The magnitudes of the Ponzo, Horizontal-Vertical, and Oppel-Kundt illusions come to a maximum at the ages around 10 years and decrease in adulthood. Piaget (1961, cited in Kato, 2005) reports that the Sander illusion (Figure 8.1m) also peaks at about this age. These inconsistent developmental findings do not seem to be captured by Piaget's distinction about the two types of illusions. In the late 20th century, there have been very few studies on this topic and a coherent explanation has yet to be proposed.

The illusion that has received most of the recent research attention is the Ebbinghaus–Titchener circles illusion (Figure 8.1g). Weintraub (1979) compared susceptibility to this illusion in children of 6, 8, 10, and 12 years of age and adults. He found the magnitude of illusion to increase with age. He interpreted the trend as showing a mixture of two processes: the contour mechanism and the context mechanism. The former is close to the assimilation effect, a kind of misjudgments of two closely presented contours, which works in all ages. The latter is more like the contrast effect coming from distinct surrounding circles, which is stronger in older ages. Káldy and Kovács (2003) also reported that perception of this illusion was weaker in 4-year-old children than adults. They related this difference to their finding that contour integration develops slowly by 14 years of age (Kovács, Kozma, Fehér, & Benedek, 1999).

However, Hanisch, Konczak, and Dohle (2001) found no developmental difference between children of 5 years old through 12 years old and adults, when they simply judge the size of the central disk with surrounding disks arranged to construct an Ebbinghaus–Titchener pattern. However, when they were asked to judge the size and then to grasp the disk, the illusory effect was larger in young children as observed by the size of the gap between thumb and the index finger. This might have been a safety response and when Duemmler, Franz, Jovanovic, and Schwarzer (2008) replicated the study, there was no age trend in size judgment between 5 year olds and 11 year olds. When observed by grasping, younger children showed a nonsignificant trend for smaller illusion rather than reversed.

A recent report shows that even 5- to 8-month-old infants may perceive this illusion (Yamazaki, Otsuka, Kanazawa, & Yamaguchi, 2010). Following a preferential looking procedure, two circles of the same size were presented side by side with small and large inducers. The target circles flashed so as to attract infants' attention to them. Infants of both ages showed a clear preference to the circle with small inducers. In a control test with isolated circles of different sizes, infants showed a preference for the larger one. Thus the preference for the circle with small inducers is likely to reflect subjective judgment of size by infants.

Doherty, Campbell, Tsuji, and Phillips (2010) tested children between 4 and 10 and adults on a version of Ebbinghaus–Titchener figure with eight inducing circles arranged in a square, rather than circular, shape. Two target circles of slightly different sizes were presented at a time and the inducers were either helpful or misleading to accurate size judgment. There was a clear developmental change; 4- and 5-year-olds showed no effect of misleading context on the size judgment, whereas children older than 5 years old did. However the effect was much smaller even in 9- and 10-year-olds than adults, indicating continued developmental increase after 10 years old.

How can we reconcile these sharply contradicting results in the developmental studies of Ebbinghaus–Titchener circles illusion? Doherty et al. (2010) noted that susceptibility to this illusion in young children may have been caused by the failure to control the size of the gap between the target disk and inducers in previous studies. In Ebbinghaus–Titchener figures, the gap between the target disk and inducers typically is smaller for figures with small inducers than those with large inducers and in fact such drawing results in more powerful illusory effect. More inducing circles may be placed for figures with small inducers to obtain still more prominent effect (see Figure 8.7). A smaller gap between the target and inducers would lead to assimilation of the target to the innermost edge of the inducing circles, which Weintraub (1979) described as a contour mechanism. On the contrary, a larger gap between them would lead to a contrast between them, which Weintraub described as context mechanism. This idea is exemplified in the concentric circles illusion, or the Delboeuf illusion. Both mechanisms contribute to the Ebbinghaus–Titchener circles illusion. It is likely that the assimilation effect works in young children or even infants, as exemplified by the Müller–Lyer illusion, which becomes weaker as they get older, as described in the first paragraph of this section. The contrast effect, on the other hand, may start to work later in the development. To solve this puzzle, more illusory figures that involve these two effects in different proportions must be tested to assess potential changes during development.

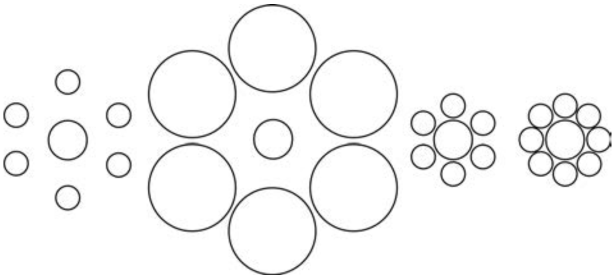

FIGURE 8.7. Various Ebbinghaus–Titchener circles figures.

CONCLUSION

This paper summarized comparative work on visual illusions in three perspectives: cross-species, cross-cultural, and developmental. In cross-species comparison, a number of nonhuman animals including fish, birds, and mammals have been tested for their susceptibility of various illusions. Although most old studies are conducted nonsystematically, more recent ones compared effects of systematic parametric modifications on the illusion in different species. There found visual illusions that are commonly found across species as well as those that are different, sometimes reversed, among species. Clearly, visual illusions are not specific to human vision, which suggests an evolutionary background of this perceptual phenomenon favored by presumably more efficient analyses of environmental stimuli by the system in regular encounters. Thus visual illusions are a consequence of such adaptive tuning, or constraints overlain on the processing function, of the visual system in inappropriate situations.

In cross-cultural studies, there also found differences in the susceptibility to various illusions among people from different cultures, which suggests important contribution of experience, or learning to the illusory perception. A recent finding that needs attention is fundamental difference in the way of paying attention between Eastern and Western cultures; the former attends more to the surroundings than the latter. This attitudinal difference may cause stronger susceptibility to some of the illusions in the former cultures.

In developmental studies, different visual illusions have been found to follow different developmental course. However, the data are not always converging. This probably shows multiple cause of illusions, such as assimilation and contrast effects, which may trace different developmental pathways.

We must admit that the data available at this moment are still short of making up a grand theory of visual illusions. However, we believe comparative visual illusion with diverse perceivers to be a powerful strategy for achieving this goal.

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SELECTIVE AND DIVIDED ATTENTION IN COMPARATIVE PSYCHOLOGY

Walter T. Herbranson

> Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things to deal effectively with others.
>
> —William James

Attention has been a central concept from the very beginnings of psychology. The quote from William James emphasizes how intuitive the notion of attention can appear. The passage also reflects James's functionalist roots by emphasizing the potentially adaptive value of attention, wherein lies its relevance to comparative psychology. An animal that can selectively attend to one of several possibilities could derive a significant advantage over another animal that cannot, and instead must devote comparable resources to all sensory inputs. Such selectivity is essential because not all environmental stimuli are equally important: The sound of an approaching predator, the colorful display of a conspecific, or the subtle odor of a scarce food may have critical consequences that demand an immediate response, and ought to take priority over the myriad of other, more trivial sensory inputs available at the same time.

Although attention is not a bit of terminology that has always been embraced by scientists studying animal behavior (e.g., behaviorism's rejection of mentalistic terms; see Sober, 1983), it nevertheless lies at the heart of many behaviors that have long been of interest to comparative psychologists and ethologists. Tinbergen's (1960) classic research on foraging, for example, reflects what many would now identify as selective attention. Tinbergen noted that seasonally abundant prey items made up a disproportionately large percentage of captures by great tits (*Parus major*), and proposed that foraging animals might use a "specific searching image" that enhances their ability to selectively identify high-frequency prey types. Although there has been some discussion over the nature of search images (Dawkins, 1971), the usefulness of such a selective process is not dependent on any specific underlying mechanism. An ability to efficiently identify high-probability targets would be potentially useful regardless of how those targets are identified. Nevertheless, the cognitive processes that give rise to such effective foraging tools are a valid and important target for research, and they have revealed insights into search images in a variety of species. For example, pigeons (*Columba livia*) are one of the most extensively studied animals in the cognitive and behavioral sciences, and laboratory experiments have shown that they also show search image effects when scanning for food targets, and that those search image effects can reasonably be interpreted as indicative of selective attention. Reid and Shettleworth (1992) presented pigeons with different types of grain on a gravel background. Grain types were visually discriminable from one another based on color, and different colored grains were presented in different proportions across sessions. If pigeons use a search image corresponding to the

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more common grain type, they would be expected to overselect grains of that type. That is, they should select the more abundant grain at a rate even greater than would be expected based on its mere availability. When different grain types differed in distribution, pigeons did in fact select the more common type at a rate greater than could be expected if pigeons did not show a preference in their search process. Furthermore, experience with a specific grain type biased birds toward that same grain type on subsequent trials. Thus, their results show classic search image effects, and suggest that pigeons' attention could be primed to favor those features that best distinguished a frequent prey type from the background.

Langley, Riley, Bond, and Goel (1996) used a similar approach to investigate the circumstances under which search images are used. In particular, they proposed that search image effects might only be seen under circumstances when a search image would be beneficial (i.e., when prey items are difficult to discriminate from the background). They investigated this possibility by presenting different colorful seed types in two contexts. One context was a multicolored tray, in which seeds were difficult to see, mimicking the way cryptic prey take advantage of their natural camouflage in the wild. The other context was a grey tray, in which seeds visually stood out because their bright colors did not match the grey background. Although there was evidence that search images were activated whether seeds were cryptic or conspicuous, search performance was influenced by seed distributions only in the cryptic context (the colorful tray). When seeds were conspicuous, high and low density prey were easily visible and both were quickly consumed. When seeds were cryptic, the typical search image effect was seen, and high density types were overselected. In a separate experiment, they also found that a brief (3 min) delay was sufficient to deactivate a search image. This relatively quick change is important, in that it indicates that search images involve a dynamic cognitive process, rather than a slower, gradual process such as associative learning. Based on their results, the authors argue convincingly that the notion of a search image conceptually parallels the concept of selective attention as it is normally used in cognitive psychology. In particular, they propose that prey encounters serve as attentional cues, influencing the likelihood of perceiving subsequent targets. In that sense, those prey encounters parallel the kinds of visual signals or base-rate manipulations that are frequently used to manipulate attention in cognitive psychology labs. Furthermore, search images and selective attention are both useful specifically when discrimination is difficult. Easy discriminations, such as the identification of conspicuous prey, do not require attentional focus. Cryptic prey, on the other hand, necessarily require a difficult perceptual discrimination between the target and a similar background. Selective attention is one of the tools that make accurate performance possible on such difficult discriminations.

Much of the value of comparative psychology is tied to the variety of species it considers, and evidence for use of search images has been found in a number of different animals, using similar types of methods. Building on the previous research on great tits and pigeons, researchers have observed comparable search image effects in a variety of other bird species with varying lifestyles: blackbirds (*Turdus merula*; Lawrence, 1985), blue jays (*Cyanocitta cristata*; Pietrewicz & Kamil, 1979), and kestrels (*Falco tinnunculus*; Viitala, Korplmäki, Palokangas, & Koivula, 1995) all overselect abundant prey types. The relevance of search images is not limited to birds, however. Mammals such as the sea otter (*Enhydra lutris*; Ostfeld, 1982) also show patterns of prey selection indicative of search images. Furthermore, the same patterns are seen in several varieties of invertebrates, including bumblebees (*Bombus fervidus*; Heinrich, 1975), butterflies (*Battus philenor*; Rausher, 1978), and spiders (*Evarcha culicivora*; Cross & Jackson, 2010). An exhaustive listing of all animals that might use a search image is beyond the scope of this chapter, but note that those that the foraging habits of each match the features indicated as important by laboratory investigations: They feed on multiple prey types that vary in spatial distribution, and those prey types are cryptic but can, with attention, be distinguished from each other and from the background. In contrast, ambush predators (or "sit and wait" predators) would not be expected to use a search image, and instead would adopt other strategies to maximize gains (Pianka, 1966). Cornell (1976), for example, pointed out that undirected searchers, such as web-spinning spiders and antlions show little selectivity and take prey in proportion to their prevalence in the environment.

Note that the term *search image* should not be interpreted as exclusively visual, since animals can use other sensory modalities to forage in the same manner. Evidence for olfactory search images has been seen in the feeding patterns of yellowfin tuna (*Thunnus albacares*; Atema, Holland, & Ikehara, 1980) and skunks (*Mephitis mephitis*; Nams, 1997), and in the search strategies of trained explosive-sniffing dogs (*Canis familiaris*; Gazit, Goldblatt, & Terkel, 2005). Similarly, rattlenakes (*Crotalus viridis*) use a chemical search image to identify prey (Melcer & Chiszar, 1989). Note again, that the variety of search-image modalities (like the diversity of search-image utilizing species) does not imply that search images are universal. They should be used specifically by those species that must perform a difficult discrimination (visual or otherwise) during a directed search.

Given these parallels between search images and selective attention, as well as the fact that many other topics in comparative psychology (memory, perception, serial learning, etc.) have benefitted from theories grounded in cognitive psychology, an understanding of theories of human attention may prove to be a useful tool in the arsenal of the comparative psychologist interested in attention. Broadbent (1958), for example, characterized attention as a selective filter that could be used to limit incoming information to a more manageable amount, and this characterization of attention as a filter resonates with the previous research on search images, in that they seem to play a similar filtering role during foraging. In fact, much of what we now know about various aspects of attention in animals has been inspired by methods and theories developed over decades of research on human attention.

Consequently, this chapter aims to provide an overview of research on the various aspects of selective and divided attention as they have been used in the field of comparative psychology. The general approach will be to identify important elements of attention according to contemporary theories of cognitive psychology, outline the methods that have been used to study those aspects of attention in humans, and then explore the ways in which those same concepts and methods have been used to study animal cognition. Given this approach, there will naturally be a bias toward visual attention (the primary sensory modality for humans, the original source of data from which the theories are derived), and animal species that are widely used in laboratory research. However, this does not imply that the concepts are not also applicable to other animals or sensory modalities, and such broader applicability will be acknowledged wherever possible.

SELECTION OF FEATURES

One of the most influential theories of human selective attention is Treisman's feature integration theory (Treisman & Gelade, 1980). The theory proposes that perception involves two stages: an early, preattentive stage, in which individual features of an object (e.g., color, shape, movement) are each automatically but separately processed; and a late, focused attention stage, in which individual features are combined into a more sophisticated, integrated perception of an object. A popular metaphor characterizes attention as the "glue" that binds together the various features of an object. Feature integration theory implies that some kinds of search tasks can be performed quickly and without attention (specifically, those relying on a single feature), whereas others require attention (those that rely on a conjunction of features), resulting in a slower, more effortful process.

Compelling evidence for feature integration theory comes from visual search tasks using stimuli that have been carefully designed to recruit either early or late stage processing. *Feature searches* involve only a single feature such as color, shape, orientation, or direction of movement, and according to feature integration theory can be done quickly and in a parallel fashion. *Conjunction searches* on the other hand, involve a combination of features (assumed to require attention), and must be done in a slower, serial fashion (Treisman, 1986). For example, an area consisting of grey shapes stands out within a field of white shapes because a search can be based on a single feature (color). Targets in feature searches are usually identified very quickly, regardless of the number of distractors. In contrast, conjunction searches (based on a combination of two features such as shape and color) typically produce much slower response times. For example, an area consisting of white squares and grey circles is not nearly as noticeable within a field consisting of grey circles and white squares (see Figure 9.1). Attention is required to bind together the combination of features that defines the target area. These results support one of the primary principles of feature integration theory: Not all visual searches are done in the same way.

Cook (1992) asked whether pigeons' visual searches also used distinct early and late stage processes depending on the type of search. Using stimuli patterned after those developed by Treisman, he trained pigeons to peck the odd region of an otherwise uniform texture display. For example, in a feature search, pigeons might search for a small region of red squares embedded within a field of green squares. In a conjunction search, pigeons might search for a small region consisting of red squares and green circles embedded within a field of red circles and green squares. Pigeons' accuracy to peck the target region was lower on conjunction searches than it was on feature searches (though still better than chance on both), consistent with the standard predictions of feature integration theory. These results suggest a two-stage process similar to that used by humans. Pigeons can use a feature search if only a single feature is sufficient for target identification, and the result is faster identification and higher accuracy. When searching for a conjunction of features, accuracy is poorer. Thus, the general pattern of results parallels the pattern seen in humans, and is consistent with the two-stage model proposed by feature integration theory.

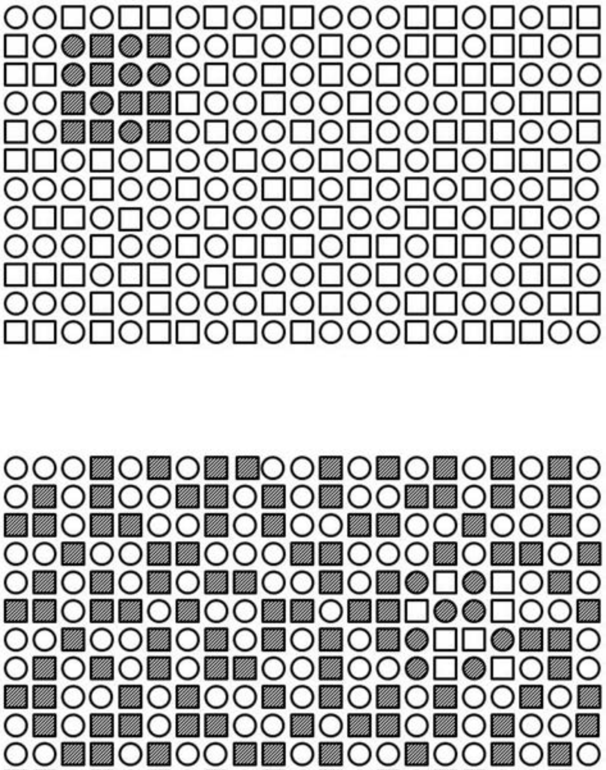

FIGURE 9.1. Visual search stimuli used to study feature integration theory. Top: A small area defined by a single feature (dark squares and circles in the top left quadrant, surrounded by light squares and circles) usually stands out. Bottom: A small area defined by a conjunction of features (light squares and dark circles in the lower right quadrant, surrounded by dark squares and light circles) is more difficult to identify and requires attention.

The relevance of feature integration theory is not limited to humans and pigeons. Bichot and Schall (1999) took a similar approach to investigating visual search in macaque monkeys (*Macaca mulatta* and *Macaca radiata*). Monkeys were trained to make an eye saccade toward a target in a visual display defined either by a feature of a conjunction of features. They performed better than chance on both kinds of searches, as humans and pigeons can. Furthermore, response times increased with set size for conjunction searches, but not for feature searches. This primary result is also consistent with Treisman's (1986) proposed two-stage model, where feature searches are done in parallel, whereas conjunction searches are serial.

The parallels between feature and conjunction searches on the one hand, and conspicuous and cryptic prey on the other, make a case for the ecological relevance of selective attention, and also provide some valuable insight into the mechanisms that may underlie the foraging behavior observed in natural settings by Tinbergen (1960). Animals, like humans, can search based on specific features or based on conjunctions of features, and depending on the type of search image, the process might require attention (conjunction searches and cryptic prey) or might not (feature searches and conspicuous prey). However, this is not the only way attention can be used to selectively favor processing of certain kinds of stimuli.

SELECTION OF SPATIAL LOCATIONS

Attention can also be used to select specific spatial locations, and cognitive psychologists have likened it to a spotlight that can move around one's field of vision (Posner, 1980). Objects falling within the spotlight receive enhanced processing relative to those in other regions. Note that attention in this sense is different from direction of gaze (see Chapter 32, this volume). In many situations, one can make maximal use of an unequal distribution of visual receptors on the retina by directing one's fovea (with its maximal density of photoreceptors) toward important areas of the environment (see Chapter 3, this volume). Humans, for example, read by moving the fovea across a line of text. However, this is not the only way of enhancing the processing of a spatial location. *Covert attention* involves attending to a location without looking directly at it. A point guard in a basketball game might, for example, disguise his intentions by looking in one direction while passing the ball in a different one. His attention is engaged on a passing target, and that target's location does not correspond to his foveal fixation point.

To investigate this aspect of attention, Posner, Snyder, and Davidson (1980) had human participants monitor a display for the onset of a light that could occur either to the left or to the right of a fixation point. On some trials, a brief flashing cue to the left or to the right of fixation provided probabilistic information about the location of the upcoming target. In particular, the cue appeared in the same location as the following target 80% of the time (called *valid cues*). The remaining 20% of the time, the cue appeared in the opposite location (*invalid cues*). Figure 9.2 provides schematic depictions of trials featuring valid and invalid cues. Participants learned to anticipate targets on validly cued trials, in that their response times were faster to validly cued targets than they were to uncued targets that appeared without any preceding cue. This result was consistent even though participants' eyes remained anchored to the central fixation point, indicating that the response time facilitation was due to a shift of attention and not to a peripheral cause, such as anticipatory eye saccades. Correspondingly, invalidly cued targets produced response times that were slower than those on uncued trials (and by extension, validly cued trials). Response times increased on invalid trials because attention had been directed away from the eventual target by the invalid cue, and that additional distance had to be covered before a response could occur. Again, these results indicate that attention can be directed to specific regions of space, and are consistent with the characterization of attention as a spotlight that can be preferentially directed to those locations that are likely to be important.

Shimp and Friedrich (1993) asked if pigeons would show similar control of spatial attention by developing a parallel task in which left and right targets were preceded by either valid (same spatial location) or invalid (different spatial location) predictive cues. Targets were red keylights appearing on one of the side keys in an operant chamber, and pecks to lit targets were reinforced with grain. Predictive cues were presented on each trial, consisting of brief (50 ms) white lights that preceded the target by various intervals of time. Their results followed the expected pattern: Response times to validly cued targets were faster than response times to invalidly

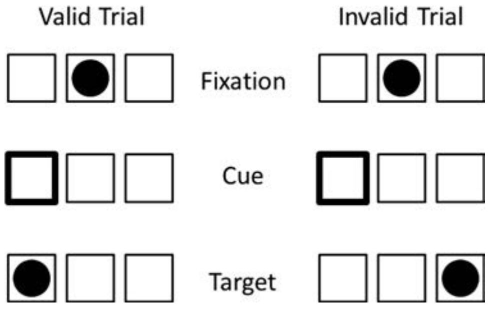

FIGURE 9.2. Schematic of valid and invalid trials in a spatial cueing task. Left: A valid trial, in which the spatial cue appears in the same location as the subsequent target. Right: An invalid trial, in which the spatial cue appears in a different location than the subsequent target. Response times to validly cued trials are consistently faster than response times to invalidly cued trials.

cued targets. This finding indicates that pigeons' attention can also be directed to different spatial locations, giving them preferential processing and producing response time facilitation. In addition, it indicates that attention shifts can occur over short time periods (i.e., the short duration between a cue and the subsequent target, using values as low as 150 ms). Note that in this operant task, direction of gaze could not be measured, as it is in the human research. Thus, on longer duration trials, pigeons could have adopted a strategy wherein they move toward the cued location and respond on the nearest available option, which would indicate a peripheral, rather than a central attentional mechanism. Such a strategy however, would be less effective on trials with short intervals, because they limit the necessary travel time. In addition, other lines of research point toward central attentional processes in similar tasks. Stonebraker and Rilling (1984) for example, used a matching to sample task, in which color samples were paired with either color comparison stimuli (identity matching) or line orientation comparison stimuli (symbolic matching). On each trial, a cue was presented along with the sample, indicating which type of comparison stimuli were to follow. Birds correctly matched both kinds of stimuli, but were impaired on occasional probe trials on which the comparison stimuli did not correspond to the type indicated by the cue. This result is indicative of prospective coding (rather than retrospective), but more important, since the location of the correct response was not cued, the cueing effect could not be accounted for by a peripheral orienting mechanism. Thus, it appears that pigeons, like humans, can direct their attention on a moment-to-moment basis if such rapid shifts are demanded by the situation.

A related phenomenon of spatial attention originating in the study of human cognition is the Simon effect. Simon (1968) noted that response times to visual stimuli were dependent on the required response. In particular, participants were faster to respond to a target if spatial aspects of the required response coincided with the location of the cueing stimulus. For example, if a participant is required to press a left response button when seeing any red light and a right response button when seeing any green light, response times are fastest if the light cue is presented on the same side as the relevant response button. In this example, the required left button press is faster if cued by a red light appearing to the left (*corresponding trials*) than if cued by a red light appearing to the right (*noncorresponding trials*). Similarly, right button presses are faster to an ipsilaterally presented green cue than to a contralaterally presented green cue (Craft & Simon, 1970).

Urcuioli, Vu, and Proctor (2005) looked for a Simon-like effect in pigeons using the same logic. They presented pigeons with color stimuli on two response keys, and trained them to peck a specific key (left or right) when an associated color (red or green) was present on either key. For example, a red key (paired with an irrelevant white key in the other possible spatial location) meant that pecks on the left key would be reinforced, and a green key (again paired with an irrelevant white key) meant that pecks on the right key would be reinforced, regardless of whether the critical color itself appeared on the left or the right key. In this manner, corresponding trials were those on which the color signal corresponded to the response location (e.g., red–left/white–right or white–left/green–right). Noncorresponding trials were those on which the relevant red or green color stimulus did not coincide with the required response (e.g., white–left/red–right or green–left/white–right). Their results showed accuracy and response time advantages for corresponding trials over noncorresponding trials, similar to the standard Simon effect seen in humans.

The existence of a parallel Simon effect in pigeons indicates several things. Primarily, it is another example of flexible spatial attention: Attention can be directed to different spatial locations based on a number of different features, and those features need not be spatial, as they are in Posner's cueing method. Second, although pigeons (and people) have control over attention, it is still influenced by nonarbitrary factors. The Simon effect decreases response times specifically on corresponding trials, in which the response specifically matches the location of the cue.

Again, such spatial aspects of selective attention are not limited to humans and pigeons. Rats (*Rattus norvegicus*) show standard cueing effects in a Posner-like spatial cueing task (Marote & Xavier, 2011), as well as a Simon effect (Courtière, Hardouin, Burle, Vidal, & Hasbroucq, 2007), pointing to similarly flexible control of spatial selective attention. In addition, Eckstein et al. (2013) adopted the spatial cueing method for humans, macaque monkeys, and honey bees, finding a spatial cueing effect in all three, though the strength of the effect was not uniform: Humans showed the strongest effect, and honey bees the weakest. Thus, although multiple species show spatial cueing effects, the details of how the "spotlight" operates may not always be identical across species.

FIGURE 9.3. Hierarchical stimuli used to investigate local/global attention. Stimuli consist of a collection of local letters, arranged into a global configuration. A given letter (T or H in these examples) can appear either at the local or global level.

SELECTION OF HIERARCHICAL LEVELS

Shifts of attention from one location to another are important, but reflect only one way that the spatial aspects of attention can be manipulated by an individual. Certain situations may instead (or also) require a shift of attention between hierarchical levels of visual organization. A common example of this kind of hierarchical organization would be the perception of a forest and its component trees. Individuals can choose to attend to a global level of analysis (the forest) or, if the situation demands, shift to a local level (a specific tree; see Chapters 5 and 8, this volume). Thus, rather than a spotlight, one might instead use a zoom lens as a metaphor for attention, reflecting the fact that attention can also be adjusted in size, encompassing a larger or smaller area. Navon (1977) investigated this kind of local/global attention dynamic in humans using stimuli having hierarchical structure like those depicted in Figure 9.3. Note that each stimulus consists of a larger configuration made up of smaller individual characters. Identification of the larger configuration requires a wider, global scope of attention, large enough to encompass multiple local characters. In contrast, identification of one of the individual characters requires a narrower, local level of attention independent of their configuration or context. Navon found that human participants could shift attention to either the local or global level of analysis as necessary, but that all other things being equal, humans had a tendency to prioritize more highly the global level of analysis in that they identified global targets more quickly than local targets.

Several animals can also process local and global aspects of stimuli with hierarchical structure, including fish (*Xenotoca eiseni*; Truppa, Sovrano, Spinozzi, & Bisazza, 2010), domestic chicks (*Gallus gallus*; Chiandetti, Pecchia, Patt, & Vallortigara, 2014), pigeons (Fremouw, Herbranson, & Shimp, 1998, 2002), domestic dogs (Pitteri, Mongillo, Carnier, & Marinelli, 2014), capuchin monkeys (*Cebus paella*; Spinozzi, De Lillo, & Salvi, 2006), rhesus macaques (Hopkins & Washburn, 2002), baboons (*Papio papio*; Deruelle & Fagot, 1998), and chimpanzees (*Pan troglodytes*; Fagot & Tomonaga, 1999; see also Chapter 5, this volume).

Fremouw et al. (1998), for example, asked if pigeons could identify local and global features of a stimulus display, and if so whether they could shift attention between local and global levels of analysis. Pigeons were presented with hierarchical stimuli like those in Figure 9.4, and trained to search for specific letter targets that could occur at either the local level or the global level. For example, presence of the letter H meant that a left response would be reinforced (whether it appeared at the local or the global level), whereas the letter S meant that pecks to the right key would be reinforced (again regardless of its hierarchical level). Pigeons learned to respond accurately to targets presented at either level. Furthermore, by presenting successive blocks of trials, during which the preponderance of targets appeared at one level or the other, they showed that birds could be primed to preferentially search at a specific level. When 85% of targets appeared at the local level, and 15% of targets appeared at the global level, response times were faster to targets appearing at the local level. Conversely, when 85% of targets appeared at the global level, the response time advantage was reversed, and pigeons were faster to

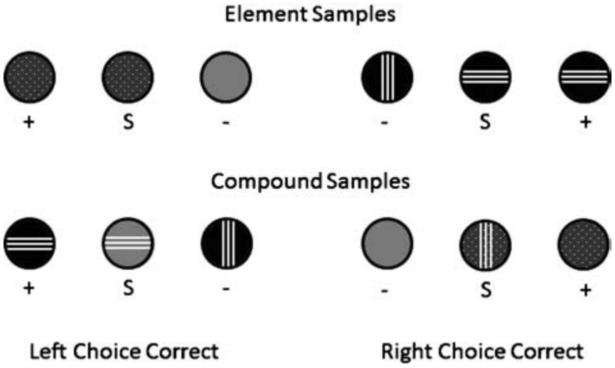

FIGURE 9.4. Matching-to-sample task used to investigate divided attention. Top: Element sample trials, in which the sample (center key) consists of either a color or line orientation. Comparison stimuli (side keys) are of the same type (color or line orientation) as the sample. The correct comparison stimulus is the one that matches the sample. Bottom: Compound sample trials, in which the sample consists of both a color and line orientation. Comparison stimuli (side keys) consist of a single element (either colors or line orientations). The correct comparison stimulus is the one that matches an element from the sample.

respond to targets at the global level. Thus, birds showed an ability to flexibly shift the hierarchical aspect of attention to take advantage of the base rates at which local and global targets appeared.

In a subsequent experiment, Fremouw et al. (2002) looked into the requisite time frame for these kinds of local/global attention shifts. The blocking procedure mentioned previously involved shifts of attention over the course of many trials across several days. This left open the question of whether pigeons could shift attention between local and global levels on a moment-to-moment basis. To answer this question, they used a trial-by-trial cueing procedure, in which a brief visual cue predicted (with 85% accuracy) the level at which an upcoming target was to appear (but not the specific target or the required response). This cueing procedure produced an effect that paralleled the earlier blocking procedure: Response times were faster to targets at the primed level than to targets at the unprimed level. This pattern of results indicates that pigeons can indeed flexibly shift their level of attentional focus based on a number of factors, and if necessary can do so quickly.

Recall that although humans can flexibly shift attention between local and global levels of analysis, Navon (1977) also found that they showed a global precedence in that they identified targets at the global level more quickly than targets at the local level. Cavoto and Cook (2001) investigated whether pigeons might also show a precedence effect, and if so, whether it would mirror humans' global precedence. Like Fremouw et al. (1998, 2002), they presented hierarchical stimuli having a target at either the local or global level, and compared accuracy on local and global targets during learning. Their results pointed toward a local precedence (notably opposite that of humans), in that birds learned to accurately identify local targets earlier in training than they did global targets. In a subsequent experiment, they presented pigeons with stimuli featuring conflicting local and global information (i.e., targets at both levels, each associated with different responses). On these conflicting probe trials, pigeons were more likely to respond in a manner consistent with the target presented at the local level.

Note that this local precedence in pigeons is different from the human global precedence, but is consistent with the local precedence found in monkeys (Hopkins & Washburn, 2002; Spinozzi et al., 2006) and baboons (Deruelle & Fagot, 1998). Chimpanzees on the other hand, do not always process the local elements faster than global (Fagot & Tomonaga, 1999). Thus, although similar methods used to study local/global attention in primates, pigeons and humans, and although each species shows an ability to shift attention between levels, the details of how those attentional shifts happen are not always identical. Note that these differences could be due to attentional processes or to various procedural and anatomical constraints. Pigeons, for example, have a much broader visual field than primates due to their side-facing eyes, and are normally much closer to presented stimuli, to facilitate pecking responses.

DIVIDED ATTENTION

Although selectivity is a fundamental attribute of attention, attention can also be divided among multiple targets. However, there is often a cost to doing so: Divided attention is usually associated with a decrement in performance relative to situations that require attention to only a single element. A classic example is the cocktail party effect (Cherry, 1953). In a situation where multiple channels of information are available, one can selectively attend to one channel, as when one focuses on a single conversation partner at a crowded and noisy cocktail party. One is bombarded by several voices, and all but one are effectively filtered out. Cherry (1953) studied the cocktail party effect using dichotic listening tasks, in which participants simultaneously listen to two different speech streams. Selective attention generally allows one to focus on one of the two speech streams, while filtering out the other. Attending to both is virtually impossible, and very little is extracted from the unattended speech stream. Although some information may break through from the unattended speech stream, this is limited to special cases, such as the participant's name, and is usually quickly forgotten (Moray, 1959). The same kinds of constraints seem to apply to visual attention as well. Neisser and Becklen (1975) used similar logic in a visual task, in which two videos were superimposed over one another, obtaining parallel results: When asked to monitor one video and ignore the other, participants were quite successful, and could report accurately on the contents of the attended (but not the unattended) video. However, tracking both videos simultaneously proved virtually impossible. Thus, the limitations of attention, and the costs of dividing it would seem to apply whether attending to auditory or visual stimuli.

The research programs described in previous sections show that pigeons are quite good at selecting specific aspects of a visual display (features, locations, or hierarchical levels). Given that pigeons' eye positioning provides them with a tremendous panoramic view of their environment, one might expect that there would be plentiful opportunities to select multiple simultaneous targets (i.e., divided attention). Maki and Leith (1973) investigated whether pigeons could simultaneously attend to two elements of a stimulus display, using a matching to sample procedure (see Figure 9.4). Samples were presented on the center key in an operant chamber, followed immediately by comparison stimuli on both side keys, and pecks to the comparison stimulus that matched the sample were reinforced. On single-element trials, all stimuli were exemplars of the same type (either colors or line orientations, but never a mixture of the two). On compound trials, samples consisted of a combination of two elements (a color and a line orientation presented on the sample key). Comparison stimuli on compound trials were the same as on single-element trials (consisting of a color or a line orientation, but never both), and the correct comparison stimulus was the one that matched either of the elements present in the compound sample. Thus, accurate performance on compound trials required that pigeons attend to both elements of the sample. Single-element trials did not require divided attention because the sample consisted of only one of the two possible elements. If there is a cost to dividing attention, then performance on single-element trials ought to be better than performance on compound trials. Indeed, Maki and Leith confirmed this expectation: Matching to sample accuracy was better when single-element samples were presented than when compound samples were presented. Note that there have been several alternative explanations proposed for this "element superiority effect" (see Zentall, 2012, for a comprehensive review). Nevertheless, superior performance on single-element trials comprises yet another similarity between established human results (the decrement in performance on divided attention tasks) and pigeons' performance on a parallel behavioral task (the element superiority effect). In both cases, there is a cost associated with simultaneous attention to multiple elements.

Similar divided attention effects have been shown in other animals. Dukas and Kamil (2001) presented blue jays (*Cyanocitta cristata*) with cryptic artificial prey on a computer monitor. Detection rates were lower when jays divided attention between searching for two different prey types at the same time, than when they searched for only a single prey type. Turchi and Sarter (1997) similarly studied divided attention in rats by requiring animals to perform a discrimination task requiring attention to either one or two possible modalities (visual or auditory). Not only was there a cost for attending to both modalities, but they were able to impair divided attention performance through a physiological manipulation. Although the neurological foundations of attention are beyond the scope of this chapter, they have been outlined elsewhere (see Posner, 2011), and this finding underscores the fact that neuroscience can contribute to comparative psychology by providing useful frameworks and relevant data, much like the frameworks and data from cognitive psychology highlighted in this chapter (see Kesner & Olton, 1990).

SELECTIVE AND DIVIDED ATTENTION IN LEARNING AND CATEGORIZATION

As with many other cognitive processes (perception, memory, etc.), selective and divided attention can be thought of as general abilities that are available to be recruited for a variety of different purposes. For example, whereas learning is a fundamental behavioral process in its own right, it can also be influenced by attention (Nissen & Bullemer, 1987). In fact, classic research on discrimination learning was influenced heavily by ideas about selective attention. Lashley (1929) made an early acknowledgement that animals faced with a discrimination problem might not attend equally to all incoming stimuli. Based on that possibility, Krechevsky (1932) proposed that the characteristic learning curve in a sensory discrimination experiment is the result of an animal adopting a series of hypotheses, sequentially abandoning inadequate ones until reaching the successful solution. The adoption of a new hypothesis involves selective attention to a new aspect of the stimulus environment (e.g., a rat attending to brightness, after shape has proven to be an inadequate solution). This is an example of a noncontinuity theory, in that it assumes that an animal does not attend to all aspects of the environment during learning, but isolates one or more stimulus dimensions relevant to the current hypothesis. In favor of this position is the observation that discrimination learning is often abrupt, transitioning quickly from chance to virtually perfect performance, as well as the regular adoption of position biases during early training (assumed to correspond to incorrect hypotheses). In contrast, continuity theory (Spence, 1940) proposes that learning is a gradual process, with the cumulative response strength of all of the various stimulus components combining to determine a response at any one time. Although with proper assumptions, either kind of theory can indeed account for most of the discrimination learning data, the important implication is that the concept of attention has important ramifications for learning (Mackintosh, 1965). That is, selective and divided attention have the potential to reach into—and influence other aspects of—cognition, such as learning and memory.

Another prominent and well-studied example of a cognitive process reliant on attention is categorization (see Chapter 5, this volume). Many animals, including humans and pigeons, learn to form useful categories that allow them to respond to novel stimuli in ways that are informed by past experiences (Goldstone & Kersten, 2003; Medin & Smith, 1984). Given that exemplars from natural categories vary along multiple dimensions (some of which are relevant to category membership and some of which are not), selective and divided attention would likely be essential components of category learning. Selective attention would allow an individual to focus on the relevant stimulus dimension (or dimensions) while ignoring the irrelevant ones. At the same time, divided attention would allow an individual to consider multiple relevant dimensions when they are jointly diagnostic of category membership.

Not surprisingly, numerous species can learn such multidimensional categories, including but not limited to chickens (Ryan, 1982), blue jays (*Cyanocitta cristata*; Pietrewicz & Kamil, 1977), African grey parrots (*Psittacus erithacus*; Pepperberg, 1983), squirrels (*Sciurus carolinensis*; Wills et al., 2009), domestic dogs (Range, Aust, Steurer, & Huber, 2008), horses (*Equus caballus*; Hanggi, 1999), squirrel monkeys (*Saimiri sciureus*; Roberts & Mazmanian, 1988), capuchin monkeys (D'Amato & van Sant, 1988), stumptailed monkeys (*Macaca arctoides*; Schrier, Angarella, & Povar, 1984), gorillas (*Gorilla gorilla*; Vonk & MacDonald, 2002), orangutans (*Pongo abelii*; Vonk & MacDonald, 2004), and chimpanzees (Hayes & Hayes, 1953). Given massive variation in methodology and categories, the specific cognitive processes used by each remain unclear.

Ashby and Gott (1988), however, developed a method that is well-suited to address such questions about multidimensional category learning, and that is simple and flexible enough to be used in comparative psychology. They simulated categories using bivariate normal distributions, which mimic some of the critical features of naturally occurring categories, while retaining experimental control of category structure and allowing for the relative importance of each dimension to be systematically and precisely manipulated. Figure 9.5 is a schematic of their method, and some conditions that can be derived to investigate attention to different attributes. The top left panel depicts two bivariate normal distributions (categories), from which stimuli can be drawn. The x- and y-axes represent two continuously varying dimensions on which stimuli can vary, such as height and width of rectangles, or frequency and orientation of Gabor patches (Yao, Krolak, & Steele, 1995). The z-axis represents the probability that a particular stimulus having attributes on the x- and y-axes will be drawn. Note that the center of a category consists of a dense collection of high-probability exemplars. As one moves away from the category center, exemplars become rarer in frequency and display less typical features (much like members of natural categories).

Categorization accuracy using this method is maximized by using a decision rule that best separates exemplars from the two category distributions. The optimal decision rule generally corresponds to a boundary, or line dividing the x–y plane such that

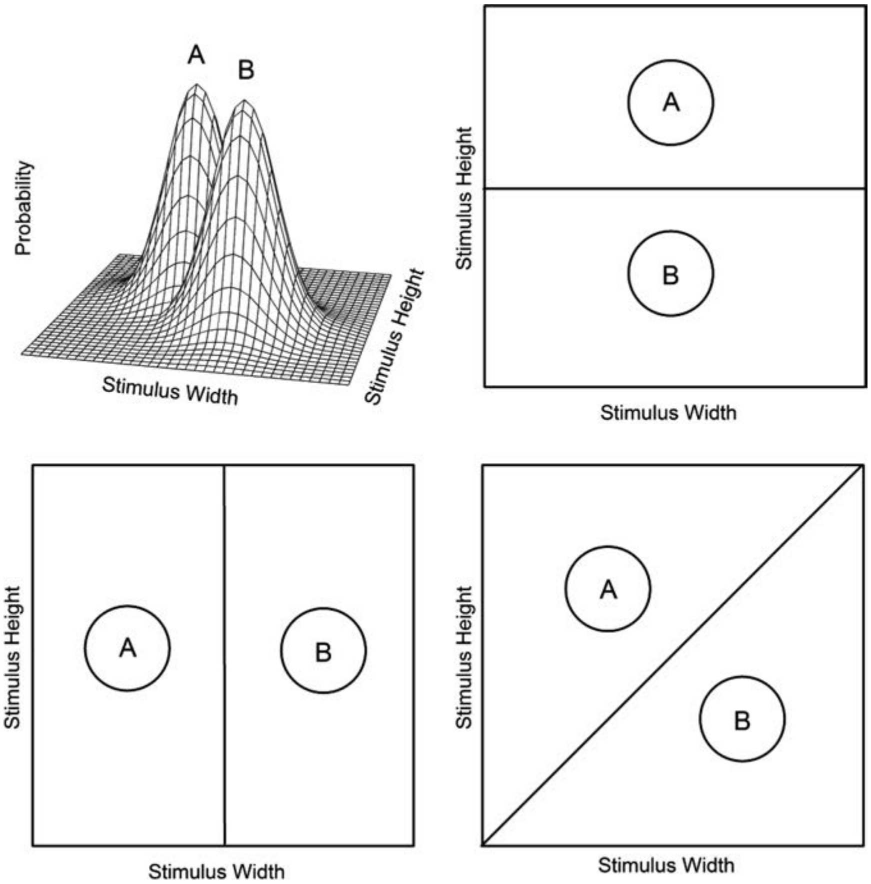

FIGURE 9.5. Multidimensional categorization task. Top left: Two approximately normal distributions (A and B) from which stimuli can be sampled. Stimuli vary along two dimensions (e.g., height and width). Top right: Summary of a categorization task requiring selective attention to height. Letters indicate peaks of each category distribution. Solid circles correspond to stimuli equally likely to be drawn from a given category. Solid line indicates points where the two categories intersect, resulting in stimuli equally likely to be drawn from either category and corresponding to the optimal decision boundary. Bottom left: Summary of a categorization task requiring selective attention to width. Bottom right: Summary of a categorization task requiring divided attention to both height and width.

stimuli falling on opposite sides of the boundary will be categorized differently. If the centers of the category distributions differ on only one dimension, the boundary will be perpendicular to that axis (and parallel to the other), and accurate performance will require attention to only a single dimension (top-right and bottom-left panels in Figure 9.5). On the other hand, if the centers of the distributions differ on both dimensions, the optimal boundary will be oblique, and accurate performance will require attention to both dimensions (bottom-right panel in Figure 9.5). When presented with stimuli generated from categories that differ on only one dimension, human participants selectively attend to the relevant dimension, using a decision bound perpendicular to the diagnostic axis. When presented with stimuli from categories that can only be discriminated by dividing attention among both dimensions, human participants are capable of incorporating both dimensions into their categorization decisions, and use a decision bound that reflects the influence of both dimensions.

Herbranson, Fremouw and Shimp (1999, 2002) used the same method to investigate categorization in pigeons using either rectangles differing in height and width or moving dots varying in speed and direction. When categories differed on a single dimension, pigeons' responses were controlled by the relevant dimension, and uninfluenced by the randomly varying irrelevant dimension. Pigeons also responded accurately when categories could only be differentiated by attending to both dimensions, indicating that they were able to incorporate information from both dimensions. Thus, pigeons were able to selectively attend to one dimension, or divide attention among two dimensions as required by the categories in effect (see Chase & Heinemann, 1972, for a similar approach).

Smith et al. (2012) used this method to investigate categorization in pigeons and three primate species: humans (*Homo sapiens*), rhesus macaque, and capuchin monkeys. Accurate performance on some conditions required attention to only one of two varying stimulus dimensions (the second varied randomly and was not diagnostic of category membership). Other conditions required attention to both dimensions, in that accurate performance was not possible without considering both stimulus dimensions. They found that pigeons could learn both kinds of categories, and that they learned both at approximately the same rate. Thus, pigeons could selectively attend to a single stimulus dimension (filtering out the other, randomly varying dimension) or divide attention among both. Meanwhile, all three primate species also learned both kinds of categories, but learned single-dimension categories more quickly than information integration categories. Thus, even though all species learned both kinds of categories, interspecies differences suggested that the cognitive tools used to do so may not have been the same for each.

LIMITATIONS AND FAILURES OF ATTENTION

Attention has been traditionally characterized as a limited resource, or information processing bottleneck. Although these characterizations originate in the study of human cognition, note that the relevant pattern of results has been generally replicated in animals: Tasks that demand more from attention result in poorer performance. Recall for example, that accuracy is impaired in visual search tasks that are defined by a conjunction of features relative to searches based on a single feature (Cook, 1992) and that matching to sample tasks with a compound sample are more difficult than tasks with a single-element sample (Maki & Leith, 1973).

Another notable demonstration of attention's limits is the phenomenon of change blindness, in which normally conspicuous changes to a stimulus display often fail to capture attention under certain specific conditions. Rensink, O'Regan, and Clark (1997) used a simple change detection task to study the conditions under which human participants would fail to notice a change. Two images, identical save for a single localized difference, were presented in successive alternation. When transitions between subsequent images were instantaneous, the changes "popped out" and were spotted almost immediately by participants. In contrast, when there was a brief interstimulus interval (ISI) between images, the change was more difficult to detect: Participants required more time to spot the difference, and performed at lower levels of accuracy. Rensink et al. also found that in the more difficult condition (featuring the ISI), changes of central interest (pertaining to the primary subject matter of the image) were spotted more quickly than changes of marginal interest. This feature of change blindness presumably serves to minimize the potential negative consequences the attention bottleneck: Changes of central interest are more likely to carry important consequences, and are thus favored for selection early in the search process.

Attention may play a similar selection function in animals, and if so, we might see comparable limitations in change detection. Laboratory investigations show that pigeons and rhesus monkeys are indeed capable of monitoring a display for change, and their performance is similar in many ways to that of humans (Cook, Katz, & Blaisdell, 2012; Elmore, Magnotti, Katz, & Wright, 2012; Leising et al., 2013). Herbranson et al. (2014) built on this change detection research by developing an analog of Rensink et al.'s (1997) flicker task that could be presented to pigeons in an operant chamber (Figure 9.6). Pigeons were presented with alternating stimulus displays consisting of line orientation elements spread across three response keys. An original and a modified display consisted of the same line features, with one exception. A single line feature was added to or deleted from the original display to create a similar, but nonidentical modified display. Individual trials featured pairs of displays, alternated for varying numbers of repetitions, and either with or without an ISI. In parallel with human change blindness results, accuracy was consistently lower on trials featuring an ISI (but still greater than chance). Furthermore, pigeons' accuracy increased with added repetitions, and patterns of responding indicated that birds had used a serial search strategy, progressing from one location to another until the change was identified. As with humans, it appears that timing has a powerful influence over selection: The presence of an ISI between subsequent

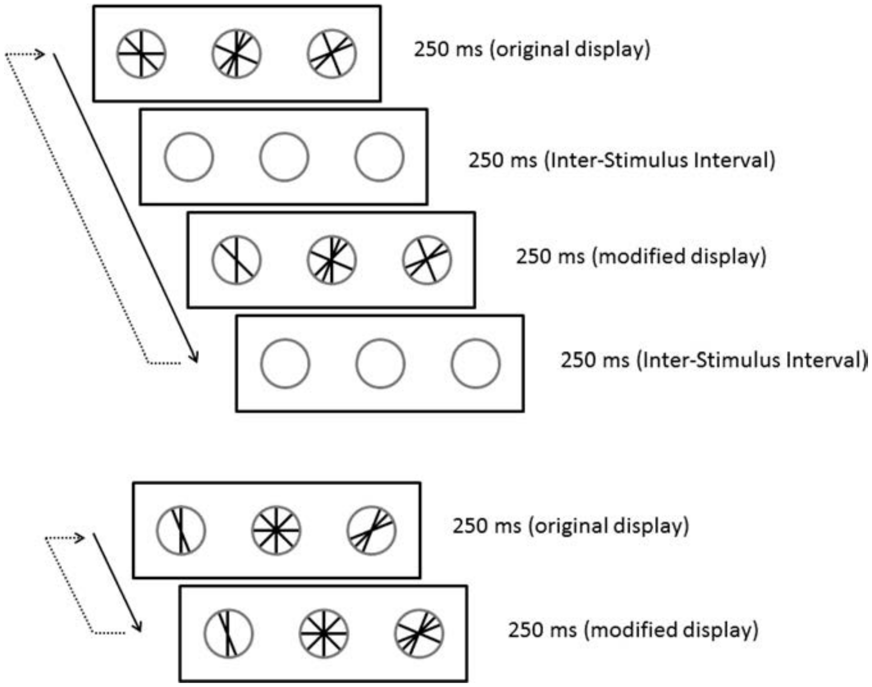

FIGURE 9.6. Example of a change detection trial using the flicker paradigm, in which two non-identical stimulus displays are alternated. Top: A trial with an inter-stimulus interval (ISI), in which there is a blank interval between each consecutive stimulus display. The correct response is to peck the key that is not the same (left key). Bottom: A trial with no ISI, in which consecutive stimulus displays are contiguous, with no intervening time delay. The correct response is to peck the key that is not the same (right key).

displays makes change detection more difficult. Change blindness indicates that not all incoming information can be processed, and that pigeons (like humans) must select partial information from the available channels.

Change detection would seem to be a critical cognitive ability, essential to a variety of activities (Rensink, 2002), and this feature makes change blindness all the more fascinating as a limitation of visual attention. Nevertheless, such a limitation is consistent with the constraints placed on other aspects of attention (the decrements in performance associated with conjunction searches, invalid cueing, and divided attention, for example). Given that animals can learn to use search images, cue information, and category structures to direct attention in strategic ways, one might also predict that animals could devise strategies to counter the negative consequences of change blindness. Cavanaugh and Wurtz (2002) found evidence for this possibility, testing rhesus macaques for change blindness, using a procedure similar to Herbranson et al. (2014). Although they still found a standard change blindness effect, change detection was improved (in terms of accuracy and response time) on trials when the location of an upcoming change was cued in advance. That is, monkeys could use predictive cues to direct their search in ways that reduced (but did not eliminate) change blindness.

CONCLUSION

The research summarized here indicates that many animals are capable of directing attention in many of the same ways humans do: They can select specific features, spatial locations, or hierarchical levels for preferential analysis, as the situation might demand. Furthermore, animals can divide attention and consider multiple aspects of their environment simultaneously, though such division may be accompanied by a decrement in performance. These fundamental processes of selective and divided attention are used in many cognitive processes including but not limited to discrimination, categorization, and change detection. Finally, as useful as attention is, it is not flawless, and is subject to strict limitations that can lead to systematic failures of selection such as change blindness.

Most of the general features of selective and divided attention in animals approximately parallel those same features of selective and divided attention in humans. Nevertheless, although the same general principles apply to multiple species, some of the details differ, and those differences are presumably due to the different environmental demands faced by the species in question. Pigeons and several species of primates, for example, seem to have a bias toward attending to the local aspects of hierarchical organization whereas humans display a global precedence (Cavoto & Cook, 2001). In addition, differential learning rates indicate that pigeons do not learn categories requiring selective and divided attention the same way that humans and other primates do (Smith et al., 2012). The contrast in how these common attentional abilities are implemented in different species are useful, in that they may provide some insights into the evolutionary origins of attention and other cognitive abilities. Smith et al. (2012), for instance, proposed that the category learning differences between pigeons and primates may reflect an important step in the evolution of explicit cognition.

The research reviewed in this chapter suggests that many of the fundamental elements of attention according to contemporary theories of human cognition can be applied in similar fashion to animals. However, one should be careful to not assume that they are universally applicable. In particular, note that most of these theories derive from research specifically on visual cognition in humans. This visual bias in research and theory is perhaps not surprising, given that visual input tends to dominate other modalities in humans (Posner, Nissen, & Klein, 1976). In turn, much of the comparative research motivated by those theories has used variations on the same visual tasks, using animals like pigeons that also show a visual dominance (Randich, Klein, & Lolordo, 1978). Nonvisual tasks or species that do not show such a strong visual bias might or might not produce the same strong parallel. Given that some of the most compelling research on selective and divided attention in humans comes from dichotic listening tasks (e.g., Cherry, 1953), the theoretical importance of auditory attention in animals should not be ignored. In fact, a wide variety of animals are indeed capable of selectively attending to individual features of complex sounds such as quality or location, while ignoring others (Heffner, 1998). Thus, there is evidence that the useful aspects of selective and divided attention can extend to other (nonvisual) sensory modalities in humans and animals. As always, much of the value of comparative psychology will rely on its ability to consider a diverse array of animals and tasks.

Finally, these programs of research have demonstrated that many of the models and theories used to study human attention can be similarly useful in the study of selective and divided attention in animals. Zentall (2013) argued that theories imported from human cognitive psychology might or might not lead to comparable results in nonhuman animals, but they do frequently motivate undeniably useful and informative experiments that would not otherwise have been conducted. In the context of the present topic for example, it is unlikely that research on local/global attention (Fremouw, Herbranson, & Shimp, 1998), the Simon effect (Urcuioli et al., 2005), or feature integration theory (Cook, 1992) would have happened in the same way without the preceding theories of human attention by which they were motivated (Navon, 1977; Simon, 1968; Treisman & Gelade, 1980). Associative learning mechanisms of course, remain an essential foundation for the study of animal behavior, but can and should be tested against predictions made by cognitive theories, such as those developed during the long history of research on selective and divided attention (e.g., Broadbent, 1958). Again, in the context of the research provided here, associative learning by itself might account for some search image effects occurring over slower time scales (Tinbergen, 1960), but the rapid shifts demonstrated in laboratory experiments (Langley et al., 1996) emphasize the usefulness of including attention in an understanding of the phenomenon.

Use of cognitive theories is furthermore appealing from a modern interdisciplinary perspective, in that it embraces potential contributions from other areas of cognitive science. For example, learning theories can benefit from an understanding of biological principles such as natural selection and genetics, which constrain and shape fundamental learning mechanisms (Papini, 2002). It is likely that the study of animal behavior could similarly benefit from concepts from other related fields such as computer science or behavioral economics. Future research will hopefully continue to add to our knowledge about attentional processes in animals and further refine theories that give those data biological and psychological meaning.

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CHAPTER 10

THE COMPARATIVE STUDY OF WORKING MEMORY

William A. Roberts and Angelo Santi

Working, or short-term, memory has been and is being extensively investigated in human and nonhuman animals. Working memory has been studied in a number of species of animals. In a recent review, Lind, Enquist, and Ghirlanda (2015) surveyed studies of working memory in 25 different species of animals, ranging from bees to primate monkeys and apes. Interestingly, they concluded that although there may be some species differences in rate of forgetting over retention intervals, immediate working memory differs little among species. Although evidence for working memory can thus be found throughout the animal kingdom, the focus of this chapter will be on theoretical mechanisms responsible for the retention and forgetting of information in working memory. We report findings mainly with a limited number of species (pigeons, rats, and monkeys) not because these animals are more important or representative than others, but because most of the theoretical research on memory mechanisms has been carried out with these species. To put the comparative study of working memory in perspective, we begin with a brief historical review of research on human working memory and then cover a number of issues in animal working memory.

HUMAN WORKING MEMORY

Although the term *comparative* usually refers to the study of animals (see Volume 1, Chapter 1, this handbook), it is important to consider the differences between the study of human and animal working memory. These differences involve procedure and theory. The American psychologist William James (1890) first suggested that there were two kinds of memory: primary memory and secondary memory. *Primary memory* referred to consciousness or that information that we are currently attending to and constitutes our present awareness. *Secondary memory* referred to the vast amount of information a person has stored in his or her brain but is not currently available to consciousness.

Because one's consciousness or current awareness appears limited, research on primary memory initially focused on its capacity. An early measure of primary memory was the memory span, used as an item on the Wechsler Intelligence Scale. A person was read a list of verbal items (often a digit span) and told to recall them in order (forward, or backward for more difficulty). The number of items that could be correctly recalled 50% of the time was a measure of a person's memory span. G. A. Miller (1956) argued that human primary memory was limited to 7±2 units of information. However, memory capacity could be expanded by the process of chunking. For example, a series of random words might be remembered as a single chunk or unit by combining them into a phrase or jingle.

A further issue concerning primary memory concerned its duration. Current ideas held in primary memory often seem fleeting. In experiments carried out by J. Brown (1958) and by L. R. Peterson and Peterson (1959), people were asked to remember a trigram (three letters that did not form a word). Over retention intervals that varied from 3 to 18 seconds, people showed rapid forgetting of the

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trigram. Importantly, subjects were prevented from rehearsing the trigram by requiring them to count backwards from a high number by threes. Two theories of this rapid forgetting from primary memory are (a) memories decay rapidly unless rehearsed or (b) memories are lost because they are displaced by new memories. Waugh and Norman (1965) presented subjects with lists of random numbers at different rates. After hearing a list, the subject was presented with a probe digit from the list and asked to recall the digit that followed it. Subjects remembered most recently presented numbers best, with rapid loss of memory for earlier numbers in the list. Rate of list presentation had little effect on memory, leading Waugh and Norman to conclude that memories did not decay over time. They argued that forgetting arose primarily through interference from subsequent items.

Waugh and Norman (1965) further suggested that information rehearsed in working memory would be transferred to secondary memory. This idea was formalized by Atkinson and Shiffrin (1968) in their modal model. This model held that information first entered memory through a sensory register, which would vary depending on the sense through which information entered the brain. Although some information would be lost from the sensory register, much of it would enter a *short-term store*. A defining characteristic of the short-term store was that items of information were stored in a rehearsal buffer. The rehearsal buffer contained a limited number of slots within which information could be maintained by a process of rehearsal. However, if new information continued to enter the buffer, old items were necessarily forgotten or displaced from the buffer. Through rehearsal or coding of items in the buffer, information was transferred from short-term store to *long-term store*. Thus, James's primary and secondary memory became short-term and long-term stores in the Atkinson and Shiffrin model. Importantly, the transfer of information between the short-term store and the long-term store operated in both directions. In fact, the short-term store may more often contain information drawn from long-term store than from a sensory register. Our ability to remember the past and to imagine the future relies on information retrieved from long-term store and processed in our immediate consciousness or short-term store (see Chapters 11 and 21, this volume).

The term *working memory* was used by Baddeley and Hitch (1974) to describe their model of short-term memory. The Baddeley–Hitch model differed from earlier conceptions by conceiving of working memory as less of a temporary storage system for information and more as the place where information from the environment and from the long-term store was compared and reorganized (worked on), involving verbal reasoning and prose comprehension. The Baddeley–Hitch model consisted of three components, a phonological loop, a visuospatial sketch pad, and a central executive. Earlier work often suggested that memory for spoken items seemed to be in an "echo-box" or to be remembered as an actual sound. In the phonological loop, recently heard speech was held in a phonemic rehearsal buffer and could be articulated by a kind of "inner voice." This component could also preserve the memory of objects by giving them a verbal label which was then articulated. The visuospatial sketch pad, on the other hand, dealt with the other major realm of human experience, visual perception of objects that were distributed and moved across a spatial field. The role of the central executive was to direct attention to one of these memory buffers or the other, to coordinate information from these two sources, and to manipulate this information, leading to inference and reasoned behavioral decisions (Baddeley, 1992). Thus, as theory developed, early conceptions of primary or short-term memory as a temporary repository for information on its way to permanent storage gave way to the conception of a working memory where very active processing of information from the environment and from long-term memory was carried out.

THE STUDY OF ANIMAL WORKING MEMORY

It could be argued that the study of short-term memory in animals began early in the 20th century. As early as 1913, the comparative psychologist Walter Hunter was interested in whether an animal could maintain the idea of a stimulus after the stimulus had been removed (Hunter, 1913). In his *delayed reaction* experiments, an animal was placed in a compartment from which it could see three doors. The animal could observe a light signal that came on over one of the doors, signalling that a reward was behind the door. However, the animal was not allowed to leave the chamber for some time after the light signal was extinguished. Hunter was particularly interested in how long the animal could wait and still choose the correct door. Rats (*Rattus norvegicus*), racoons (*Procyon lotor*), and dogs (*Canis domesticus*) were all tested on this task, and the percentage choice of the correct door was above chance (33%) for all three species over repeated trials with different doors correct. Species differences were apparent. Although dogs could respond correctly after a delay as long as 5 min, racoons could delay for 25 s, and rats for only 10 s. These findings convinced Hunter that animals could maintain what he called *sensory thought* in the absence of direct stimulation. In the case of dogs, however, he was concerned that their ability to delay for up to 5 min and still choose correctly was mediated by postural orientation. In other words, a dog continued to orient toward the correct door throughout the delay period and then simply ran to the door at which it was pointed.

Hunter's experiments sparked considerable interest. For several subsequent decades, investigators looked for the limits of delayed responding in a number of species of animals. Various techniques were used to prevent an animal from using postural orientation to mediate the delay, some rather extreme, such as anaesthetizing the animal or rotationally spinning it at a high speed. The general outcome of these experiments was that a variety of animals could make accurate delayed responses without postural orientation. An important reason for much of this research was to establish a hierarchy of animals, on the basis of the length of time they could delay and still respond accurately. It eventually became apparent that this was a somewhat futile endeavor, because the length of time an animal could delay and still make the correct response was more dependent on the apparatus and procedure used than on the species of the animal (Roberts, 1998).

Modern readers may be surprised to know that during the period in which considerable research on delayed response was carried out, the word *memory* was rarely used. During the first half of the 20th century, behaviorism and stimulus-response psychology dominated studies of animal learning and behavior. Animals were assumed to learn to make responses to stimuli through Pavlovian or operant conditioning. Even the study of human memory was largely conceived of in terms of the maintenance of stimulus-response associations, with forgetting arising from interference between associations. The cognitive revolution in human psychology began in the 1950s and blossomed during the 1960s. Human memory was now thought of as a number of interconnected information processing systems, such as the Atkinson–Shiffrin and Baddeley–Hitch models previously described. Retention and forgetting arose from retrieval or failure to retrieve information from storage systems.

Undoubtedly heavily influenced by this paradigm shift in the study of human memory, researchers now began to investigate short- and long-term memory in animals (Honig & James, 1971). Although the new work on short-term memory bore a resemblance to the older investigations of delayed response, new techniques were developed that readily avoided the problem of delay mediation by response orientation that plagued earlier studies. The theoretical orientation had also changed. Instead of examining how long animals could delay and respond accurately as a measure of their intelligence, the new research was more interested in what factors promoted retention and forgetting in animals. Thus, retention curves were examined under conditions that varied the way in which animals initially were exposed to information to be remembered, the conditions animals were exposed to during a retention interval, and the stimulation they were exposed to at the retention test.

Delayed Matching-to-Sample

A procedural paradigm called *delayed matching-to-sample* became immensely popular for the study of short-term memory in pigeons (*Columba livia*) and nonhuman primates (see Chapter 15, this volume). Animals were often tested in operant chambers, with stimuli projected on keys or response panels. Figure 10.1 shows the stimuli that

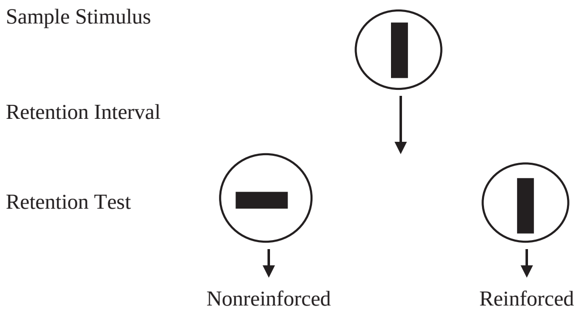

FIGURE 10.1. **Diagram of a delayed matching-to-sample trial in which a sample stimulus (vertical bar) is initially seen and then must be pecked after a retention interval to obtain food reinforcement.**

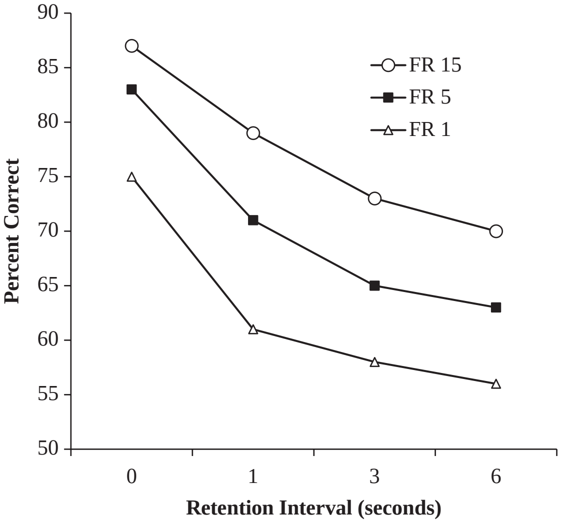

FIGURE 10.2. **Short-term retention curves shown by pigeons after pecking the sample stimulus 1, 5, or 15 times. FR = fixed ratio. Reprinted from "Short-Term Memory in the Pigeon: Effects of Repetition and Spacing," by W. A. Roberts, 1972, *Journal of Experimental Psychology, 94,* p. 76. Copyright 1972 by the American Psychological Association.**

would be presented to a pigeon in a delayed matching experiment. The pigeon faces three keys on which different patterns or colors can be projected, and a peck to any key is recorded by a computer. At the beginning of a trial, only the center key is illuminated with a black vertical bar projected on a white background (the sample stimulus). After the pigeon pecks this key a fixed number of times, a fixed ratio schedule, the key is darkened, and the pigeon must wait during a delay or retention interval to have its memory tested for retention of the sample stimulus. At the end of the retention interval, the side keys are illuminated, one with a vertical bar and the other with a horizontal bar (the comparison stimuli). A peck on the key containing the vertical bar that matches the sample causes a food hopper to operate that allows the pigeon to eat grain reinforcement for a few seconds. Choice of the key containing the horizontal bar, however, leads to termination of the trial without reinforcement. After an intertrial interval of some seconds, a new sample stimulus appears on the center key to begin a new trial. Note that the sample stimulus changes randomly from one trial to the next, making it impossible to respond accurately on all trials by pecking the same comparison stimulus. Further, the left–right positions of the comparison stimuli change randomly from one trial to the next. The beauty of this procedure is that orienting toward and pecking the left or right key would lead to only chance accuracy (50%). The pigeon can only earn reinforcement on the majority of trials by remembering the sample stimulus.

Retention curves were obtained by plotting the percentage of correct choices made on a number of test trials against the retention interval. Figure 10.2 shows a set of retention curves obtained from a delayed matching-to-sample experiment (Roberts, 1972). Notice that the curves represent different conditions in which pigeons had to peck the sample stimulus one, five, or 15 times. As the length of time the pigeon was exposed to the sample stimulus increased, the overall height of the retention curve increased. Pigeons remembered better at every retention interval as the exposure duration increased. Notice also that forgetting takes place quite rapidly over the 6 s retention interval and that the most forgetting takes place early in the retention interval. These findings are similar to those found in human short-term memory experiments (Hellyer, 1962).

The trial diagrammed in Figure 10.1 shows that a correct choice involves choosing the vertical bar comparison stimulus that matches the sample stimulus. Although the experimenter has arranged it so that the correct response matches the sample, this need not be the case. Pigeons can also learn *symbolic delayed matching-to-sample* in which the sample and comparison stimuli come from different dimensions and bear no relationship to one another. Thus, pigeons can readily learn that a red sample requires choice of a vertical bar comparison stimulus for reinforcement and that a green sample requires choice of a horizontal bar comparison stimulus.

The earlier discussion of human working memory outlined the Baddeley–Hitch model in which a central executive directed attention to slave sensory processing systems and integrated their information. Although Honig (1978) used the term working memory to describe the study of short-term memory in animals, and this term has remained in common usage, the theoretical processes associated with working memory in humans are more controversial when applied to studies of animal working memory. Whether animals actively rehearse and transform information in working memory will be discussed in the following sections.

The Radial Maze

The radial maze was introduced by Olton and Samuelson (1976) and has become a very popular tool for the study of working memory in rats (see Volume 1, Chapter 6, this handbook and Chapter 21, this volume). Figure 10.3 shows a top view of a typical radial maze. It consists of eight arms that radiate outward from a central hub, with a reward container placed at the end of each arm. The maze is typically elevated above the lab floor, and rats quickly learn to run down the arms of the maze to collect food rewards. Of particular interest, rats enter all eight of the arms on the maze with little repetition of arms already visited, suggesting that they remember previous visits and avoid re-entering arms where they have already collected the reward. One objection to this interpretation is that rats might be using an algorithm, such as turning right into the arm adjacent to the one just exited, thus obviating the need to remember arms entered. To test this possibility, rats were given a two-phase test. In a *study phase*, a rat was put on the maze with only four randomly chosen arms available (the other four were blocked). In a subsequent *test phase*, the rat was placed back on the maze with all the arms open but food placed on only the arms not previously visited. Rats proved excellent at this task, visiting only the arms containing reward at a high level of accuracy (Zoladek & Roberts, 1978). Although rats show forgetting with the passage of time, they show retention of working memory in this task for several hours (Beatty & Shavalia, 1980). Note that a defining characteristic of this working memory task, as with delayed matching-to-sample, is that the information to be remembered changes on every test trial.

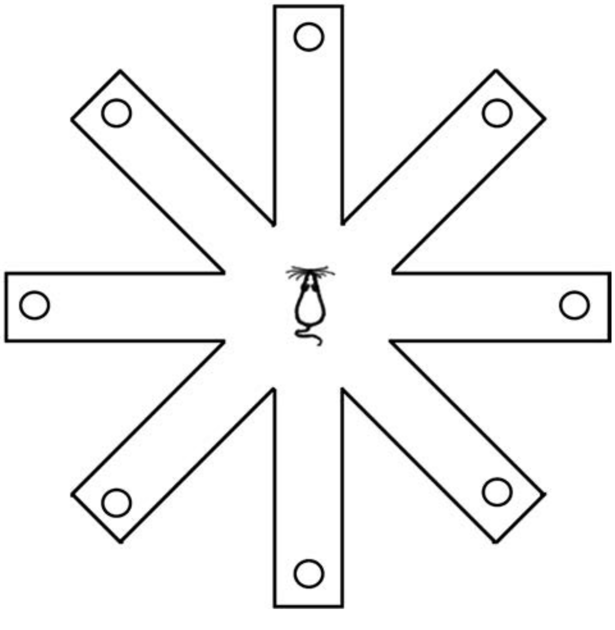

FIGURE 10.3. A top view of a radial maze used to test working memory in rats.

Interference Effects in Working Memory

An early question asked about working memory was whether the events experienced after a memory was formed could interfere with its retention. This form of memory interference is called *retroactive interference*. In the case of animals tested on delayed matching-to-sample in an operant chamber, it was found that the most effective way to create retroactive interference was simply to turn a light on during the retention interval. It was found in capuchin monkeys (*Cebus paella*; D'Amato, 1973) and pigeons (Grant & Roberts, 1976; Roberts & Grant, 1978) that much faster forgetting takes place when a house light was turned on during the retention interval than when animals were left in darkness. One theoretical explanation of this effect is that animals can see stimuli within the chamber when it is lit and that processing new information during the retention interval prevents consolidation of memory of the sample stimulus. The consolidation hypothesis predicts that light introduced at the beginning of a retention interval should cause more forgetting than light introduced at the end of a retention interval, because memory should be at least partially consolidated by end of the retention interval and thus not disrupted by new information. Quite to the contrary, however, it has been found that illumination at the end of the retention interval causes more interference with retention than illumination at the beginning of the retention interval (Calder & White, 2014; Roberts & Grant, 1978). In fact, White and Brown (2011) showed that pigeons actually recover from forgetting induced by light exposure at the beginning of a retention interval. They suggest that temporal distinctiveness is responsible for memory recovery.

Interestingly, rats do not suffer retroactive interference effects when tested on spatial working memory in the radial maze. Rats were forced to enter four randomly chosen arms on an eight-arm maze; before they were given a retention test to see how well they could choose the remaining arms, they were subjected to lights, sounds, a distinctive odor, or feeding in the center of the maze. None of these treatments reduced working memory accuracy relative to control tests with no treatment (Maki, Brokofsky, & Berg, 1979). Roberts (1981) attempted to produce interference by having rats run down arms on a second maze placed beside or on top of the test maze between study and test phases. Even this treatment failed to produce retroactive interference. Only one treatment yielded evidence of interference. After a study phase of entering four arms, rats were placed directly on the ends of the remaining correct arms and allowed to eat a food reward. When given the test phase, rats tended to avoid the now correct arms where they had been previously rewarded. Apparently, rats could recognize these places from the center of the maze, even though they had not run to that location. These findings suggest that rats encode a very precise memory for their location in space and that this memory is little disturbed by new incoming information.

It may be that the greater resistance to retroactive interference by rats on the radial maze than by pigeons in delayed matching-to-sample experiments arises more from a difference between spatial and visual memory than between rats and pigeons. That is, spatial memory may be more robust than visual memory. Compared to visual working memory, studies of spatial working memory indicate a large storage capacity in rats (Cole & Chappell-Stephenson, 2003), food-hoarding birds such as marsh tits (*Parus palustris*; Shettleworth & Krebs, 1982) and Clark's nutcrakers (*Nucifraga columbiana*; Balda & Kamil, 1988), and chimpanzees (*Pan troglodytes*; Menzel, 1973). Spatial working memory can be maintained over long retention intervals in rats (Crystal & Babb, 2008) and birds (Balda & Kamil, 1988; Hitchcock & Sherry, 1990).

THEORETICAL ISSUES IN COMPARATIVE WORKING MEMORY

Whereas theories of human working memory have emphasized active processing of information so that it can be better coded for later retrieval, whether any such processes are involved in animal working memory has been a controversial issue. Can animals actively rehearse new information to improve its retention? Can they transform information into a new code that makes it more memorable? Can they deliberately forget information for which they will have no further need? The following sections address these questions.

Memory for Temporal Durations

Studies of memory for temporal duration in pigeons have typically used a symbolic delayed matching-to-sample task in which a pigeon is trained to peck one comparison stimulus (e.g., red) on trials initiated by a short-sample stimulus (e.g., 2 s) and to peck a different comparison stimulus (e.g., green) on trials initiated by a long-sample stimulus (e.g., 8 s). The durations are typically signalled by illumination of a key light, house light, or feeder light. Following training in this task, retention functions for the temporal samples are obtained within-session by varying the duration between the end of the sample stimulus and the presentation of the comparison stimuli (see Chapter 23, this volume). Numerous studies have shown that at extended delays pigeons respond with high accuracy on trials initiated by the short sample, whereas accuracy on trials initiated by the long sample drops to below 50% correct (see Figure 10.4; e.g., Grant & Spetch, 1991; Spetch & Wilkie, 1983). Thus, this effect is often referred to as the *choose-short effect* because choice of the comparison stimulus mapped on the short sample duration becomes increasingly the preferred response as the retention interval increases.

The study of memory for temporal duration in *rats* has not produced consistent evidence of a choose-short effect. Although some studies have reported a choose-short effect (e. g., Church, 1980; Santi, Weise, & Kuiper, 1995), other studies have reported a choose-long effect (Meck, Church, & Olton, 1984; Santi, Stanford, & Coyle, 1997; Van Rooyen, McMillan, & Santi, 2008). Unfortunately, no single procedural variable or combination of variables appears to be clearly linked to the occurrence of a choose-short or a choose-long bias during delay testing in rats.

In pigeons, on the other hand, the occurrence of a choose-short effect is a robust phenomenon whenever memory for an interval filled with visual stimulation serves as the sample and a choice symbolic matching-to-sample task is used. The initial explanation for the choose-short effect was proposed by Spetch and Wilkie (1983) and was called the *subjective-shortening hypothesis*. According to this hypothesis, the working memory representation of the long sample shortens and increasingly becomes more similar to the representation of the short sample as the delay interval increases. In support of this hypothesis, studies have shown that if instead of training at a 0 s baseline delay, pigeons are trained at a longer baseline delay (e.g., 5 s or 10 s) and then tested at different delays, a choose-short effect is observed at test delays longer than the baseline delay and a choose-long effect occurs at delays shorter than the baseline delay (Spetch, 1987; Spetch & Rusak, 1989). Presumably, the choose-long effect occurs at shorter test delays because the memory representation for the sample appears longer than the foreshortened representation which occurred at the longer baseline training delay.

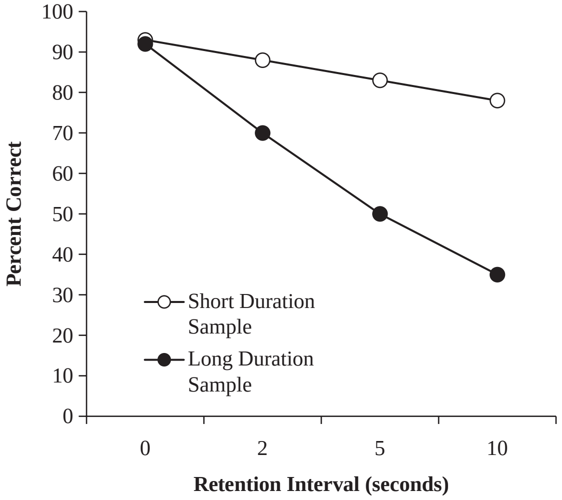

FIGURE 10.4. The choose-short effect in memory for temporal duration is shown by the rapid drop in the long duration sample retention curve caused by increasing preference for the short comparison stimulus as the retention interval becomes longer.

Several alternative accounts of the choose-short effect have been offered. Grant and Spetch (1994) suggested that the effect arose from asymmetric coding in which only the long sample is coded into working memory. In the absence of the long-sample memory, the alternative comparison stimulus (short sample) is chosen by default. Thus, choice of the default stimulus remains high after short samples and increases as the long-sample memory is forgotten. A somewhat similar explanation for the choose-short effect was proposed by Gaitan and Wixted (2000). On the basis of a signal detection approach, they suggested that pigeons respond to comparison stimuli on the basis of their memory for the occurrence of the most salient sample (i.e., the long-sample stimulus). In the absence of a memory for the long sample, the detection model claims that the birds respond to the comparison stimulus associated with the short sample. Unlike the Grant and Spetch model, the detection model holds that the short and long samples are coded but that only the memory of the more salient sample is retrieved.

A quite different explanation of the choose-short effect has been offered by Zentall and his colleagues (Zentall, 1997, 2007). They argue that the choose-short effect arises from methodological artifacts of the procedure rather than from temporal foreshortening in working memory. According to their instructional ambiguity/confusion hypothesis, because pigeons are typically trained in the absence of delays, the delays introduced during testing are novel. As a result, pigeons confuse the novel delays with the intertrial interval, particularly when they share similar ambient illumination conditions (e.g., the house light is either on or off during the intertrial interval and the delay). Consequently, when presented with choice stimuli at the end of a delay, pigeons may respond as if they are in the intertrial interval and no sample stimulus has been presented. Because the absence of a sample is more similar to a short sample than to a long sample, pigeons are biased to respond to the comparison stimulus which is correct for the short sample.

Experiments using a duration-comparison procedure to investigate subjective shortening have also been conducted on humans, pigeons, and rats. In the duration-comparison procedure, rather than being presented with a single-sample duration, as in delayed matching-to-sample procedures, a subject is presented with a standard duration (s) followed by a comparison duration (c), and the subject must make one response if c < s, and another if c > s. The duration-comparison procedure requires the subject to make a relational decision between s and c, so it naturally involves working memory, even if the subject is trained with a 0 s delay between s and c. The initial duration-comparison studies conducted with humans (Wearden & Ferrara, 1993) and with pigeons (Fetterman & Dreyfus, 1986; Fetterman, Dreyfus, Smith, & Stubbs, 1988) reported an increased likelihood of reporting that c was longer than s, as the s–c delay was increased. It is unlikely that the pigeons would have confused the intertrial interval with the s–c delay, because the house light was on during the sample presentation phase as well as during the s–c delay, but not during the ITI. Fetterman, Dreyfus, and Stubbs (1989) suggested that the increase in long responding may have been because of subjective shortening of s over the s–c delay. However, in the Fetterman et al. (1988) study, the increase in long responding could have occurred because pigeons added the s–c delay to c and then compared the total against the duration of s. To minimize this problem, Van Rooyen and Santi (2009) trained pigeons with duration pairs that were constructed so that neither the absolute duration of s or c, nor the total length of a trial provided a reliable cue for responding. Regardless of whether the s–c delay was identical to or different from the intertrial interval, they found that long responding increased as a function of s–c delay length, even on trials in which the duration of c was uninformative with respect to whether a long response was or was not reinforced on training trials. They also reported analyses of their data which made it unlikely that the increase in long responding was because of the pigeons' adding the s–c delay to c and comparing the total against the duration of s. The Van Rooyen and Santi study provided strong evidence in pigeons that the increase in long responding with an increase in s–c delay was due to subjective shortening of s.

Using a similar comparison-duration methodology, Santi, Hoover and Simmons (2011) demonstrated that rats can also acquire relational duration discriminations. As with pigeons, rats exhibited an increase in long responding as the s–c delay was lengthened, even when the illumination condition during the s–c delay differed from that during the intertrial interval. Thus, there appears to be strong evidence for subjective shortening of event duration in working memory in humans, pigeons, and rats, but the occurrence of this phenomenon appears to be complexly affected by procedural variables as well as species differences in some paradigms.

Prospective Versus Retrospective Coding

Note that the accounts of the choose-short effect discussed all suggested that pigeons remembered the initial duration of the sample stimulus. This form of memory is called *retrospective* or *analogical*. Honig and Thompson (1982) suggested that as an alternative to retrospective coding, animals might code sample stimuli into *prospective memories* or instructions on how to respond at the end of a retention interval. Thus, in a symbolic delayed matching paradigm in which a long-sample stimulus requires a response to a green comparison stimulus and a short-sample stimulus requires a response to a red comparison stimulus, the samples might be coded into the instructions "peck green" or "peck red." Although several experimental paradigms have been devised to test retrospective versus prospective coding, we will examine two of them here.

One approach to the coding question has been to vary the discriminability of the sample stimuli and comparison stimuli to determine whether at increasing delays the errors increased more as a function of sample confusability or comparison stimulus confusability. Roitblat (1980) used a choice symbolic delayed matching-to-sample procedure in which different sample colors were mapped on different line tilt comparison stimuli so that the degree of similarity between the colors and the orientation of line tilts was varied. Most of the confusion errors made by the pigeons were due to comparison stimulus similarity and not sample stimulus similarity. As a result, Roitblat concluded that pigeons were retaining a prospective code in working memory, not a retrospective code. Wilkie and Willson (1990) adapted this procedure to study the nature of coding of temporal samples. They trained pigeons to discriminate 2 s, 8 s, and 10 s presentations of house light illumination by pecking red, orange, and green comparison stimuli keys, respectively. Thus, the easy to discriminate samples (2 s vs. 8 s) were mapped on hard to discriminate comparisons (red vs. orange), whereas the difficult to discriminate samples (8 s vs. 10 s) were mapped on easy to discriminate samples (orange vs. green). Wilkie and Willson found that as task difficulty was increased, the change in the discriminal distance scores was consistent with retrospective coding of event durations, not prospective coding. One interpretation of these conflicting findings is that pigeons prefer to code colors prospectively and time durations retrospectively (see Chapter 23, this volume).

Rainer, Rao and Miller (1999) trained rhesus monkeys (*Macaca mulatta*) with a symbolic delayed matching-to-sample procedure in which the confusability of samples and comparison stimuli was varied. Although they did not vary delay length, they found that the monkeys made errors which were related to comparison stimulus similarity rather than sample stimulus similarity. More important, they recorded neural activity in the prefrontal cortex (PF) of the monkeys while they were performing the task and found that during and very shortly after the sample, the firing rate of single neurons in the lateral PF reflected the nature of the sample stimulus. However, toward the end of the fixed delay interval, the neural firing rate in the PF began to reflect the nature of the anticipated comparison stimulus. This result is consistent with lateral PF activity reflecting the prospective coding of visual objects in working memory.

Another approach to the coding question has been to directly or indirectly vary the memory load on the basis of retrospection or prospection. Grant (1982a) trained pigeons to respond to one comparison stimulus (red) after each of three different sample stimuli (red key, 20 pecks on the sample key, or food delivery), and to respond to a different comparison stimulus (green) after each of three different sample stimuli (green, one peck, and no food). During critical test trials, Grant presented the pigeons with the same physical sample stimulus presented three times or the three physically different samples mapped on the same comparison presented once each. Equivalent levels of accuracy were observed for these two trial types, suggesting that a memorial representation of the correct comparison stimulus was being encoded.

Santi and Roberts (1985) trained two groups of pigeons, one group in a one-to-many condition (OTM) and the other group in a many-to-one condition (MTO). In the OTM condition, red and green sample stimuli were followed by one of three sets of comparison stimuli (line tilts, colors, or shapes). In the MTO condition, samples of red, vertical line or circle required a response to a red comparison stimulus, whereas green, horizontal line or triangle samples required a response to a green comparison stimulus. It was reasoned that from a retrospective processing perspective, there should be no difference in difficulty between the OTM and MTO conditions. However, from a prospective processing perspective the MTO condition should be easier than the OTM condition. In the MTO condition, a pigeon must retrieve one response instruction from reference memory which corresponds to the particular sample stimulus being presented. In the OTM condition, a pigeon would need to retrieve three response instructions from reference memory and to maintain all of these codes in working memory until one of them can be used to choose between the particular set of comparison stimuli presented on a trial. The extra load on working memory should often lead to loss of one or more of these codes. As predicted by a prospective processing hypothesis, poorer performance was obtained in the OTM condition compared to the MTO condition. On the other hand, research that manipulated the encodability of sample and comparison stimuli showed evidence for retrospective retention of sample stimuli (Urcuioli & Zentall, 1986).

Evidence for changes in coding strategy as a function of task demands has also been found in studies of spatial memory in rats (Cook, Brown, & Riley, 1985; DiMattia & Kesner, 1984), college students (Kesner & DeSpain, 1988), and pigeons (Zentall, Steirn, & Jackson-Smith, 1990). In the studies with rats, a radial arm maze was used which required visits to a number of arms baited with food. Following acquisition of the task, the rats were tested by inserting a delay interval after different numbers of visits. The initial findings indicated that as the point of insertion of the delay interval increased from a small number of arms chosen to an intermediate number, the probability of making an error increased, but as the insertion point increased to a larger number of arms chosen, the probability of making an error decreased. This error pattern, which has been shown for rats, pigeons, and humans, suggested that subjects are relying on a retrospective memory code when only a small number of spatial choices have been made, but that they rely on a prospective memory code later in the trial when there are only a small number of spatial choices remaining. Although there has been some controversy with respect to this conclusion (M. F. Brown, Wheeler, & Riley, 1989; Gipson, Digian, Miller, & Zentall, 2008), the overall findings with pigeons, rats, monkeys, and humans suggest that they may code either retrospectively or prospectively, depending on which code is most advantageous for the type of memory test they confront.

The Differential Outcomes Effect

Closely related to the issue of retrospective versus prospective coding is the *differential outcomes effect*. In the typical delayed matching-to-sample experiments thus far described, a choice of the correct comparison stimulus mapped on each sample stimulus leads to the same reward. Suppose, however, that choice of each comparison stimulus in a symbolic delayed matching-to-sample experiment led to a different reward. For example, after seeing red as a sample, choice of the vertical lines comparison stimulus leads to delivery of Food A, and choice of the horizontal lines comparison stimulus leads to nonreinforcement; after seeing green as a sample, choice of the horizontal lines comparison stimulus leads to delivery of Food B, and choice of the vertical lines comparison stimulus leads to nonreinforcement. The effect of a differential outcomes manipulation is to substantially increase the rate at which delayed matching is learned and to produce much higher levels of retention on delayed matching tests at long retention intervals (G. B. Peterson, Wheeler, & Armstrong, 1978; G. B. Peterson, Wheeler, & Trapold, 1980). Other variations on differential outcomes are also effective, such as following a sample-comparison choice with reinforcement and the other sample-comparison choice with nonreinforcement. Differential probabilities of reinforcement (e.g., 20% vs. 80%) are also effective.

One explanation for the benefits of differential outcomes is that they arise from participants developing differential reinforcement expectancies that come to be elicited by sample cues (Trapold, 1970). In two-process associative theory, samples become associated with unique trial outcomes and eventually elicit expectancies of the outcomes that then act as cues for the correct choice of a comparison stimulus. In the example given in the previous paragraph, the red sample would elicit an expectancy of Food A, and the Food A expectancy would then cue choice of the vertical lines comparison stimulus ($S_{\text{red}} \rightarrow E_{\text{food A}} \rightarrow R_{\text{vertical lines}}$); similarly, the green sample would elicit an expectancy of Food B, and the Food B expectancy would then cue choice of the horizontal lines comparison stimulus ($S_{\text{green}} \rightarrow E_{\text{food B}} \rightarrow R_{\text{horizontal lines}}$). The mediating expectancy may be thought of as a prospective code that guides choice between the comparison stimuli.

An alternative account of the differential outcomes effect is that the differential outcomes simply increase the discriminability of the sample and comparison stimuli and thus lead to improved learning and memory (Urcuioli, 2005). Several lines of evidence argue against this interpretation and in support of expectancy theory as an account of the differential outcomes effect. One experimental test has been to reverse the outcomes. In our example, suppose that after learning the original mapping of color samples on line orientation comparison stimuli, the choice of vertical lines after the red sample is now reinforced with Food B and choice of horizontal lines after the green sample is now reinforced with Food A. Notice that the relationships between the samples and correct comparison stimuli stay constant; only the outcomes have been reversed. This manipulation should have little effect if these outcomes are just making the sample and comparison stimuli more discriminable. However, in fact outcomes reversal has a major disruptive effect on matching performance, driving it to chance accuracy or below (G. B. Peterson & Trapold, 1980). From expectancy theory, this is quite understandable: The new expectancy elicited by the red sample (Food B) tells the subject to choose the incorrect comparison (horizontal lines), and the new expectancy elicited by the green sample (Food A) tells the subject to incorrectly choose vertical lines.

Another finding that clearly supports expectancy theory is *transfer of control*. Suppose that after pigeons learned delayed matching of vertical lines to a red sample with Food A as the outcome and matching of horizontal lines to a green sample with Food B as the outcome, they were then given the simple task of pecking a blue key for Food A and pecking a yellow key for Food B. After this training, the pigeons are put on a new delayed matching-to-sample problem that involves learning to choose vertical lines after seeing a blue sample stimulus and to choose horizontal lines after seeing a yellow sample stimulus. Because the pigeons have never before encountered these combinations of sample and comparison stimuli, we might expect their performance to be at chance (50%). Quite to the contrary, they immediately match at a high level of accuracy near 90%. Expectancy theory allows us to understand this high level of positive transfer. The intermediate training with blue and yellow keys led pigeons to form a blue→Food A expectancy and a yellow→Food B expectancy. If these expectancies served as the primary cues for the choice of vertical and horizontal lines comparison stimuli in original delayed matching training, then it was these expectancies, and not the blue and yellow samples, that cued correct matching on the transfer test. Thus, the chains of events that led to highly accurate matching were $S_{\text{blue}} \rightarrow E_{\text{food A}} \rightarrow R_{\text{vertical lines}}$ and $S_{\text{yellow}} \rightarrow E_{\text{food B}} \rightarrow R_{\text{horizontal lines}}$. Demonstrations of transfer of control (Urcuioli, 1990; Urcuioli & Zentall, 1992) and the effect of outcome reversal, among other findings, convincingly indicate that expectancies elicited by a sample stimulus (a form of prospective code) guide choices between comparison stimuli (Urcuioli, 2005).

Active Versus Passive Processing in Working Memory

As discussed earlier, models of human working memory emphasize the maintenance of information in working memory through rehearsal and coding. A major question in comparative memory then is whether animals can also develop processes to extend the life of information in working memory. The alternative possibility is that forgetting in animal working memory experiments arises from passive decay (Roberts & Grant, 1976). However, evidence for active maintenance of information in working memory has been suggested by the following empirical results: (a) the improvement in memory as a result of practice, (b) the enhanced memory for surprising events, (c) directed forgetting effects, and (d) serial-position effects.

The improvement in memory as a result of practice. If forgetting in animals was only due to passive decay from working memory, there would be no basis for anticipating that animals could improve their accuracy as a result of experience with long delays. However, Grant (1976) showed that if pigeons are given extended training in delayed matching-to-sample with a sample duration of at least 4 seconds or more, they become capable of above chance matching performance with delays as long as 60 seconds. Not only does training pigeons at fixed delays improve accuracy at longer delays, it also alters the nature of the forgetting function. Sargisson and White (2001) trained four groups of pigeons in a delayed matching-to-sample procedure with a fixed delay interval, either 0 s, 2 s, 4 s, or 6 s, from the start of training. Sufficient training was provided at the longer delays to ensure comparable levels of accuracy in all four groups. The pigeons were then tested at delays of 0 s, 2 s, 4 s, 6 s, 8 s, and 10 s. Matching accuracy remained highest at the training delay but was lower at delays shorter and longer than the training delay. Sargisson and White concluded that the forgetting function is essentially a generalization gradient of choice behavior along the temporal dimension of delay duration. Thus, remembering can be trained and is maximal at the training delay duration but shows decreasing levels of generalization to delays shorter or longer than the training delay. An alternative account of these findings is that pigeons learned to expect a retention test at a particular delay and showed lower accuracy at shorter and longer delays because they were not prepared for the unexpected test at those delays. Additional evidence for the contribution of generalization decrement to forgetting functions was provided by Rayburn-Reeves and Zentall (2009). They found that forgetting functions were significantly shallower for pigeons trained with variable delays than for pigeons trained with a 0 s delay and tested with longer delays. When subsequently tested at even longer delays, the pigeons exhibited a continuous rather than discontinuous decrease in matching accuracy, suggesting that memory loss alone was responsible for the decrease in accuracy at the longer test delays.

Enhanced memory for surprising events. On the basis of a design first used in Pavlovian conditioning experiments with rabbits (*Oryctolagus cuniculus*; Wagner, Rudy, & Whitlow, 1973), Maki (1979) was the first to report enhanced memory in pigeons for surprising sample stimuli. Maki trained pigeons to discriminate between two line tilts, one of which was followed by food (S+) and the other of which was followed by no food (S–). The pigeons had previously been trained in symbolic delayed matching-to-sample to choose a red or a green comparison stimulus on the basis of whether a food sample or a no-food sample had initiated the trial. During subsequent probe trials, these two discriminations were chained together such that S+ signaled samples of expected food or surprising no food and S– signaled samples of surprising food or expected no food. The accuracy of delayed matching was greater for surprising samples than for expected samples.

Grant, Brewster, and Stierhoff (1983) noted that the enhanced accuracy for surprising samples reported by Maki (1979) did not occur early in testing, but only appeared with repeated testing. Although surprising probe trials of S–/food and S+/no-food were always followed by a test of retention, the expected probe trials began with the sequences S+/food and S–/no-food, which on the majority of trials were simple discrimination trials and only occasionally were followed by a retention test. Thus the pigeons may have learned to rehearse the sample on the surprising sample trials but not the expected trials. Grant et al. (1983) introduced procedural modifications to evaluate this hypothesis and found that a surprise effect was present from the outset of testing, thus ruling out the possibility that birds "learned to rehearse" during test trials. They also found that the effect of surprise was more marked at longer retention intervals of 5 s and 10 s than at the 0 s retention interval. In fact, there was little forgetting at all of surprising sample stimuli but marked forgetting of expected sample stimuli. These observations led Grant et al. to conclude that surprise does indeed trigger a rehearsal process that maintains sample information in working memory.

Directed-forgetting effects. Studies with humans have shown that they do not remember items they are told to forget as well as items they are told to remember (Bjork, 1972). This finding suggests that people perform postperceptual processing of information that promotes its retention or loss. In similar experiments with animals, using a directed-forgetting procedure, cues presented after the presentation of a sample stimulus signal whether the trial will end with presentation of the comparison stimuli. A choice test occurs following a remember (R) cue but not after a forget (F) cue. Following training in this procedure, occasional probe trials are presented during which the animal is presented with a choice test between the comparison stimuli after an F cue. Compared to trials with an R cue, pigeons tend to show decreased accuracy on F-cue probe trials (Grant, 1981, 1984; Kendrick, Rilling, & Stonebraker, 1981; Maki & Hegvik, 1980; Santi &

Savich, 1985). In addition, the reduction in accuracy on F-cued probe trials is greater at longer retention intervals (Grant, 1981; Maki & Hegvik, 1980) and when the F cue is presented early rather than late in the retention interval (Grant, 1981; Stonebraker & Rilling, 1981). Directed forgetting has also been found in rats (Grant, 1982b; W. S. Miller & Armus, 1999) and in monkeys (Roberts, Mazmanian, & Kraemer, 1984; Tu & Hampton, 2014; Washburn & Astur, 1998). One account of these findings is that animals perform postsample rehearsal after an R cue but not after an F cue.

Although evidence of a directed-forgetting effect appears to indicate an active rehearsal process in working memory, an alternative perspective has been advanced. Zentall and colleagues (Roper & Zentall, 1993, 1994; Zentall, Roper, & Sherburne, 1995) have argued that nonmemorial processes can account for much of the directed forgetting data. In a majority of studies, an F cue is established by using an omission-training procedure in which neither comparison stimuli nor the opportunity for reinforcement follows the presentation of an F cue. Thus, the drop in accuracy that occurs on F-cue probe trials could be due to a disruption of responding caused by any or all of (a) the unexpected presentation of comparison stimuli, (b) a negative emotional state elicited by an F cue that has been associated with nonreinforcement during training, or (c) inattention to the comparison stimuli. As a result of the limitations of the omission procedure, a number of studies have used *substitution procedures* in which F-cued trials end with a memory test. Substitution procedures involve F-cued training trials that terminate in the presentation of one or more discriminative stimuli and thus provide opportunity for reinforcement on some proportion of the trials. The substitution stimuli may be two cues unrelated to the sample and comparison stimuli, with choice of one cue (S+) yielding reinforcement. Although directed-forgetting effects have been found in some experiments using substitution procedures, Roper and Zentall (1993) argued that the effect arises because the substitution procedure establishes a pattern of responding on F-cued training trials that is incompatible with accurate responding to comparison stimuli during test trials. However, Roper, Kaiser, and Zentall (1995) showed convincingly that F cues lead to poorer retention than R cues when the F cues serve as sample stimuli for choice between an alternate set of comparison stimuli.

Evidence for directed forgetting when a substitution procedure was used was reported by Grant and Soldat (1995). They used a training procedure in which the R cue and the F cue were associated with the same probability of end-of-trial reinforcement and pattern of discriminated test responding. As a result, the F-cue effect could not be due to the F cue triggering negative affect, indiscriminate responding, failure to attend to test stimuli, or a pattern of responding incompatible with accurate matching performance. Grant and Soldat obtained an F-cue effect and concluded that their results provided additional evidence that an F cue terminates the active maintenance of information coded in working memory.

Tu and Hampton (2014) studied directed forgetting in rhesus monkeys in which memory for the sample stimulus was tested following R-cues, and a visual object discrimination was presented following an F cue. In addition to the standard F-cue probe trials, they included R-cue probe trials, in which the R cue was followed by an unexpected discrimination test. This was done to assess whether the accuracy decrement on F-cue probe trials was due to reduced maintenance of memory for the sample, or to disruption because of the presentation of an unexpected test. Although Tu and Hampton obtained a directed-forgetting effect which could not be explained by nonmemorial factors, they also noted this finding did not conclusively establish that the R cue engaged an active rehearsal of the sample in working memory, because it was possible that the F cue generated a prospective memory for the target of the discrimination problem presented on substitution trials. This prospective memory code could have displaced memory for the sample stimulus initially presented at the beginning of the trial and resulted in reduced accuracy on F-cue probe trials (i.e., an interference effect rather than a change in rehearsal). To reduce the likelihood of this prospective coding, Tu and Hampton trained the monkeys with multiple randomized discrimination tests following the F cue and still produced a strong directed-forgetting effect. In a final experiment, they presented two consecutive samples followed by a single cue and tested memory for both of the presented samples. Monkeys demonstrated generalized use of the R and F cues to the tests with two-item lists, showing superior accuracy on R-cue probe trials compared with F-cue probe trials.

Serial-position effects. The serial position function is a ubiquitous empirical finding in studies of human list-memory. It is characterized by a primacy effect, which leads to good memory for the first items in the list, reduced memory for items in the middle of the list, and a recency effect, which leads to good memory for the last items in the list. According to the Atkinson and Shiffrin (1968) modal model of memory, the primacy effect arises because the initial items in a list are rehearsed more in the short-term store than subsequent items and thus are more frequently transferred to permanent memory in the long-term store. The recency effect was accounted for by the immediate recall of items just placed in the short-term store.

Early attempts to find a primacy effect in list memory with animals failed and suggested that only humans possessed a rehearsal mechanism that resulted in a primacy effect. Sands and Wright (1980a, 1980b) were the first to report evidence for a primacy effect for lists of visual items in a rhesus monkey. After observing a list of 10 visual images, a monkey's memory was probed by presenting it with an image that was or was not in the list, and the monkey had to move a lever in one direction for a "yes" response and in the opposite direction for a "no" response. Serial position curves obtained when images from each serial position were probed on test trials are shown for monkey and human subjects in Figure 10.5 and clearly show primacy and recency effects for both species. Since these findings, primacy and recency effects have been reported for a number of species including chimpanzees (Buchanan, Gill, & Braggio, 1981), rhesus monkeys (Basile & Hampton, 2010; Castro & Larsen, 1992; Wright, Santiago, Sands, Kendrick, & Cook, 1985); squirrel monkeys (*Saimiri sciureus*; Roberts & Kraemer, 1981), capuchin monkeys (Wright, 1999), dogs (Craig et al., 2012), rats (DiMattia & Kesner, 1984; Harper, McLean, & Dalrymple-Alford, 1993; Williams, McCoy, & Kuczaj, 2000), black-capped chickadees (*Parus atricapillus*; Crystal & Shettleworth, 1994), and pigeons (Santiago & Wright, 1984; Wright et al., 1985).

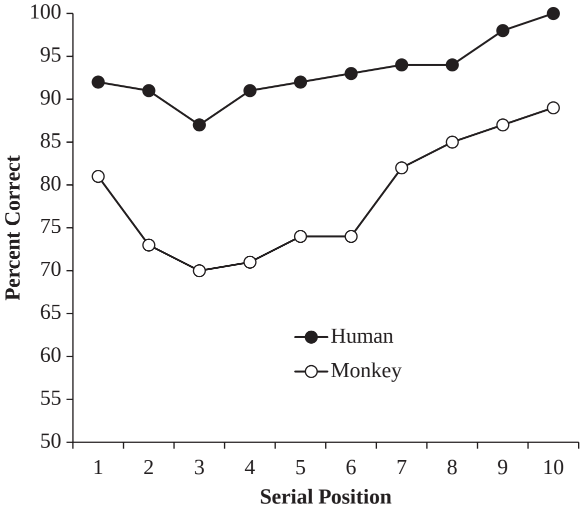

FIGURE 10.5. Serial position curves for a human and rhesus monkey subject showing primacy and recency effects. Reprinted from "Serial Probe Recognition Performance by a Rhesus Monkey and a Human With 10- and 20-Item Lists," by S. F. Sands and A. A. Wright, 1980, *Journal of Experimental Psychology: Animal Behavior Processes, 6,* p. 390. Copyright 1980 by the American Psychological Association.

Visual-list memory in humans is improved by increasing the interval between items (i.e., ISI), an effect attributed to the greater opportunity to rehearse items (e.g., Intraub, 1980). Unlike humans, however, monkeys do not benefit from increasing the ISI between items in a visual-list memory task (Cook, Wright, & Sands, 1991; Roberts & Kraemer, 1984). This observation suggests that monkeys do not engage in rehearsal between items and that primacy effects in visual-list memory experiments may not be due to a rehearsal process. Furthermore, rhesus monkeys, capuchin monkeys, pigeons, and humans tested with four-item lists of visual images show the same changes in their serial position functions as the retention interval is systematically varied (Wright, 2007, 2013). Although there are differences among the four species in the retention intervals at which changes in the serial position function occur, for all species increasing the retention interval strengthens the primacy effect and weakens the recency effect.

Wright (2007) argued that these systematic changes in serial position functions are the result of the opposing effects of proactive interference (past items preventing the recall of recent items) and retroactive interference (recent items preventing the recall of past items) over time. Wright's model suggests that at short retention intervals, retroactive interference is strongest and thus suppresses memory for initial items. At long retention intervals, proactive interference is strongest and suppresses memory for later items. Memory for the middle items is poorest because they are subject to proactive and retroactive interference. Basile and Hampton (2010) reported serial position effects in rhesus monkeys which they argued are difficult to explain using the interference account. In their study, robust primacy and recency effects were obtained when monkeys were tested with items drawn from small (six) and medium (60) image sets, but not from very large image sets (2400). In addition, the serial position curves were stable across various retention intervals (0.2 s–50 s). Basile and Hampton suggested that the images in the small and medium sets were more familiar because of repeated presentation and thus were easier for the monkeys to rehearse, contributing to a primacy effect.

Unlike the visual-list memory effects previously described, increasing the retention interval in an auditory-list task with rhesus monkeys produces a different pattern of serial position changes. That is, the primacy effect weakens with longer retention intervals, whereas the recency effect gets stronger (Wright, 1998). These findings create further difficulties for the idea that primacy effects are due to differential rehearsal of early items in a list. Although the differences in serial position functions for visual and auditory lists in rhesus monkeys is not completely understood, there is some empirical support for the operation of time-dependent proactive and retroactive interference effects in auditory-list memory (see Wright & Roediger, 2003).

RECENT FINDINGS IN COMPARATIVE WORKING MEMORY

Two recent areas that provide new insights into comparative working memory are change detection and interaction between memory systems.

Change Detection

Visual working memory has been increasingly studied in humans using a change detection task (Luck & Vogel, 2013; see also Chapter 9, this volume). A briefly shown array of items is followed by a blank retention interval and then a test array is presented. The subject is required to indicate the presence or absence of a change, and, in the case of a change, the subject may be asked to identify the specific item which changed. Recent studies have demonstrated that rhesus monkeys (Elmore et al., 2011; Heyselaar, Johnston, & Paré, 2011) and pigeons (Gibson, Wasserman, & Luck, 2011; Wright et al., 2010) are capable of performing a change detection task using experimental procedures that are very similar to those used with humans. As the complexity of visual objects increases, humans and pigeons exhibit a decrease in change detection performance (Magnotti et al., 2013).

The study of change detection in nonhuman animals is important for the insights that it can provide on theoretical controversies regarding capacity limitations in working memory. Traditionally, research and theory on human working memory has maintained that there is a capacity limitation of approximately 4±1 unrelated items (Cowan, 2001; Luck & Vogel, 1997). Although the concept of a limited working memory capacity is not in dispute, the idea that there are a limited number of slots (i.e., the "discrete-slot" model) has recently been strongly challenged by a "continuous-resource" model in which visual working memory is viewed as a limited resource that is distributed among many items, resulting in a noisy internal representation of each item (Luck & Vogel, 2013; Ma, Husain, & Bays, 2014). On the basis of a comparison of change detection performance in humans and rhesus monkeys using almost identical experimental procedures and analytical techniques, Elmore et al. (2011) derived capacity estimates of approximately three items for humans and one item for monkeys. Other analyses, however, led Elmore et al. to reject a fixed-capacity model in favor of the continuous-resource model. For example, monkeys showed confusion in change detection between similar colors (purple and blue) but not between more dissimilar colors (red and green). Fixed-capacity models hold that an item is either perfectly stored and not confusable or not stored at all. Color confusion is more understandable from the idea that all items are stored within a noisy representation in which items of similar appearance will be more difficult to discriminate from one another. By applying a signal-detection model on the basis of memory as a continuous resource, they showed that memory accuracy (d') declines as an inverse power law function of display size in humans and monkeys (Elmore & Wright, 2015). The lower memory capacity found in monkeys is explained not by an inability to store as many visual items as humans but by reduced attention to these items that causes increased difficulty in extracting a signal from a noisy representation.

Interaction Between Memory Systems

A phenomenon familiar to most people is confusion between working memory and more permanent reference memory. A friend may give you his/her new telephone number which you rehearse several times in working memory. If soon thereafter you need to call your friend, you will dial the new number. If some time goes by before you call, it is very likely that you will revert to calling the old number that you have habitually used in the past. Thus reference memory interferes more and more with working memory as the retention interval increases. Well learned memories or habits are often described as implicit, automatic, and unconscious, whereas memories for more recent one-time events are described as explicit and conscious. Jacoby (Hay & Jacoby, 1996; Jacoby, 1991) developed the *process dissociation procedure* (PDP) to compute the strength of working memory and reference memory or habit in tasks that vary learning and retention variables. Application of PDP equations to memory experiments with humans indicates the independence of working and reference memory systems. Thus, variables that determine the strength of a habit, such as repetition, affect only reference memory scores and not working memory scores. Variables that cause loss of working memory, such as retention interval, affect working memory scores, and not reference memory scores.

Recent research suggests that similar memory system competition and interaction may be found in animals. A key feature of the PDP approach is that it uses *oppositional testing* of memory. That is, on some trials working and reference memory dictate the same response; working and reference memory are said to be congruent. On other trials, working and reference memory may be put in opposition, as they dictate different or incongruent responses. Tu and Hampton (2013) used a delayed matching-to-sample task to test working memory in rhesus monkeys. Monkeys were shown a clip-art image on a screen as a sample stimulus and then had to select that image from among four comparison images for a reward. Habit or reference memory was manipulated by presenting different sets of four test images (quads) so that a given image was the correct choice on 100%, 75%, 50%, or 25% of the training trials. Thus, on different tests, the correct image that matched the sample corresponded to a relatively strong habit image (congruent) or corresponded to a relatively weak habit image (incongruent). Tu and Hampton found results very similar to those obtained with humans. When the retention interval was increased, one-trial working memory PDP scores dropped but reference memory PDP scores were unaffected. When the probability of a sample-match pair was varied between 25% and 100%, reference memory or habit PDP scores increased but working memory PDP scores remained unchanged.

Roberts, Strang, and Macpherson (2015) have recently extended the study of memory systems interaction to the pigeon. Pigeons were initially trained to perform a symbolic delayed matching-to-sample task. A pigeon was required to make 10 pecks on a red or green sample stimulus to advance to the retention test. On the retention test, the pigeon was presented with comparison stimuli consisting of vertical lines on one key and horizontal lines on another key, with a peck on vertical lines reinforced after the red sample and a peck on horizontal lines reinforced after the green sample. Once pigeons had learned to match at 90% accuracy, they were given 64-trial reference memory training sessions on a visual discrimination in which only vertical lines and horizontal lines were presented on each trial, and choice of one of these cues (say vertical lines) was always rewarded. After each daily session of discrimination learning, pigeons were tested on delayed matching at retention intervals of 0 s, 3 s, 6 s, and 10 s on the next daily session. The important thing to notice in this experiment is that on trials when a red sample was presented, working memory and reference memory were congruent because they both indicated choice of vertical lines on the memory test. On trials when a green sample was presented, however, working memory and reference memory were incongruent because the sample stimulus cued choice of the horizontal lines comparison stimulus but the discrimination learning trials (reference memory) cued choice of the vertical lines comparison stimulus.

The results of this experiment are shown in Figure 10.6. It plots accuracy of delayed matching for congruent and incongruent trials as a function of the retention interval. The left panel shows performance on the first session of testing, and the right panel shows performance on all five sessions of testing. Notice that the effect of congruency is small at the short retention intervals and grows as the retention intervals get longer. In other words, working memory dominates when it is relatively strong at short intervals, but reference memory dominates at the longer intervals as working memory weakens. The other thing to note in Figure 10.6 is that the curves taken after just one session of discrimination training (left panel) look much the same as the curves shown for the average of all five sessions. It appears that competition between working and reference memory develops quite early in reference memory formation.

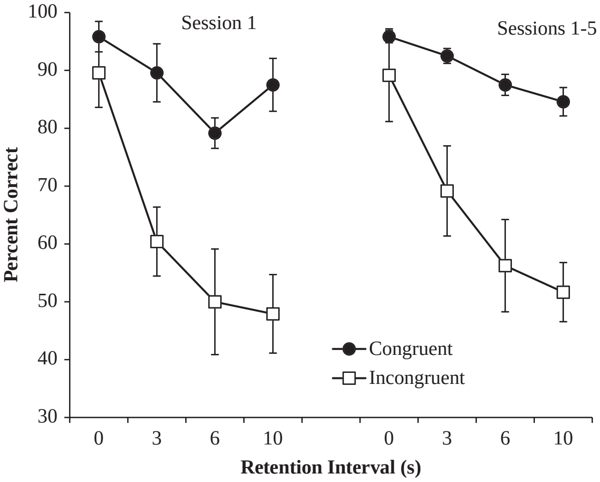

FIGURE 10.6. Tests of working memory in pigeons when working memory and reference memory are congruent and incongruent. Reprinted from "Memory Systems Interaction in the Pigeon: Working and Reference Memory," by W. A. Roberts, C. Strang, and K. Macpherson, 2015, *Journal of Experimental Psychology: Animal Behavior Processes, 41,* p. 154. Copyright 2015 by the American Psychological Association.

Further experiments with pigeons showed that working memory and reference memory were independent. When exposure time to the sample stimulus was varied, a PDP analysis showed it affected working memory but not reference memory. When the level of discrimination learning was varied through variation in the probability of reinforcing vertical and horizontal lines during discrimination learning, the PDP analysis showed it affected reference memory but not working memory. Thus, it appears that independent working and reference memory systems compete and interact in humans, monkeys, and birds.

CONCLUSION

The study of comparative working memory has expanded vastly since the early studies of delayed response. In many ways, more recent studies of short-term or working memory show strong similarities between humans and other species of animals. Recent work indicates that change detection memory varies in capacity between monkeys and humans but this difference can be explained by differences in noise within a continuous-resource model. Serial position curves showing primacy and recency effects were once thought to be unique to human working memory but now are commonly found in monkeys, rats, and pigeons. The interactive competition between independent working and reference memory systems familiar to humans has now been shown in monkeys and pigeons. Other research suggests that animals do not just passively encode events and forget them as they decay. Although decay may be one process leading to forgetting of working memory, evidence has accumulated suggesting that animals process information in various ways that improve its chances of being remembered or forgotten. Thus, remember and forget cues lead to substantial differences in performance on retention tests. Surprising events appear to be remembered better than expected events through a process of postsample stimulus rehearsal. Animals appear to recode sample stimuli into memory codes that improve retention. Evidence for prospective coding suggests sample information may be recoded into a response instruction or into an outcome expectancy that guides choice between comparison stimuli. Very exciting new work recording neural firing in an animal's brain is revealing evidence online about working memory codes (Browning, Overmier, & Colombo, 2011; Milmine, Watanabe, & Colombo, 2008; Rainer et al., 1999; Rose & Colombo, 2005; Veit, Hartmann, & Nieder, 2014). Clever behavioral designs combined with new neural recording technology promise to yield further important insights into comparative working memory processes.

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CHAPTER 11

EPISODIC-LIKE MEMORY AND MENTAL TIME TRAVEL IN ANIMALS

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As the White Queen assiduously remarked to Alice in Lewis Carroll's poignant tale *Alice Through the Looking Glass*, "it's a poor sort of memory that only works backwards." Our personal memories of the past are intimately entwined with our thoughts about the future precisely because we rely on our episodic cognition, our mental time travel system, to reminisce, and that is one reason why our memories need to travel forward as well as backward in time.[1] Mental time travel refers to the ability to project the self in time, to remember the past (episodic memory), to imagine future scenarios (episodic future thinking), and in so doing to re-experience and often re-evaluate our memories of what we have experienced. There are two important points to note here. The first is the distinction between episodic cognition and semantic knowledge, which Tulving (1983) coined *remember-know*. Episodic cognition is concerned with memories and preremembrances about the past and future respectively, which is necessarily subjective and involves the projection of the self in time and space. By contrast semantic, or factual, knowledge of the past and future does not necessarily require an awareness of the projection of the self or time and largely consists of a series of selfless timeless labels (the obvious exception being the semantic knowledge of one's birth date, which is not accompanied by any episodic remembrance of one's actual birth). To illustrate this distinction between semantic knowledge and episodic cognition, consider the following example: I know that Rambert is England's flagship touring dance company and that its dancers are trained in contemporary dance and ballet—these are semantic facts about the world. My memories of working at Rambert, however, are largely episodic, involving personal memories of what I have experienced in my role as scientist in residence with the dance company.

At the phenomenological level, the episodic cognition system contains two key features that the semantic knowledge system does not, namely an awareness of the subjective sense of time, of re-experiencing now an event that happened in the past (*chronesthesia*; Tulving, 2002), coupled with an awareness of being the author of these memories and forethoughts (*autonoesis*; Wheeler, 2000). This idea that remembering involves the subjective projection of self in time was captured succinctly in the famous quote by William James (1890): "Memory requires more than the mere dating of a fact in the past. It must be dated in *my* past" (p. 6509).

The second important point to note is that there has been considerable debate as to whether mental time travel is uniquely human (e.g., Suddendorf & Corballis, 1997), or whether we share this cognitive ability with other animals (e.g., Clayton, Bussey, & Dickinson, 2003; Corballis, 2013, 2014). The issue is not about whether animals can store, process, and retrieve information about the past, but rather whether they use episodic cognition, the mental time travel system, to do so. One problem is that, in the absence of any agreed behavioral markers of consciousness in nonlinguistic animals, it is not

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[1] A second reason is that humans also have prospective memories, which is the ability to remember to do something in the future (e.g., making a mental note in the morning to buy a bottle of wine on the way home from work for a dinner party that evening).

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possible to evaluate empirically whether or not the phenomenological aspects of mental time travel, namely autonoesis and chronesthesia, are unique to humans (Griffiths, Dickinson, & Clayton, 1999).

What we can do, however, is to focus on the behavioral criteria, and this has been termed *episodic-like memory* to explicitly acknowledge that such criteria are entirely on the basis of behavior and ignore the possible involvement of phenomenological consciousness (Clayton, Bussey, & Dickinson, 2003; Clayton & Dickinson, 1998; Griffiths et al., 1999). My colleagues and I have argued that the retrospective component, episodic-like memory, needs to fulfill three criteria to meet the behavioral properties of episodic memory as defined for humans: namely content, structure, and flexibility (Clayton, Bussey, & Dickinson, 2003). First, the subject must remember what happened where and when on the basis of a single past experience. The what, when, and where components are in fact inspired by Tulving's (1972) original definition of episodic memory, which emphasized the spatio-temporal relations between events, and the single past experience acknowledges the fact that episodic memories are encoded automatically (see Morris & Frey, 1997). Second, the what, where, and when components are integrated into a bound structure, which allows the subject to discriminate between similar episodes that occurred at different times and/or places. Finally, the information must show flexible deployment so that the information contained in the memory can be updated at a later date and the information can be generalized across situations.

In the next section of this chapter I review the evidence that some nonhuman animals do have episodic-like memory. I then evaluate the extent to which they can also plan for the future. This is an important question because a key prediction is that if the processes involved in episodic-like memory do engage the mental time travel system then it necessarily follows that any subject that uses episodic-like memory to recall the past should also be able to think about the future and plan for it accordingly. Indeed, human cognitive neuroscience supports this claim about the relationship between episodic memory and forethought in two ways. The first is by demonstrating that patients who are unable to remember the past are also impaired in their ability to imagine the future, even when they have access to a semantic knowledge of past and future (e.g., Klein, Loftus, & Kihlstrom, 2002; Rosenbaum et al., 2005), and that hippocampal amnesics are impaired in their ability to imagine and construct future scenes (e.g., Hassabis, Kumaran, Vann, & Maguire, 2007; see also Volume 1, Chapter 25, this handbook). The second is that fMRI studies of healthy human subjects show that the same patterns of brain activation are found when they are asked to remember the past and imagine the future (e.g., Schacter, Addis, & Buckner, 2007, 2008; Schacter et al., 2012).

In the final section, I discuss whether such prospective cognition must engage the same cognitive process as that involved in episodic-like memory, namely whether future planning relies explicitly on episodic-like future thinking. For, if the ability to plan for the future need not necessarily involve episodic cognition, then perhaps we need to rethink the behavioral criteria for future planning and their relationship to mental time travel.

EPISODIC-LIKE MEMORY IN ANIMALS

The work on episodic-like memory in animals began with a series of studies that investigated the mnemonic abilities of western scrub-jays (*Aphelocoma californica*). Like many food-caching animals, these birds are renowned for their ability to hide food caches and remember where they have been hidden (Vander Wall, 1990). At issue is whether the birds could episodically recall specific past caching episodes in terms of what happened, where it happened, and when it happened (Clayton & Dickinson, 1998).

Corvids Remember Specific Past Caching Episodes

The experiments capitalized on the fact that these birds readily hide perishable items such as worms that degrade over time as well as nonperishable nuts, and as they do not eat rotten worms, they recover the perishable food caches only when the worms are fresh. To investigate whether or not the scrub-jays can remember which foods they have hidden where and how long ago, the birds were given the opportunity to cache worms and peanuts and then recover these caches either after a short delay of 4 hr or a long delay of 124 hr (i.e., 5 days plus 4 hr). This procedure ensured that the birds were tested at the same time of day in both conditions so that they could not use a circadian rhythm (see Volume 1, Chapter 29, this handbook) to discriminate between short and long delays but instead had to remember how long ago the caching event had occurred. There were two groups of birds, both of which had been hand-raised to ensure that they could not have learned beforehand about whether or not the worms perish. The degrade group had the opportunity to learn across four trials that the worms were fresh after the short delay, but that the worms had degraded by the long delay. By contrast, for the replenish group, at the long delay the worms were replaced with new worms to ensure that the birds always received fresh worms at both delays (Figure 11.1).

Although the jays had no cue to predict whether or not the worms had perished other than the passage of time between caching and recovery, the birds in the degrade group rapidly learned that the highly preferred worms were still fresh when recovered 4 hr after caching, whereas after 124 hr they had perished. Consequently, the jays avoided the wax worm caches if they had been cached 124 hr earlier, and

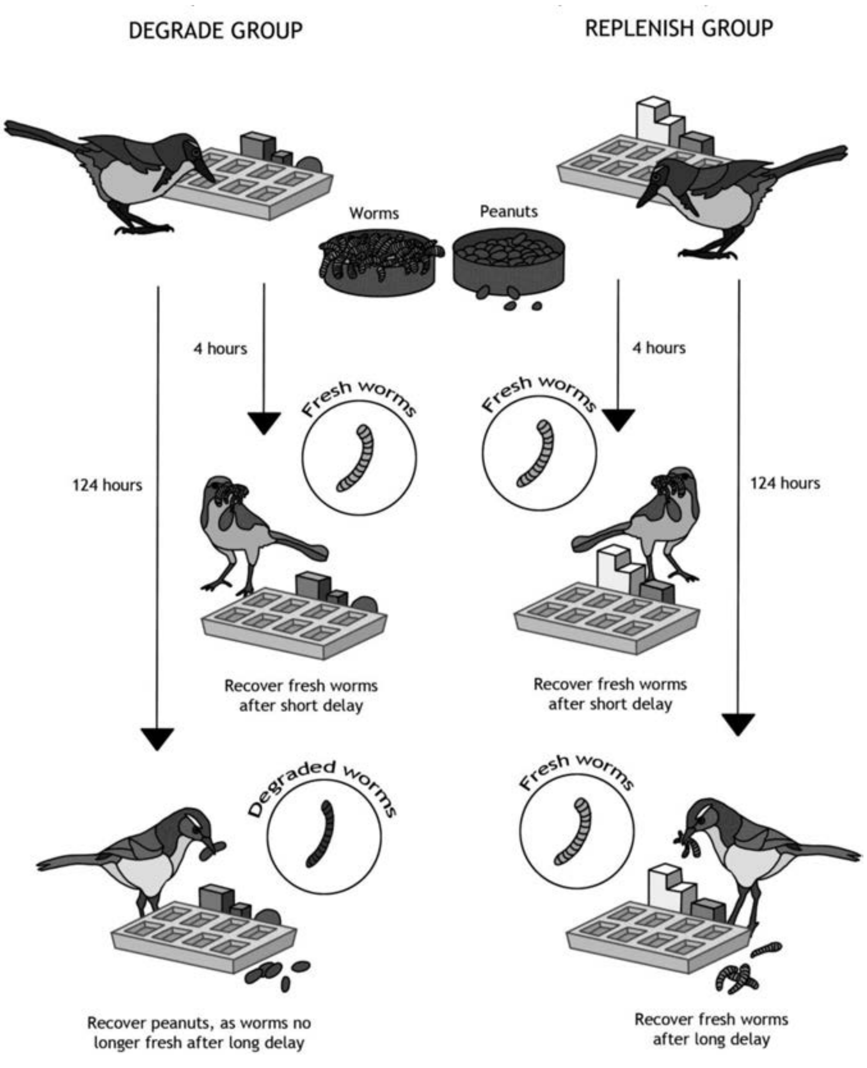

FIGURE 11.1. The design of Clayton and Dickinson's (1998) experiment to test whether western scrub-jays can remember what they cached where and when.

instead only recovered and ate the peanuts, which do not perish. The replenish group continued to recover the worms after both delays because their worms never perished.

After the birds had received this experience of caching and recovering worms and peanuts after the short and long delays, test trials were introduced in which the food was removed prior to recovery to ensure that the birds relied on their memory of what they had cached where and how long ago as opposed to olfactory or visual cues emanating directly from the food (Figure 11.1). On these test trials the birds clearly remembered what they had cached, where, and how long ago. The replenish group continued to search in those sites in which they had cached the worms after both delays, whereas the degrade group searched in those sites in which they had cached worms after the short delay, but switched to searching in those sites where they had cached the nuts after the long delay (Clayton & Dickinson, 1998). The fact that only the degrade group switched their searching behavior suggests that the scrub-jays were able to remember what happened, where, and how long ago, and the fact that the replenish group continued to search for worms after the long delay demonstrates that the switch in behavior shown by the degrade group could not be explained by the birds forgetting the worm caches after the long delay.

Subsequent tests have revealed that the jays also remembered which types of perishable foods they have hidden where and how long ago, irrespective of whether the foods decayed or ripened (Clayton, Dally, Gilbert, & Dickinson, 2005; Clayton, Yu, & Dickinson, 2001; de Kort, Dickinson, & Clayton, 2005). The birds also kept track of which individual was watching when they cached (see Chapter 32, this volume), and protect those caches accordingly (Dally et al., 2006), for example by rehiding those caches once the potential pilferer has left the scene (Dally et al., 2006; Emery & Clayton, 2001). The jays also discriminated between similar episodes that occurred at different times and places, demonstrating that they formed integrated what, where, and when components (Clayton et al., 2001), thereby satisfying the structural component of episodic-like memory as well as the content criterion (Clayton, Bussey, & Dickinson, 2003).

Clayton, Yu, and Dickinson (2003) also found that the jays could update and generalized across situations, and therefore that these episodic-like memories also met the flexible deployment criterion. They tested this by allowing the birds to cache and recover perishable and nonperishable foods using an interleaved procedure in which the birds cached in different trays on three subsequent days, and only once they had completed the caching trials did the birds receive the opportunity to recover their caches from each tray. If the birds were capable of the flexible deployment criterion for episodic-like memory, then they should be able to update their knowledge about the rate of perishability of the food and consequently change their search behavior at recovery accordingly, even though the episodic information about what they cached where and when was encoded prior to the acquisition of the new knowledge about the decay rates. This is precisely what the birds did. When the jays cached perishable and nonperishable items in different locations in one tray and then subsequently discovered that the perishable items from another tray had degraded more quickly than they expected, the birds immediately switched their search preference in favor of the nonperishable nuts when given the original tray back. The birds continued to search for the perishable food if it had been cached recently, thereby showing that they had not simply developed a general aversion to searching for food that might rot. As far as I am aware, this is the only published demonstration of the declarative flexibility with which animals can update their information after the time of encoding (Clayton, Yu, & Dickinson, 2003).

Episodic-Like Memory in Other Animals

A number of other laboratories have subsequently investigated whether or not animals have episodic-like memory using paradigms analogous to those used with the scrub-jays. There is now good evidence that a diverse range of animals can remember the what, where, and when of past events including rats (*Ratus norvegicus*; Babb & Crystal, 2006a, 2006b), mice (*Mus muscularis*; Dere, Huston, & De Souza Silva, 2005), meadow voles (*Microtus pennsylvanicus*; Ferkin, Combs, delBarco-Trillo, Pierce, & Franklin, 2007), magpies (*Pica pica*; Zinkivskay, Nazir, & Smulders, 2009), chickadees (*Poecile atricappillus*; Feeney, Roberts, & Sherry, 2009), chimpanzees (*Pan troglodytes*), orangutans (*Pongo abeli*), and bonobos (*Pan paniscus*; Martin-Ordas, Haun, Colmenares, & Call, 2010) and most recently cuttlefish (*Sepia apama*; Jozet-Alves, Bertin, & Clayton, 2013). All of these studies focused on the content criterion for episodic-like memory,[2] however, so it remains unclear as to whether they also satisfy the structure (integrated binding of what, where, and when memories) and flexible deployment criteria.

Other researchers have focused on the animal's ability to remember what happened, where, and in which context as opposed to the temporal component of when. There is now a large body of evidence to suggest that rodents form accurate what, where, and which memories of past events (e.g., Eacott & Easton, 2010; Eacott & Norman, 2004; Easton, Webster, & Eacott, 2012; Easton, Zinkivskay, & Eacott, 2009).

Of course the critic would argue that these what-where-and-when and what-where-and-which memories in animals need not involve mental time travel. In the absence of any agreed behavioral markers of consciousness in nonlinguistic animals there is no way of knowing whether or not nonhuman animals possess the phenomenological aspects of conscious awareness, namely autonoesis and chronesthesia, that accompany this form of remembering in humans. Absence of evidence is not evidence of absence, however, and consequently it remains an open question as to whether or not these episodic-like memories in animals rely in the same cognitive processes as the recollection of episodic memories in humans do.

In acknowledgement of this, other comparative psychologists, such as Zentall, have taken a different approach to studying episodic-like memory in animals, namely asking whether the animal can spontaneously recall "unexpected" information about a past event given that a fundamental feature of episodic memory in humans is the "automatic recording of attended information" (Morris & Frey, 1997, p. 1489).

Asking an Unexpected Question

Zentall, Clement, Bhatt, and Allen (2001) argued that the problem with the studies on episodic-like memories in animals is that the subjects have necessarily received a series of training trials in which they have effectively been trained to remember what, where, and when or what, where, and in which context. Although the stimuli on any given test trial are trial-unique and therefore must be episodically encoded, if the animal can generalize across tests then, in principle, the animal could predict the question that is likely to be asked on the test trial (e.g., "What did I hide where and when?"; "In which context was I when I encountered the object in that particular place"). Zentall et al. argued that with such knowledge, an individual can prepare accordingly, just as humans do when making a prospective memory of what will need to be recalled later. When the subject is asked an expected question, however, that individual does not have to go back mentally in time to revisit the memory and recall the details about what happened. Instead, they could simply recall what they had aimed to remember. Zentall at al. developed a paradigm that might circumvent these problems by asking the pigeons unexpected questions about their recent behavior.

In phase 1, the pigeons were trained to peck a red light if they had just pecked the screen, and to peck a green light if they had just refrained from pecking that screen. During phase 2, the pigeons were trained to peck a yellow light that was always associated with a food reward, and to avoid pecking a blue light was not followed by food. On test trials a yellow or blue was presented first followed by a choice between the red and green lights. In other words, the pigeons were first asked to peck (yellow) or not peck (blue), and then they were given the opportunity to report what they had just done, namely whether or not they had just pecked (red = pecked; green = not pecked). The pigeons performed above chance level from the start of the test trials thereby excluding the possibility that they had learned the correct answers during training. Transfer tests using novel stimuli, namely a circle

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[2] There are some potential candidates: Henderson, Hurly, Bateson, and Healy (2006) reported memory for when and where (but not what) in hummingbirds; Salwiczek and Bshary (2011) found evidence of what and when memory (but not where) in cleaner wrasses; and Pahl, Zhu, Pix, Tautz, and Zhang (2007) showed that honeybees can remember what they coined a "circadian time episodic-like memory in bees" (i.e., the when is a biological clock as opposed to the subjective passage of time).

versus no stimulus (what Zentall et al., 2001, called the *dark response key*), showed that the birds quickly learned to peck the circle and to avoid the dark response key, and then to choose the red light if they had just pecked the screen, and the green one if they had not. In short, in this unexpected question task, the pigeons were required to recall what the previous stimulus had been and how they had reacted to formulate a correct response and thus receive a food reward.

COMBINING EPISODIC-LIKE MEMORY TESTS WITH THE UNEXPECTED QUESTION TASK

Experiments by Skov-Rackette, Miller, and Shettleworth (2006) combined both of these approaches, by using the unexpected question task to test the structural criterion of episodic-like memory to investigate whether or not the pigeons (*Columbia livia*) could form an integrated memory of what, where, and when. In the first experiment the pigeons were trained on a series of delayed-matching-to-sample tasks to test whether they remembered what, when, and where independently or whether they were able to episodically recall them in a bound integration (Figure 11.2).

The birds first saw one of two symbols in one of eight possible locations at the periphery of the monitor (Figure 11.2A). After a delay of either 2 s or 6 s, a cross appeared in the center of the screen (Figure 11.2B). When the bird pecked at this cross, one of three possible screens appeared (Figure 11.2C).

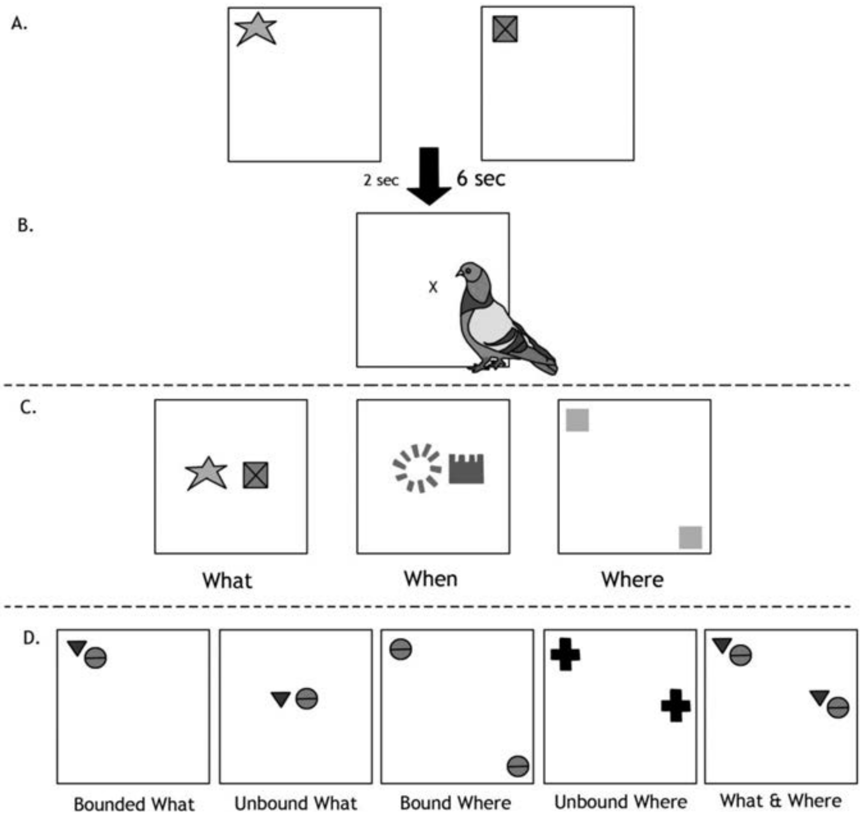

FIGURE 11.2. The design of the experiment by Skov-Rackette, Miller, and Shettleworth (2006) testing whether pigeons can remember what, where, and when using an operant procedure to test whether or not the birds could remember what symbol had been shown in stage A and where and whether it had appeared 2 s or 6 s before. Stage C tested for the individual components, whereas stage D explored whether the pigeons could remember integrated memories of what and where, when and where, and whether the memories were unbound individual what, where, and when components.

The *what* memory screen consisted of the initial item plus one other item being presented in the center of the screen, whereas the *where* memory condition consisted of two novel symbols, with one at the location where the initial item had been seen, and the *when* memory consisted of two symbols different from the previously seen items, one representing the 2 s delay and the other representing the 6 s delay. Once the pigeons had been trained to reliably select the correct what, where, and when items, the birds entered the critical two-test phase in which the birds went through steps (Figure 11.2A–C) on the first trial, but on the next trial (Figure 11.2A) was skipped and the cross was presented again before another unexpected alternative appeared. The assumption was that once the birds reliably answered the individual what, where, and when questions, they must have encoded the three characteristics of a given episode because they did not know which of these questions they would be asked on part two of the two-phase trials, hence reference to the unexpected question approach. Interestingly the pigeons, unlike the scrub-jays, were unable to form bound memories of what, where, and when. Indeed, the pigeons' performance dropped as soon as the birds received the first block of trials combining what, where, and when, and interestingly loss of accuracy mainly affected the when component (for detailed discussion, see Skov-Rackette et al., 2006). This was also the case in a second experiment, which investigated whether the pigeons could spontaneously bind the individual components together in the absence of specific training (Figure 11.2D). The results of both experiments suggested that the pigeons remember the what, where, and when features independently rather than in an integrated memory that bound the individual what and where components. Of course the comparisons between the pigeons and scrub-jays are not direct, given the manner in which the two species were tested. For example, it remains to be seen whether or not the scrub-jays could pass such tests using the operant chamber procedure.

A Comparative Approach

Taken together, the results of these investigations suggest that there is evidence that some nonhuman animals have episodic-like memories about the past, but further studies are required to understand more about why some species pass such tests and others fail, and under what conditions. For example, rhesus macaques (*Macaca mulatta*) have been found to remember what and where but not when (Hampton, Hampstead, & Murray, 2005), which seems surprising given that a number of other birds and mammals pass these what, where, and when tasks. And in the case of rats, the evidence is mixed with the subjects failing some tests of episodic-like memory (e.g., McKenzie, Bird, & Roberts, 2005), yet passing others (e.g., Babb & Crystal, 2006a, 2006b). Details of the differences in methodology and species ethological needs may help to illuminate this issue. Future work should also investigate whether or not the animals that meet the content criterion for episodic-like memory also show evidence for the integrated structure and flexible deployment, which is what one would predict if the ability to remember what, where, and when is truly indicative of episodic cognition.

It would be also interesting to know whether, and to what extent, performance on the unexpected question task correlates with the tests of what-where-and-when and what-where-and-which memories. Recent work on different tests of episodic memory in young children suggest that these abilities do not necessarily correlate (Cheke & Clayton, 2015). Perhaps this is not surprising. As pointed out by Crystal (2009) and Salwiczek, Dickinson, and Clayton (2008), episodic memory is defined as a long-term memory system, yet the unexpected question experiments carried out by Zentall et al. (2001) and Skov-Rackette et al. (2006) use very short retention intervals of just a few seconds (see Chapter 10, this volume) in contrast to the longer delays used in the what-where-and-when memory tests. One clear prediction is that if these of episodic-like cognition really do tap into the episodic cognition system then subjects that pass these tests should also pass tests of future planning, as alluded to in the introduction. Is there any evidence to support this claim?

Can Animals Plan for the Future?

Clayton, Bussey, and Dickinson (2003) argued that, as with episodic-like memory, we should be able to identify behavioral criteria for future planning, and that do so we need to differentiate between an observed behavior that is controlled by prospective cognition as opposed to one that is simply prospective in nature. Consider food-caching—an animal that stores food with the intention of retrieving it later would certainly seem to exhibit some form of prospective cognition, but it is also plausible that evolution has endowed the animal with a hard wired desire to cache food, oblivious to the future benefits of doing so. Clearly the task is to identify instances in which an animal acts for the future with the future in mind (Thom & Clayton, 2015). Future planning provides a profound cognitive challenge to the motivational system because the subject has to suppress thoughts about their current motivational state to allow them to imagine future needs and dissociate them from current desires.

DISSOCIATION OF FUTURE AND PRESENT MOTIVATIONAL STATES

Suddendorf and Corballis (1997) argued that the ability to dissociate current from future motivational states is a critical feature of episodic future thinking. In formulating their Bischof–Köhler hypothesis, the authors argued that nonhuman animals are incapable of anticipating their future needs, and as a consequence nonhuman animals are stuck in the present and therefore bound to their current motivational state. Falsification of the Bischof–Köhler hypothesis is the current gold standard for claims of prospective cognition in nonhuman animals, and indeed Suddendorf and Corballis's proposal has led to a number of empirical tests of whether or not animals can dissociate current from future motivational needs.

Primate Evidence

The first study to test this directly was conducted by Naqshbandi and Roberts (2006), who provided squirrel monkeys (*Simia sciureus*) with the opportunity to choose between eating one versus four dates. Eating dates makes monkeys thirsty, and the monkeys were then given some water after a long or a short delay. In fact, the monkeys received water after a shorter delay if they had chosen the one date rather than the four dates. The monkeys gradually reversed their natural preference to choose four dates over one date, suggesting that they could anticipate their future thirst. The problem is that one can give a simple alternative associative explanation in terms of reinforcement of the anticipatory act because the monkeys received repeated trials in which they had the opportunity to learn about the consequences of their choices.

Corvid Evidence

More convincing evidence for a dissociation between current and future motivational states comes from a study by Correia, Dickinson, and Clayton (2007) on the food-caching choices of western scrub-jays. Here they tested whether the jays would choose to cache the food they want now or whether they would choose the food they think they will want when they come to recover their caches at a later date. To do so Correia et al. capitalized on the specific satiety effect, namely that having eaten a specific type of food to satiety, the subject will no longer desire more of that food, but if presented with a new food they will eat some of the new type of food.

At the start of the experiment the birds cached the food they desired at the time, but the birds rapidly switched to caching the food they would want at the time of recovery, despite continuing to eat the food they desired at the time. This result suggests that the jays can plan future actions on the basis of what they anticipate they will desire in the future as opposed to what they need now. In a commentary on Correia et al.'s (2007) study, Suddendorf and Corballis (2008) raised two key criticisms. The first is that the jays in the *same* group (who had been prefed the same food prior to caching as that they had been prefed prior to recovery) had been presented with more of the prefed food type across the course of the experiment than jays in the *different* group (who had been prefed a different food prior to caching than that they had been prefed before recovery). This is true, but it is unclear why this feeding schedule should have affected the birds' motivational states. All birds in both groups had prior experience of the prefed food types from previous studies, and all birds had *ad libitum* access to a range of maintenance food types in between trials. Furthermore, subsequent work with Eurasian jays (*Garrulus glandarius*), another corvid cousin, replicated the findings of Correia et al. using a within-subject design that prevents this problem (Cheke & Clayton, 2012).

The second criticism focuses on the use of proportions of food types cached in the analysis, rather than absolute numbers, reflecting a reduction in caching of the prefed food, rather than an increase in caching of the nonprefed food. In other words, the birds did not appear to anticipate a future need for the nonprefed food, but instead to anticipate that they would not need the prefed food. However, this is precisely what one ought to expect given that they began on trial 1 by caching both food types (Clayton et al., 2008). If the birds had anticipated that they would want more of any food at retrieval they would be wrong! The prefeeding with one food type before retrieval reduced the value of that food type most, but also reduced the value of all foods through its effect on general satiety. Put in lay terms, knowing that you plan to have cheese leftovers for dinner should stop you from buying yourself more cheese now, not encourage you to buy extra chocolate (Cheke, Thom, & Clayton, 2011).

Taken together the evidence from the jay caching experiments described in this section (Cheke & Clayton, 2012; Correia et al., 2007) appear to contradict the Bischof–Köhler hypothesis, by suggesting that these two species of jay can indeed dissociate future needs from current ones and act for what the birds will want in the future. It is not, however, clear that we can conclude from this that jays are able to engage in prospective mental time travel, that they need to project their self into a future time to do so. It seems entirely possible that they could use a nonepisodic, semantic-like knowledge to dissociate future and current needs.

The critic may also wish to argue that the fact that all the evidence in the jays comes from studies of food-caching might imply a rather narrow focus for their abilities that contrasts with the broad range of future experiences that humans can envisage (Suddendorf & Corballis, 2010). Yet, the emphasis on caching is a matter of empirical convenience rather than a cognitive limitation—the scrub-jays may well be capable of foresight beyond a caching context, but this has not been tested. Absence of evidence is not evidence of absence.

Recent work conducted on Eurasian jays hints at a potentially new avenue for research into foresight in a noncaching context. The male jays share food with their partners in breeding season, and they do so by transferring one food item at a time, which means that we can quantify how many items and of which type the males choose to share with their female partner. Using this behavior, Ostojić, Shaw, Cheke, and Clayton (2013) have been able to ask whether the male jays anticipate their partners' food desires when doing so. The females were prefed on one of two food types to induce specific satiety, and then the males were given a choice of food types to share. The males preferentially shared the nonprefed food, in accordance with their partners' motivational states. Importantly, this preference was only seen when the males could observe their mate being prefed, so the females were not just cueing the males' choices behaviorally. Subsequent work suggests that the males' food selection is partially driven by their own motivational state (Ostojić et al., 2014). The important point here is that the birds had to overcome their own desires to act to satiate their partner's desires. Given that the selection of food was necessarily made before sharing, and because the Bischof–Köhler hypothesis does not state how far into the future a "future need" should be (Paxton & Hampton, 2009), it could be argued that food-sharing provides evidence of foresight outside of the caching context.

It should be noted, however, that neither the food-caching scrub-jay and Eurasian jay, or the food-sharing Eurasian jay needs to project itself in time to imagine a future situation to solve these tasks. I alluded to this previously, in terms of a nonepisodic semantic knowledge account. One possible mechanism, proposed by Clayton, Russell, and Dickinson (2009), is that the act of recovering a particular food might trigger the memory of the time the bird cached that food. If the bird is hungry for that particular food then recovering that food type will be rewarding, thereby directly reinforcing the act of caching that particular food type through the memory and associated motivational state of doing so. Such memory-mediated reinforcement does not require the jay to project itself in time to imagine what its future motivational state will be. Indeed, it may be for this very reason why the jays are so adept at dissociating current and future motivational states, namely because they do not need to use their mental time travel system to do so.

The Bischof–Köhler hypothesis was intended to be a conservative test of nonhuman foresight, and consequently there may be instances of behavior for which foresight might be a plausible explanation as the previous example illustrates, but where competing explanations such a memory-mediated reinforcement cannot be ruled out. It is also likely to be the case that the narrow focus of the Bischof–Köhler hypothesis on anticipation of future needs so restricts the range of behaviors from which prospective cognition can be inferred that caching provides one of the few conclusive examples. If this is so, perhaps we should question whether the Bischof–Köhler hypothesis continues to be a useful tool for research into prospective cognition.

Perhaps it might be helpful to consider the application of the Bischof–Köhler hypothesis to our own species; after all, humans are certainly able to anticipate future needs and cache food accordingly. Going to the supermarket to buy food for the week is a case in point. If a holiday is approaching and family are visiting for several days, then we will buy more food than usual. This is clearly an example of acting for the future with the future in mind. Nonetheless, it is not necessarily the case that we dissociate completely from the context of our present motivational state when we engage in this behavior. Indeed, shopping for food is very much influenced by current hunger (Nisbett & Kanouse, 1969), even though we know that the hunger we are experiencing is a temporary state, one that is unlikely to affect our needs for the rest of the week. It may be precisely because we are relying intuitively on our mental time travel system that we make such mistakes (e.g., Gilbert, 2006). Given these problems with tests of the Bischof–Köhler hypothesis, are there any other tests that may better, or more generally, evaluate future planning in animals and specifically prospective mental time travel, which we might term episodic-like future thinking?

TULVING'S SPOON TEST

Tulving (2005) has argued that it is possible to test whether or not animals are capable of such episodic-like future-thinking using the Spoon test, on the basis of an Estonian children's story tale, which he argues is a "future-based test of autonoetic consciousness that does not rely on and need not be expressed through language" (p. 43). In the original story, a young girl dreams about going to a birthday party. All of her friends are eating her favorite desert, a delicious chocolate mousse. All she can do is watch, however, because the rules of the game are that no one is allowed to eat it without their own spoon, and she hasn't brought one with her. So as soon as she is back home she goes to the kitchen to find a spoon which she caches it under her pillow for safe keeping, knowing she will have one to hand in the future should a similar scenario come to exist once more—be it a real birthday party or even just a dream about future birthday parties.

To pass the Spoon Test the subject must act analogously to the little girl, using a specific previous past experience (an episodic memory) to take action now for an event that might happen at a future event, namely caching a spoon so that it is ready to take to a new party at some point in the future. It is important that the spoon that has been obtained in another place and at another time, in a distinctly separate event not just a continuation of the current episode. Tulving (2005) argued that these decisions specifically involve episodic cognition—remembering a specific episode in the past, imagining similar future scenarios, and taking a specific action in the present in order to facilitate the positive outcome for such future events. At issue then is whether there is any evidence that some animals can pass this Spoon Test.

Primate Evidence

Mulcahy and Call (2006) were the first to devise a Spoon Test experiment for nonhuman great apes. They trained bonobos and orangutans to use a tool to obtain a food reward that would otherwise have been out of reach, and then gave the apes the opportunity to choose one of the tools from the experimental room, which they could carry into their sleeping quarters to be used the following morning. Although most of them sometimes chose the correct tool, the individual pattern of success for each subject was not consistent across subsequent trials, as one would expect if the apes had a proper understanding of the task. A simpler explanation in terms of reinforcement of the anticipatory act cannot be ruled out because the apes received a number of training trials (Raby, Alexis, Dickinson, & Clayton, 2007; Shettleworth, 2007; Suddendorf, 2006). It is therefore possible that the observed behavior can be attributed to long-delay instrumental conditioning (Cheke & Clayton, 2010). Furthermore, we know nothing of the subjects' motivational states at the time of testing. This same criticism applies to a more recent replication of Mulcahy and Call's first experiment by Dufour and Sterck (2008). The apes could plausibly have experienced a present desire for juice without entertaining any particular expectation of an encounter with the apparatus. In the absence of an obvious cost to selecting and keeping the correct tool, we might expect a present desire for juice to drive the observed behavior and in which case there is no requirement for a dissociation of present from future motivational states.

A more convincing case of future planning was provided by Osvath and Osvath (2008), who overcame this hurdle by introducing a self-control element, in which present desires and future needs are juxtaposed by design. Two chimpanzees and one orangutan were given the opportunity to select a tool from a tray of alternative items, and this tool could be used to access some highly valued fruit soup after a 70 min delay. Initially, the alternative items were nonfunctional tools, and all three subjects reliably chose the functional tool. In the second experiment, however, one of the alternative items was a piece of the animal's favorite fruit. The subjects therefore faced a choice between an immediately available piece of fruit, and the prospect of future access to an even more valuable fruit reward using the functional tool. All three subjects selected the tool on significantly more than the expected 0% of trials.

A third experiment controlled for the possibility that the functional tool had become a secondary reinforcer through its association with the fruit soup. The subjects were now given two choices instead of one: The first was between a functional tool and several nonfunctional alternatives; the second was between another functional tool, a piece of fruit, and some nonfunctional tools. If the tool had previously been preferred to the fruit because it had acquired its own reinforcing properties, then the apes should have chosen the functional tool twice. Instead, each of the subjects selected the fruit in the second choice on every trial. Osvath and Osvath (2008) argued that the apes were anticipating their future encounter with the fruit soup and their consequent need for a single functional item. In a final experiment, all subjects showed an above-chance preference for a novel functional tool over some equally novel nonfunctional alternatives, a finding that might be taken to suggest that the subjects were preexperiencing their interaction with the apparatus containing the fruit soup, to identify which tool they would need.

In response to this publication, Suddendorf, Corballis, and Collier-Baker (2009) issued a commentary suggesting a more cautious account of the findings, noting in particular that tool-selection in the second experiment was compared to 0%, not to chance. Osvath (2010) argued that chance is not the correct comparison, because the presence of an attractive alternative (the favorite fruit item) would lead a "future blind" ape to select the functional tool less often than chance. This line of reasoning seems plausible, but it remains to be tested. A simple control could confirm this using a less attractive fruit alternative, which should result in more choices for the functional tool, and fewer for the fruit (and still none for the nonfunctional tools). Applying this control the third experiment could also strengthen those findings: Because the value of the fruit is always greater than that of a second functional tool, the apes should behave identically and always choose the fruit.

The claims of Osvath and Osvath (2008) rest primarily on the validity of their third experiment, which purports to control for associative learning. Suddendorf et al. (2009) suggested that the apes may have held an expectation of an immediate encounter with the apparatus containing the fruit soup, and that this is what motivated their initial choice. This claim seems surprising because the subjects were never given the opportunity to use the tool immediately after selection. However, there is one aspect of the apes' behavior that does appear to be inconsistent with anticipation of future tool-use, namely that the experimenters were able to retrieve the tool after each testing session. Why did the apes not guard the functional tool for future use, given that they received a succession of trials involving the same scenario, namely the use of a tool to obtain the fruit soup?

Suddendorf et al. (2009) also questioned whether the paradigm used by Osvath and Osvath (2008) is capable of testing the Bischof–Köhler hypothesis. Because it is not clear that desire for the fruit and desire for the fruit soup are qualitatively different motivational states, there may be nothing to dissociate from. This criticism betrays an ambiguity at the heart of the Bischof–Köhler hypothesis in its description of present and future needs. The interpretation of needs as drive states is convenient for empirical work, but it is nevertheless rather limiting if applied universally. If the apes were indeed pre-experiencing a future encounter with the apparatus containing fruit soup, would anticipation of the need for the tool not be sufficient to be considered a case of episodic foresight?

That said, it is hard not to be impressed with the apes' behavior from a comparative perspective: When long-tailed macaques were tested on a tool-transport paradigm similar to that of Mulcahy and Call (2006), the monkeys only learned to select and transport tools following shaping with immediate rewards (Dekleva et al., 2012). Furthermore, this behavior mostly stopped with a longer delay of 20 min, whereas the apes tolerated a 14 hr delay. If the apes show a greater propensity for future-oriented behavior than some other primates, it is important to determine whether this is due to a greater capacity for foresight. That is why it is important to consider the evidence for prospective cognition in other species.

Corvid Evidence

Food-caching scrub-jays also pass the Spoon Test, spontaneously planning for tomorrow's breakfast without reference to their current motivational state (Raby, Alexis, Dickinson, & Clayton, 2007). The birds were given the opportunity to learn across 6 days that they received either no food for breakfast in one end compartment (the hungry room), and that they received food for breakfast in the other end compartment (the breakfast room). For the rest of the day, from 11:00 a.m. onwards, the birds had free access to both compartments and also to a central arena. During this time the birds were maintained on powdered food, which they could eat but not cache. This was to ensure that the birds were neither rewarded nor punished for caching, and therefore one could not invoke a reinforcement of the anticipatory act to explain the results. Having been confined to each end compartment at breakfast time for an equal number of times, the birds were unexpectedly provided with the opportunity to cache food in both compartments at 5:00 p.m., a time when there was plenty of food for them to eat and therefore no reason for them to be hungry, by placing a bowl of whole food items in the central arena and two caching trays, one in each end compartment (Figure 11.3). If the jays can plan ahead they should cache food in the hungry room, given they do not know which compartment they will find themselves tomorrow and thus whether or not breakfast would be provided the next morning at 7:00 a.m.

That is precisely what the birds did, suggesting that the jays could anticipate their future need for breakfast tomorrow, at a time when they would be hungry, and even though they were not hungry at the time when they had the opportunity to cache. Furthermore, as mentioned previously, an explanation in terms of mediated reinforcement of the anticipatory act can be ruled out because the birds had not been given the opportunity to cache during training. Indeed Shettleworth (2007) argued that

> two requirements for genuine future planning are that the behaviour involved should be a novel action or combination of actions . . . and that it should be appropriate to a motivational state other than the one the animal is in at that moment. . . . Raby et al. describe the first observations that unambiguously fulfil both requirements. (p. 825)

A CALL FOR MORE COMPARATIVE WORK

What these studies demonstrate is the capacity for some nonlinguistic animals, namely the apes and

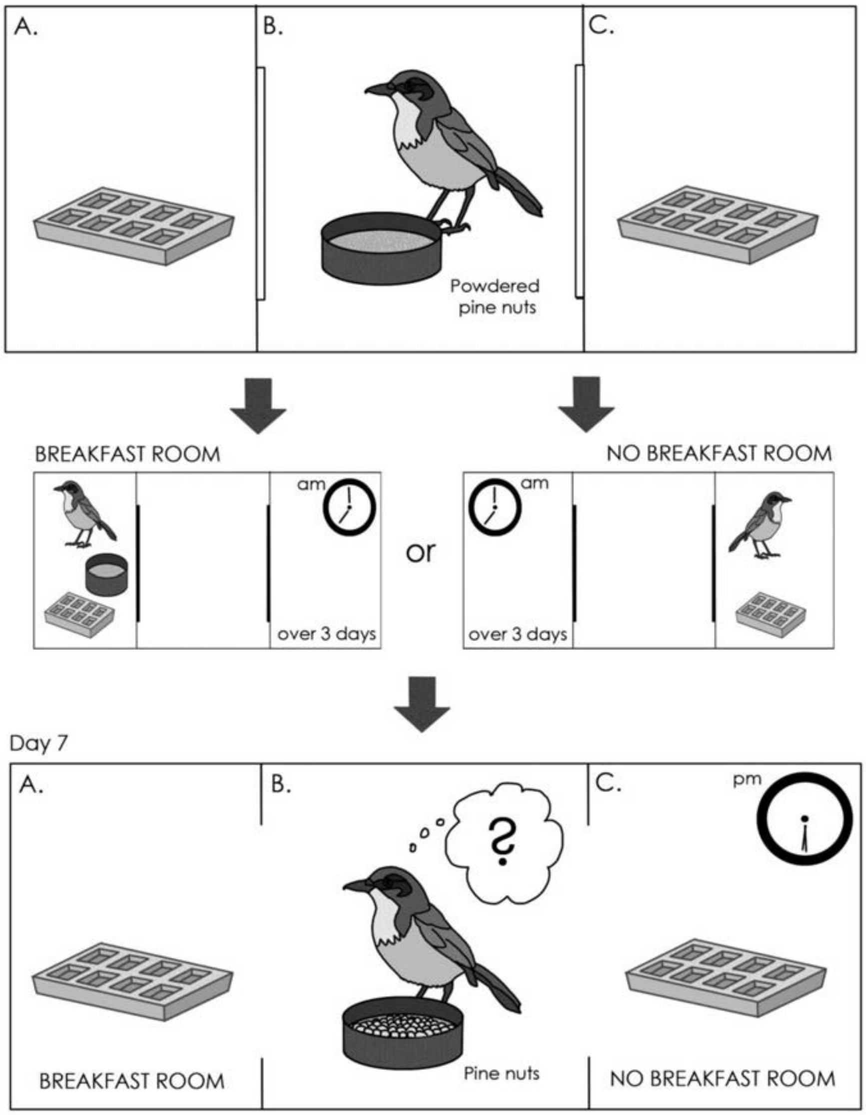

FIGURE 11.3. **The design of the experiment by Raby, Alexis, Dickinson, and Clayton (2007) testing whether western scrub-jays can plan for future breakfasts.**

the scrub-jays, to plan for a future motivational state that stretches over a timescale of at least tomorrow. These results challenge the assumption that the ability to anticipate and act for future needs evolved only in the ape lineage (Raby et al., 2007). More comparative studies are needed to assess whether the ability to pass the Spoon Test is restricted only to the apes and scrub-jays and also over what time scales, given that the long-tailed macaques were unable to cope with a delay of more than 20 min whereas the apes and corvids tolerated a delay of 14 hr. Furthermore, as stated in the introduction, it is important to know whether or not those species that pass episodic-like memory tasks also pass these future planning tasks, and where the notable exceptions might lie.

A recently published study of apparent route planning in chimpanzees is interesting in this regard. Janmaat, Polansky, Ban, and Boesch (2014) conducted 275 days of detailed observations of the movements, nesting, and feeding behaviors of five female chimpanzees in the wild. The chimpanzees traveled to a fruit tree for breakfast every morning as part of their daily ritual, but they left the site earlier when competition for the fruit was likely to be greater, for example, when there were smaller fruit that could also be eaten by other, smaller species. If the next day's breakfast was to be figs, which were typically depleted rather quickly, then the chimpanzees tended to choose sleeping nests en route to the breakfast tree. This finding might be taken to suggest that the chimpanzees appeared to plan their routes to arrive at the breakfast tree before all the fruit had been eaten, and that in doing so they also planned their sleeping nest sites accordingly. One issue, of course, is that when studying a wild population, it is impossible to control for confounds arising from previous life experience (Thom & Clayton, 2015). Perhaps future work inspired by these careful and detailed observations could be conducted in the laboratory, because controlled manipulations are required to make unambiguous predictions about an animal's behavior given differing present and future needs.

THE DISTINCTION BETWEEN FUTURE PLANNING AND FUTURE EPISODIC THINKING

There is one final issue I shall address, and that is whether these tests of prospective cognition engage the same cognitive process as that involved in episodic-like memory. The issue is whether or not these Spoon Test tasks really require the use of episodic-like future-thinking in the first place. In the absence of language there is no way of knowing whether the jays' ability to plan for future breakfasts is based on a projection of the self in time, which is what would be required to satisfy an episodic future-thinking account. The same reasoning applies to the apes' ability to choose tools. It is entirely possible that the jays and apes rely on a semantic knowledge-based sense of the future, in which they take prospective action but without any personal mental time travel into the future (Raby et al., 2007). To solve the Spoon Test, all the subject has to do is to decide what has to be done to ensure the implement will be at hand, be it a spoon, another tool, or a food-cache, without the need to imagine one's self in possible future episodes or scenarios (Raby & Clayton, 2009).

What we are left with, then, is a criterion that is neither sufficient nor necessary to indicate prospective mental time travel or so-called episodic-like future thinking. The Bischof–Köhler hypothesis and the Spoon Test have provided an important focus for comparative research into prospective cognition in animals but they are rather restrictive as null hypotheses. The hope is that future research will benefit from the development of new criteria for future-oriented cognition, ones that will be more tightly linked to the behavioral criteria for episodic-like memory. Without such a link, it is far from clear why future planning and episodic-like memory abilities should go hand in hand, and how this relates to mental time travel.

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PART II

LEARNING AND MOTIVATION

CHAPTER 12

ETHOLOGICAL AND EVOLUTIONARY PERSPECTIVES ON PAVLOVIAN CONDITIONING

Mark A. Krause and Michael Domjan

Pavlovian conditioning is a fundamental mechanism guiding behavioral change. It enables organisms to adjust to their environments and facilitates their interactions with ecologically relevant resources, conspecifics, and threats. Associative learning is extraordinarily common, and even exists among invertebrates with remarkably simple nervous systems. The biological and evolutionary foundations of conditioning are built on studies of a diversity of species that encounter unique, species-specific ecological problems. These foundations were established as long-standing historical debates about the relative contributions of nature and nurture took place. Resolution on the issue is ongoing and is aided by incorporating ethological and evolutionary perspectives into studies of animal learning. Researchers of Pavlovian conditioning have long offered special insight into these questions because their work involves studying reflexive or unconditioned responses (UR) and the ways that experience alters how these responses occur.

In this chapter we review the outcome of ethologically and evolutionary-based investigations of Pavlovian conditioning. We seek to bring together information about all of the major biologically informed perspectives on conditioning, including consideration of the evolutionary origins of conditioning, the biological functions of conditioning, as well as ecological, adaptationist, and behavioral systems approaches. We begin with a brief overview of the historical debate about learning and instinct because it provides the historical context for the ethological and evolutionary perspectives offered in this chapter.

HISTORICAL ANTECEDENTS: LEARNING VERSUS INSTINCT

Historically, behavior was classified as either learned or instinctive. Instinctive behaviors were presumed to be primarily a function of the genetic history of the organism, whereas learned behaviors were a product of individual experiences or ontogenetic history. However, a strong distinction between "learned" and "instinctive" is no longer tenable. Phenomena generally referred to as "biological constraints on learning" illustrate that how a particular learning procedure shapes behavior depends on how the procedure interacts with the pre-existing behavioral organization and instinctive repertoire of the organism.

Breland and Breland (1961) characterized constraints on instrumental conditioning in their research as instances of "misbehavior" due to "instinctive drift," because instinctive behaviors intruded into the responses that they were trying to condition. Thus, a longstanding challenge to understanding learning is to figure out how learning processes interact with instinct. Unfortunately, the question can no longer be expressed in those terms because the term *instinct* has fallen into disfavor (see Volume 1, Chapter 17, this handbook).

The term instinct took center stage with the work of biologists who founded the field of ethology, which focuses on understanding the biological bases of behavior observed in naturalistic environments. Although ethologists discovered learning phenomena such as imprinting, their emphasis

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was on “naturalistic” behavior instead of seemingly arbitrary responses studied by psychologists in laboratory experiments on learning. In particular, ethologists were interested in responses (e.g., courtship, incubation behavior, territorial defense) that occur pretty much in the same fashion in all males or females of a species. Because these species-specific behaviors were essential for biological success and were present in most individuals, they appeared to be “instinctive.” Niko Tinbergen, one of the founding fathers of ethology, even titled his seminal tome *The Study of Instinct* (Tinbergen, 1951).

The Study of Instinct triggered a vehement attack on the concept of instinct from Daniel Lehrman, an American ethologist (Lehrman, 1953), who studied courtship behavior in ring doves (see Volume 1, Chapter 2, this handbook). Lehrman argued that labeling a behavior as instinctive did not provide any information about the possible underlying mechanisms or origins of the behavior. Characterizing something as instinctive does not tell us how the behavior may emerge during ontogenetic development, what its physiological and neural mechanisms may be, or how and what kinds of environmental input may be necessary for the normal emergence of the behavior.

Lehrman’s attack on the concept of instinct had a huge impact and nearly led to the abandonment of the notion that behaviors could be categorized as instinctive versus learned (Bateson & Mameli, 2007; Marler, 2004). The enduring impact of the critique is supported by modern biology, which rejects a dichotomy between genetic and environmental effects. The current guiding principle is that genetic determinants of phenotypical behavioral and physiological traits depend on an interaction of genes and the environment in which those genes operate (Champagne & Mashoodh, 2009; Crews, 2011; see also Volume 1, Chapters 11 and 18, this handbook). Such epigenetic mechanisms are becoming increasingly evident as key players in learning and memory (Lattal & Wood, 2013).

Rejection of the term instinct has created something of a void in the study of learning. If we cannot talk about instincts, we cannot talk about interactions between learning and instinct or instinctive drift. How, then, are we to characterize biological constraints on learning or specialized, seemingly genetic influences on what is learned and how conditioning works? Clearly, different approaches are needed, with a different vocabulary. We explore these alternatives in the following sections.

A FUNCTIONAL PERSPECTIVE ON PAVLOVIAN CONDITIONING

One possibility to resolve the instinct versus learning conundrum is to adopt a functionalist perspective on Pavlovian conditioning. Because learning in naturalistic settings takes place in an evolutionarily relevant context, we can predict that what organisms learn about (and how they learn) will involve species-typical response patterns that are functionally designed for biological ends. At the same time, behavior systems have to be flexible enough to be modified by experience in ways that promote effective feeding, drinking, mating, avoiding predators, and other survival-relevant behaviors.

A functional/evolutionary approach has not been widely adopted by investigators of Pavlovian conditioning. There is an extensive literature on the importance of cornerstone principles of associative learning, such as the roles of contingency, contiguity, and various stimulus factors in learning (Boakes & Costa, 2014; Gallistel & Gibbon, 2000; Pearce & Bouton, 2001; Rescorla & Wagner, 1972). This work has revealed important insights into the mechanics of associative learning. However, the evolutionary relevance of these processes, and whether they adequately account for how learning occurs in natural situations, has been the subject of far less empirical and theoretical attention.

Components of a functional conditioning system include unconditioned reflexes and physiological responses that, by definition, do not require prior training or learning. Unconditioned stimuli (US) either pose direct threats to survival (e.g., predatory attack) or sustain survival (e.g., food, water) so long as UR are elicited. The associative piece to this system of learning involves the acquisition of a conditioned response (CR) to a conditioned stimulus (CS) or context that was paired with a US. An auditory or visual CS that reliably predicts a pending predatory encounter (a US) can help the organism take evasive or defensive action. Correspondingly, gustatory or olfactory CSs can serve as signals about whether to consume or reject a food source. Such cues are initially ineffective and are therefore referred to as CSs. A putative effect of Pavlovian conditioning is that it leads to adaptive conditioned responding to initially irrelevant events experienced by individual organisms (Hollis, 1997). From an evolutionary perspective, the newly acquired information provided by a CS enables conditioned individuals to cope more effectively with a biologically challenging US.

Pavlovian conditioning is studied almost exclusively in laboratory settings where stimulus inputs and response measures, and their often complex arrangements, can be carefully controlled. Table 12.1 summarizes a number of basic Pavlovian conditioning paradigms. The table lists the USs and URs, and common CSs and CRs used in experiments. The table shows that Pavlovian conditioning occurs in a wide range of situations. In later sections of this chapter, we will closely examine a few of them that are particularly relevant to evolutionary questions.

Several aspects of this summary table are noteworthy. First, USs that occur in nature are relatively easy to model or simulate in laboratory conditions. One exception is the use of shock, which is rarely encountered in nature. Nonetheless, shock reliably elicits defensive URs in many organisms, and is therefore regarded as a good proxy for actual

TABLE 12.1

Examples of Associative Learning With Respective Conditioned and Unconditioned Stimuli and Conditioned and Unconditioned Responses

Behavioral system/ response	Unconditioned stimuli	Unconditioned responses	Conditioned stimuli	Conditioned responses
Appetitive	Food, water	Salivation, eating, enzyme and hormone release	Tone, light, or context	Salivation, sign tracking, enzyme and hormone release
Caloric	Caloric depletion	Hunger	Flavor paired with needed food	Flavor preference
Aversive/poison	Illness	Nausea	Flavor	Avoidance/suppression of behavior
Aversive/fear	Shock	Species dependent; attack, escape, increased sympathetic activity	Audio, visual, or combined cue, context	Species dependent; avoidance, escape, increased sympathetic activity
Eye blink	Air puff	Blinking	Tone	Blinking
Sex	Receptive partner	Sexual arousal, activity	Light, objects[a]	Sign or goal tracking, endocrine/gonadal responses
Aggression	Rival animal	Pursuing, fighting	Light	CS-directed threats, increased effectiveness in aggressive encounter
Drug tolerance	Drug	Drug contingent (e.g., pain relief, arousal)	Context	Tolerance or sensitization
Hypoalgesia	Shock	Species dependent; attack, escape, increased sympathetic nervous system activity	Context	Freezing, pain sensitivity
Nursing	Mother–infant interactions	Hormone release supporting milk letdown and release	Olfactory and social/ contextual cues	Hormone release supporting milk letdown and release
Immunomodulation	Drug (e.g., cylophosphamide)	Immunosuppression, malaise	Gustatory cue	Immunosuppression

Note. These examples are of individual conditioning. Important bodies of work in several paradigms have used observational conditioning procedures.

[a] See Figure 12.2 for diagrams of the CS objects used.

encounters with threats to survival (e.g., predators). Second, URs are reflexively elicited by the USs, and involve activity of the central nervous system and circuitry with the sympathetic and parasympathetic nervous systems (e.g., fear and nursing, respectively). Despite the somewhat artificial laboratory environments in which these studies are conducted, the US and UR relationships are based on natural, species-specific stimulus sequences (Domjan, Cusato, & Krause, 2004).

Another observation about Table 12.1 that is particularly critical to this chapter concerns the CSs that are listed. Few of them resemble anything an organism would encounter in its natural environment. This is not surprising given that traditional textbook definitions of associative learning emphasize the arbitrary and neutral nature of the CS, and note that the CS only elicits a CR after being paired with a US. Thus, learning in the laboratory is often based on situations that are by design highly artificial. Departures from this tradition are found in research programs examining how naturalistic CSs affect conditioning (Domjan, 1998), and in studies in which common laboratory CSs are manipulated to test the null hypothesis of equipotentiality against an experimental hypothesis stemming from evolutionary logic (Domjan, 2015). Finally, the CRs listed in Table 12.1 differ in magnitude or topography from their respective URs (or oppose the UR, as is the case in drug tolerance), and evidence for Pavlovian conditioning requires that they occur in response to the CS alone after it has been paired with a US. Depending on the behavioral system, the CR may serve to prepare the organism for the US, or modify the UR in other ways (Domjan, 2005; Domjan, Cusato, & Villarreal, 2000).

GENERAL OR SPECIALIZED PROCESSES?

The ubiquity of basic Pavlovian processes among numerous vertebrate and invertebrate species (see Chapter 13, this volume) lends face validity to the view that associative learning is an all-purpose mechanism for useful modifications of behavior on the basis of experience. On the other hand, the diverse ecological and evolutionary circumstances of various species have given rise to specialized expressions of learning. Different labels have been given to biologically based views and interpretations of learning, such as preparedness, belongingness, adaptive specializations, and constraints on learning. Discussion on different meanings of these terms can be found elsewhere (see Domjan & Galef, 1983; Rozin & Kalat, 1971), but each one converges on the conclusion that individual species may evince learning in ways that reflect the influence of species-specific ecological and evolutionary processes, and that general learning processes do not satisfactorily account for some key findings about how animals learn and what they learn about.

Landmark papers by Seligman (1970) and Rozin and Kalat (1971) summarized work on preparedness and adaptive specializations, respectively, and proposed different directions that psychologists have taken to understand learning in an ecological and evolutionary context (see also Domjan & Galef, 1983; Shettleworth, 1993). Studies of taste aversions, specific hungers, language, and various aspects of instrumental responding were offered as evidence that general process theories and the assumption of equipotentiality could not account for many unique and interesting findings.

In what follows, we review differing but complementary perspectives on evolutionary approaches to Pavlovian conditioning. We address two major questions: (a) What are the origins and circumstances that gave rise to Pavlovian conditioning? (b) To what extent have evolutionary processes influenced how conditioning occurs in different behavioral systems and species?

EVOLUTIONARY ORIGINS OF PAVLOVIAN CONDITIONING

Simply put, associative learning requires a biological mechanism for detecting co-occurring events. The raw materials to accomplish this include afferent and efferent reflexive circuitry supporting US-elicited unconditioned responding (e.g., reflexive gill withdrawal in *Aplysia*). In addition, mechanisms for “molecular memory” at individual synapses are necessary but not sufficient for Pavlovian conditioning. A critical component is a CS pathway linking to the motor systems that are a part of the UR circuit, and a modulatory neuron linking the CS and US pathways.

This general description of the raw materials required for Pavlovian conditioning may sound nervous system-centric. Experience-based adaptive changes in behavior have been measured in microorganisms (*E. coli* and *S. cerevisiae*; A. Mitchell et al., 2009), and some have claimed to have replicated processes analogous to Pavlovian conditioning by studying *in silico* evolution through computer and statistical analyses of chemical networks that appear to form "memory traces" (McGregor et al., 2012). This is interesting work in its own right. Establishing that other systems behave in ways analogous to Pavlovian conditioning might give us a sense of the evolutionary origins of Pavlovian conditioning. However, such evidence falls short of telling the actual story of how Pavlovian conditioning evolved. There are many multicellular organisms that do not show Pavlovian conditioning (Ginsburg & Jablonka, 2010), suggesting that the evolutionary origins of this type of learning will not be discovered among unicellular organisms, or in the union of organic and inorganic compounds.

The contemporary evolutionary methods that are most germane to tracing the origins of Pavlovian conditioning include, principally, phylogenetic comparative methods, as well as corroborating evidence from the fossil record and molecular genetic techniques. To map the origins of Pavlovian conditioning, we can begin with a macroevolutionary phylogeny, derived largely from fossil and molecular methods, and examine whether different organisms across the phylogeny show evidence for it. Ginsburg and Jablonka (2010) used this approach to hypothesize that associative learning originated during the Cambrian explosion (545 million–520 million years ago). Fossil evidence from this period reveals a massive diversification of morphological characters, ecological expansions, and speciation events within major animal phyla. Biotic and abiotic changes that occurred during the Cambrian period created conditions that favored the evolution of an increasingly complex nervous system. Ginsburg and Jablonka hypothesized that associative leaning not only originated during this period, but also contributed to evolutionary diversification. The behavioral flexibility afforded by associative learning may have facilitated invading new niches, and may have been the ontogenetically adaptive mechanism that led to fixed behaviors via genetic accommodation (see Exhibit 12.1 for summary of this hypothesis).

Concomitant origins and evolution of sensory and motor capacities, and the neural systems supporting them, further facilitated massive Cambrian diversification. This scenario, summarized in Exhibit 12.1, gathers support from comparative data. Some of the organisms that arose during the Cambrian period have extant representative species with associative learning capacities. For example, the chambered nautilus (*Nautilus pompillus*) is a sole remnant of a lineage that originated during the Cambrian and is the closest living relative of a derived group of cephalopods that have well-established associative learning abilities (cuttlefish, squid, and octopuses). Despite the lack of a specialized neural region for learning and memory, the primitive neural architecture of the nautilus supports conditioning (Crook & Basil, 2008).

Figure 12.1 shows the distribution of associative learning among Metazoan animals. Nephrozoa, the most relevant phylum to the discussion, includes bilaterally symmetrical animals with a centralized nervous system, or at least a diffuse but integrated circuitry of

Exhibit 12.1

Scenario and Hypotheses for the Cambrian Origins of Associative Learning

1. The Cambrian explosion involved biotic and abiotic changes that facilitated massive evolutionary change and expansion into new ecological niches.
2. Some of these changes, such as increased oxygen availability and nutrient cycles, facilitated increased complexity of the nervous system.
3. Organisms that could learn by association were better prepared for dealing with threats to survival and the availability of food resources.
4. Diversification was further reinforced by the evolution of stress responses. The fight or flight response enhanced predator avoidance and associative memory for threatening events further enhanced survival.
5. Genetic assimilation processes (e.g., epigenetics) led to the canalization of associative learning, leading to fixed nonassociative behavioral patterns.

Note. Data from Ginsburg and Jablonka, 2010.

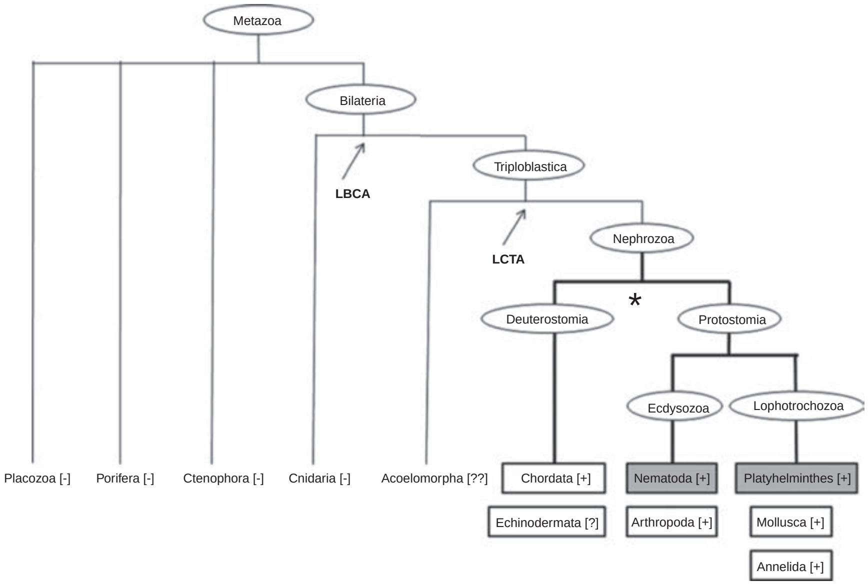

FIGURE 12.1. Phylogenetic distribution of associative learning in animals. Lineages originating during the Cambrian explosion are highlighted with thick lines (Nephrozoa). A potential modification would designate + for Cnidaria, as Haralson, Groff, and Haralson (1975) reported classical conditioning in sea anemones (*Cribrina xanthogrammica*). * = hypothesized emergence of associative learning; LBCA = last bilateral common ancestor; LCTA = last common triploblastic ancestor; [?] = insufficient evidence to conclude associative learning; [??] = learning capacities have not been studied in this phylum. From "The Evolution of Associative Learning: A Factor in the Cambrian Explosion," by S. Ginsburg and E. Jablonka, 2010, *Journal of Theoretical Biology*, *266*, p. 14. Copyright 2010 by Elsevier. Reprinted with permission.

sensory and motor ganglia (chordates, arthropods, mollusks, and worms). Although associative learning may have evolved prior to Nephrozoan organisms, it appears to have become an evolutionarily conservative trait within this group. Associative learning among chordates is pervasive, and given the structure and functionality of the chordate nervous system, it would be surprising if a species within this phylum lacked the capacity for Pavlovian conditioning.

Numerous species of Ecdysozoan animals, which includes insects, crustaceans, and nematodes, show evidence of Pavlovian conditioning. Members of the Lopotrochozoa include flatworms (*Platyhelminthes*), segmented worms (*Annelids*), and mollusks. Evidence for associative learning in flatworms has been reported in work on planaria (*Dugesia tigrina*; McConnell, Jacobson, & Kimble, 1959; Ramakrishnan et al., 2014). Segmented worms such as leeches (*Hirudo medicinalis*) also have well-established associative learning abilities (Sahley & Ready, 1988). And, of course, the mollusk *Aplysia californica* is an iconic animal model for studies of the neural basis of conditioning (Walters, Carew, & Kandel, 1979).

The combined factors of Cambrian environmental conditions, macroevolutionary changes, and the origins of physiological systems that could support learning set up a plausible scenario for why associative learning would have, and could have, evolved. It should be noted that although associative learning is common among Nephrozoans, not all extant representative species of the groups in the phylogeny shown in Figure 12.1 have been tested. Thus, current evidence does not fully resolve whether associative learning is of monophyletic or polyphyletic origin. The possibility of multiple origins of associative learning cannot be ruled out until more species across different phyla are tested.

ECOLOGICAL RELEVANCE AND BEHAVIORAL SYSTEMS THEORY

In addition to addressing evolutionary origins, the ethological and evolutionary approach to associative learning can also be tested more directly by using ecologically informed behavioral and physiological measures, as well as by quantifying the reproductive benefits to conditioning. Ethologically informed laboratory experiments on Pavlovian conditioning are designed in reference to naturalistic encounters that the study species would likely have, and also the species-specific behavioral and sensory repertoires that would be involved in learning in the animal's natural habitat. Work stemming from this orientation has tested how manipulating naturalistic and arbitrary CSs differentially affects conditioning (learning and ecological relevance), and how different phases of species-typical response patterns are affected by experience (behavior systems).

Learning and Ecological Relevance

A consideration of ecological factors suggests that one may be able to predict how rapidly something is learned by considering the ecological circumstances in which a species evolved (Domjan, 2008). Within this framework, laboratory learning paradigms that are highly similar to the natural ecology of the species (such as taste-aversion learning and some forms of fear conditioning) are predicted to generate rapid learning. In contrast, learning paradigms that involve CSs and USs that an organism is not likely to encounter in its natural environment will produce much slower (or less prepared) learning.

Domjan, Cusato, and Krause (2004) tested the proposition that learning phenomena may be a function of the extent to which a laboratory procedure uses cues that mimic what animals encounter in their natural habitat. The experiments were done in the context of sexual conditioning of male quail (*Coturnix japonica*). In this situation, the US is copulatory access to a female quail. In the quail's natural habitat, sexual encounters with a female are preceded by visual cues of the female at a distance. Because quail live in grassy areas, prior to encountering a female, the male is likely to see only the female's head and possibly neck. Domjan et al. replicated this sequence of events in the laboratory by preparing a taxidermic model of the female's head and neck (Figure 12.2). Conditioning trials consisted of presenting this head and neck model to a male quail as a CS shortly before the male had an opportunity to copulate with a live female quail (which was the US). For a control group, the CS was a three-dimensional object of similar size and general shape as the head and neck model, but the

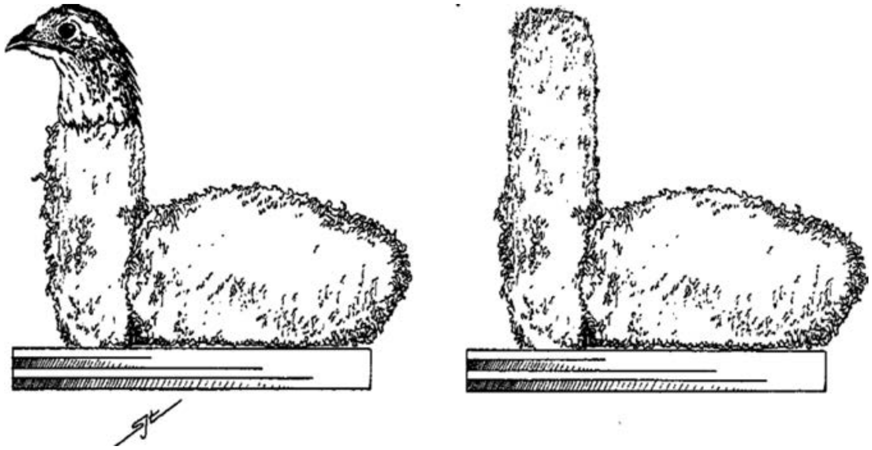

FIGURE 12.2. **Model conditioned stimuli used in studies of conditioned sexual behavior in Japanese quail. From "Learning With Arbitrary Versus Ecological Conditioned Stimuli: Evidence From Sexual Conditioning," by M. Domjan, B. Cusato, and M. Krause, 2004, *Psychonomic Bulletin and Review, 11,* p. 235. Copyright 2004 by the Psychonomic Society, Inc. Reprinted with permission.**

control CS was made of terrycloth and did not have quail feathers or a beak. Male quail used in these studies received a 5 min pretest for copulatory behavior, but otherwise had no sexual experience.

The results strongly supported the proposition that more robust learning occurs with a naturalistic CS. Not only did conditioning proceed more quickly with the head and neck model CS, but the naturalistic CS came to elicit a broader range of CRs. With the terrycloth model, only approach responses became conditioned to the CS. The males also showed conditioned approach to the head and neck model CS. However, they also grabbed, mounted, and made cloacal contact responses to the CS. Conditioned responding to the naturalistic CS was much more difficult to extinguish than responding to the terrycloth object (Krause, Cusato, & Domjan, 2003). In addition, the learning could not be blocked by concurrently presenting a previously trained CS (Köksal, Domjan, & Weisman, 1994) or by increasing the CS–US interval (Akins, 2000). The naturalistic CS also supported more second-order conditioning (see Domjan et al., 2004, for further details).

The contrasting results obtained in conditioning with a naturalistic versus arbitrary CSs indicate that any evolutionary influences on learning have to be considered within the context of the ecological environment in which a species might have evolved. These results also suggest that evolutionary and ecological factors influence not only the speed and strength of learning, but also the types of conditioned responses that develop and whether the learning is sensitive to blocking or increases in the CS–US interval. Given these findings, one can conceive of a continuum of learning on the basis of the extent to which the CS and US used in the learning procedure are related to the ecology of the species (Domjan, 2008). Such a continuum has some resemblance to the preparedness continuum proposed by Seligman (1970) but unlike the original preparedness hypothesis, the ecological view is not circular because ecological relevance can be determined independently of the outcome of a learning experiment.

Behavior Systems Theory

How the relationship between stimuli, responses, and their shared evolutionary history affects the outcomes of learning experiments has been most systematically considered in behavioral systems theory. Behavior systems theory postulates that the outcome of a conditioning procedure depends on how that procedure interacts with the pre-existing behavioral organization of the species. That behavioral organization is conceived of in terms of different functional systems that have evolved to deal with critical biological challenges such as procuring food, defending oneself from predators, and successfully reproducing. Each behavior system is assumed to be organized into a hierarchy of subsystems, modes, and modules. Within each of those units, organisms show increased sensitivity to certain kinds of stimuli and are likely to exhibit specific sets of responses.

Behavior systems have been characterized for feeding (Timberlake, 2001), defense (Rau & Fanselow, 2007), and reproduction (Akins & Cusato, 2015; Domjan, 1994). In each system the particular subsystem or response mode that is activated depends on how far the organism is from the goal object or US in distance or time. In the defensive behavior system, this organization has been characterized in terms of the imminence of attack by a predator or the *predatory imminence continuum* (e.g., Rau & Fanselow, 2007). The actual point of attack elicits a circa strike response, which is akin to a discrete UR or reflex. If a rat (the prey object) is bitten by a snake (the predator), the circa strike response is leaping into the air. Prior to the actual attack but at a time and place where the attack is imminent, the defensive mode results in freezing behavior or remaining still. Freezing presumably evolved because potential prey are more difficult to detect in their natural environment if they do not move (Suarez & Gallup, 1981). Rats that are farther removed in space and time from the point of actual attack are in “pre-encounter” mode, and likely engage in cautious foraging and fewer trips out of the burrow. At a time and place when there is no chance of a predatory attack, the rat engages in recuperative behaviors and various nondefensive behaviors such as foraging, mating, and care of young.

The feeding behavior system is activated when the organism is hungry and begins to search for food. When there are no cues relevant to finding food, the organism is in the general search mode, in which increased locomotion is the most prominent behavior and there is presumed sensitivity to contextual cues. Once a potential food source is identified, behavior switches to a focal search mode and is guided by more localized stimuli. The actual identification of a food item causes yet another change response mode, with increases in reactivity to the specific features of the food item and activation of responses relevant to manipulating and ingesting the food (Timberlake, 2001).

The sexual behavior system is similar to the feeding system in that it involves an appetitive reinforcer or US (access to a potential sexual partner and copulation). At a time and place where a sexual partner has not yet been identified, a general search mode is activated, which is characterized by increased locomotion and increased reactivity to broad contextual cues. This may be followed by a focal search mode, with approach to cues indicative of the appearance of a sexual partner. Once the partner is available, response modes related to courtship and copulation are activated (Akins & Cusato, 2015; Domjan, 1994).

Behavior systems theory assumes that a laboratory conditioning procedure is superimposed on the pre-existing behavior organization that is activated in a particular learning situation. The theory has been most successfully applied to predicting the nature of the CR in Pavlovian conditioning procedures when different CS–US intervals are used. A short CS–US interval is predicted to elicit responses closer to the end of the behavior sequence, whereas long CS–US intervals should elicit responses appropriate to earlier response modes such as general search. Consistent with this prediction, Akins (2000) found that in the sexual behavior system, a 2 min CS–US interval results in conditioned approach to the CS, whereas a 20 min CS–US interval results in increased locomotor behavior when the CS is presented.

REPRODUCTIVE SUCCESS AND PAVLOVIAN CONDITIONING

Biological constraints and behavior systems perspectives are concerned with how the evolutionary history of a species shapes learning processes, determining what is learned rapidly or slowly, and what response modules are activated as a result of Pavlovian conditioning. But, the relationship between learning and evolution may not go in just one direction. Learning processes may also determine the course of evolution (see Volume 1, Chapter 15, this handbook and Chapter 20, this volume).

The driving force for evolution is reproductive success. Pavlovian conditioning no doubt contributes to reproductive success indirectly by facilitating the organism's interactions with a variety of biologically significant events and challenges. Coping with pain, digesting food, effectively nursing offspring, and territorial defense are all facilitated by Pavlovian conditioning and no doubt contribute to reproductive success (see Domjan, 2005, for a review). The evolutionary benefits of such learning have to be weighed against the costs of maintaining the relevant learning systems. Such calculations are difficult to make. But, given the prevalence of Pavlovian conditioning, it may be safe to assume that on balance the benefits of Pavlovian conditioning have been greater than its costs.

The evolutionary benefits of Pavlovian conditioning are perhaps most obvious in the area of sexual conditioning (Brom et al., 2014; Coria-Avila, 2012; Pfaus, Kippin, & Centeno, 2001; see also Volume 1, Chapter 37, this handbook). Early research with rats demonstrated that exposure to a sexual CS reduces the latency of males to ejaculate when copulating with a female (Zamble et al., 1985). Decreased latencies to copulation were also observed in sexual conditioning studies with male quail (Domjan et al., 1986). This conditioning effect is of biological significance because it provides an advantage when two males compete for sexual access to a single female (Gutiérrez & Domjan, 1996).

Sexual conditioning also influences the copulatory behavior of females. In female domesticated quail, the CR is increased squatting and other forms of proceptive behavior (Gutiérrez & Domjan, 1997, 2011). These female behaviors in turn enable males to mount and copulate more easily and efficiently, and that in turn is correlated with increased fertilization of eggs (Domjan, Mahometa, & Mills, 2003).

Although most studies of sexual conditioning have focused on conditioned behavioral responses, a growing number of experiments have also been conducted that document reproductive success more directly. The first of these was conducted in a fish species, the blue gourami (*Trichogaster trichopterus*; Hollis et al. 1997). Pavlovian conditioned males sired significantly more offspring when given a chance to interact with a female as compared with a nonconditioned control group. The increased reproductive success of the Pavlovian males was accompanied by reduced aggression toward the female, more nest building behavior, and increased clasp frequency.

Initial studies with domesticated quail showed that Pavlovian conditioned males release more sperm than males in a control group (Domjan, Blesbois, & Williams, 1998), probably because exposure to a CS elicits cloacal gland contractions (Holloway, Balthazart, & Cornil, 2005). The first direct demonstration in quail that Pavlovian conditioning can increase rates of fertilization of eggs was by Adkins-Regan and MacKillop (2003), who demonstrated that conditioning of either the male or the female quail increased rates of fertilization. Mahometa and Domjan (2005) replicated this basic conditioned fertility effect and the phenomenon was subsequently extended to a wide range of conditioning parameters. The conditioned fertility effect was obtained when females were conditioned with CS durations ranging from 30 seconds to 20 minutes. The phenomenon was observed with arbitrary and naturalistic CSs, and was also demonstrated with contextual cues signaling copulatory opportunity (Domjan, Mahometa, & Matthews, 2012). However, in the Domjan lab, increased rates of fertilization only occurred when both the male and the female in a copulatory interaction received access to the sexual CS.

In the standard conditioned fertility paradigm, rates of fertilization are measured following a copulatory episode involving one male and one female. However, as we mentioned earlier, Pavlovian conditioning may also determine the outcome of sexual competition in which a female copulates with more than one male. Observing an overall increase in fertilization rates as a consequence of Pavlovian conditioning is not helpful in such a situation without some way to determine which male sired which offspring. Using microsatellite-based DNA analysis, Matthews et al. (2007) were able to assign paternity to each fertilized egg that a female produced after copulating with two males in succession. Of these two males, one copulated with the female after exposure to a sexual CS, whereas the other received exposure to a control cue. The microsatellite analysis showed that the conditioned males sired 72% of the total fertilized eggs that were produced. Furthermore, of the 14 females that produced fertilized eggs in the experiment, 10 produced more eggs fertilized by a conditioned male than a control male. This experiment clearly shows that Pavlovian conditioning provides a reproductive advantage in sexual competition.

In the initial study by Matthews et al. (2007), the two males copulated with the same female right after one another. Under these circumstances, the baseline fertilization rate is 50/50 for the two males. How about if a 5 hr interval separates when each of two males copulates with the same female? With a 5 hr separation, the second male usually has a great advantage in fertilizing the eggs that are subsequently produced. In fact, Matthews et al. found that if neither of the males received a sexual CS, the second male fertilized 74% of the subsequent eggs whereas the first one fertilized only 26% of the eggs (Domjan, Mahometa, & Matthews, 2012). However, if the first male received a sexual CS, the first-male disadvantage was substantially attenuated. With the sexual CS, the first male's fertilization rate increased to 43% (with a concomitant decrease to 57% for the second male). This provides another dramatic illustration of the power of Pavlovian learning to influence the outcome of sexual competition.

How about a situation in which the same male copulates in succession with two females? Under those circumstances, fertilization rate is usually governed by sperm depletion. In the absence of sexual conditioning, a male is expected to fertilize more eggs produced by the first female it copulates with than the second female. Indeed, in a control test with a 15 min interval between the two copulations, Matthews found that the first copulation fertilized 24% of the eggs whereas the second only fertilized 6%. However, with the same interval between exposures to the two females, if the male received a sexual CS prior to copulating with the second female it's fertilization rate for the eggs produced by the second female went up to 27% (Domjan, Mahometa, & Matthews, 2012).

These results indicate that Pavlovian conditioning can overcome what is usually attributed to sperm depletion. Apparently, the depletion effect evident in the large decrease in fertilization rates from the first to the second female is not actually due to a lack of sperm but a failure to deposit those sperm into the female. As we noted previously, a sexual CS can elicit cloacal gland contractions in anticipation of copulation (Holloway et al., 2005) and increased sperm release (Domjan et al., 1998). Evidently, those mechanisms are sufficient to overcome the lower fertilization rates that occur with repeated copulations.

Studies of the conditioned fertility effect clearly indicate that Pavlovian conditioning can significantly influence the reproductive success of a copulatory episode. These effects occur under a wide range of conditioning parameters and result in increased sperm release, increased fertilization rates in isolated copulations, greater success in sexual competition, and attenuation of the usual sperm depletion effect. Because Pavlovian conditioning has such wide-ranging effects on reproductive success, there is no doubt that Pavlovian mechanisms can influence genetic transmission and thereby the course of evolution. Thus, learning is not only the product of evolution but may determine the future course of evolution

EVOLUTIONARY CONVERGENCE AND ADAPTIVE PLASTICITY: CONDITIONED FEAR AND ANTIPREDATOR RESPONSES

Another productive approach to testing evolutionary hypotheses involves examining relationships among environmental variables and their mapping to phylogenetic relationships among multiple species (see Volume 1, Chapter 12, this handbook). Closely related species may undergo divergent evolution as their respective populations respond to unique selection pressures. Or, parallel evolution may result in the evolution of similar traits between related species from different clades in response to common selection pressures. Another evolutionary process, convergent evolution, occurs when distantly related species arrive at a similar adaptive solution to a common selection pressure. Numerous examples of convergent behavioral and cognitive evolution have been described in the literature, owing in large part to an expanding diversity of species that have been studied from an evolutionary perspective. Convergent evolution is thought to account for the complex sociocognitive abilities found among cetaceans, canids, and primates (Marino, 2002; Topál et al., 2009), as well as capacities for tool use, social cognition and mental time travel among corvids and apes (Emery, 2006; Emery & Clayton, 2004). Thus, despite very different anatomical and neural organization, diverse organisms have evolved similar behavioral and cognitive abilities.

Evolutionary convergence may account for some aspects of the Pavlovian conditioning of defensive behavior among diverse organisms. Conditioned fear and antipredator responses appear to be specialized for dealing with evolutionarily relevant threats (see Volume 1, Chapters 39 and 40, this handbook). Selectively strong associations develop to CSs that are inherently related to long-standing threats to survival in several species that have been tested. In addition, in some cases conditioned fear and antipredator responses appear specialized in ways that do not conform to general process accounts of learning.

Conditioned Fear and Evolutionarily Relevant Threats

Snakes have posed an enduring threat to the survival of individuals of many species of primates and other animals. Throughout their evolutionary histories many primates, including humans, have overlapped geographically with venomous and large constrictor species of snakes. Behavioral and comparative neuroanatomical studies reveal specialized, perceptual biases for detecting snakes. For example, Isbell and colleagues (Isbell, 2006; Van Le et al., 2013) have demonstrated that the primate visual cortex has evolved adaptively specialized processes for perceiving snakes, and developmental work shows that human infants and children have an attentional bias toward snakes and spiders in comparison to other animals (LoBue, 2014; Rakison & Derringer, 2008). For many species, snakes seem to be in a category by themselves as a perceived threat to survival. Additional support for this claim comes from individual and observational Pavlovian conditioning experiments done on humans and rhesus macaques (*Macaca mulatta*).

Öhman and Mineka (2001, 2003) reviewed a large body of work showing that people acquire particularly strong conditioned sympathetic arousal to photos of snakes (the CS) paired with a shock US, in comparison to conditioned responding to nonthreatening CSs (flowers) and ontogenetically acquired threat CSs (guns). Similarly, rhesus monkeys rapidly acquire conditioned fear responses to snake CSs relative to arbitrary CSs. Individual and observational learning processes result in conditioning that is stronger to snakes than to biologically irrelevant stimuli (e.g., flowers). A common interpretation of this work is that natural selection favored individuals that were quick to acquire a selectively strong association between snakes and potentially lethal injury (see also Davey, 1995).

Tammar wallabies (*Macropus eugenii*) also acquire selectively strong associations to evolutionarily relevant predatory stimuli. Griffin, Evans, and Blumstein (2001) exposed wallabies to a stuffed fox (the CS) paired with a threatening US (a person approaching with a capture net in hand). A control group experienced the same duration of CS and US exposures in an unpaired fashion. After only four CS–US pairings, the wallabies engaged in significantly more conditioned antipredator responses (vigilance or escaping) to the fox CS, whereas the control group showed no conditioning to the fox CS. Also, conditioned antipredator responses generalized to a different threatening stimulus (a model of a cat) that had not been paired with the US, but not to a nonpredatory animal (a goat; see also Griffin, Evans, & Blumstein, 2002).

The research on conditioned fear to snakes in humans and rhesus monkeys, and antipredator responses in wallabies, shows that specific qualities of the CS determine the magnitude of conditioned responding. Possibly, adaptive learning about specific predatory or threat stimuli evolves among organisms that have consistent encounters with such predators over their evolutionary history. In addition to having a predisposition to learn about these types of threat, prey organisms may benefit from plasticity of conditioned responding to predatory cues.

Plasticity in Antipredator Responses: Social Cues, Latent Inhibition, and Learned Irrelevance

Successful predators arrive and attack at unpredictable times from the perspective of their prey. Animals that predators want to eat benefit from rapidly learning about predators, such as the way they look, sound, or smell, and when their presence is most likely. In addition, prey species use conspecific social cues such as alarm calls or olfactory signals to detect the presence of predators (see Volume 1, Chapters 30 and 40, this handbook and Chapter 4, this volume). Socially mediated associative learning involving conspecific cues (USs) and predatory cues (CSs) has been documented in several species. For example, Carib grackles (*Quiscalus lugubris*) and Indian mynahs (*Acridotheres tristis*) acquire one-trial predator avoidance and vigilance responses after either forward or backward pairings of a model CS (stuffed pigeon or pheasant) and conspecific alarm call playbacks (the US; Griffin, 2008a, 2008b; Griffin & Galef, 2005). This work simulated real-world social interactions experienced by both species. Observing threats or predation on a conspecific facilitates the acquisition of strong, adaptively significant avoidance responses (Griffin & Haythorpe, 2011).

Several species of crayfish acquire olfactory-based, conditioned inhibitory responses to predatory cues. Crayfish show unconditioned defensive responses to alarm odors, which are emitted by injured conspecifics. Pairing a novel and nonpredatory odor CS (goldfish, which are herbivores) with the alarm odor US results in conditioned inhibition of feeding behavior in response to goldfish odor alone in four species of crayfish (*Orconectes spp.*, *Procambarus spp.*; Hazlett, Acquistapace, & Gherardi, 2002). Only 2 hr of pairing the CS and US odors were required for conditioning to occur. Interestingly, the learned association was more robust in an invasive crayfish species (*O. rusticus*) compared with a native species (*O. virilis*). On the basis of similar data from invasive and native pairs of *Procambarus* crayfish, Hazlett et al. (2002) concluded that associative learning abilities are enhanced in invasive species, which may facilitate their relative success in inhabiting new ecological niches.

For prey species, learning can be critical for survival and reproductive success. Because predatory threats can fluctuate over time and space, it behooves prey species to learn not only when to be vigilant and defensive, but also when to temper their responses so as not to waste energy or miss opportunities to do other things such as acquiring resources (Ferrari & Chivers, 2006). Two learning processes, latent inhibition and learned irrelevance, are thought to play important roles in conditioned predator recognition. *Latent inhibition* occurs when repeated, unreinforced exposure to a CS attenuates conditioning if that CS is subsequently paired with a US. For example, conditioned antipredator responses to olfactory cues emitted by a predator may be acquired relatively slowly or not at all if those odors are not paired with an actual aversive encounter. Repeated false alarms also come at a cost. For crayfish, repeated exposure to goldfish odor alone results in latent inhibition of conditioned defensive responses when the goldfish odor is subsequently paired with conspecific alarm odor (Acquistapace et al., 2003). Latent inhibition of conditioning to predator cues has also been reported in frog tadpoles (*Pelophylax perezi*; Gonzalo, López, & Martín, 2013), fathead minnows (*Pimephales promelas*; Ferrari & Chivers, 2006), and coral reef fish (*Pomacentrus moluccensis*; M. D. Mitchell et al., 2011).

Learned irrelevance occurs when the CS and US occur randomly with respect to each other, resulting in diminished conditioning when pairings subsequently do occur (Mackintosh, 1973). Conditioned responding may be attenuated by random encounters with the CS and US if those random presentations occur prior to CS–US pairings, afterward, or both. Learned irrelevance occurs in crayfish when goldfish and alarm odors occur randomly with respect to each other, either before or after trials in which they occur simultaneously (Hazlett, 2003). As with latent inhibition, learned irrelevance occurs in other predator–prey species systems (Gonzalo et al., 2013).

In addition to learning to recognize predators, learning about when they are more likely to be present is also important. Remarkably, stimulus exposure during embryonic development affects subsequent CS-responding in newly-hatched wood frog (*Rana sylvatica*) tadpoles (see Volume 1, Chapters 11 and 19, this handbook). Ferrari, Manek, and Chivers (2010) exposed freshly laid clutches of wood frog eggs to either water (control), salamander odor, or crushed conspecific tadpoles combined with salamander odor in either the morning or the evening over a 7 day period. Salamanders prey on larval frogs, and injured tadpoles give off alarm odors that elicit evasive action by conspecifics. Two weeks after hatching, activity levels (line crosses) were measured during exposure to water (negative control), crushed conspecific odor (a positive control), and salamander odor. Inhibition of line crosses was the assay for antipredator responding. The tadpoles that were exposed to crushed tadpole and salamander cues during embryonic development inhibited their movements in response to salamander odor during test trials. This effect was strongest when the timing of conditioning (morning or evening) matched the time of testing (also morning or evening). Thus, learning about predatory cues by tadpoles was sensitive to the circadian-based activity patterns of their potential predators (see Volume 1, Chapter 29, this handbook).

Applications to Species Conservation

The role of conditioning in the development of antipredator responses and predator recognition has implications for conservation efforts. One strategy for species conservation is to reintroduce captive-born animals into natural or semi-natural habitats. However, unless key survival skills are learned and practiced in captivity, reintroduction efforts may have limited success. For example, animals may need to learn appropriate evasive and vigilance responses to predators and predatory cues that they will likely encounter in the wild. Methods for accomplishing this include exposure and sensitization procedures, observational learning, and Pavlovian conditioning (Braithwaite & Salvanes, 2005; Griffin, 2010).

Conditioning procedures have been used to train appropriate defensive responses and enhance subsequent postrelease survival in juvenile, captive-born prairie dogs (*Cynomys ludovicianus*; Shier & Owings, 2006). During conditioning, the prairie dogs in the experimental group experienced separate conditioning trials with natural predatory stimuli, including a live ferret (*Mustela nigripes*) and snake (*Crotalus viridis*), and a stuffed red-tail hawk (*Buteo jamaicensis*; the CSs). Played-back conspecific alarm calls were used as the US, with alarm barks paired with ferret and hawk CSs and jump-yip calls paired with the snake. A control group had no exposure to either predators or alarm calls. Prairie dogs in the treatment group showed vigorous conditioned vigilance responses and alarm vocalizations toward predatory stimuli alone compared with the control animals. Furthermore, following conditioning the natural conditioned predatory stimuli elicited more vigorous defensive responses than did a nonpredatory control species (cottontail, *Sylvilagus auduboni*). Following the conditioning phase, the prairie dogs were released to a natural prairie dog town. Animals from the experimental group had a higher survival rate one year after release into the wild compared with controls (see also Shier & Owings, 2007).

Although conditioning procedures can be a valuable component of conservation efforts, it should be noted that learning about predators and other natural situations in no way guarantees survival advantages, as additional variables are in play (Moseby et al., 2012). Compared to wild-caught animals that have been relocated, captive-born and wild-introduced carnivores experience higher mortality rates because of starvation, disease, and human-related activity (Jule et al., 2008).

DISCUSSION

We began the chapter with a review of the learning vs. instinct controversy, and how mounting evidence for biological constraints on learning altered some prevailing views about learning held by comparative psychologists in the middle of the twentieth century. No single "critical experiment" could have resolved scientific debate about whether a given behavior was learned or instinctive. Rather, ethologically-based experiments, which have increasingly included genetic and epigenetic measures, demonstrate how ecological and evolutionary factors guide the development and expression of behavioral phenotypes. These shifts in perspective are apparent in the past several decades of research on Pavlovian conditioning. Seligman's (1970) proposal of a continuum of biological preparedness for learning and Rozin and Kalat's review (1971) reflected these changes at one point in time. However, they fell short of changing prevailing views that learning was a generalized process that could be fully understood without considering the natural history of the study species.

The concept of preparedness provided a convenient term with which to categorize behaviors that could be learned rapidly (one trial, in some cases) from those that required extensive training. However, the concept provided no more insights into underlying mechanisms than the concept of instinct. In fact, all of the criticisms that Daniel Lehrman leveled against instinct could be just as well be applied to preparedness. The term *preparedness* continues to be used in introductory discussions of learning, but it has been abandoned by researchers because it is entirely circular (Domjan & Galef, 1983). Because the rate of learning is used to identify the level of preparedness, it cannot be used to explain why some things are learned faster than others.

Ethological and Functional Views of Learning

The contemporary functional approach to Pavlovian conditioning has helped break this circularity. Conditioning in naturalistic contexts involves CSs that have a pre-existing relationship to the US. Furthermore, conditioning alters how organisms respond to biologically relevant USs, not CSs (Domjan, 2005; Dukas, 1998; Hollis, 1997). Investigations of natural learning paradigms in such systems as poison-avoidance learning, caloric conditioning, sexual and fear conditioning, and maternal nursing confirm the vitality of a functional approach to Pavlovian conditioning (summarized previously in Table 12.1). In addition, a critical component of the functional approach is that Pavlovian conditioning either directly or indirectly affects survival and reproductive success. The experiments on sexual conditioning and conditioned fear and antipredator responses reviewed in this chapter have confirmed that this is indeed the case.

The relationship between Pavlovian conditioning and reproductive fitness has been clearly established in research with several different vertebrate species, such as Japanese quail (*Coturnix japonica*; Domjan et al., 2012), poison dart frogs (*Dendrobates tinctorius*; Gaalema, 2013), and fish (*Trichogaster trichopterus*; Hollis et al., 1989, 1997). Research on invertebrates, namely *Drosophila*, has the distinction of not only highlighting conditions under which sexual conditioning might evolve but also how adaptively specialized or prepared learning evolves. Regarding the former, Reif and colleagues (2002) experimentally tested the functional significance of inhibitory conditioning in male *Drosophila melanogaster*. Recently-mated female flies release a pheromone from their cuticle that inhibits mating attempts by males. The pheromone becomes a CS that inhibits wasted copulatory attempts. This type of conditioning would be favored when population densities are high. Under those circumstances inhibiting copulation with competitors would reduce resource competition. The data confirm this hypothesis, as over the course of 21 generations inhibitory courtship became increasingly advantageous if males had extensive contact with females (2 weeks) relative to brief contact (18 hr).

Use of Traditional Evolutionary Methodologies

A worthy component of an ethological and evolutionary discussion of Pavlovian conditioning includes asking to what extent established evolutionary methodologies have been applied to the research (Krause, 2015). One approach to understanding the adaptive value of a trait is to examine its phylogenetic origins and distribution. Applying this methodology confirms just how common Pavlovian conditioning is among a diversity of organisms, even among species that have evolved a relatively simple sensory and motor circuitry (Ginsburg & Jablonka, 2010).

Comparative and experimental psychologists have long incorporated evolutionary logic into the interpretation and design of research on learning. Interpreting human and animal behavior in evolutionary terms certainly has advanced the respective fields of comparative and evolutionary psychology (Vonk & Shackelford, 2012), but the risk of "just-so story telling" looms large (Gould & Lewontin, 1979; Panksepp & Panksepp, 2000). Thus, it is worth examining what has been a rather wide disparity between designs used by psychologists and those used by evolutionary biologists for testing adaptive hypotheses (see Chapter 14, this volume). Within evolutionary biology, methods for testing behavioral adaptations include phylogenetic comparative methods, genetic techniques, modeling, common garden designs, and other experimental approaches that include measures of reproductive fitness and survival in relation to phenotypic variation.

Species comparisons are certainly common in the animal learning literature, but formal phylogenetic comparative methods (see Volume 1, Chapter 10, this handbook) have not been applied to test hypotheses about the adaptive value of conditioning—namely, claims about adaptive specializations of learning (Krause, 2015). Sample sizes required are among the challenges to applying comparative methodology to complex behavioral traits (but see MacLean et al., 2014). Rapid and robust fear conditioning to snakes may be evolutionarily adaptive to many primates, but work that builds on what has been done with humans and rhesus monkeys, and the implementation of comparative methods, would be required to directly test an adaptive hypothesis. Currently, the evolutionary relevance of this research leans heavily on the modular brain and design feature perspectives common within popular evolutionary psychology (Öhman & Mineka, 2001).

Another approach, behavioral genetic data from monozygotic and dizygotic twin comparisons, demonstrates a heritable basis for Pavlovian fear conditioning, and shows that heritability of fear conditioning to snake-like stimuli may differ from that of responses to arbitrary shapes (Hettema et al., 2003). In humans, self-reported fear to natural threats such as animals and social situations is moderately heritable in comparison to situational fears (e.g., fear of fire or desolate highways; Skre, Onstad, Torgersen, Lygren, & Kringlen, 2000). At a molecular level, variation in COMT and 5-HTT alleles correlates with individual differences in fear learning and anxiety disorders (Lonsdorf et al., 2009; Oehlberg & Mineka, 2011). Given these data, from an evolutionary perspective the hypothesis that fear conditioning is itself a target of natural selection, and that selection has resulted in specialized learning to natural threats, has equivocal support from genetic research. Measures involving survival in relation to fear/antipredator responses suggest an adaptive advantage to learning (Shier & Owings, 2006, 2007).

Genetic contributions to biological constraints on learning can also be examined by breeding successive generations in environments that do (or do not) involve special CS–US correlations. Dunlap and Stephens (2014) successfully simulated conditions in which selectively strong associations could be formed in *Drosophila*. By manipulating the reliability of different CS (color or odor) and US (quinine) pairings over the course of 40 generations, they were able to quantify genetically based changes in selective associations to the different CSs. When a color CS and quinine were paired 100% of the time, and the odor CS and quinine were paired 50% of the time, there was a selectively strong association formed to the color CS across generations. The converse held true when the odor CS and quinine were paired 100% and the color CS and quinine were paired 50% of the time. Such research directly addresses the long-standing problem of circular reasoning with regard to preparedness, and provides empirical evidence for logical inferences psychologists have been making about the role of evolution in modifying the expression of Pavlovian conditioning.

CONCLUSION

We have come a long way since research on biological constraints on learning forced investigators of conditioning to seriously consider the pre-existing behavior systems their organisms brought to a learning situation. Contemporary scientists take as given that the outcome of a learning process depends on how evolution has shaped organisms to cope with various ecological challenges. These behavioral substrates no doubt develop through epigenetic processes, but the details of how that occurs remain to be elucidated. The last thirty years of research has yielded much information about the role ecological variables have played in learning, and has also shown us how the products of learning can shape the future course of evolution. The rich and multifaceted approach evident in contemporary research on the interactions of evolution and learning promises an exciting future for this area of comparative psychology.

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CHAPTER 13

COMPARATIVE LEARNING AND EVOLUTION

Mauricio R. Papini and Carmen Torres

Learning refers to the ability of animals to acquire, consolidate, and retrieve information from individual experience. Experience may be defined as any sort of information arising from the internal milieu (e.g., pain, sickness, effort), the physical environment (e.g., food, water, shelter, predators), or the social environment (e.g., mates, competitors, offspring). Psychologists have applied comparative methods to understand the evolution of learning mechanisms by developing a wide variety of behavioral assays that test the organism's ability to adjust to particular situations (see Volume 1, Chapter 6, this handbook). Such adjustment is often related to the nature of the situation, internal conditions, prior experience, and the species' ecological and phylogenetic history. Comparative studies are concerned with explaining species similarities and differences in learning, and they are used to gain an understanding of the diversity of learning mechanisms—a remarkable function of nervous systems.

There are two fundamental questions about the evolution of learning mechanisms:

- Are species similarities understandable in terms of homology or homoplasy?
- Are species differences attributable to evolutionary divergence?

Homology, homoplasy, and divergence are evolutionary outcomes (see Volume 1, Chapter 12, this handbook). *Homology* refers to phenotypic similarity attributable to common ancestry (e.g., all primates have nails). *Homoplasy* refers to phenotypic similarity attributable to independent evolution in response to similar environmental pressures (e.g., similar body shape of sharks and whales). *Divergence* refers to the split of lineages with regard to a particular trait (e.g., grasping feet of chimpanzees vs. flat feet of humans). Applying these concepts to the study of learning requires recognizing a distinction between learning phenomena and learning mechanisms. *Learning phenomena* are typically induced under laboratory conditions and involve a comparison between experimental and control groups in terms of behavioral differences. Learning phenomena must be the result of *learning mechanisms*—a set of processes that account for the behavioral phenomenon. But what is a learning mechanism? There are at least four levels of mechanistic analysis in the study of learning (M. R. Papini, 2002, 2008):

- *Psychological level*: This is the traditional level of analysis developed by comparative psychologists. The methodology consists of dissecting learning phenomena through experimental design contrasting different training conditions (e.g., Chapter 15, this volume). Psychological concepts offer a guide to interpret the effects of manipulations at lower levels of analysis on behavior (Bitterman & Woodard, 1976).
- *Neural circuitry level*: This involves specifying the neural network necessary to produce a given

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learning phenomenon. Typical methodology involves lesions, stimulation, recording, and imaging of brain regions to determine their role in a given learning phenomenon (e.g., Volume 1, Chapter 25, this handbook).

- *Neurochemical level*: At this level, synaptic processes, including synaptic plasticity, are implicated in learning. Methodological manipulations include the administration of psychoactive drugs and genetic interventions (e.g., knockout strains) affecting synaptic transmission, among others (e.g., Volume 1, Chapter 23, this handbook).
- *Cell-molecular level*: Cellular cascades, including gene expression and protein synthesis, are necessary for learning. Its methodology includes drug and genetic manipulations that affect cellular processes involved in synaptic plasticity (e.g., Volume 1, Chapter 22, this handbook).

According to this view of learning mechanisms, a homology hypothesis of similarity by common ancestry is strengthened when a learning phenomenon occurring in two or more species depends on the same processes at all four levels of analysis. By contrast, a homoplasy hypothesis of similarity because of common ecological pressures is strengthened when similar learning phenomena across species depend on different processes at one or more levels of analysis. A divergence hypothesis of phenotypic differentiation is favored when similar environmental conditions lead to different learning phenomena, which, in turn, are shown to depend on different mechanisms at one or more levels of analysis. In all cases, the alternative hypothesis is that similarities or differences in learning phenomena are caused by species differences in contextual mechanisms, such as sensory-perceptual, motivational, and motor processes (Bitterman, 1975). Because the role of contextual variables is difficult to dismiss completely, the conclusions drawn in the next section are expressed in tentative terms.

SPECIES SIMILARITIES IN LEARNING MECHANISMS

The simplest nervous systems are the diffuse networks of radially symmetrical animals (e.g., sea anemones, coral, jellyfish: *Cnidaria*). Cnidarian neurons show a similar set of physiological functions as those of other animals (Anderson, 1985). Thus, it is hardly surprising that these animals exhibit familiar learning phenomena, including classical conditioning (Haralson, Groff, & Haralson, 1975). However, underlying mechanisms have yet to be identified. Most animals exhibit a bilateral symmetry, with central and peripheral nervous systems. Classical conditioning has also been reported in species from several Phyla, but these studies are also limited in terms of identifying underlying mechanisms, with some notable exceptions.

The round worm *Caenorhabditis elegans* (*Nematoda*) allows for a combination of behavioral, physiological, and genetic manipulations of associative and nonassociative (e.g., habituation) learning enabled by the striking simplicity of its central nervous system. With only 302 neurons, all identified and with a known connectivity, and a mapped genome, studies using *C. elegans* demonstrate that simple circuitry is sufficient for learning (McDiarmid, Ardiel, & Rankin, 2015). The mechanisms of simple learning processes are well understood in the sea hare *Aplysia californica* (*Mollusca*), especially at the cell-molecular level (Roberts & Glanzman, 2003), and in the honeybee *Apis mellifera* (*Arthropoda*), especially at the behavioral level (Bitterman, 1996; Prete, 2006). With its complex sensory systems and refined behavior, honeybees have produced an impressive list of learning phenomena familiar from research with vertebrates, including overshadowing, latent inhibition, and the partial reinforcement extinction effect, among many others.

From a comparative perspective, it is remarkable that species so distantly related as nematodes, mollusks, and arthropods exhibit such a degree of similarity in learning phenomena relative to mammals. Such similarity can be understood in terms of deep homology, massive convergence, or parallel evolution of learning mechanisms (M. R. Papini, 2008). If one assumes that at least some of these phenomena are dependent on neural architecture, then deep homology can be dismissed on the assumption that the nervous systems of insects and mammals have evolved largely independently (although invertebrate and vertebrate nervous systems do share some molecular markers; see Benito-Gutiérrez & Arendt, 2009). For example, there is no homologue to the vertebrate hippocampus in insects. Massive convergence would be consistent with different mechanisms at all levels, whereas parallel evolution would require homologies at lower levels of analysis. Current data suggest that parallel evolution on the basis of homologous cell-molecular processes has played a significant role in the evolution of learning mechanisms. It is plausible that mechanisms of synaptic plasticity established early in animal phylogeny (e.g., second-messenger cascades) have been preserved and coopted to new neural architectures in different lineages (Kaplan & Abel, 2003; Mayford & Kandel, 1999; McGuire, Deshazer, & Davis, 2005).

SPECIES DIFFERENCES IN LEARNING MECHANISMS

To understand differences in learning mechanisms, comparative psychologists have traditionally emphasized either adaptive significance (Domjan, 1997; see also Chapter 12, this volume) or phylogenetic history (Bitterman, 1975). Adaptive significance is suggested by a variety of learning phenomena, including most prominently conditioned taste aversion (CTA). In CTA (Garcia & Koelling, 1966), rats (*Rattus norvegicus*) exposed to pairings of a taste or an audiovisual conditioned stimulus with either gastrointestinal intoxication or a physical pain unconditioned stimulus later exhibited selectivity. They responded to the taste when paired with intoxication but not with pain, but responded to the audiovisual stimulus when paired with pain but not with intoxication. This selectivity may reflect an adaptive specialization. Testing the adaptive significance hypothesis requires comparisons among closely related species with different ecology (e.g., Daly, Rauschenberger, & Behrends, 1982). Adaptive significance implies that species differences in learning should map to different mechanisms at one or more levels of analysis. This view anticipates a myriad of neural mechanisms for dealing with one functional problem across species with contrasting ecologies (e.g., learning about food location in species foraging on different food resources).

Phylogenetic history is suggested by differences in learning phenomena observed among distantly related lineages. Consider successive negative contrast (SNC), an example of divergence related to phylogenetic history. In SNC, an animal rejects a small reward after a downshift from a large reward. SNC has been described in mammals and in one isolated experiment with a bird species, but not in any other vertebrate species studied thus far (M. R. Papini, 2014). In teleost fish, amphibians, reptiles, and some avian species a reward downshift causes a gradual adjustment without the strong rejection typically observed in mammals. This outcome is called a *reversed SNC effect*. A similar distinction between mammals and teleost fish also appears in other learning phenomena involving reward downshifts. The reason why history, rather than adaptive significance, is a good candidate relates to the fact that SNC and reversed SNC effects have been observed in species that differ widely in ecological adaptations. This should not imply that the underlying mechanisms are maladaptive or even not adaptive; rather, it implies that the adaptation provides a fit to an ecological dimension cutting across many types of niches (Dickinson, 1980).

Accounts of comparative data in terms of adaptive significance and phylogenetic history share a problem, namely, to distinguish between species differences in learning mechanisms versus nonlearning mechanisms that can also affect behavior. Behavioral plasticity can evolve by affecting so-called contextual factors, that is, changes in sensory-perceptual, motivational, and motor processes. In fact, it is possible that natural selection achieves adaptive behavioral outcomes more often than not by fine-tuning of contextual factors, rather than by modifying neural plasticity per se. This would have the possible advantage of minimizing the phenotypic impact of the changes (i.e., learning can affect a variety of behaviors) by restricting necessary genetic changes in brain circuitry. There is no simple way to distinguish between an effect of evolution on learning mechanisms versus one on contextual factors. Comparative psychologists tend to deal with this complex issue by systematically varying factors that affect behavior while observing the outcomes in different species (Bitterman, 1975). To illustrate this point, we turn now to a comparative analysis of SNC.

SUCCESSIVE NEGATIVE CONTRAST: A CASE STUDY IN COMPARATIVE LEARNING

During the 1960s evidence started to emerge that learning phenomena involving incentive shifts were not general among vertebrates (Bitterman, 1975). Whereas mammalian species tended to show the SNC effect, experiments with species from more conservative evolutionary lineages, such as teleost fish and turtles, provided a different picture. These animals show sensitivity to reward magnitude, but reward downshift leads to a gradual adjustment of behavior without a hint of contrast. Subsequent research has extended the database, suggesting that an evolutionary transition occurred possibly in the ancestors of extant mammals, leading to an emotional adjustment in situations involving reward downshift (M. R. Papini, 2014). Characterizing such a transition requires an understanding of these effects in mammals at the behavioral, neural circuitry, synaptic, and cell-molecular levels of analysis (M. R. Papini, 2002, 2008). This research has revealed some of the key determinants of the SNC effect, including its dependence on the degree of reward disparity and type: ratio invariance regulates the detection of a reward downshift, incentive contrast phenomena require limbic and prefrontal cortex processing, GABAergic and opioidergic pathways are critically and specifically involved in regulating these effects, and these effects require the expression of specific genes in neural tissue (Flaherty, 1996; M. R. Papini, 2009; Torres & Sabariego, 2014). The research on learning phenomena involving reward downshifts reviewed later in this chapter provides a window into the type of knowledge and problems derived from comparative research on learning.

Research With Mammals

Two papers published in 1928 were turning points in the psychology of learning, driving the field away from a simple stimulus → response (S→R) theoretical framework into a cognitive view emphasizing the role of expectations. Tinklepaugh (1928) gave a female monkey (*Macaca fascicularis*) named Psyche a choice between two containers after observing the experimenter deposit a piece of food under one of them. In some trials, the food was a piece of banana (a preferred reward), whereas in others it was a piece of lettuce (a less preferred, but acceptable reward). After learning to choose the baited container to eat the food, Psyche rejected the lettuce in occasional trials when she had seen the experimenter placing a piece of banana under the cup (see Chapter 26, this volume). Tinklepaugh (1928) described these probe trials as follows:

> She extends her hand to seize the food. But her hand drops to the floor without touching it. She looks at the lettuce, but (unless very hungry) does not touch it. She looks around the cup and behind the board. She stands up and looks under and around her. She picks the cup up and examines it thoroughly inside and out. She has on occasions turned toward observers present in the room and shrieked at them in apparent anger. After several seconds spent searching, she gives a glance forward the other cup, which she has been taught not to look into, and then walks off to a nearby window. The lettuce is left untouched on the floor. (pp. 224–225)

Simultaneously, Elliott (1928) reported similar results in work with rats trained to find food in a complex maze with many blind alleys. A group that ate bran mash in the goal box learned to reach the goal faster than one that ate sunflower seeds. After 9 daily trials, the bran mash was replaced by sunflower seeds. Whereas both groups were under the same reward conditions, downshifted rats exhibited an increase in the number of entries in blind alleys and took more time to reach the goal than the unshifted controls that kept eating sunflower seeds at the goal. Elliott's (1928) interpretation was that the rats had learned a precise representation of the reward and the change had caused them to look for the missing reward elsewhere in the maze.

These results, hardly surprising for anybody who has experienced an event involving a loss (e.g., looking for missing keys), were important because they provided experimental evidence against a view of learning on the basis of pure S→R associations. This view had been introduced by Thorndike (1911) as an attempt to explain animal learning without reference to mental representations. Thorndike (1911) argued as follows, using strikingly current terminology:

> The connections formed between situation and responses are represented by connections between neurones and neurones, whereby the disturbance or neural current arising in the former is conducted to the latter across their synapses. The strength or weakness of a connection means the greater or less likelihood that the same current will be conducted from the former to the latter rather than to some other place. The strength or weakness of the connection is a condition of the synapse. What condition of the synapse it is remains a matter for hypothesis. Close connection might mean protoplasmic union, or proximity of the neurones in space, or a greater permeability of a membrane, or a lowered electrical resistance, or a favorable chemical condition of some other sort. (pp. 246–247)

It took mounting evidence from a variety of experiments before theorists could absorb the implications of results such as those originally reported by Tinklepaugh and Elliott (e.g., Amsel, 1958; Hull, 1952; Spence, 1956). Zeaman (1949) used different amounts of cheese to reinforce rats in a runway and found that upshifts and downshifts in magnitude caused changes in latency that were more extreme than the extrapolated performance level of the same groups before the change. The lack of unshifted controls (i.e., groups receiving always the same amount of food, whether large or small), required by today's standards, does not allow firm conclusions about the presumed reward comparison mechanism underlying these effects. However, the labels used by Zeaman to describe the upshift and downshift effects, *positive contrast* and *negative contrast*, respectively, were subsequently adopted and extended (e.g., Flaherty, 1996). The extensions relate to the particular procedures used to introduce reward shifts: successive, simultaneous, behavioral, and anticipatory contrast effects (see Chapter 15, this volume). For example, in successive contrast procedures, the organism experiences one magnitude during several sessions and then is shifted to another magnitude, whether larger or smaller, during several additional sessions. Whereas the behavior observed in these procedures seems superficially analogous and involving comparisons between incentive conditions, the underlying mechanisms are different (Flaherty, 1996). Here we center on *successive contrast* effects, which typically involve a single, sequential transition in reward quality or magnitude, and widely spaced training conditions. Four major types of successive contrast have been distinguished depending on the type of hedonic transition (positive or negative) and the behavioral measure (consummatory or instrumental). Table 13.1 describes these procedures and their corresponding acronyms.

TABLE 13.1

Types of Successive Contrast Effects

		Reward shift	
		Positive (less to more)	**Negative (more to less)**
Behavioral measure	Instrumental or Pavlovian (anticipation: latency, response rate)	iSPC	iSNC
	Consummatory (ingestion: fluid intake, lick rate)	cSPC	cSNC

Note. Describing the shifts as "less to more" and "more to less" emphasizes quantitative shifts, but there can be qualitative shifts, for example, from a more preferred to a less preferred type of food. The prefixes *i* and *c* denote instrumental and consummatory procedures, respectively. Some experiments use Pavlovian training to test for contrast effects, so the label "anticipatory" would seem more general than "instrumental." However, we keep the labels shown here for consistency with the literature. SPC = successive positive contrast; SNC = successive negative contrast.

Reward shift experiments imply that the two qualities or magnitudes have different hedonic value, an implication often assumed but examined only occasionally via preference tests (e.g., M. R. Papini, Ludvigson, Huneycutt, & Boughner, 2001). Of course, the very presence of successive positive or negative contrast effects demonstrates that the incentives have differential value. However, the absence of these effects may reflect that the incentives do not have differential value, that their differential value does not affect behavior, or that the underlying contrast mechanisms are not engaged in that situation. In the absence of direct tests, different behavioral levels during preshift trials are taken to indirectly demonstrate that the incentives have different value, although such differential performance is not always observed (see, e.g., Flaherty, 1996). For example, in consummatory experiments the larger incentive may cause satiety or sensory adaptation, leading to a lower performance level in preshift trials than the lower incentive. Moreover, different reward magnitudes not always support differential performance because of ceiling or floor effects.

To a lay person, contrast effects may seem of restricted value, a curiosity interesting only to scientists with little appreciation for the problems of "real life." There is, however, basic and translational value in the study of reward comparison effects (M. R. Papini, Fuchs, & Torres, 2015). As shown in the rest of this chapter, just one instance of contrast, SNC, has shed light on fundamental issues in associative learning (stimulus-response vs. cognitive theories), on reward comparison processes, and on the interaction between cognition (reward representation, expectancy), motivation (how internal states assign value to external events), and emotion (connection between unrealized expectations and frustration) in the control of behavior. SNC does not appear to be a general phenomenon across vertebrates, which poses an evolutionary puzzle: Exactly what is the adaptive advantage of adjusting to reward changes? In the hands of creative scientists, incentive contrast effects have become models for a variety of problems that afflict a large number of individuals, including coping with physical pain and stress, anxiety disorders, depression, and addiction, to name but a few. This chapter cannot cover these areas in detail, but it provides sufficient leads to orient interested readers in the appropriate direction. We begin with some general characterization of SNC in terms of parameters and consequences.

Behavioral processes. Research with mammals shows that SNC is modulated by a variety of parameters, including the spacing of trials, deprivation level, retention intervals, reward disparity, and type of reward, among others (see Flaherty, 1996). The last two will be highlighted here because they lead to issues of comparative relevance.

Reward disparity refers to the distance in incentive value between the rewards presented during preshift (sessions of exposure to the initially large reward) and postshift sessions (sessions of exposure to the downshifted reward). Incentive value is an intervening variable and, therefore, it is usually operationalized in terms of the objective magnitude of the reward. This is one reason why most research on contrast involves magnitude, rather than quality; the incentive values of qualitatively different rewards (e.g., banana and lettuce in Tinklepaugh's original experiment) are difficult to quantify exactly. In iSNC (instrumental successive negative contrast) and cSNC (consummatory successive negative contrast) procedures (see Table 13.1), the size of the effects is directly related to the size of the difference between preshift and postshift rewards (Di Lollo & Beez, 1966; Flaherty, Becker, & Osborne, 1983). Thus, a downshift of 32% to 4% sucrose leads to greater consummatory suppression than a downshift of 8% to 4% sucrose, a fact that raises the question of how such reward downshift is detected. Detecting a difference between two rewards is necessary, but not sufficient for SNC. Thus, an organism may be able to perceive the difference and even show a preference for one of the rewards, but if the difference is not significant enough, it may not affect behavior. For example, rats given access to either 1 ml of 30% sucrose or one 45 mg food pellet showed similar latency to approach each of the two goals; however, when given a choice in the absence of the rewards, rats exhibited a clear preference for the cup associated to sucrose (M. R. Papini et al., 2001).

In the cSNC situation and after, say, a downshift of 32% to 4% sucrose, the animal must compare the current 4% sucrose with the retrieved long-term memory of the 32% sucrose last received during preshift sessions a day before. The cSNC effect occurs when the animal fails to recognize the current reward as that expected on the basis of previous experience. In the iSNC situation, however, the memory demands are different. An animal that has already experienced the pre- and postshift rewards must be able to reactivate two long-term memories as it moves toward the goal for its anticipatory behavior to be influenced: The memory of the preshift reward and the memory of the downshift event. Thus, the iSNC effect depends on cued-recall memory. Although similar, cSNC and iSNC depend on different types of memory, recognition and cued-recall memory (M. R. Papini & Pellegrini, 2006), and thus it is expected that they will not always be influenced by the same factors.

An important common mechanism determines the detection of the reward disparity in both situations: *ratio invariance* (M. R. Papini & Pellegrini, 2006; Pellegrini, López-Seal, & Papini, 2008; Pellegrini & Papini, 2007). In the cSNC situation, for instance, the degree of consummatory suppression observed after a reward downshift depends not on the absolute magnitudes of the reward or on the size of their difference, but on their ratio. Thus, rats exposed to an 8:1 ratio between preshift and postshift sucrose concentrations, whether it is a downshift of 32% to 4% sucrose or 16% to 2% sucrose, exhibit comparable levels of consummatory suppression.

The problem of detection is also important in comparative terms. Because some species of vertebrates do not show evidence of SNC in analogous experiments, one possibility is that the detection process is based on different mechanisms (see section on Comparative Models).

Type of reward refers to the goal events that support SNC effects. Rats, for example, exhibit the iSNC effect when rewarded with solid food pellets, but not when rewarded with sucrose solutions. The latter effect is paradoxical because the same rats that fail to exhibit the iSNC in the stem of a runway do show the cSNC effect when arriving at the goal (e.g., Sastre, Lin, & Reilly, 2005). The reasons for these discrepant results are not completely understood; it may reflect the relative difficulty of cued-recall and recognition memory when comparing sucrose solutions of different magnitudes. Still, this information can be used to explore other issues. For example, the ratio invariance mentioned previously was still observed in rats exposed to a downshift in sucrose solutions in an instrumental situation which, as expected, did not yield evidence of an iSNC effect (Pellegrini & Papini, 2007). The implication is that ratio invariance is a fundamental mechanism of reward comparison which does not depend on the presence of an SNC effect, at least for rats.

Other types of rewards have been used in incentive contrast experiments, including aversive stimuli. Several experiments using escape from a noxious stimulus have provided evidence of iSNC. Using a runway procedure, an increase in the intensity of an electric shock delivered to the animal's feet led to a reduction in running speed below the level of an unshifted control—iSNC. Interestingly, a reduction in shock intensity led to an increase in running speed above the unshifted control, a rare example of iSPC (instrumental successive positive contrast Nation, Wrather, & Mellgren, 1974). SPC is usually difficult to observe in rats, although occasional reports have been published (Flaherty, 1996). Using a runway submerged in water, swimming as the response, and a change in temperature at the goal as the reward, Woods (1967) reported that a downshift in temperature led to an increase in latency above the level of an unshifted control—iSNC. However, in this case, an upshift in temperature yielded no evidence of an iSPC. A series of experiments using a one-way avoidance procedure and manipulating the time spent in the safety compartment produced good evidence of an iSNC effect (Cándido, Maldonado, Megías, & Catena, 1992) and iSPC (Cándido, Maldonado, Rodríguez, & Morales, 2002; Maldonado et al., 2007). Although usually these training situations are described in terms of the termination of an aversive event (a retrospective process of negative reinforcement), these experiments demonstrate that there is also a prospective process involving incentive expectancy in avoidance learning. That is, the expectation of a rewarding event (e.g., time spent in safety) also influences escape or avoidance learning. Consistent with this view, iSNC in the one-way avoidance situation shares a common neurochemical basis with iSNC in the runway situation and cSNC in the consummatory situation (see section on Psychopharmacology).

There is also evidence that the cSNC effect is connected to physical pain and emotional stress in a complex manner (M. R. Papini et al., 2015). Whereas exposure to reward downshift reduces pain sensitivity in the hot plate (Mustaca & Papini, 2005), exposure to peripheral pain by a subcutaneous injection of formalin in a hind paw increases the size of the cSNC effect (Ortega, Daniel, Davis, Fuchs, & Papini, 2011). cSNC is also enhanced by presession exposure to restraint stress (Ortega et al., 2013). The cSNC itself leads to an increase in the release of stress hormones (Pecoraro, de Jong, & Dallman, 2009).

Psychopharmacology. Systemic drug effects have identified the role of several neurotransmitter systems in SNC effects. Here we concentrate on GABA (gamma aminobutyric acid) and opioid receptors (see Volume 1, Chapter 23, this handbook). These receptors are widely distributed in the mammalian brain (Mansour, Fox, Akil, & Watson, 1995; Young & Chu, 1990) and are also present in nonmammalian species (Dreborg, Sundström, Larsson, & Larhammar, 2008; Gou, Wang, & Wang, 2012).

Benzodiazepine (BZ) tranquilizers and ethanol tap GABA_A receptors and have an anxiolytic effect on situations involving reward downshift. BZs consistently attenuate the behavioral effects of reward loss in cSNC and iSNC situations. This effect was reported for chlordiazepoxide (Flaherty, Grigson, & Lind, 1990; Rosen & Tessel, 1970), midazolam (Flaherty & Driscoll, 1980), flurazepam (Flaherty, Becker, Checke, Rowan, & Grigson, 1992), and diazepam (Liao & Chuang, 2003; Morales, Torres, Megías, Cándido, & Maldonado, 1992; Mustaca, Bentosela, & Papini, 2000). BZs reduce cSNC in a dose-dependent manner, whether administered systemically or intracranially, but selectively on the second downshift session. The effects of BZs seem to be selective for the downshift condition because these drugs do not affect the performance of unshifted controls. These effects are also eliminated by coadministration of GABA_A antagonists, such as flumazenil (Torres, Morales, Megías, Cándido, & Maldonado, 1994).

Paradoxically, although BZ administered *before* downshift sessions attenuate SNC, they enhance at least one form of contrast, cSNC, when administered *after* downshift sessions (Ortega, Glueck, Daniel, Prado-Rivera, White, & Papini, 2014). This effect is rather specific to the downshift experience and it seems to reflect a memory-interfering effect of BZs on experience with the downshifted reward. Thus, whereas presession BZ administration may have an anxiolytic effect, postsession BZ administration may interfere with memory consolidation.

Although ethanol has actions on several types of synaptic receptors, its anxiolytic effects are mainly related to GABA_A binding (Morrow, Suzclak, & Paul, 1988). The administration of ethanol reliably reduces the cSNC effect in a dose dependent manner and, like the BZs, only after some experience with the downshifted reward (Becker & Flaherty, 1982). Moreover, ethanol and chlordiazepoxide can influence cSNC in an additive fashion; marginally effective doses of these drugs have a potent effect if combined (Becker & Flaherty, 1983). Ethanol and chlordiazepoxide administered during partial reinforcement training negate the usually ameliorating effects of partial reinforcement on recovery from cSNC (Kamenetzky, Mustaca, & Papini, 2008; Pellegrini, Muzio, Mustaca, & Papini, 2004).

Opioid receptors are also implicated in the modulation of behavior in reward downshift situations. Pharmacological studies on cSNC include selective and nonselective opioid agonists and antagonists. For example, Rowan and Flaherty (1987) found that the nonselective agonist morphine reduced cSNC in the first and the second downshift sessions, and this effect was blocked by the nonselective antagonist naloxone. Naloxone enhances cSNC when administered before the first or second downshift sessions (Pellegrini, Wood, Daniel, & Papini, 2005) and it also disrupts the ratio invariance property characterizing the detection of the incentive mismatch during the first downshift session (Daniel, Ortega, & Papini, 2009). Interestingly, the effect of selective opioid-receptor compounds on cSNC depends on the level of experience with the downshifted reward. Thus, whereas the kappa receptor agonist U50,488H modulates the cSNC effect when administered before the second downshift session (Wood, Norris, Daniel, & Papini, 2008), the delta receptor agonist DPDPE [D-Pen(2),D-Pen(5)-enkephalin] and antagonist naltrindole reduced and enhanced the cSNC effect, respectively, when administered before the first downshift session (Pellegrini et al., 2005; Wood, Daniel, & Papini, 2005). These results suggest that reward devaluation induces a compensatory response based on the release of endogenous opioids.

The role of GABA and opioid receptors in situations involving reward downshift in nonmammalian species remains to be explored. Particularly interesting from a comparative perspective is the delta opioid receptor, which appears to be selectively involved in the modulation of the initial stages of downshift detection (M. R. Papini, 2009).

Brain circuitry. Brain mechanisms underlying reward downshift can be described in terms of a top-down activation of the cortex and critical subcortical nuclei that organize appetitive behavior and brainstem-based mechanisms that control consummatory behavior. This is perhaps more clearly seen in the case of cSNC than in iSNC, because consummatory behavior (i.e., taste licking) is organized as a relatively stereotypical action pattern. This action pattern is under the partial control of brainstem nuclei, including the nucleus of the solitary tract and parabrachial nucleus processing taste input, and the hypoglossal nucleus controlling movements of the tongue. It is likely that the feeding behavior of a variety of vertebrates is under the control of a homologous brainstem circuit (Wainwright, 2002), although its relevance to reward downshift in nonmammalian species remains to be explored.

Lesions of the parabrachial nucleus disrupt three properties of the cSNC effect (Grigson, Spector, & Norgren, 1994). Instead of a drastic reduction in lick frequency, rats with lesions displayed a gradual reduction without contrast; the number of licks per burst is usually reduced below unshifted levels after the downshift, but lesions equate them across downshifted an unshifted groups; and whereas sham animals adjust the interburst interval to the level of unshifted controls, animals with lesions retain lower intervals than unshifted controls after the downshift. Thus, lesions of the parabrachial nucleus disrupt the organization of the taste-licking action pattern and prevent the development of the cSNC effect.

Efferents from the parabrachial nucleus reach two structures that also play an important role in cSNC and are highly conserved in vertebrates: gustatory thalamus and amygdala. Lesions of the gustatory thalamus (Reilly & Trifunovic, 2003) prevent contrast under various retention intervals between preshift and postshift trials. This suggests that the deficit is not related to memory of the preshift solution. The amygdala is clearly involved in the cSNC and iSNC effects. Liao and Chuang (2003), for example, infused the benzodiazepine diazepam into the amygdala and observed a reduced cSNC effect; similar infusions in the hippocampus yielded no effects. Reversible inactivation of the amygdala before the first downshift session reduces cSNC and iSNC (Kawasaki, Glueck, Annicchiarico, & Papini, 2015; Salinas & White, 1998). The precise function of the amygdala, however, is still poorly understood; is it storing an emotional memory of the downshift event or tagging it as aversive?

Identifying the components of the neural circuit activated by reward loss can be aided by molecular techniques that detect increased activity in various brain sites after a downshift event. For example, using c-Fos immunoreactivity, Pecoraro and Dallman (2005) observed increased neural activation in several cortical areas, including the anterior cingulate, medial prefrontal, orbital, and insular cortex, as well as several subcortical areas, such as the nucleus accumbens, amygdala, bed nucleus of the stria terminalis, and lateral habenula, among others. Some of these areas were also identified in terms of the expression of phosphorylated CREB (cyclic AMP response element-binding protein), a marker of synaptic plasticity, after the first downshift event in the cSNC situation (Glueck, Dennis, Perrotti, Torres, & Papini, 2015), including the anterior cingulate and the prelimbic section of the medial prefrontal cortex. In addition, increased CREB expression was found in the dorsomedial striatum. This information is useful to identify potential targets for further analysis using, for example, lesion techniques. This would help narrow down the search. Lesion studies have shown effects of some of these areas on cSNC. For example, lesions of the insular cortex

(Lin, Roman, & Reilly, 2009) and of the anterior cingulate (Ortega, Uhelski, Fuchs, & Papini, 2011) have opposite effects, the former eliminating and the latter enhancing the cSNC effect.

Individual differences. Rats exposed to the SNC situation exhibit distinct profiles of recovery from the reward devaluation experience. An extensive secondary analysis of such profiles using latent-growth mixture modeling detected three distinct trajectories (S. Papini, Galatzer-Levy, & Papini, 2014). The majority (83%) of rats exhibited the usual response suppression followed by recovery to control levels of consummatory behavior, but two minority groups showed either little or no evidence of contrast (6%) or very little recovery from the suppressive effects of reward downshift (11%). Interestingly, the contrast and slow-recovery profiles did not differ in performance during the initial exposure to the reward downshift but rather in the subsequent recovery. Research with fast- and slow-recovery subsamples has also shown differential sensitivity to opioid blockage. Naloxone treatment affects slow-recovery rats more than fast-recovery rats in an activity test (Pellegrini et al., 2005). These data suggest that there is sufficient genetic variability in lab rats for artificial selection to affect performance in the cSNC situation.

Artificial selection techniques provide the closest approach to understanding the evolution of learning mechanisms in the laboratory. Many studies of selective breeding for behavioral divergence show a rapid response, indicating the presence of hereditary factors through which a differential set of alleles can bias specific behavioral traits. Several studies have explored the genetic basis of sensitivity to reward loss (see Chapter 16, this volume) by using strains of rats selectively bred for divergent emotional reactivity, fearfulness, or anxiety, as well as with respect to their divergence in the size of the cSNC effect (M. R. Papini et al., 2015; Torres & Sabariego, 2014).

Flaherty, Krauss, Rowan, and Grigson (1994) selectively bred Sprague-Dawley rats showing large versus small cSNC effects over seven generations. This gave rise to two lines diverging in reactivity to reward downshift, the large contrast line being more stable (i.e., less influenced by selective breeding) than the small contrast line. Interestingly, strains did not differ in other behavioral tests, including reactivity to novelty, response to the absolute value of different rewards, or anticipatory negative contrast. Similarly, Ortega, Norris, López-Seal, Ramos, and Papini (2014) selectively bred Long-Evans rats on the basis of differences in their rate of recovery from cSNC—fast versus slow recovery. They also included randomly mated rats as controls. After five generations it was found that the size of the cSNC was reduced in the fast-recovery line, whereas slow-recovery and random lines did not differ across generations. Fast-recovery rats from this generation also failed to show increased resistance to extinction after training with partial reinforcement, as opposed to slow and random lines. Another experiment conducted with animals from the sixth generation revealed that fast-recovery infants exhibited more vocalizations in the mother–infant separation test in comparison to slow and control groups. When they were adults, these animals differed from the other groups in terms of lower sensitivity to the actions of naloxone. The results cannot be explained in terms of group differences in water intake, sucrose sensitivity, activity levels in the open field test, or consummatory behavior before the sucrose devaluation. One implication of this research is that selective breeding led to changes in the opioid system that resulted in reduced (but not enhanced) response to reward downshift (Ortega, Norris, et al., 2014).

Differences in reward devaluation phenomena have also been studied in strains of rats divergent in anxiety situations other than incentive contrast. For example, Syracuse low-avoidance (SLA) and Syracuse high-avoidance (SHA) rats originally bred on the basis of their poor or good active avoidance learning, respectively, exhibited correlated differences in incentive contrast. SLA rats showed larger cSNC effects than SHA rats (Flaherty & Rowan, 1989). Maudsley reactive (MR) and Maudsley non-reactive (MNR) rats, which were originally selected on the basis of their high or low defecation rate in an open field, also exhibited correlated effects. Paradoxically, MNR rats showed larger cSNC effects than MR rats (Rowan & Flaherty, 1991). Likewise, Okamoto hypertensive rats showed a stronger cSNC effect than their controls, Wistar-Kyoto strain (Bentosela & Mustaca, 2005).

The most extensive effort to explore this topic has been conducted in the inbred Roman high-avoidance (RHA) and Roman low-avoidance (RLA) strains of rats, selectively bred for extreme divergence in a two-way avoidance learning task. Originally selected from Wistar rats, RHA and RLA rats differ in anxiety or emotional reactivity (low in RHA, high in RLA rats), as well as with respect to novelty seeking, impulsivity, drug consumption and abuse, psychotic-like symptoms, offensive aggression, sensitivity to antidepressant, and sexual behavior (M. R. Papini et al., 2015; Torres & Sabariego, 2014).

Roman strain differences in emotional reactivity could underlie differences found in a variety of reward loss situations, including cSNC and iSNC. For example, the high-anxiety RLA rats recover more slowly from a downshift of 22% to 4% sucrose than low-anxiety RHA rats (Gómez, Escarabajal, et al., 2009). Similarly, RLA rats show the iSNC effect in a runway procedure after a downshift of 12 to 2 pellets, whereas RHA rats do not (Rosas et al., 2007; Sabariego et al., 2013). Interestingly, when animals receive partial reinforcement during preshift sessions (an experience of chronic reward loss known to increase tolerance to frustration), strain differences in iSNC are not observed (Cuenya et al., 2012). Compared to RHA rats, RLA rats (and Wistar controls) show a larger iSNC effect in the one-way avoidance situation (Donaire, Sabariego, Gómez, Fernández-Teruel, & Torres, 2013; Torres et al., 2005). Similar strain differences are obtained in instrumental appetitive extinction (Gómez et al., 2008; Gómez, de la Torre, et al., 2009).

Inbred Roman strains are also being used to understand the psychogenetic basis of reward loss. Recent microarray studies have identified differential patterns of genetic expression in the brain that could underlie strain differences observed in reward loss paradigms. A number of genes are differentially expressed under resting conditions in the whole brain of RHA and RLA rats. Five of them were validated by qRT-PCR (EPHX2, PRL, CAMKK2, CRHBP, and HOMER3); these genes were selected because of their relevance in biobehavioral traits known to be divergent in RHA and RLA rats (Sabariego et al., 2011). Sabariego et al. (2013) exposed Roman rats to iSNC and subsequently analyzed strain differences in hippocampal gene expression. As expected, only the RLA strain exhibited a contrast effect. Moreover, five qRT-PCR-validated genes were up-regulated in the RLA contrast group relative to the RHA contrast group, some of which have been related to neurobehavioral processes known to be divergent in Roman rats, such as neuropsychiatric disorders (TAAR2), fear memory (THAP1), taste sensitivity (PKD2L1), and hippocampal development (NANOS1).

Comparative Models

The genetic diversity present in rats generates strains that yield an incentive contrast profile strikingly similar to that of more conservative vertebrate species (e.g., the Roman high-avoidance strain). What seems to do the job is a decrease in the level of emotional reactivity to unrealized appetitive expectancies (see Volume 1, Chapter 23, this handbook and Chapter 34, this volume). These “mammalian guidelines” have to make their way into comparative research with other vertebrate models that seem to show a different type of adjustment to reward downshift—a research endeavor that is just beginning.

Two promising animal models include toads, which provide prima facie evidence of evolutionary divergence in SNC effects, and pigeons, which provide an interesting case to test evolutionary homoplasy in learning mechanisms underlying incentive contrast effects (M. R. Papini, 2014). Amphibians can be trained by taking advantage of their daily need for access to water and their complex assessment and intake of fluids via skin absorption. The toad *Rhinella arenarum* (formerly *Bufo arenarum*) is a terrestrial anuran that searches for and returns to water ponds frequently to reestablish fluid balance. Toads respond to reward magnitude by acquiring a runway response faster under large rather than small amounts of water absorption. However, reward downshift leads to an adjustment without contrast (a reversed iSNC effect), whether with multiple trials per day (Schmajuk, Segura, & Ruidiaz, 1981) or a single trial per day (M. R. Papini, Muzio, & Segura, 1995). An assessment of water uptake also yielded evidence of a reversed cSNC effect

(M. R. Papini et al., 1995). Thus, the behavior of toads in reward downshift situations is regulated by the magnitude of the current reward. Toads also fail in a related contrast situation involving extinction after training with different reward magnitudes (reward-to-nonreward downshift). Large rewards produce slower extinction than small rewards (Muzio, Segura, & Papini, 1992; M. R. Papini et al., 1995), the opposite of what is typically found in rats (M. R. Papini et al., 2001). The toad's skin detects the concentration of sodium in a fluid, allowing the organism to stay in fluids that contain smaller amounts and escape from saturated fluids (Daneri, Papini, & Muzio, 2007). Using sodium concentration as the reward, toads display reversed iSNC and iSPC effects in shifts between distilled water and a sodium-neutral solution as measured in terms of runway performance, consummatory behavior, changes in coloration of the ventral skin where water uptake occurs, contact time with the reward, and rubbing behavior during water uptake (Muzio et al., 2011).

Little is known about the neurobiological control of instrumental behavior in toads. Intriguing results come from experiments in which the toad's medial pallium was lesioned before exposure to reward downshift. The amphibian medial pallium is considered homologous to the CA fields and subiculum of the mammalian hippocampus on the basis of anatomical connections (Northcutt & Ronan, 2004). In rats, lesions of the hippocampus eliminate the iSNC, leading to little behavioral change after reward downshift (Flaherty, Coppotelli, Hsu, & Otto, 1998; Franchina & Brown, 1971). Toads, which exhibit little behavioral change to begin with, show even greater resistance to change after lesions of the homologous medial pallium (M. R. Papini et al., 1995).

Amphibians exposed to reward devaluation exhibit a lack of behavioral flexibility when compared to rats. A similar picture can be drawn from research with pigeons, at least with respect to SNC effects. Pigeons (*Columba livia*) can be trained with similar procedures to those used with rats. Pigeons trained in a Skinner box to peck at a key under spaced-training conditions (one trial per day) show faster acquisition with a large food reward than with a small one. However, when exposed to a downshift of 15 to 1 pellets they show a gradual adjustment without contrast—a reversed iSNC (M. R. Papini, 1997). Their extinction performance is also faster after a small-to-nonreward downshift than after a large-to-nonreward downshift (M. R. Papini, 1997; M. R. Papini & Thomas, 1997). Interestingly, a similar effect was obtained with male quail (*Coturnix japonica*) rewarded by sexual access to either several or just one female (Baquero, Puerta, & Gutiérrez, 2009). However, evidence of cSNC was reported in another avian species, starlings (*Sturnus vulgaris*), exposed to a qualitative reward downshift (Freidin, Cuello, & Kacelnik, 2009). Thus, the status of SNC effects in birds remains uncertain. It is possible that these differences among avian species are related to procedural factors. In rats, for example, cSNC seems more robust than iSNC (Sastre et al., 2005), so it is possible that consummatory tasks may also prove more sensitive with birds, as seems to be the case with starlings.

However, direct comparisons between pigeons and rats suggest they use different mechanisms to adjust to reward downshifts. As pointed out previously, rats use ratio invariance to detect downshifts in reward value whether SNC is induced or not, whereas pigeons respond on the basis of the absolute magnitude of the preshift reward (M. R. Papini & Pellegrini, 2006; Pellegrini et al., 2008; Pellegrini & Papini, 2007). Moreover, pigeons trained in spatial discrimination reversals adjust by making anticipatory errors before the reversal and perseverative errors after the reversal, whereas the behavior of rats is controlled by the response-outcome contingencies of previous trials (Rayburn-Reeves, Stagner, Kirk, & Zentall, 2013). These results suggest that there is a component of flexibility in the behavior of rats trained under shifting reward conditions that seems to be attenuated or missing in pigeons and toads.

EVOLUTION OF INCENTIVE CONTRAST MECHANISMS

The field of associative learning has been dominated by two evolutionary frameworks, one (general-process view) emphasizing the species generality of learning process and the other (ecological view) emphasizing the adaptive significance of learning processes (M. R. Papini, 2002). The general-process view is consistent with the wide taxonomic distribution of basic learning phenomena (e.g., acquisition, extinction, generalization) but has failed to distinguish between two sources of commonality: homology from common ancestry versus homoplasy from common selective pressures. The ecological view is consistent with behavioral differences in learning tasks among closely related species but has failed to dissociate the contribution of learning versus the influence of contextual factors (e.g., motivation, sensory-perception, motor) to behavior. Comparative research on the SNC and related effects does not fit well in any of these two camps. Unlike the general-process view, there is growing recognition of an evolutionary transition that sets mammals apart from other vertebrates. The core hypothesis is that frustration-related mechanisms are not general but restricted to the mammalian brain, and, thus, they may not be needed to understand associative learning in other vertebrates. However, this hypothesis also seems, at least on the surface, to contradict the adaptationist approach assuming that species-specific selective pressures determine the type of learning mechanisms that evolved in any particular species. None of these views agrees well with what we know about biological evolution in general (M. R. Papini, 2008). There are traits that are general only within a restricted taxon (e.g., feathers occur in birds but not in other living vertebrates), and there are adaptations above the species level (e.g., feathers occur in all birds, not in only a particular species of bird). There is not a priori reason to expect that learning mechanisms would deviate from this. Therefore, concerning incentive contrast, a key question for comparative psychologists is this: What are the selective pressures, which, combined with preadaptive constraints, could have led to the evolution of frustration-related mechanisms only in mammals? In trying to provide an educated answer to this specific question, we also provide a general framework for answering questions about the evolution of learning mechanisms involved in a variety of behavioral functions.

There is extensive evidence that the SNC effect is accompanied by negative emotion in mammals (M. R. Papini et al., 2015). Compelling evidence comes from studies in which rats are allowed access to anxiolytics after the training session. For example, rats exhibit a selective increase in preference for ethanol or chlordiazepoxide immediately after being exposed to sessions of appetitive extinction (Manzo et al., 2014) or cSNC (Manzo, Donaire, Sabariego, Papini, & Torres, 2015). Such negative emotion has traditionally been referred to as frustration (Amsel, 1992). If one assumes that frustration induced by reward loss is unique to mammals, then the key question becomes this: What is the adaptive value of frustration?

Stout, Muzio, Boughner, and Papini (2002) speculated on a possible evolutionary scenario combining adaptive significance with possible constraints from preadaptations that differentiate mammals from other vertebrates. They suggested that frustration may accelerate the detachment from a signal or location previously paired with reward. This process, termed *incentive disengagement* (M. R. Papini, 2003), may induce escape behavior and facilitate a switch to a searching mode that increases chances of finding a new source of reward. With a high metabolic rate, it is costly for mammals to stay attached to a site that used to yield food but no longer does so. The selective pressures exerted by a high metabolism and activity levels were met by a series of preexisting conditions. In the case of mammals, preadaptations may have been related to the role of olfaction in foraging and the direct connections between olfactory pathways and limbic structures associated to negative emotion, including the amygdala, already present in reptiles. In extant insectivores, the most conservative order of placental mammals, the size of the olfactory bulbs correlates with the size of the centromedial amygdala, but not with nonlimbic structures. As noted previously, the mammalian amygdala plays a critical role in iSNC and cSNC. With the exception of birds, other vertebrates have substantially lower metabolic rates, thus presumably experiencing weaker selective pressures for incentive disengagement. What would set birds apart from mammals is their reliance on visual cues for foraging and the relatively less direct connections between visual input and limbic structures, a fact that would have promoted the evolution of nonemotional strategies to deal with reward loss.

The evolutionary scenario just presented leads to a number of predictions, some of which have been tested, although much remains to be done. That the brain mechanisms responsible for frustration may not be present in nonmammalian vertebrates does not imply that these animals are devoid of emotional states (see Chapter 34, this volume). In fact, for example, avoidance learning in teleost fish shares some common brain circuitry with fear conditioning in mammals (Portavella, Torres, Salas, & Papini, 2004). Because teleosts do not show evidence of any of the phenomena associated with frustration in reward loss situations (Bitterman, 1975; M. R. Papini, 2006), and fear and frustration are controlled by a host of similar neural processes (M. R. Papini et al., 2015), the possibility has been suggested that the evolution of these mechanisms is correlated. One possibility is that frustration-related brain mechanisms evolved in early mammals by cooption from preexisting fear-related mechanisms (M. R. Papini, 2003).

The evolutionary scenario presented by Stout et al. (2002) would also be consistent with independent neural control of seemingly similar behavioral adjustments. This has been studied using a behavioral preparation known as the *partial reinforcement extinction effect* (PREE), obtained under spaced practice (e.g., one trial per day), and also involving repeated reward downshifts. The PREE involves greater resistance to extinction after training under partial reinforcement (e.g., only a random half of the trials ends in reward and the animal cannot predict the outcome) rather than continuous reinforcement. In rats, the PREE is known to be eliminated by the anxiolytic chlordizepoxide (e.g., Feldon & Gray, 1981), but in pigeons, the same drug retards its emergence but does not eliminate it (Thomas & Papini, 2003). The implication is that, although superficially similar, the PREEs in rats and pigeons are based on different neurotransmitter systems.

Additional results are consistent with the view that frustration plays a secondary role, if any, in the control of instrumental behavior in pigeons. Procedures that increase responding after surprising nonreward in rats (Stout, Boughner, & Papini, 2003), a drive-inducing property of frustration (Amsel, 1992), do not invigorate key pecking in pigeons (M. R. Papini & Hollingsworth, 1998; Stout et al., 2002). However, contrary to this view, pigeons and other birds exhibit aggressive behavior toward signals of reward omission (Terrace, 1972) and toward another pigeon present during appetitive extinction (Azrin, Hutchinson, & Hake, 1966; Kuhne, Sauerbrey, & Adler, 2013). Pigeons also learn to turn off a visual stimulus signaling nonreinforcement (Terrace, 1971). These aggressive and escape behaviors are similar to what has been described in mammalian species exposed to analogous conditions (see M. R. Papini & Dudley, 1997). There is also an already mentioned report of cSNC in starlings (Freidin et al., 2009). These phenomena must be studied at a neural level before a clearer picture of the degree of homology versus homoplasy in mechanisms controlling the adjustment to incentive downshifts among birds and mammals can be ascertained.

CONCLUSION

Incentive contrast effects provide a case study to illustrate the use of comparative methods in the study of learning. Learning mechanisms are one source of behavioral control contributing to many functions, including feeding, reproductive behavior, and defensive behavior. To understand the evolution of these mechanisms, scientists need to share some minimum number of concepts. These include an understanding of what is meant by a learning mechanism, what criteria differentiate cases of homology from cases of homoplasy, and a convergence perspective that integrates behavioral data with the results of manipulations at lower levels of analysis, including neural circuitry, neurochemical factors, and cell-molecular cascades involved in synaptic plasticity. Progress in comparative learning and evolution is likely to be accelerated by applying such a convergence approach to a family of behavioral effects (e.g., effects involving reward downshifts) in a selected group of species.

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CHAPTER 14

ON THE STRUCTURE AND ROLE OF OPTIMALITY MODELS IN THE STUDY OF BEHAVIOR

Marco Vasconcelos, Inês Fortes, and Alex Kacelnik

The use of optimality models in behavioral biology and comparative cognition stems from the view that the mind is a product of the same evolutionary process that leads to kidneys, wings, petals, eyes, or monkeys' tails. The chief participant in this process is natural selection, a mechanism identified in its fundamentals by Charles Darwin and Alfred Russel Wallace toward the middle of the 19th century. Its essence is that randomly originated, heritable variation inevitably leads to evolutionary changes, because traits that best promote reproduction and survival increase their representation in the species across generations and thus progressively become the species' norm. In the long-term, biological traits, including psychological mechanisms, appear as if they had been designed to maximize reproductive success, and mathematical models that assume optimal, fitness-maximizing design can be used to generate testable hypotheses about decision mechanisms.

Optimality techniques are common in many areas of biology, as when anatomists examine the shape of wings as being designed either for flapping or gliding flight. George Williams (1966) highlighted the relevance of assuming fitness-maximizing design to psychology, by asking rhetorically "Is it not reasonable to anticipate that our understanding of the human mind would be greatly aided by knowing the purpose for which it was designed?" (p. 16). Williams, like us, uses the term *design* in a nonteleological, process-based way, and not in the contorted irrational sense that is predicated by supporters of the *intelligent design* idea. In Williams's approach, the mind's design purpose (on which optimality techniques rely) is different from the goals driving the behavior of the organism in which the mind is embodied. The mind's biological purpose *sensu* Williams can be described as the goal or directionality of natural selection, not the goals of the acting agent. For instance, mating behavior may be driven by an organism's pursuing of sexual desire, but the purpose to which biological optimality refers is reproductive output, with desire being the tool through which the organism's behavior is manipulated by its genes. Similarly, fear, hunger, aggression, or maternal love are all tools of natural selection to make individuals "do the right thing," namely, maximize their representation in future generations. Thus, agents' motivations appear as designed for a purpose, namely to maximize fitness. Those ancestors whose mental traits we inherited were not necessarily the happiest, most emotionally balanced, or most intelligent ones, but those whose minds led to maximize the recruitment of descendants to the breeding population.

Optimality is thus a framework for devising hypotheses about how animals work and what is important to selection, and our overall message is that this framework may be very useful to psychologists, provided it is properly understood and used in conjunction with empirical research. To make the optimality work it is especially important to

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avoid several trivial but frequent misrepresentations, namely that evolutionary biologists expect animals to behave perfectly, that optimality models require the organism to compute optima to act, and that the hypothesis under test is whether animals are optimal. The assumption of those using optimality techniques is not that organisms make perfect fitness-maximizing choices in all circumstances, but that their psychological mechanisms reflect those of ancestors that outperformed their contemporaneous conspecifics. Inasmuch as present circumstances reflect the species' past, such mechanisms are expected to cause decisions that are, on average, adaptive for present members of the species. One way to dispel such misinterpretations is to focus on the structure of optimality models and to follow some examples in detail. This is our objective in the present chapter, and we'll pursue it by illustration, describing how the optimality approach has aided research in a few clear examples.

COMPONENTS OF OPTIMALITY MODELS

There are alternative ways to carve up models' components, but here we follow the approach of Kacelnik and Cuthill (1987). They argued that optimality models are an assemblage of at least three interconnected assumptions, all of which are in turn hypotheses, because they are independently testable: the *strategy set*, the *feedback function,* and the *currency*.

The Strategy Set

For the purpose of modeling, optimality practitioners see all behavior as choice, but this does not mean conscious deliberations. The choice may be between discrete alternatives such as different food types (e.g., Pulliam, 1974), mates (e.g., Slagsvold & Dale, 1991), or forms of locomotion (walking or flying; e.g., Bautista, Tinbergen, & Kacelnik, 2001), or between points along a continuum, such as intensity of parental effort (e.g., Wright & Cuthill, 1990), flying velocity (e.g., Houston, 1986), or size of an ejaculate (e.g., Parker & Pizzari, 2010). This means that right from the start, models define the range of potential behaviors, or strategy set. The strategy set used in a particular model is then a hypothesis inspired by observing the organism in its normal circumstances, as the range of alternatives must be realistic (i.e., when studying decision making in horses one can compare trotting with galloping, and when studying decision making in starlings one can compare walking with flying, but species and choices cannot be swapped). This is not as trivial an issue as it may seem, because although anatomical constraints may be obvious, psychological ones are not. For instance, shiny cowbirds (*Molothrus bonariensis*) in the Americas parasitize the reproductive effort of other species, and their offspring share the nest with those of their hosts (Gloag, Fiorini, Reboreda, & Kacelnik, 2011). Hosts seem unable to feed preferentially their own offspring, probably because of psychological mechanisms evolved to drive parental behavior in unparasitized nests, and so the strategy set for some optimality models of host behavior includes a choice between abandoning the present brood or not, but not the choice of which nestling to feed. These constraints introduce elements of circularity, because a model can only produce as an output a member of its hypothetical strategy set. Although it is important to be aware of this issue, this is not a flaw of the optimality approach, because as we have said from the start, the strategy set is a hypothesis, and thus is itself subject to recursive testing and improvement.

The Feedback Function

Each action within the strategy set would have different consequences as a function of the state of the organism and its environment. For instance, a threatened zebra choosing to gallop rather than walk increases its probability of escaping from a stalking lion, but also increases metabolic rate and interrupts grazing, so that the relative payoff of each behavior is not only affected by the probability of escape but also by how hungry the animal is and how easy it is to find food. The feedback function in a model dealing with choice of mode of locomotion would describe probability of escape and/or nutritional consequences as a function of mode of locomotion. The feedback function is thus a hypothesis about what happens to the actor as a function of what it does, and it is meant to be refined with accumulated knowledge. To create a new model, the modeler makes informed guesses to include a manageable number of state-dependent, action-consequence relations considered to have influenced the evolution of the organism's psychology.

The Currency

Optimality models are predominantly normative rather than descriptive, because decisions are predicted as if the actor intends to maximize Darwinian fitness, but they are not just normative, as they cannot avoid including assumptions about mechanisms of behavior. This is in part because Darwinian fitness, defined as the contribution to the species' gene pool in later generations, is not measurable at the time scale of behavioral studies. Each action may have a minute effect, but the pattern of choice integrated along a lifetime and across generations may impact the fitness of individuals and of the alleles (variants of genes) that they carry. To build optimality models that are testable at a behavioral time scale, the modeler identifies short-term, measurable variables that are good candidates to have a clear relation to long-term fitness. Examples of such variables are rate of intake, vulnerability to predation, probability of avoiding starvation, or balance between nutrients. As with the other two categories of model components, these currencies are hypotheses: If an animal does not act so as to maximize a candidate currency, it may be that that particular variable is not a significant bottleneck with respect to natural selection, and new models will modify the currency assumption.

PREDICTIONS OF OPTIMALITY MODELS

Optimality models are used to predict or explain behavior in natural and experimental circumstances, and to design experimental protocols that challenge those predictions. To predict behavior, the modeler asks which member(s) of the strategy set maximizes the currency given the feedback function. It is mainly in the interaction with empirical data that the value of this research program has to be judged. Like all scientific ideas, the predictions of optimality models sometimes succeed and sometimes fail. Confirmation of the predictions is valuable if the predictions supported are novel, previously unexplained, and to some degree counterintuitive. Failed predictions are just as informative (often even more) as those corroborated. If a model's prediction is falsified, at least one of the component hypotheses must be wrong, and a new model needs to be formulated after revision. Once again, the method does not intend or allow for corroboration or falsification of claims that animals are optimal. The assumption that natural selection is an optimizing process plays a metatheoretical role for biologically inspired behavioral science: It is not tested, but it underlies its validity. Optimality models thus help to shift behavioral sciences from a descriptive toward a hypothetico-deductive approach, and increase the precision and explicitness of our reasoning.

We will not review optimal foraging models exhaustively (for detailed treatments, see Houston & McNamara, 1999; Kacelnik & El Mouden, 2013; Stephens, Brown, & Ydenberg, 2007; Stephens & Krebs, 1986). Instead, we aim at showing with examples from our own work, predominantly using European starlings (*Sturnus vulgaris*) as experimental systems, that the functional rationale underlying research in behavioral ecology is a powerful tool, sometimes underestimated by experimental psychologists (just as behavioral ecologists often overlook the importance of mechanisms). In our view, the optimality approach complements rather than competes with the mechanistic approach prevalent in the psychological sciences. We believe that cross-fertilization between evolutionary biology and animal psychology is the best way to fulfill Tinbergen's (1963) desideratum of a behavioral science straddling across mechanisms, adaptive value, ontogeny, and phylogeny.

PATCH EXPLOITATION: THE MARGINAL VALUE THEOREM

Economists have long been aware that benefit often increases less than linearly with effort invested (Samuelson, 1937). For instance, a baker may sell more loaves by increasing his opening hours, but not at a constant rate: as a larger fraction of neighborhood residents have bought tomorrow's bread, the additional loaves sold in yet another opening hour (the marginal benefit) decline, and at some point the baker benefits more by allocating his time to other sources of revenue, such as making cakes instead. The analysis of strategies for switching between activities has received much attention in foraging contexts, and one of the best-studied optimal foraging models is known as the marginal value theorem (MVT; Charnov, 1976b; Parker & Stuart, 1976). One specific scenario where the MVT applies is in *central place foraging*, as embodied by a bird that provisions dependent nestlings. Brood provisioning is amenable to modeling because it can be decomposed in regular cycles: The parent leaves the nest, lands at a foraging patch, gathers a certain amount of food (a fraction of which it eats), and at some point flies back to deliver a load of food to its brood. Over the day, it repeats this cycle hundreds of times, and virtually all of the daylight hours are occupied flying to and from the foraging patches, collecting food, and delivering it to the nestlings. As discussed previously, to formulate a model one has to decide on a currency, a strategy set, and a feedback function. We now see how this works in the present case.

Because food provisioning affects the chicks' fitness, the rate at which food is delivered is a sensible a priori candidate as a model's currency. As for the strategy set, one could consider all actions that are under the bird's control, including allocation of captures between the parent and the brood, the time when to stop collecting food to fly back toward the nest, or distribution of food among the nestlings. Different models and experimental studies address each of these decisions (e.g., Kacelnik, Cotton, Stirling, & Wright, 1995; Kacelnik & Cuthill, 1990), but here we focus on when to stop gathering food. In this example, the strategy set is defined by the range of potential time in the patch, which is a continuous variable, and the feedback function is how the currency (provisioning rate) varies as a function of time in the patch. The analogy with the baker's example arises from the fact that when birds collect multiple prey in their beaks in each trip, load does not increase linearly as a function of patch time, because prey already held slow the bird down. The MVT then applies in a very straightforward manner, as follows.

The maximized currency (provisioning rate, R(t)) can be expressed by

$$R(t) = \frac{G(t)}{\tau + t} \tag{1a}$$

where G(t) is the gain curve, expressing the load accumulated as a function of time since arrival at a patch, τ is the mean travel time for round trips between nest and feeding patch, and t is the time between landing in the patch and taking off (called *patch time*). The problem is to find the value of t that maximizes R(t) given the shape of G(t) and the value of τ. If it is known that capture rate decreases with time in the patch (i.e., the 2nd derivative of G(t) is negative), then we know from calculus that the optimal t is the point at which the first derivative of R respect to t is null,[1] provided that at that point the 2nd derivative is negative. This value, t_{op}, is the predicted patch time. Because patch time and load are directly related through G(t), predicting t_{op}, also specifies the optimal load per trip, $G(t_{op})$.

Figure 14.1a depicts the problem graphically, plotting lines passing through a notional start of a foraging cycle and loads at different possible departure times. The slope of these lines is given by the ratio of total gain G(t) over total cycle duration ($\tau + t$), which is precisely R(t), the currency we want to maximize. The steepest of these lines has slope $R(t_{op})$ and is tangent to G(t). At this point, the first derivative of G(t) equals R, the overall rate of provisioning taking into account travel time as well as the shape of G(t) and t. In this example, the first derivative of G(t) is a monotonically decreasing function of t, whereas R (which is what we aim at maximizing) has a peak at t_{op}.

According to the model, the rate-maximizing policy is obtained by adhering to a (mathematically) simple rule: Stay in the patch as long as the

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[1] The first derivative of R(t) is given by $\frac{dR}{dt} = \frac{G'(t)(\hat{\tau}+t) - G(t)}{(\hat{\tau}+t)^2}$, which is zero when $G'(t)(\hat{\tau}+t) = G(t)$ or $G'(t) = \frac{G(t)}{(\hat{\tau}+t)}$ namely when the first derivative of G(t) equals the overall rate of provisioning.

local rate (G'(t), the first derivative of G(t)) exceeds the expected overall rate R. This rule is prospective, because the ideal decision maker simply chooses where to invest its next unit of time. The strategy set in the case of this model includes the capacity to tune behavior to the overall rate R in the environment, either by learning from experience (McNamara & Houston, 1985) or by reading some environmental clue. It also includes the capacity to directly perceive the local rate G(t) as it drops as

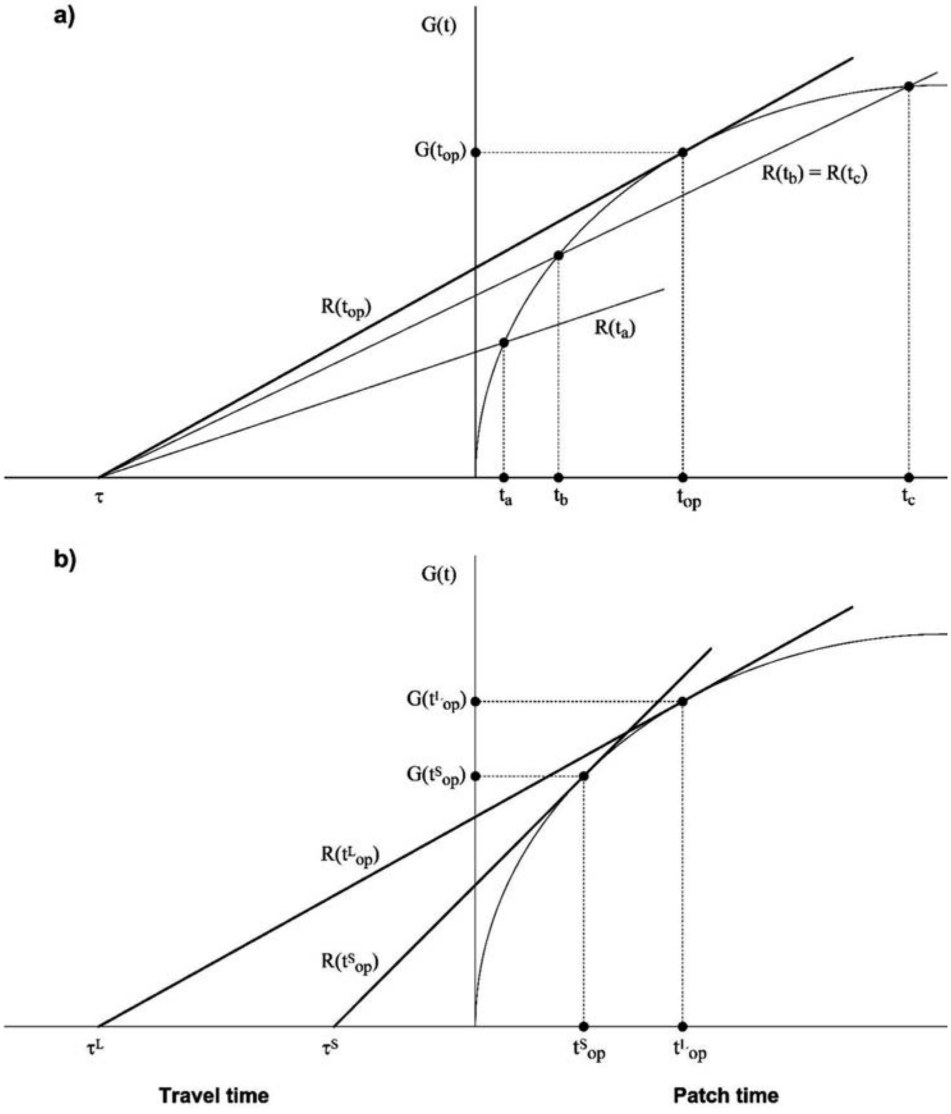

FIGURE 14.1. Graphical representation of the marginal value theorem as applied to a central place forager. The origin of coordinates is set at the arrival time to a patch. The horizontal axis shows the total travel time (round trip) growing to the left and patch time growing to the right; the vertical axis shows accumulated food, with the curvilinear function showing total gains as a function of patch time. An animal leaving all patches after collecting food for a time t will experience an overall rate of returns R, given by the ratio of accumulated gains to the sum of travel and patch times. In (a) several potential leaving times are shown. The line with slope $R(t_{op})$ represents the maximum rate of prey acquisition, and serves to identify the optimal patch leaving time. Also shown for comparison are two alternative strategies, with rates $R(t_a)$ and $R(t_b) = R(t_c)$, both less profitable than $R(t_{op})$; (b) shows the effect of travel time. When the round trip travel decreases so does the optimal patch residence time and consequently the optimal load size. Notice that only at the optimal departure time is the slope of G(t) identical to the overall rate R.

a function of patch time. The mutual dependence between R and t_{op} is solved through convergence until experienced and expected R are equal.

Figure 14.1b shows how travel time, τ, affects optimal patch time. As τ increases from τ^S to τ^L, the optimal residence time and consequently the optimal load increase. This is intuitive because the less time spent traveling the higher is the overall rate of return R, and G(t) drops to R earlier. To our knowledge, the prediction that longer travel time should lead to longer patch times was met in every published experimental test of the MVT.

The MVT as described so far incorporates simplifications, including the following:

- G(t) is a continuous function, but foraging animals encounter discrete prey items, so that responding according to how its slope declines with patch time may pose implementation problems.
- Foraging cycles are assumed to be identical, and parameters are entered in the model only as averages, but in practice patches differ from each other as do travel times to them, so that variance, as well as averages, may have an impact.
- The currency R is provisioning rate, but parents must engage in other activities such as territorial defense or antipredator behavior, and this may impose trade-offs.
- The model deals just with maximizing provisioning rate, but the parent needs to eat to stay alive.
- The currency as discussed so far does not take into account known metabolic costs of foraging and flying.
- The model is mute regarding mechanism: The agent does not need to compute the optimum as the modeler does, but it must acquire and process the relevant information somehow.

Exposing these simplifications is an important contribution of the model. All of these simplifications are amenable to theoretical refinements and experimentation, and have been dealt with in the foraging literature. Kacelnik (1984), for example, applied the MVT to European starlings feeding nestlings. Starling pairs usually make between them in the order of 400 foraging trips per day, bringing up to eight prey per trip. In a field experiment, starlings learned to collect mealworms from an artificial patch that was reset in every visit, and where G(t) was implemented by delivering worms at increasing intervals. The delivery rule was a discrete approximation to $I_i = e^{(i/1.52)}$ where I_i is the time between landing and delivery of the i_{th} prey in each visit, in seconds. As the birds collected prey as they were delivered, they experienced $G(t) = 1.52 \ln(t)$.

To test the impact of travel time, the distance (travel time) between patch and nests was also manipulated, allowing for a priori predictions of the optimal patch time, or equivalently of the optimal load. For the traveling distances tested (up to 1 km from the nest), the observed loads increased with travel time and were close to the predicted optima. However, the model showed a quantitative deviation: It slightly but systematically underpredicted the loads carried by the birds. One of the model's simplifications turned out to be the culprit: The currency (gross rate of delivery) treated all time components in the cycle as equivalent (i.e., they all caused the same loss of foraging opportunity), but flying time is more energetically costly than foraging on the ground or time spent in the nest. A realistic improvement of the currency hypothesis to include energetic costs (Cowie, 1977; Kacelnik & Houston, 1984) increased the quantitative fit between model and data (Figure 14.2).

In addition to linking foraging behavior to economics, the MVT applies to many other biological problems. One classic example is that of male dung flies (*Scatophaga stercoraria*), that compete for the opportunity to mate with females arriving at cowpats to lay their eggs. Copula in these flies takes variable times for two reasons: because the transfer of sperm increases with copulation time and because males guard females after ejaculation, to prevent them from copulating with other males. Parker (1970; see also Parker, Simmons, Stockley, McChristie, & Charnov, 1999; Parker & Stuart, 1976) has shown that the sperm of a second male copulating with a female fertilizes about 80% of the eggs. So the strategic question here for each male is how long to spend in each copula. The returns of added copulation time diminish rapidly (in terms of the expected proportion of eggs fertilized) and there is also the opportunity cost of encountering other females. The time each male

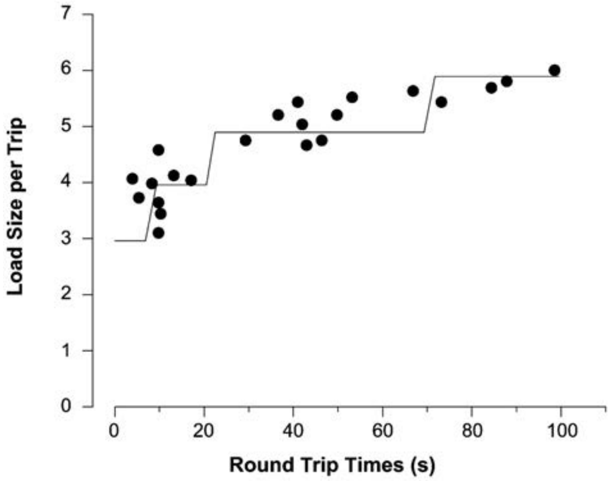

FIGURE 14.2. Load size as a function of round trip times in a field experiment with starlings as subjects. Each dot represents the average number of mealworms collected over approximately 50 trips to the same foraging site; the line represents the predicted optimal number of prey according to the MVT when physiological costs are considered. From "Central Place Foraging In Starlings (*Sturnus vulgaris*). I. Patch Residence Time," by A. Kacelnik, 1984, *Journal of Animal Ecology, 53*, p. 292. Copyright 1984 by the British Ecological Society. Adapted with permission.

spends guarding the present female until she lays her eggs plus the time to search for a new female (the analogue of travel time in the starling experiment) can be used to predict the time a male should spend copulating with a female, and the predictions work reasonably well (Parker, 1978).

The Role of Psychology in Optimal Foraging

In summary, animals in many cases do follow the predictions of the MVT, but in its simplified versions, this does not address the proximate mechanism(s) by which they do. Behavioral ecologists often address this by postulating that animals may follow simple rules, known as *rules-of-thumb*, capable of engendering behaviors close to the predicted optima (e.g., Davies, Krebs, & West, 2012). Many such rules have been proposed, each to deal with particular features of a problem. Examples include *hunting by expectation* (the animal should leave the patch after a given number of captures; e.g., Gibb, 1958, 1962a, 1962b, 1966), *giving-up time* (the animal should leave the patch when the time since the last capture exceeds a given threshold; e.g., Croze, 1970; McNair, 1982), *patch-residence time* (the animal should leave the patch after a certain exploitation time; e.g., Krebs, 1973), and even Bayesian updating rules that can cope well with variability between patches (e.g., R. F. Green, 1980, 1984). These hypothetical rules are close to the heuristics favored by some critics of optimality in the study of human decision making (e.g., Gigerenzer & Goldstein, 1996; Gigerenzer, Hertwig, & Pachur, 2011), and have similar shortcomings. Their main virtue is that they show that animals can approximate optimal behavior without making the same computations as the scientist. For those that support bounded rationality as if it were an alternative to optimality, heuristics illustrate the same point, namely that individuals do not make the computations required to identify optima and instead follow algorithms that converge to sufficiently appropriate behavior under the ecological conditions in which the decision maker lives. But we are concerned with some shortcomings.

First, most of the rules proposed are domain-specific. For instance, a foraging bird may use waiting time between two prey items as a proxy for the reciprocal of G'(t), departing when experiencing a given interval, or a baseball player may catch a ball not by computing the ball's parabolic trajectory but by running so as to maintain a constant angle of gaze to the ball as it flies, until both converge. We fear that such rules are probably unsuitable for animals inhabiting heterogeneous habitats and facing a multitude of daily tasks. Members of species that face different demands within and across generations would have to use the correct rule-of-thumb in each particular situation, which implies the existence of an extensive library of such rules and a mechanism to select the correct one in each case. Second, the approach mostly ignores psychological mechanisms known in the parallel, but highly related field, of animal learning and cognition. Mechanisms such as reinforcement learning (loosely defined as increasing the frequency of actions that work well) may adjust the organism to a very broad class of problems, ranging from rate maximizing patch times to the right movements to catch a flying ball.

The adaptive algorithm is then a learning and developmental process, rather than a specific rule of thumb or heuristic for each individual problem.

As stated previously, we argue that optimality models are a framework to integrate functional and mechanistic hypotheses. Just as adaptive function constrains which psychological mechanisms evolve, broad-domain psychological mechanisms determine the nature of the problems each animal solves.

To illustrate this view we turn our attention to how learning theory and psychophysics relate to the foregoing discussion of the MVT. It is clear from the previous discussion that optimal foraging models involve sensitivity to time intervals such as travel time and intercapture intervals. This by itself suggests that mechanisms known under the heading of *interval timing* (psychological processing of learned intervals typically in the seconds to minutes range) might be directly relevant (see Chapter 23, this volume). This was demonstrated by Brunner, Kacelnik, and Gibbon (1992; see also Kacelnik & Brunner, 2002) using a laboratory task in which starlings traveled between perches to reach a virtual patch, where on arrival started to receive food pellets with fixed intercapture intervals (fixed-intervals [FIs]). The rate of capture did not decline gradually, but after an unpredictable and unsignaled number of deliveries the patch went dead, and the bird could renew the process by traveling to a new patch. The choice in this case is how long to wait since the last reward, before abandoning each patch. The optimal policy for an animal with perfect timing would be to leave immediately after a FI had lapsed without a delivery, as that was a sure sign that the patch was exhausted, regardless of the mean and variance of travel time between patches. However, animals process time intervals with some level of error, well mapped in the field of interval timing. For instance, the standard deviation of birds' estimates of when food is due, as expressed in the temporal location of the peak in their pecking rate, is known to be proportional to the interval lengths. This is a regularity known in psychophysics as Weber's law (see Chapters 1, 23, and 25, this volume). This means that as time waiting for a prey item lapses, the bird gets a gradual rather than stepwise increase in its level of certainty about the patch status. This gradual increase in the certainty that the patch is depleted transforms the task into one of choosing between a declining function expressing the potential of the present patch as a function of waiting time and the expected reward rate in the environment. The lower the environmental rate, the longer should the optimal decision maker wait before leaving. This task is equivalent to the problem of when to stop loading prey in the MVT, but for different reasons: Instead of the local reward potential declining objectively as a function of time since arrival, here the estimated reward potential declines gradually since the last capture because of the animals' psychology. The authors reasoned that starlings should approximate the optimal solution taking into account these constraints. To test this, they manipulated interprey intervals and travel time between patches. Across conditions they corroborated that the predictions of this psychologically determined version of the MVT were upheld, as follows. First, maximum pecking rate was consistently centered around the FI parameter but the spread of the timing function increased with the length of the FI, as expected from Weber's Law for timing. This was incorporated as an assumption of the model. Second, the time between the moment when reward would have been due and the time at which birds stopped responding or initiated a new travel kept a roughly linear relation to the FI. This makes sense because of the Weber Law assumption: If timing accuracy were independent of the FI an optimal animal would give up on a patch after waiting a constant time after the last reward, but one whose precision is inversely proportional to the typical FI (as assumed by Weber's law) needs to vary its waiting time to reach the same level of certainty about a patch's potential for reward. This interlocking between optimality modeling and psychological research is preferable to ad-hoc rules-of-thumb or heuristics, because the properties of psychological timing do not need to be seen as dedicated mechanisms to solve a particular experimental situation.

Optimality and Environmental Variability

Thus far we have dealt with models that are only sensitive to average parameters. For instance, in Equation 1a, the maximized currency is the ratio of average gains to the average sum of travel plus patch times. Equation 1a is thus insensitive to variability in these parameters, but this is not true for how animals behave. Cuthill and colleagues (1990; see also Cuthill, Haccou, & Kacelnik, 1994), for example, found that when starlings experience a mixture of travel times, patch exploitation is affected by the most recently experienced travel time, thus causing variability in patch times. In a different study, Kacelnik and Todd (1992) compared patch residence time in a MVT task between conditions with equal mean travel time but different variance. They found that pigeons (*Columba livia*) decreased patch times with increasing travel time variance. This result can be understood by reference to a mathematical result called Jensen's inequality, which in its simplest form states that if F(x) is a concave function of x and x is variable, then the mean of F(x) is less than or equal to F(mean of x), with the opposite holding for convex functions. Let us consider a bird foraging in an MVT task but in either of two conditions differing only in the variability of travel times. In the constant condition C_c, the travel time τ is always the same, whereas in the variable condition C_v there are two equiprobable travel times, $\tau+\delta$ and τ-δ. The average travel time is the same in both conditions, hence the optimal strategy should be the same under constant or variable travel time, because the rates of return are identical:

$$R(t)=\frac{G(t)}{\tau+t}\equiv\frac{G(t)}{\frac{1}{2}\big[(\tau+\delta)+(\tau-\delta)\big]+t} \qquad (1b)$$

Thus, and in contrast with the empirical results showing that birds actually do show cycle-to-cycle variability in patch times when travel time is variable, an ideal model animal should leave all patches after the same patch time. This predicted insensitivity is intuitively important to underscore that the MVT predicts decisions taking into account expected (i.e. future) average opportunities rather than paying the travel costs already incurred (sunk costs; see Chapter 15, this volume). The ideal forager leaves its current patch when it expects, on average, to get a higher payoff elsewhere, given the statistical properties of the environment. If the environment has a random mixture of travel times, then the mean of this mixture defines the rate of gain to be obtained in the future. But the future can only be anticipated by measuring the statistics of the past, and sensible algorithms for using the past to predict the future include some weight for recency, to take into account that conditions may change. Recency effects in turn can cause persistent modifications of patch time (see Chapter 10, this volume).

Even if these fluctuations in patch time are left aside, variation in mean patch time as a function of variance in travel, such as that described by Kacelnik and Todd (1992) can be attributed to a mixture of optimality and mechanistic considerations. Imagine, for instance, a forager that is sufficiently adjusted to the fact that short and long travels are in an unpredictable temporal sequence that it does not vary its patch time between cycles, but modifies patch time gradually according to the discrepancy between the rate of gain it expects and that experienced in each cycle (McNamara & Houston, 1985). In cycles where the preceding travel was short it estimates that the rate of returns is relatively high, and in cycles when preceding travel was long, that it is lower. On average, its subjective estimate is given by Equation 2a:

$$R_v(t)=\frac{1}{2}\left(\frac{G(t)}{\tau+\delta+t}+\frac{G(t)}{\tau-\delta+t}\right) \qquad (2a)$$

that can be simplified to

$$R_v(t)=\frac{G(t)}{\tau+t-\dfrac{\ddot{\delta}^2}{\tau+t}} \qquad (2b)$$

Given that the only difference between Equations 1a and 2b is that Equation 2b has a smaller denominator, it follows that $R_v(t) > R(t)$, and a forager that computes average rate in the future as a cycle-by-cycle running average will perceive the world as being richer. Because perceived lost opportunity while in the patch is greater in a richer environment, the animal would leave all patches sooner, as reported by Kacelnik and Todd (1992). This is another combination of optimality and psychological considerations. Shorter term fluctuations in patch time as reported by Cuthill et al. (1994, 1990) add another layer of mingling between psychology and optimality.

The differences between strategies predicted on the basis of objective rates and strategies that, because of computational mechanisms, lead animals to optimize respect to biased subjective estimates is related to the *fallacy of the averages* which is another idea related to Jensen's inequality, described previously. Someone committing this fallacy fails to see the distinction between computing a mean of a variable and then applying a function to it, and applying a function to each case of the independent variable and then computing the average (Templeton & Lawlor, 1981; Turelli, Gillespie, & Schoener, 1982). In the previous example, Equation 1b (a function of expected values) leads to predictions different from those of Equation 2a (the expected value of a function). The original fallacy is only of historical interest, because the issues are now well understood, but the problem of which algorithm predicts behavior remains, and boils down to whether including psychological mechanisms is a fair practice in optimality models. Regarding rate maximizing, the experienced rate of return of an animal over a certain period is given by the quotient between mean gains and mean times over the period, but it is perfectly possible that real foragers instead respond psychologically to the mean of the ratio of gain over time across hunting episodes, thus "committing the fallacy," as it were. Including such mechanisms has methodological costs, because one builds into the model what should ideally be the model's output, but it is to some extent unavoidable if the models are conceived as being refined with relation to behavioral data. In their original conception, optimality modelers assumed that the constituent hypotheses of each of their preferred models were objectively known. The role of experimentation at the time was aimed, in practice, to illustrate the action of natural selection, and to generate predictions for previously unknown behavioral adaptations. The hypotheses involved in constructing the models were not explicitly seen as such, leading to the illusion that functional behavioral models could ignore mechanisms.

THE SELF-CONTROL PROBLEM IN INTERTEMPORAL CHOICE

Another research field that benefits from integrating functional and mechanistic approaches is the study of self-control in intertemporal choice (see Chapter 24, this volume). Intertemporal choices involve decisions between outcomes at different times in the future, and they are pervasive in human and nonhuman daily life. Consider once again a foraging bird that provisions its chicks, this time facing a choice between two feeding patches, one providing a large prey after a long search time (LL) and the other a small prey after a brief search (SS).[2] For simplicity let's assume that the bird carries only one prey per trip. Because the bird spends all its daytime provisioning its young, natural selection favors individuals that maximize the food mass delivered over the day. We can now compare the adaptive advantages of choosing to hunt for LL or SS. Because the birds are judged by the amount of food delivered, they would be indifferent when the ratio of reward size to search time plus travel time is the same in both sites:

$$\frac{Size_s}{\tau + t_s} = \frac{Size_L}{\tau + t_L} \tag{3a}$$

or

$$Size_s = \frac{\tau + t_s}{\tau + t_L} Size_L \tag{3b}$$

In other words, the biological value of a large reward is equivalent to that of a small reward provided that the ratio of times involved exactly compensate for the size difference. One way to express this is to say that delayed rewards are discounted as a function of the extra time costs. Equations 3a and 3b are based on the assumption that time is a limiting resource.

Many laboratory studies examine intertemporal choice in animals using protocols wherein subjects, typically pigeons or rats (*Rattus norvegicus*), choose repeatedly between alternatives that differ in reward size and delay in trials separated by intertrial intervals. In a prototypical example, as soon as a trial starts a pigeon chooses between two colored keys,

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[2] The reader may notice some similarities between this situation and the patch-exploitation problem (for a detailed analysis see Stephens & Anderson, 2001; Stevens & Stephens, 2010).

each associated with a particular amount and delay to food. SS may give one pellet of food after a delay of 10 s and LL two pellets after 20 s. In different conditions, experimenters manipulate the delays to and/or amounts of food so as to map how animals trade amount for time. Given these values, if there is no intertrial-interval (ITI; or if the subjects do not include it in their computations, as we discuss later), according to Equation 3b the two items should be equally valuable, but this has not been the intuitive expectation in most of the psychological literature on temporal discounting.

In treatments of this problem by experimental psychologists, although in their experiments the animals face iterated choices, the two most frequent mathematical descriptions consider the choices as if the animal made only one choice. The question asked is not "which relation between size and delay would equalize rate of gain?" as is typical in optimal foraging theory, but instead "what function describes the value of a reward as a function of waiting time?" This function is normally called the *discounting function*. Because of the implicit one-shot perspective, lost opportunity is not in the frame, and the results are often described saying that animals forego long-term gains in favor of more immediate but less valuable food rewards (e.g., L. Green, Fisher, Perlow, & Sherman, 1981; Mazur, 1987; McDiarmid & Rilling, 1965), as if this were irrationally impulsive (the phrase "inability to delay reinforcement" is sometimes used). Pigeons, for example, are said to find rewards delayed just one second as half as attractive as an immediate reward (Mazur, 1984). According to the rate of reward analysis, if it were possible (and this is of course not the case) for a reward to be found and consumed in no time at all, the corresponding rate of gain would tend to infinity, and there is no size of a more delayed reward that equalizes the value of an immediate delivery.

Within the one-shot framework there are normative and descriptive accounts of temporal discounting. Normative (i.e. optimality) models of temporal discounting, suggested by economists (Samuelson, 1937) and biologists (Kagel, Green, & Caraco, 1986), predict that the discounting function should take an exponential form (see Chapter 24, this volume). This is because if there is a constant probability of the reward being lost per unit of waiting time, the probability of collecting the reward is a declining exponential function of the delay. This is known as the *discounting-by-interruptions* hypothesis, and has been central to treatments of intertemporal choice in behavioral ecology (e.g., Houston & McNamara, 1999; Kagel, Battalio, & Green, 1995; Kagel et al., 1986; Sozou, 1998). This is perhaps surprising as the one-shot logic contrasts with the classical optimal foraging treatments that see time as a limiting resource and focus on multiple decisions and repeated cycles.

A descriptively successful and widely accepted alternative to exponential discounting, termed *hyperbolic discounting*, has been put forward by Mazur (1987). According to this model, value declines with delay as follows:

$$V_i = \frac{S_i}{1 + kt_i} \tag{4}$$

where S_i is the subjective value of the reward if it were available immediately, k is a free parameter with dimensions reciprocal to time, and t_i is the delay between the evaluation moment and the outcome for that prey. Variations in k are used to describe differences between individuals and between species. This function has been successful in fitting animal choice data and useful in clinical settings, where research has shown an association between the parameter k and addictive behavior, such as gambling, substance abuse, and obesity (Odum, 2011; Odum & Baumann, 2003).

Although derived descriptively rather than normatively, hyperbolic discounting is almost identical to Equation 3a. Let us assume that the subjective value of a prey immediately available is well represented by its size. Then the delays at which two prey LL and SS have equal value are given by

$$\frac{S_s}{1 + kt_s} = \frac{S_L}{1 + kt_L} \tag{5a}$$

or

$$S_s = \frac{1 + kt_s}{1 + kt_L} S_L \tag{5b}$$

In addition to the fact that Equation 3b has a normative interpretation under repeated cycles whereas 5b is descriptive and frames discounting as a one-shot problem, the main differences between them are as follows: In Equation 3b the proportionality constant is nondimensional because it is the ratio of two times, whereas in Equation 5b the time dimension is eliminated by the fitted constant k. Equation 3b includes the ITI, whereas Equation 5b replaces it by a small constant that is influential only for very short delays. And finally, 5b has a fitted parameter that allows for different discounting rates across subjects or species, whereas Equation 3b is rigid in this respect.

There remains a further consideration that will serve us, once again, to examine the relation between optimality models and what we may call "real" psychology. Equation 3b implies equal sensitivity to all time components, namely the delay between choice and outcome *t* and the travel time or intertrial interval τ, but, because they deal with one-shot problems, Equation 5b only addresses sensitivity to the delay between choice and outcome. Available evidence, although scarce, suggests that intertrial intervals have very little effect in animal self-control experiments (Mazur & Romano, 1992) or other designs including choices between simultaneous opportunities. This is puzzling, because in the patch-exploitation problem, travel time, which can be seen as closest to the intertrial interval in self-control studies, has a strong and highly predictable impact. Consistently with the view expressed elsewhere (Kacelnik, 2003), we argue that the answer lies in the temporal position of the time components of the cycle relative to the moment at which the subject makes its choice. In a patch foraging problem, the forager's decision is when to leave the current patch to initiate a cycle by traveling to a new site, hence travel costs occur between the decision and its consequences, the reinforcing experience on arrival at the new patch. In the self-control paradigm, the decision is the choice between SS and LL and the delays occur between that decision and its outcome, with the ITI placed after the choice consequence, be this a large or small reward (Figure 14.3).

Our view is that animals are very sensitive to times between decisions and outcomes, but relatively insensitive to intervals other than those, because of the problem of *credit attribution*. From an evolutionary standpoint, it makes sense that when

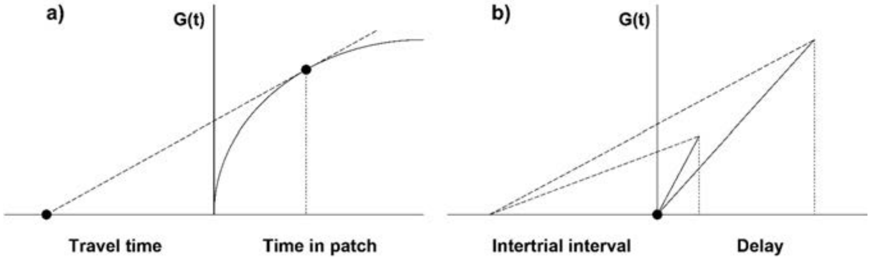

FIGURE 14.3. The effect of travel time and intertrial-interval (ITI) on decisions. (a) In the depleting patch problem, the decision being modeled is patch departure, which marks the start of a new foraging cycle. Travel time occurs between the decision, indicated by the two black dots, and a new patch arrival. Given the cyclical nature of the problem, the two dots mark the same point in time; (b) in the discounting problem, the decision between two options and the programmed delay occurs between the decision, occurring at the moment indicated by the black dot, and either outcome. Travel time (or ITI in lab simulations) occurs between outcomes and new choices. Although the overall rate of reward, as indicated by the slope of the broken lines, shows that travel time has the same effect on rate of reward in both the depleting patch and the discounting problems, reinforcement analysis expects them to be substantially different, and predicts that travel time will control decisions in the marginal value theorem while ITI will be irrelevant in the discounting problem.

the animal obtains a reward (SS or LL) after a short or long delay respectively it attributes the "responsibility" of such outcome to its preceding decision. It may be expected, on conditioning and foraging arguments, that the reinforcing effect of the outcome declines with the interval since that decision, and increases with the magnitude of the outcome. This is adaptive in a world where the animal needs to learn the consequences of its decisions by the ensuing outcomes (e.g., Bouton, 2007).

With suitable adjustments, Equation 3a can be applied to situations where the effect of energetic costs on choice is examined. Consider a situation where the forager faces alternatives that differ in net energy content S_i (net content is the absolute content minus the metabolic expenditure during handling time), handling time t_i, search time τ_i, and metabolic rate during searching, m_i. In such a case, the net rate that would result from using exclusively option i is given by:

$$NetR_i = \frac{S_i - m_i \tau_i}{\tau_i + t_i} \tag{6}$$

This model was applied by Bautista et al. (2001) in a laboratory study of starlings choosing between searching for food by flying or by walking. The question was, given that flying is more metabolically expensive than walking, how would the birds integrate time and metabolic costs to make their choices, starting with the prediction that they might be expected to maximize Equation 6. The birds were given iterated choices between two options delivering food rewards of equal size, one requiring a certain (manipulated) length of time flying and the other an adjustable length of time walking. For each experimentally fixed flight time, the walking cost was automatically varied to establish by titration the value at which the birds were indifferent between the options, considering that flying delivered food faster but at greater cost per unit of time than walking. The results were also compared to two alternative currencies, gross rate of energy gain (ignoring metabolic costs) and energetic efficiency (energy gained per unit of energy spent, ignoring the times involved). The results were very close to those predicted by Equation 6, indicating that the birds do indeed include time and energy costs in determining their preferences between sources of food. This is another form of hyperbolic discounting, because by flying a bird gets expensive food sooner, whereas by walking it gets cheap food later, but the protocol is enriched by the inclusion of energetic costs to reflect the foraging perspective.

In summary, hyperbolic discounting is the form of discounting in intertemporal choices predicted by optimality models on the basis of rate maximization. Some deviations from its predictions in special cases are as expected by learning processes, where decisions are reinforced by their consequences. With one exception, to our knowledge, single-shot choices between SS and LL rewards are not appropriate to model animal choices, given that the animals are instructed of the parameters of the protocols by iterating multiple trials. The exception is Stevens, Rosati, Ross, and Hauser (2005) work with cotton-top tamarins (*Saguinus oedipus*) and common marmosets (*Callithrix jacchus*), where delay could be anticipated from visual cues. More generally, many results of choice experiments with nonhumans can be explained by identifying the decision facing the subject and considering the way actions are reinforced by their consequences. The overwhelming selection pressures may have been those designing the existing reinforcement mechanisms, rather than specific solutions to unique choice protocols, and for this reason the search for rules of thumb may not be the most fertile approach to relate optimality models to psychological processes.

THE STRUCTURE OF FORAGING ENVIRONMENTS AND CHOICE

A common assumption in the study of decision making is that most, perhaps all decisions imply tradeoffs. As we have just discussed, animals need to choose between foraging opportunities that differ in magnitude and time costs. From such a starting point it is tempting to assume that decisions involve comparisons between alternatives and therefore cognitive effort and time. As we will see, this assumption is not always supported.

We incorporate the hypothetical structure of foraging environments in our modeling approach by arguing that animals mostly choose in contexts where alternatives are faced sequentially rather than simultaneously. An example is when a predator decides between pursuing a detected prey or skipping it and continuing to search for alternatives that may be more profitable because they are larger, less likely to escape, or require less engagement time and hence less lost opportunity. The ideas in this section are encapsulated in the Sequential Choice Model (SCM; Kacelnik, Vasconcelos, Monteiro, & Aw, 2011; Shapiro, Siller, & Kacelnik, 2008) whose main assumption is that choice mechanisms evolved as adaptations to environments in which sequential encounters (i.e., finding one option at a time) are common, whilst direct choice opportunities (i.e., finding two or more options simultaneously) are rare (e.g., Stephens & Krebs, 1986). Thus, the psychological mechanisms acting in choices between simultaneously available options are adaptations for the broader need of learning to improve performance in more frequent situations, such as when deciding whether to engage with a given option or let it pass to pursue other alternatives (closer to a go/no-go psychological protocol).

According to this framework, animals develop a subjective valuation of each source of reward (similar to its associative strength in learning models) whenever they encounter that prey type, through the mechanisms of reinforcement learning. With the same lost opportunity reasoning used so far, this valuation is a function of the remembered profitability of each prey type relative to the rate of gain in the environment as a whole, including time costs and information about the mixture of alternatives in the habitat. We further hypothesize that when animals face single options, relative valuation is expressed as the immediacy of their response (latency). In nature this latency would correlate with the probability of skipping the opportunity to search for alternatives. Latencies in encounters with single options should decrease when the options' objective profitability increases (e.g., ratio of amount of reward to the delay between action and outcome; Bateson & Kacelnik, 1996; Mazur, 2010; Shapiro et al., 2008), and increase with the energetic reserves of the animal during learning (e.g., Aw, Holbrook, Burt de Perera, & Kacelnik, 2009; Pompilio & Kacelnik, 2005; Pompilio, Kacelnik, & Behmer, 2006; Vasconcelos & Urcuioli, 2008; see also Chapter 16, this volume) and the profitability of the available alternatives in the same context (Fantino & Abarca, 1985; Mazur, 2010; Shapiro et al., 2008). Because of random noise, successive sequential encounters with an option result in a probability density function of latencies. We further hypothesize that when two or more options are met simultaneously, each option elicits a sample from its own distribution of latencies and the shortest sample is expressed as a choice.

In this hypothetical mechanism no deliberative comparison between options occurs at the time of choice; instead, the mechanism underlying sequential decisions is primed for each option in parallel, with the option yielding the shortest sample dictating behavioral allocation and censoring the alternative (Kacelnik et al., 2011). Formally, the probability P_A of choosing option A over B is given by the joint probability of the latency for A equaling x and the latency for B exceeding x, integrated for all possible x:

$$P_A = p\left(l_A < l_B\right) = \int_0^\infty f_A(x).\left[1 - F_B(x)\right]dx \qquad (7)$$

where l_A and l_B are random samples from the respective distributions, f_A is the probability density function of latencies for A, F_B is the cumulative distribution function of latencies for B, and x is a particular latency value.

In summary, the SCM's assumptions are that the latency to accept sequentially encountered options is a joint function of three variables: the options' objective properties, the average rate of gain in the environment given the mixture of options and their respective search times, and the energetic state of the subject at the time of learning (i.e., not at the time of the choice). Moreover, the mechanism that determines choice when two or more options are met simultaneously depends on random independent sampling from each option's latency distribution. Under this hypothetical mechanism the latency distribution of the options present in a simultaneous choice censor each other, as only the shortest of the sampled latencies will be recorded. In other words, the SCM is what is known as a race model in the decision making literature, as opposed to models postulating a competitive evaluation between attractors such as diffusion models (Bogacz, 2007; Bogacz, Brown, Moehlis, Holmes, & Cohen, 2006; Pelé & Sueur, 2013).

The assumptions of this model combine empirical observations and the overarching logic of optimal foraging theory. One departure from *a priori* optimality that is empirically driven is the very existence of a latency to respond to single options. If (as it happens in many laboratory experiments) a predator has no choice other than take the present option or remain in that situation forever, it should take it immediately. Typically consuming the prey immediately resets the scene to searching anew, meaning that any waiting time is a loss of opportunity. In spite of these expectations, Shapiro et al. (2008; see also Mazur, 2010) found that latencies in starlings facing exactly those circumstances were strongly dependent on the parameters, namely were shorter when the present option was richer and when the alternative option in the environment was leaner (Figure 14.4). Posthoc arguments for the adaptive significance of these latencies have been elaborated since, for instance the suggestion that latencies in the laboratory are an artifact of the animals' lack of choice: In nature foragers can always skip a prey to forage for further opportunities, and the conditions under which a prey should be skipped are exactly those that cause longer latencies in single encounters in the laboratory (Charnov, 1976a). Whatever the adaptive history of the mechanisms that cause such orderly latencies, once their presence is established optimality models need to include them in the strategy set, lest the models are condemned to failing from scratch. Models including these assumptions can make novel and counterintuitive predictions. For instance, according to this model it ought to be possible to predict preferences in simultaneous choices from the distributions of latencies in sequential encounters.

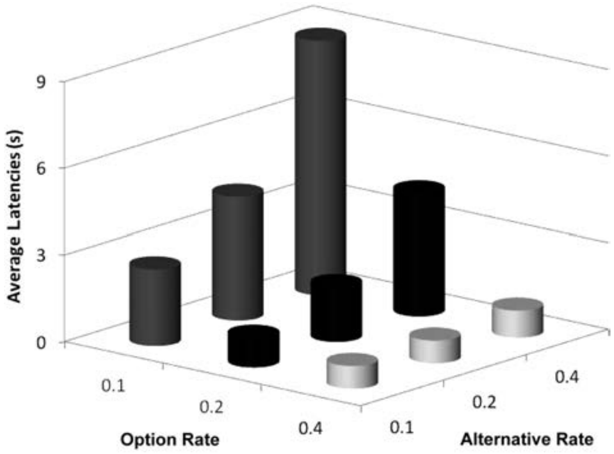

FIGURE 14.4. Median latencies to accept each option during sequential encounters as a function of the option's profitability and that of the alternative option that could potentially be encountered in the same environment, averaged across subjects. Adapted from "Simultaneous and Sequential Choice as a Function of Reward Delay and Magnitude: Normative, Descriptive and Process-Based Models Tested in the European Starling (*Sturnus vulgaris*)," by M. S. Shapiro, S. Siller, and A. Kacelnik, 2008, *Journal of Experimental Psychology: Animal Behavior Processes, 34*, p. 82. Copyright 2008 by the American Psychological Association.

The SCM predicts a deviation from indifference in simultaneous choices if, and only if, different latency distributions are observed during sequential encounters. The option with the most leftwards distribution of latencies in sequential encounters should be chosen more often, and thus be less severely censored than the alternative. The less preferred alternative will seldom be chosen, and when it does the observed latencies should on average be shorter than when the same option is encountered alone. Through this censorship mechanism the SCM makes the counterintuitive prediction that latencies observed in simultaneous choices should be shorter than the ones observed with those same options in sequential encounters. Moreover, the shortening of latencies in choices with respect to sequential decisions should be more extreme for the less relatively profitable and less frequently chosen option.

The prediction of a latency shortening contradicts models of choice that assume the existence of comparative cognitive processes at the time of making each choice. Such comparisons should logically take time, and thus animals would be expected to act faster when options are met without competition than when multiple options are presented simultaneously. This intuitively expected increase in choice time with number of options is encapsulated in the Hick–Hyman Law (Hick, 1952; Hyman, 1953). The assumption is that every choice involves a trade-off between accuracy (i.e., choosing the better option) and the (temporal) cost of evaluation.

Similarly to other proposals for individual decision making (e.g., Blough, 2011; Ratcliff, Van Zandt, & McKoon, 1999; Smith & Ratcliff, 2004) and collective decision making in social insects (Robinson, Franks, Ellis, Okuda, & Marshall, 2011; Seeley et al., 2012), the SCM proposes that choice processes resemble a horse race rather than a tug-of-war. The idea is that the vertebrate's brain operates at least partly like a eusocial insect colony, where options are represented by some form of bidding in the absence of an executive system that ponders their relative strength.

The model was inspired by experimental results obtained with starlings foraging in two-alternative environments (Shapiro et al., 2008), but has since been successfully applied to risk-sensitive foraging (Aw, Monteiro, Vasconcelos, & Kacelnik, 2012) and multialternative environments (Freidin, Aw, & Kacelnik, 2009; Vasconcelos, Monteiro, Aw, & Kacelnik, 2010). Simultaneous choice can be predicted in multiple ways under the SCM rationale. One, which we call *molar*, uses the complete distribution of latencies from sequential encounters with each option to predict the overall proportion of choices. The alternative, which we call *molecular*, attempts to predict the outcome of each particular choice using only the most recent sequential encounters with each option, thus considering potential local fluctuations in motivation. Figure 14.5 shows experimental results and model predictions in two- and multialternative environments. Figure 14.5a includes only molecular predictions whereas Figure 14.5b includes molecular (left axis) and molar predictions (right axis).

Support for the prediction that latencies for each option should be shorter in the presence of alternatives than when the option is alone is weaker so far, but two features make testing this prediction difficult. First, latencies have a lower but not an upper limit, which frequently constrains the detection of shortening by floor effects, unlike the opposing lengthening hypothesis which is not limited by physical constraints. Second, the best chance to observe shortening is in the less preferred option because it is more severely censored, but by definition this option is chosen infrequently and thus the sample size of latencies for this option in simultaneous choices is typically small. Nonetheless, shortening (Shapiro et al., 2008) or a tendency in that direction (Mazur, 2010; Vasconcelos, Monteiro, & Kacelnik, 2013) has been observed on several occasions, whereas signs for the increase in choice time expected from the hypothesis that choice takes some deliberation time have not been reported so far.

In sum, the basic idea of the SCM is that choices made when facing alternatives simultaneously can be predicted by behavior observed during sequential encounters with one alternative at a time, but not the other way around. The significance of sequential encounters and the logic of lost opportunity is an ubiquitous feature of optimality models since the early days of optimal foraging theory, through Charnov's diet choice model (Charnov, 1976a) and marginal value theorem (Charnov, 1976b), both of which predict preferences as a consequence of a tradeoff between exploiting the current source of reward and the background average opportunities offered by the environment as a whole; taking the present option causes lost opportunity elsewhere. The main contrast with psychological accounts of choice is that the latter must be applied to the individual's experience, and the MVT explains behavior as if it were shaped by the transgenerational species' past so as to maximize reward in the future. It should be apparent that it makes no sense to explain behavior resorting to only one or the other. Charnov's ideas from early on inspired empirical tests (Cowie, 1977; Krebs, Erichsen, Webber, & Charnov, 1977) that are now classic in behavioral ecology, but these early tests and most of those that followed did not make sufficient contact with psychological research. In experimental psychology, meanwhile, the study of decision making has been dominated by descriptive models of simultaneous choice paradigms, without sufficient interest in the adaptive consequences of animal preferences. Refocusing on the contrast between single options and their background context, and incorporating known psychological mechanisms into the strategy set of optimality models allows for a productive link between these diverse approaches.

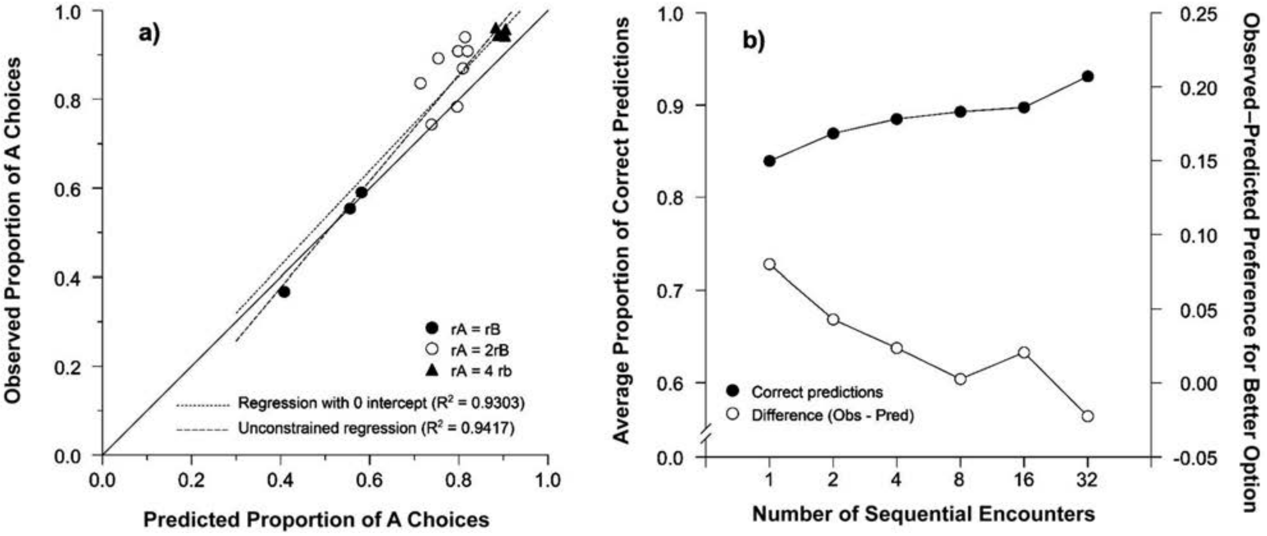

FIGURE 14.5. Illustration of the sequential choice model (SCM) ability to predict simultaneous choice from sequential encounters. (a) Obtained versus predicted proportion of choices for the option yielding higher rate of reward (always labeled A) according to the SCM. Each rate is represented by a different symbol. Two linear regression lines are included. The dashed line corresponds to an unconstrained regression and the doted one is constrained to pass through the origin. Adapted from "Simultaneous and Sequential Choice as a Function of Reward Delay and Magnitude: Normative, Descriptive and Process-Based Models Tested in the European Starling (*Sturnus vulgaris*)," by M. S. Shapiro, S. Siller, and A. Kacelnik, 2008, *Journal of Experimental Psychology: Animal Behavior Processes, 34,* p. 85. Copyright 2008 by the American Psychological Association. (b) Average proportion of choices accurately predicted by the SCM (solid circles, left axis, molecular predictions), and difference between observed and predicted preference strength (open circles, right axis, molar predictions) as a function of the number of preceding sequential trials used to predict each choice in simultaneous presentations. From "Choice in Multi-Alternative Environments: A Trial-By-Trial Implementation of the Sequential Choice Model," by M. Vasconcelos, T. Monteiro, J. Aw, and A. Kacelnik, 2010, *Behavioural Processes, 84,* p. 439. Copyright 2009 Elsevier B.V. Adapted with permission.

CONCLUSION

We have argued that because behavior and cognitive processes are products of evolution by natural selection, behavioral research can benefit from optimality modeling. This approach assumes that the psychology of organisms makes sense from a fitness-maximization design standpoint, but does not amount to say that animals always behave optimally. Instead the models are sets of hypotheses subject to empirical refinement.

We have illustrated these ideas with optimality models of foraging behavior, one dealing with the decision on when to switch from a reward source with diminishing returns, another with intertemporal choice and discounting, and finally one considering how choices between simultaneously presented opportunities reflect mechanisms evolved to more ecologically relevant sequential choices.

It should be clear that although optimality modeling uses an evolutionary logic, at its best, it is supported by specific psychological hypotheses that are directly tested experimentally. For example, the MVT typically is used to discuss the functional problem of foraging strategies for gradually depleting patches, but because each testable implementation requires hypotheses for a strategy set, a feedback function, and a currency, it cannot detach itself from behavioral mechanisms. These components are hypotheses that can be rejected empirically, and in proper implementations they often are rejected. Data can show that the feedback function is inaccurate or that the animal maximizes a different currency, and combined laboratory experiments with field work are needed to disentangle these possibilities (see Volume 1, Chapters 3 and 7, this handbook). Models respond to data by being modified to include previously unforeseen constraints, changing the currency, or specifying the statistical structure of the foraging environment more precisely, and making new, testable predictions on these bases. Good models account for what is known and predict what hasn't been explored as yet. What persists is the models' functional rationale: The biological system, including its psychological mechanisms, reflects the action of natural selection.

It is widely appreciated that testing environments seldom match precisely the environment under which the behavioral mechanisms evolved (the problem of the domain of testing vs. the domain of selection; see, e.g., Stevens & Stephens, 2010). This can be tackled using artificial selection experiments. For instance, Dunlap and Stephens (2009) have succeeded in using optimality considerations to anticipate the rapid evolution of learning parameters across just 30 generations of fruit flies (*Drosophila melanogaster*). But even when optimality predictions tested against current ecological conditions may fail because of environmental mismatching, the models provide a strong framework for the study of behavioral mechanisms. Functionally inspired models help understanding animals' responding to experimental protocols, by relating them to possible natural equivalents, for instance relating intertrial intervals to travel time, food caching to spatial memory tasks, perception of probability and partial reinforcement to risk sensitivity, and so on.

In our view, a truly integrative study of animal behavior and cognition must combine evolutionary and psychological approaches. They are often seen as orthogonal topics, but through model-inspired experimentation they can and do converge.

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CHAPTER 15

DECISION MAKING: RATIONAL AND IRRATIONAL CHOICE

Thomas Zentall

All learning can be viewed as decision making or choice because choice, broadly conceived, involves any context involving a response or even absence of a response (one can choose not to choose). Initial presentation of a stimulus generally produces an *orienting response* (a "what was that" response). If nothing of consequence follows that stimulus and it occurs repeatedly, the orienting response will undergo extinction, or *habituation*. If something of consequence follows the stimulus (e.g., food or shock) it will likely undergo *Pavlovian conditioning*. If a consequence (e.g., food for a deprived animal) requires a response such as lever pressing, the probability of a lever press will tend to increase (*instrumental conditioning*).

Rational choice is defined as choice that tends to maximize the probability of reinforcement. When choice is *irrational*, it means that an organism chooses suboptimally (i.e., it chooses an alternative that results in a lower probability of reinforcement). In the sections that follow, I will first examine contexts in which animals generally choose rationally and will then examine several cases in which they tend to choose irrationally (or suboptimally).

RATIONAL CHOICE

Rational choice involves most learning in which performance improves and accuracy approaches optimality. Often researchers ask what is learned, in addition to the correct response. To determine what else is learned generally requires a test of the transfer of training to new stimuli.

Simultaneous Discriminations

In a simultaneous discrimination, typically, an organism is given two (or more) alternatives from which to choose, one stimulus is followed by a biologically important outcome (e.g., for an animal, response to the positive stimulus [S+] is typically followed by food, the reinforcer); the other stimulus (the negative stimulus [S−]) is not. Initially, choice might be based on a preferred spatial location so the spatial location of the S+ and S− is randomized over trials. If an animal is appropriately motivated, the appearance of the two stimuli is sufficiently different, and the response required reasonably is easy to make; with experience, most choices are to the S+. The simultaneous discrimination can be used to determine the discriminability of the stimuli: For example, how large a physical difference in the stimuli is needed before the one associated with reinforcement is preferred (e.g., hues of different wavelength).

The learning process. An important use of the simultaneous discrimination is to help identify the nature of the underlying associative learning process. For example, according to classical learning theory (e.g., Hull, 1943), the preference for the S+ should be a monotonic function of the amount of training provided. It follows then that if the discrimination is reversed (the S+ and S− are interchanged), the number of trials to reverse the preference should be directly related to the amount of original training provided. However, the typical finding is that if animals are overtrained

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(i.e., they are trained beyond a usual criterion of success, beyond 90% correct) reversals are more quickly acquired than when they are merely trained to criterion (see Mackintosh, 1965). Such findings have suggested that animals learn not only which stimulus is correct but to identify the relation between the S+ and the S− (e.g., a difference in brightness), and attention to the brightness dimension acquired during overtraining may facilitate the reversal relative to a shift to a different dimension (see Mackintosh & Little, 1969).

Probability learning. Another interesting choice phenomenon occurs in a discrete-trial simple discrimination when there is some probability of reinforcement associated with both alternatives but reinforcement following the choice of one is more probable (e.g., 75%) than following the choice of the other (25%). If the trials are independent, then the stimulus associated with 75% reinforcement should be chosen on all trials and that is what animals often do (Graf, Bullock, & Bitterman, 1964); however, humans show a pattern of choices that closely match the probability of reinforcement associated with each of the alternatives (Koehler & James, 2009). That is, if the probability of reinforcement associated with the two alternatives is 75% and 25%, humans often choose the first alternative about 75% of the time and the second alternative about 25% of the time. Thus, whereas the animals are correct on about 75% of the trials, the humans are correct on about only 62.5% of the trials (75% x 75% plus 25% x 25%). This suboptimal choice by humans may be attributed to a bias to assume that there is a pattern of responses that will do better than 75% correct (see Gaissmaier & Schooler, 2008).

A related, although somewhat more complex, probability learning phenomenon in which pigeons appear to perform better than humans is known as the *Monty Hall dilemma*. With this problem, subjects are initially given a choice among three alternatives, one of which has been randomly chosen to be correct, but before the results of the choice are revealed, one of the unchosen alternatives is revealed to be incorrect and is removed. The subject is then permitted to choose between its original choice or switch to the remaining alternative. Because the revealed alternative was explicitly removed because it was incorrect, the probability that the original choice is correct is .33 whereas the probability that the remaining alternative is correct is .67 (see Figure 15.1). With only two remaining alternatives, humans generally assume that the probability of being correct for staying with their original choice or switching to the remaining alternative is the same and so they typically stay with their original choice. However, if humans are given several hundreds of trials to learn about the actual probabilities of staying or switching, they gradually become more likely to switch, but rather than learning to switch all of the time, as with the probability learning procedure, they usually learn to match the probability of reinforcement associated with staying versus switching. That is, they stay about 33% or the time and switch about 67% of the time (Herbranson & Schroeder, 2010). With sufficient experience, however, pigeons learn to switch almost all of the time (Herbranson & Schroeder, 2010; Stagner, Rayburn-Reeves, & Zentall, 2013). Once again, humans tend to match probabilities, whereas pigeons tend to choose close to optimally.

Relational learning. Historically, learning theorists have debated whether acquisition of a discrimination involves learning about the absolute properties of the stimulus (e.g., S+ is a gray stimulus of a

	Option1	Option 2	Option 3	Stay	Switch
Outcome 1	Win	Lose	~~Lose~~	Win	Lose
Outcome 2	Lose	Win	~~Lose~~	Lose	Win
Outcome 3	Lose	~~Lose~~	Win	Lose	Win

FIGURE 15.1. The logic of the Monty Hall dilemma. Assume there are three options and that the subject chooses Option 1. Before revealing the outcome, the experimenter removes one of the remaining (losing) options and asks if the subject would like to stay with his/her original choice or switch. If Option 1 is the winner, the subject wins by staying and loses by switching. If Option 2 is the winner, the subject loses by staying and wins by switching. If Option 3 is the winner, the subject loses by staying and wins by switching. Thus, in two out of the three cases switching wins.

particular brightness; Spence, 1937) or learning the relation between the S+ and the S− (e.g., the S+ is the darker of the two stimuli; Köhler, 1929). After training chickens on a simultaneous discrimination to peck at a gray card (S+) and to refrain from pecking at a darker gray card (S−), Köhler (1929) presented the chickens with a choice between the light gray card (former S+) and a card that was still lighter (a novel stimulus). He found that the chickens tended to peck at the novel stimulus and reasoned that the chickens had learned to respond to the lighter of the two gray cards. Köhler concluded that the fact that animals showed *transposition* suggested that discrimination learning was relational.

Spence (1937) argued, however, that an absolute theory of learning together with stimulus generalization could account for transposition effects (see Figure 15.2). Transposition, he said, results from the algebraic summation of the positive generalization gradient around the S+ and the negative generalization gradient around the S–. Because the negative gradient subtracts more from the positive gradient at the value of the S+ than it does at the novel stimulus the peak value of the net gradient is shifted to the left, away from the S+ in the direction away from the S–.

The absolute theory of discrimination learning is supported by the finding that if two test stimuli have values that are further removed from the training stimuli, transposition is no longer found (Ehrenfreund, 1952; Kendler, 1950). However, further research suggested that both theories may be correct depending on the conditions tested. A critical test of relational theory involves the intermediate stimulus problem. According to Spence (1942), if the discrimination involves three stimulus values with the middle value S+ and the outer values S−, according to the absolute theory of discrimination learning, because the generalization gradients should be symmetrical, transposition should not occur; and that is what he found. However, Gonzalez, Gentry, and Bitterman (1954) found that animals will transpose if the size difference between the stimuli is reduced. Thus, it appears that when the stimuli are highly discriminable animals may learn about their absolute properties, however, when comparison between stimuli is needed to acquire the discrimination, their relational properties are likely to be important (Riley, 1968).

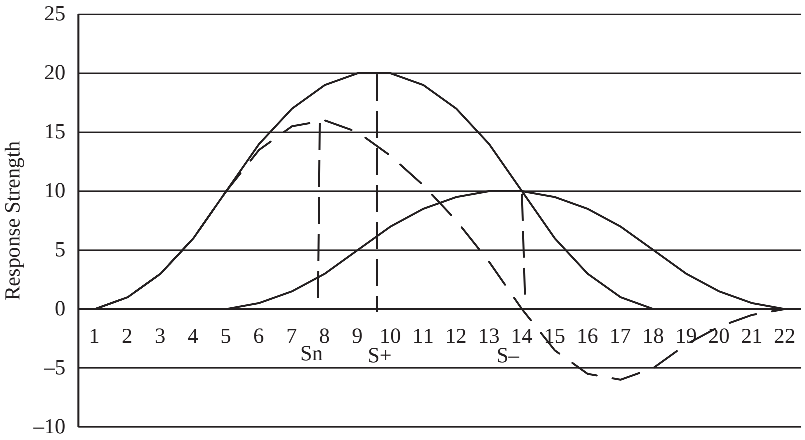

FIGURE 15.2. Spence's (1937) account of transposition. As the result of training on a simple discrimination involving a stimulus associated with reinforcement (S+) and one associated with the absence of reinforcement (S−), an excitatory gradient develops around the S+ value and an inhibitory gradient develops around the S− value. The difference between the two gradients (the dashed line) indicates the response strength at all values along the stimulus dimension. From the figure it can be seen that the response strength to a novel stimulus (Sn), a value removed from the S+ in the direction away from the S−, is stronger than to the S+ itself.

Conditional Discriminations

In a conditional discrimination the correct response to one of two comparison stimuli depends on the recent presence of a third stimulus (the conditional stimulus). Although the conditional stimulus and the correct comparison stimulus may be the same (identity matching; if the conditional stimulus in the center is a red light, the correct response is to the red light on the side; if the conditional stimulus is a green light in the center, the correct response is to the green light on the side) the relation between them may be quite arbitrary (symbolic matching; if the conditional stimulus is a circle in the center, the correct response is to the red light on the side; if the conditional stimulus is a plus in the center, the correct response is to the green light on the side). Although much of the research on conditional discrimination learning has been conducted with pigeons, it also has been found in rats (Holland, 1983) and monkeys (D'Amato, 1973; Worsham, 1975; see also Chapter 10, this volume).

Identity concept learning. Identity matching training can be used to ask if the identity relation between the sample and correct comparison stimulus is meaningful to pigeons (see Chapter 17, this volume). For example, Zentall and Hogan (1976) trained one group of pigeons on identity matching with shapes and another group on identity mismatching with shapes (with mismatching the rule is to choose the shape that is different from the sample). Then, half of each group was transferred to identity matching with colors and the other half was transferred to identity mismatching with colors. Zentall and Hogan found that pigeons that were transferred from matching to matching and mismatching to mismatching acquired the new task significantly faster than the pigeons that were transferred from matching to mismatching or from mismatching to matching. That is, when the second task was conceptually consistent with the second, learning was facilitated relative to when the second task was inconsistent with the first. Thus, the pigeons appeared to benefit from the conceptual relation (identity or different) between the sample and the correct comparison stimulus when it could be used in the second task (see also Cook, Katz, & Cavoto, 1997; Wright, Cook, Rivera, Sands, & Delius, 1988; Young & Wasserman, 1997).

Differential outcomes. Matching to sample can also be used to ask if animals can anticipate the nature of the expected outcome and use that anticipation as the basis for choice of the comparison stimulus. For example, if in a red/green matching task correct responses to the red comparison are followed by one outcome (e.g., food) and correct responses to the green comparison are followed by a different outcome (e.g., water), there is evidence that task acquisition is faster (Peterson, Wheeler, & Armstrong, 1978) and delayed matching accuracy is improved (Peterson, Wheeler, & Trapold, 1980; see also Chapter 10, this volume). Furthermore, when animals were trained on two identity matching tasks with differential outcomes that were the same between tasks (e.g., two different kinds of grain), positive transfer was found when the samples from one task were exchanged for the samples from the other task (Edwards, Jagielo, Zentall, & Hogan, 1982). Thus, pigeons appeared to be able to use the anticipated outcome elicited by the sample as the sole basis for correct comparison choice.

Conclusion. Matching to sample is a useful task for assessing complex learning in animals. Transfer tests can tell us the degree to which the similarity between the sample and the correct comparison stimulus is meaningful. Furthermore, they can demonstrate that animals can anticipate outcomes and use their representation as the basis for comparison choice.

IRRATIONAL CHOICE

Although much of the research in animal decision making has examined the extent to which human cognitive abilities can be found in other animals (see Zentall & Wasserman, 2012), recently there has been an emerging interest in the degree to which animals engage in a class of human behaviors that are distinguished by the fact that they result in biased behavior (when the alternatives are associated with equal probabilities of reinforcement) and even suboptimal behavior (when the alternatives are associated with unequal probabilities; see Chapter 16, this volume); among these are justification of effort (on the basis of cognitive dissonance), sunk cost, commercial gambling, the less-is-more effect, and base rate neglect. The importance of this research with animals is that if analog processes can be found in other animals, it suggests that those behaviors thought to be unique to humans very likely do not result from culture or language but can be attributed to more basic behavioral processes.

Justification of Effort

Justification of effort is a phenomenon in which humans tend to value outcomes in proportion to the effort required to obtain them. It is considered a subcategory of an attempt to reduce cognitive dissonance, the unpleasant feeling that comes about when there is a discrepancy between one's beliefs and one's behavior (Festinger & Carlsmith, 1959). For example, groups that have difficult initiations may be valued more by aspiring members than those that have easy initiations (Aronson & Mills, 1959). This differential value occurs presumably because one needs to justify subjecting oneself to the difficult initiation. However, in practice, it is often the case that the value of an outcome is proportional to the difficulty of the task, so if no other information is available, task difficulty may serve as a useful heuristic for the value of the outcome. Thus, past experience may encourage humans to use this rule of thumb. Alternatively, the effort that goes into a task may actually change the subjective value of the outcome and it may do so by way of a mechanism that is simpler than cognitive dissonance. To explore this possibility, one can ask if other animals would also show a justification of effort effect (see Chapter 16, this volume).

To study justification of effort in animals Clement, Feltus, Kaiser, and Zentall (2000) presented pigeons with a task (see Figure 15.3) in which, on some trials, a single peck to a white light presented them with a red and a yellow light and pecking the red light provided them with a reward (2 s access to mixed grain). On other trials, 20 pecks were required to the white light which presented them with a green and a blue light and pecking the green light provided them with the same reward (see also Friedrich & Zentall, 2004; Kacelnik & Marsh, 2002). After considerable training, when the pigeons were given a choice between the two stimuli associated with reinforcement (i.e., red and green lights) they showed a significant preference for green light (the stimulus that required 20 pecks to obtain).

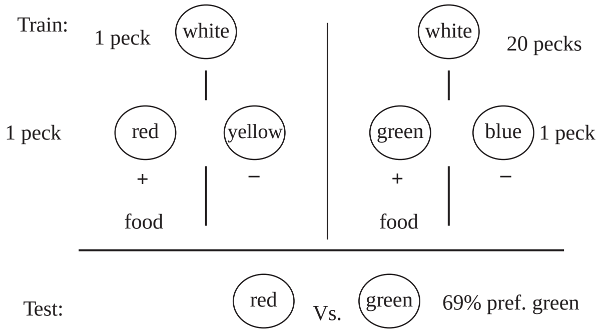

FIGURE 15.3. Design of the justification of effort experiment (Clement, Feltus, Kaiser, & Zentall, 2000). On some trials pigeons were required to peck once to receive a simple simultaneous discrimination (red+/yellow−). On other trials they were required to peck 20 times to receive a different simple simultaneous discrimination (green+/blue−). On probe trials, when the pigeons were given a choice between the two S+ stimuli (red and green) they showed a preference for the green.

Clement et al.'s (2000) explanation of this justification of effort effect does not require the reduction in dissonance caused by the discrepancy between behavior (making 20 pecks) and beliefs (one should not have to work so much harder for the same reward; Festinger & Carlsmith, 1959). Instead, they proposed that the effect could be explained by the contrast between the state of the organism immediately prior to the appearance of reward and the reward itself, or in the case of the experiment described, the appearance of the signal (color) for reinforcement (see Figure 15.4). As this contrast effect is somewhat different from other well-known contrast effects (incentive contrast, behavioral contrast, and anticipatory contrast; see Chapter 13, this volume) it is referred to as *within-trial contrast*.

According to this model, the 20-peck requirement results in a decrease in the hedonic state of the organism (analogous to fatigue or frustration), and then reinforcement (or the signal for reinforcement) results in a greater improvement in hedonic state than the appearance of the signal for reinforcement following a single peck.

The interesting characteristic of this model is the prediction that any relatively aversive event that

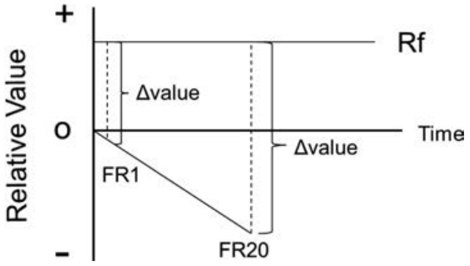

FIGURE 15.4. **Within-trial contrast model of the justification of effort effect.**

occurs prior to the appearance of the discriminative stimuli should result in a somewhat negative hedonic state and the appearance of the discriminative stimuli should result in greater contrast than would occur on trials on which the prior event was less aversive. Consistent with this prediction, researchers have also found that pigeons prefer a stimulus associated with food if it was preceded by a delay rather than no delay (DiGian, Friedrich, & Zentall, 2004) or if the stimulus was preceded by the absence of food rather than food (Friedrich, Clement, & Zentall, 2005). Hunger can also be thought of as a relatively aversive event. To test the prediction that pigeons would prefer stimuli associated with reinforcement more if they were preceded by food restriction, Vasconcelos and Urcuioli (2008) trained pigeons to peck one colored light on days that they were tested following moderate food restriction and to peck a different colored light on days that they were tested following less food restriction (by prefeeding them). When they were later given a choice between the two colored lights, the pigeons strongly preferred the color encountered when they were not prefed, and they did so independently of their level of food deprivation at the time of test (see also Marsh, Schuck-Paim, & Kacelnik, 2004; Pompilio & Kacelnik, 2005; Pompilio, Kacelnik, & Behmer, 2006; see also Chapter 14, this volume). Thus, the within-trial contrast effect appears to have considerable generality and it provides a more parsimonious account of the justification of effort effect found with humans.

The Sunk Cost Effect

Another example of suboptimal choice by humans is the *sunk cost effect* (or Concorde fallacy). After embarking on a project, if there are indications that one is very unlikely to be successful, humans often continue to expend resources in a losing cause. For example, in the case of a business that is failing, humans often continue to invest time and money in the business because, they argue, if they quit, the investment they have made in it would be lost. Prospect theory (Kahneman & Tversky, 1979) suggests that the sunk cost effect results from loss aversion, the fact that people are typically willing take greater risks to avoid a loss than to obtain a comparable gain.

Although it has been argued that the sunk cost effect is limited to humans (Arkes, & Ayton, 1999), several investigators have found evidence for it in birds. For example, Navarro and Fantino (2005) trained pigeons to peck a response key for food. On a random half of the trials, 10 pecks were required for reinforcement, on 25% of the trials 40 pecks were required, on 12.5% of the trials 80 pecks were required, and on the remaining 12.5% of the trials 160 pecks were required. However, at any time, the pigeons could peck a second response key which would advance the program to the next trial. Given this procedure, the optimal strategy would be to make 10 pecks and if no reinforcement was forthcoming, to advance the program to the next trial. Staying with the current trial would result in a 50% chance of having to make 30 more pecks for reinforcement, whereas advancing to the next trial would result in a 50% chance of having to make only 10 pecks for reinforcement (see also Macaskill & Hackenberg, 2012; Magalhães & White, 2014; Pattison, Zentall, & Watanabe, 2012). In spite of the benefit of advancing the trial once 10 pecks had been made, the pigeons generally failed to do so and persisted in responding to the original key. There is also evidence that it can be found in starlings (Kacelnik & Marsh, 2002). This line of research suggests that the sunk cost effect can be found in animals other than humans and although it is not clear if evidence for it can be found in nonhuman mammals the evidence suggests that the mechanism responsible for the effect is not likely to be a culturally acquired “do not waste” rule as has been proposed to account for the effect in humans (Arkes & Ayton, 1999).

The Less-Is-More Effect

The *less-is-more effect* (Hsee, 1998) can be demonstrated when humans are asked to estimate the value of two alternatives, one of which is objectively of greater value than the other but also includes items of lesser value. For example, at a flea market, subjects were asked to judge the value of a set of 40 dishes consisting of 31 intact dishes together with 9 broken dishes or to judge the value of 24 intact dishes (Hsee, 1998). Although objectively the 24 intact dishes should be given less value than the 31 intact dishes, on average they were actually given over 40% more value. Apparently, when some of the items in a set have a value that is lower than the others, the lower-valued items have a tendency to devalue the higher-valued items (see also Chernev, 2011; List, 2002).

Interestingly, animals also appear to experience this kind of suboptimal judgment. For example, Silberberg, Widholm, Bresler, Fujito, and Anderson (1998) found that monkeys (and a chimpanzee) who showed a preference for bananas over apples were indifferent when offered a choice between a banana and a banana plus an apple. Although Silberberg et al. proposed that humans would likely give greater value to the option that provided the greater amount of resource, the previous example from research with humans (e.g., Hsee, 1998) suggests that humans can fall prey to similar violations of economic principles.

One might hypothesize that in the Silberberg et al. (1998) study the value of the added apple may not have been detected by the primates, however, more recently, Kralik, Xu, Knight, Khan, and Levine (2012) repeated this experiment with a preferred grape and a less preferred cucumber slice and actually found a significant preference for the grape alone over the grape plus the cucumber slice (see also Beran, Evans, & Ratliff, 2009).

Similar effects have been found in dogs (Pattison & Zentall, 2014) and in pigeons (Zentall, Laude, Case, & Daniels, 2014), however, Zentall et al. (2014) reported that the less-is-more effect with pigeons occurred only when the pigeons were only modestly hungry (4 hr without food) rather than the more typical 24 hr. Thus, the less-is-more effect may be found only when the level of motivation is moderately low (as it was in the experiments with monkeys, dogs, and presumably humans). Interestingly, Beran et al. (2009) found a less-is-more effect when the time between trials was relatively short (20 s) but not when it was somewhat longer (3 min), an effect that might also be attributed to differences in motivation.

The less-is-more effect can be described as an example of inappropriate reward averaging, rather than the more appropriate reward summation. It may be that the effect results from the contrast between the values of the two kinds of reward. By itself, the reward of lower value may be contrasted with the absence of reward and thus has some value. When placed together with the reward of greater value, however, the negative contrast may actually cause the two food items to have less value than the more valued one alone. Although this contrast account may be appealing, it does not explain why there is no compensatory positive contrast that accrues to the more preferred food item resulting from the presence of the less preferred item.

Suboptimal Choice in a Gambling-Like Task

Natural selection should favor decision mechanisms that over time maximize the net rate of reinforcement while minimizing energy and time invested (Schoener, 1971). Similarly, expected utility theory, originally proposed by Von Neumann and Morgenstern (1944), suggests that rational, risk-neutral organisms should be prefer options that have the greater expected outcome. Often, however, these predictions are not supported. For example, small immediate reinforcements are preferred over larger more optimal (in amount per unit time) delayed reinforcements, a phenomenon known as delay discounting (Odum, 2011). Furthermore, if two options have identical expected outcomes, but the delay to reinforcement is variable it is preferred over the same amount of reinforcement at a fixed delay. In contrast, if time is held constant, a schedule involving a fixed amount of food is preferred over schedule involving a variable amount food (Kacelnik & Bateson, 1996).

When monkeys are trained on an exchange task in which one experimenter always gives them a fixed amount of food in exchange for any amount of food some of them learn to offer only the minimum amount of food. However, when a different experimenter always doubles the amount of food offered, the monkeys generally fail to learn to offer the maximum amount of food (Steelandt, Dufour, Broihanne, & Thierry, 2011). Thus, under these conditions monkeys do not appear to be sensitive to the differential contingencies of reinforcement. However, exchange tasks involve not only a delay of reinforcement but also a tendency not to want to give up what one already has (Kahneman & Tversky, 1973; Thaler, 1980) sometimes called *the endowment effect*. Furthermore, there is the perceived uncertainty of what will be returned (risk aversion; Simonsohn, 2009).

When humans experience several sequential events they sometimes develop biases that are inconsistent with the actual events experienced. One of these, the gambler's fallacy, comes from the knowledge that a randomly determined, equally likely, two-alternative outcome should produce the same number of the two alternatives (e.g., a coin toss). If people experience a number of the same outcome (heads), they often believe the other outcome (tails) will be more likely to occur next (Falk & Konold, 1997). This bias results from the mistaken belief that the events are not independent and must compensate by increasing the probability of the other outcome. A similar phenomenon in animals is not known.

Paradoxically, humans sometimes show the opposite bias known as the *hot-hand effect* (Tversky & Kahneman, 1971). When humans feel that they have some control over their performance (e.g., shooting a basketball) they often attribute a string of successes to a hot hand. In fact, however, given a series of successes, the probability of the next success is no better than given a series of failures (Gilovich, Vallone, & Tversky, 1985). A similar effect was recently reported with monkeys (Blanchard, Wilke, & Hayden, 2014), however, with their procedure, the probability of a repeated correct choice for making the same response was manipulated. Evidence for a hot-hand effect was the finding that the monkeys repeated the previously correct response at a level greater than would have been expected by chance (a win-stay bias). An even stronger win-stay bias has been found in pigeons using an analog of a radial maze procedure (Zentall, Steirn, & Jackson-Smith, 1990). Pigeons were trained to peck each of five colored keys for food but returning to the same key was considered an error and was not reinforced. Although the pigeons were able to acquire this task, initially they made twice the number of errors one would expect by chance had they been choosing randomly (with replacement). That is, they showed a significant tendency to return to the key they had just pecked and received reinforcement. Rats, on the other hand, have a natural tendency to shift to a different response, a phenomenon sometimes referred to as spontaneous alternation (Tolman, 1925). The way that this phenomenon has been studied in animal is likely to reflect a bias resulting from the natural ecology of the species.

Thus, several of the biases shown by humans appear to be inconsistent with the predictions of expected utility theory and some of these can be found in animals, as well. But even more inconsistent with expected utility theory is what occurs when humans engage in commercial gambling (e.g., lotteries, slot machines, roulette), games in which winning is entirely based on probabilistic outcomes (i.e., skill plays no role). When humans engage in commercial gambling, on average, the amount likely to be won is less than the amount invested. That is, in a mathematical sense, the expected outcome is negative.

Several popular explanations have been given for what would generally be considered suboptimal human behavior. One view is that people often are unaware of the odds of winning and if they are, they may have a difficult time interpreting the meaning of those odds (Gilbert, 2011). This difficulty can be derived from the hyperbolic function associated with probability discounting (Rachlin, Raineri, & Cross, 1991). Thus, as the odds against winning become high, the difference in the relative value of 1:100, 1:1000, and 1:1,000,000 become quite small, yet the odds of the payoffs are quite different. Of course, one could consider this poor discriminability the result of inadequate experience but there is no evidence that added experience lessens the probability of gambling behavior (consider the problem gambler who continues to gamble in the face of poor odds).

A second account of human gambling has to do with the fact that in most public gambling, when someone wins, it is more salient than when someone loses. Bells ring and lights flash at casinos when someone wins big, and big winners of lotteries are often mentioned on the news, whereas losses are rarely mentioned. This is sometimes referred to as an example of the availability heuristic (Tversky & Kahneman, 1974).

A third possibility is that humans are social animals and there is often additional social reinforcement that accompanies winning (e.g., at casinos). Finally, people who engage in gambling behavior often describe the activity as enjoyable, independent of wins and losses. (Narayanan & Manchanda, 2012).

Each explanation of human gambling described implies that other animals should not choose suboptimally under similar gambling-like conditions; however, research on the brain activity of problem gamblers suggests that basic reward processes involving dopamine are involved (Paglieri et al., 2014). Consistent with the hypothesis that basic brain structures are involved is research with animals, which suggests that they too make suboptimal choices under conditions similar to human gambling. For example, Stagner and Zentall (2010) trained pigeons on a task analogous to human gambling. In this experiment, pigeons were offered a choice between a gambling-like alternative in which the pigeons received a red stimulus on 20% of the trials that signaled 100% reinforcement (the winning outcome) or they received a green stimulus on 80% of the trials that signaled 0% reinforcement (the losing outcome). Choice of the uninformative alternative always resulted in a stimulus (blue or yellow) that signaled a 50% chance of reinforcement (see Figure 15.5). Thus, the pigeons could choose between reinforcement an average of 20% of the time (the suboptimal alternative) or reinforcement an average of 50% of the time (the optimal alternative). All of the pigeons were given forced trials to ensure familiarity with the conditions of reinforcement associated with the two alternatives and the different colors that followed. Under these conditions, the pigeons chose the informative alternative almost all of the time (see also Gipson, Alessandri, Miller, & Zentall, 2009).

Although the results of Stagner and Zentall (2010) clearly demonstrated suboptimal choice by

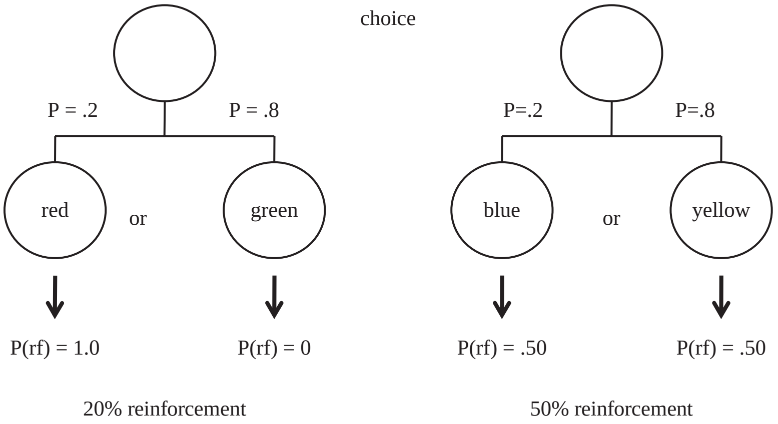

FIGURE 15.5. Design of suboptimal choice (gambling) experiment (Stagner & Zentall, 2010). Pigeons chose between one alternative (left) that produced a color on 20% of the trials that predicted a 100% chance of reinforcement or that produced a different color on 80% of the trials that predicted a 0% chance reinforcement and the other alternative (right) that produced one of two colors, each of which predicted a 50% chance of reinforcement. Pigeons showed a strong preference for the alternative on the left.

pigeons, when humans gamble, the alternatives generally involve different magnitudes of reinforcement (typically money) rather than different probabilities of reinforcement. Thus, one may purchase a lottery ticket for $1 in hope of winning a large amount of money. It is possible that the effect Stagner and Zentall observed with the manipulation of probability of reinforcement occurred because the pigeons were avoiding the alternative that resulted in stimuli associated with an uncertain outcome (.50 probability of reinforcement). If the effect that they found with pigeons is a good analog of human gambling behavior, it should be possible to find a similar effect by manipulating the magnitude of reinforcement, rather than the probability of reinforcement, and removing the uncertainty of the outcome associated with the nongambling alternative.

To study pigeons under conditions more similar to human gambling, Zentall and Stagner (2011) gave pigeons a choice between two alternatives: Choice of the gambling alternative produced a stimulus on 20% of the trials that always predicted the delivery of 10 pellets of food (the "jackpot") and produced a stimulus on the remaining 80% of the trials that always predicted the delivery of no pellets (no gain). Thus, this alternative was associated with an average of two pellets per trial (see design in Figure 15.6). Choice of the nongambling alternative always produced one of two stimuli each of which always predicted the delivery of three pellets. Thus, the second alternative was associated with a consistent three pellets per trial. Once again, if pigeons are sensitive to the amount of food they obtain over time, they should select the three-pellet option. However, contrary to this prediction, the pigeons showed a strong preference for the variable two-pellet alternative over the fixed three-pellet alternative. In a follow up experiment, Zentall and Stagner showed that the preference for the gambling alternative was not just for the variable outcome (10 pellets or no pellets vs. a certain three pellets) because when both colors associated with the suboptimal alternative predicted 10 pellets 20% of the time, all of the pigeons chose optimally (the three-pellet alternative).

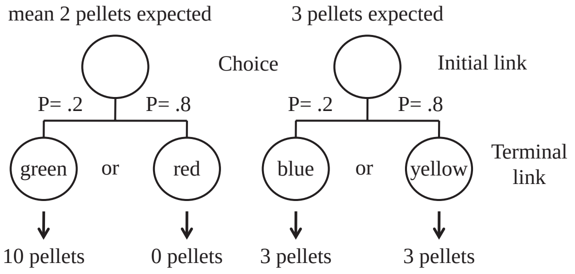

FIGURE 15.6. Design of suboptimal choice (gambling) experiment (Zentall & Stagner, 2011). Pigeons chose between one alternative (left) that produced a color on 20% of the trials that predicted 10 pellets of food or produced a different color on 80% of the trials that predicted 0 pellets, and the other alternative (right) that produced one of two colors, each of which predicted 3 pellets.

It is quite clear that during training the stimulus associated with the high probability of reinforcement or large magnitude of reinforcement became a strong conditioned reinforcer. The question is why the stimulus associated with the absence of reinforcement did not become a strong conditioned inhibitor, especially as it occurred four times as often as the conditioned reinforcer in the Stagner and Zentall (2010) and Zentall and Stagner (2011) experiments. This question was addressed in a further investigation using this gambling-like task in which the negative value of the conditioned inhibitor was assessed as a function of training (Laude, Stagner, & Zentall, 2014). The research suggested that as the amount of training with this task increased, the negative value of the stimulus associated with the absence of food (a loss) decreased as well. The reduction in inhibition produced by losses that appears to occur with training is consistent with human gambling research. Breen and Zuckerman (1999) reported that humans who gamble regularly have been found to attend more to their wins and less to their considerably more frequent losses than occasional gamblers. If the percentage of losses is relatively unimportant in the choice of the suboptimal alternative, it suggests the counterintuitive possibility that the percentage of wins is also relatively unimportant. That is, it may be that the frequency of stimuli associated with a win is less important than the value of the win when it occurs.

If it is the outcome of a win, and not its frequency, that is responsible for choice of the suboptimal choice, it follows that if the outcome of a win is held constant, one should be able to show that pigeons are not sensitive to the frequency of winning. To test this hypothesis, Stagner, Laude, and Zentall (2012) gave pigeons a choice between two gambling alternatives: If the pigeons chose one alternative, 20% of the time they were presented with a stimulus that was always associated with reinforcement and 80% of the time they were presented with a stimulus associated with the absence of reinforcement. If they chose the other alternative, 50% of the time they were presented with a stimulus associated with reinforcement and 50% of the time they were presented with a stimulus associated with the absence of reinforcement (see Figure 15.7). Thus, both alternatives were associated with gambling alternatives but one provided reinforcement 2.5 times as often as the other. As predicted, however, the pigeons were indifferent between the two alternatives. That is, they appeared to be insensitive to the frequency of winning. This finding may account for why humans play the lottery. That is, they are attracted by the outcome associated with winning but are relatively insensitive to the very low probability of winning (Paglieri et al., 2014).

One caveat that should be mentioned in comparing human gambling behavior to analog tasks with animals is the difference between risk of losing and failing to win. Humans typically risk money already earned, whereas animals typically do not lose anything but fail to win. It is not obvious how this difference might affect differences in behavior but it might be possible to institute a mild punishment for a loss rather than the absence of reinforcement. Zeeb, Robbins, and Winstanley (2009) attempted such a procedure by associating losses with an extended time out (reducing the opportunity to obtain additional food). However, Spetch, Mondloch, Belke, and Dunn (1994) found that increasing the duration of the stimulus associated with the absence of reinforcement, a manipulation that should have a punishing effect similar to that of an extended time out, had little effect on the preference for the suboptimal alternative. Thus, although, in principle, one can differentiate between risk of losing and failing to win, in practice the two may not be very different.

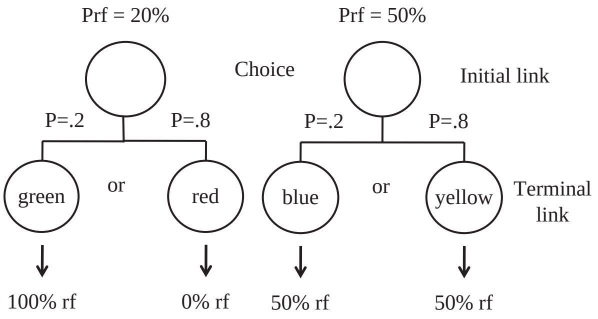

FIGURE 15.7. Design of experiment (Stagner et al., 2012) that compared the preference for the alternative that produced discriminative stimuli with a low probability of reinforcement (.20) with the alternative that produced discriminative stimuli with a high probability of reinforcement (.50).

It is interesting to speculate about why animals are relatively sensitive to the probability of reinforcement in a simple probability learning experiment (Graf et al., 1964) but choose suboptimally in the gambling analog experiments. A likely answer lies in the fact that the gambling analog experiments use conditioned reinforcers that signal the coming of reinforcement and conditioned inhibitors that signal the absence of reinforcement. Given that in the present procedure conditioned inhibitors tend to lose their negative value with training all that remains is the highly positive value of the conditioned reinforcer associated with choice of the suboptimal alternative.

Problem gambling by humans has been associated with impulsive choice (Alessi & Petry, 2003; Dixon, Marley, & Jacobs, 2003; MacKillop, Anderson, Castelda, Mattson, & Donovick, 2006; Petry & Casarella, 1999; Petry, 2001). That is, the immediate possibility of winning a large amount of money outweighs the long term, substantially more probable likelihood of losing. To test the hypothesis that pigeons' choice of the gambling alternative is also associated with impulsive choice, Laude, Beckmann, Daniels, and Zentall (2014) tested pigeons on a delay discounting task, using as a measure of impulsivity, the delay at which the pigeons were indifferent between a choice between a delayed four pellets of food and an immediate single pellet of food. They then trained the pigeons on the suboptimal choice task and found that there was a significant correlation between the pigeons' degree of suboptimal choice and their impulsivity.

Although there are several procedural differences between the pigeon task and human slot-machine gambling, recent research suggests that the pigeon task is a reasonable analog of human gambling. When humans who reported frequent gambling behavior were exposed to a task similar to the pigeon task, they chose the suboptimal alternative significantly more often than controls who reported that they never gambled (Molet et al., 2012).

Interestingly, consistent with the proposal that there is a relation between suboptimal choice and impulsivity, it has been found that adults with lower incomes discount delayed rewards more steeply than do adults with higher incomes (Green, Myerson, Lichtman, Rosen, & Fry, 1996). Furthermore, people from a lower socioeconomic status tend to gamble proportionally more than those from a higher socioeconomic status (Lyk-Jensen, 2010).

Parallel findings exist in the animal literature. For example, there is evidence that greater levels of food restriction are associated with greater rates of delay discounting by animals (Eisenberger, Masterson, & Lowman, 1982). That is, hungry rats (Bradshaw & Szabadi, 1992) and pigeons (Snyderman, 1983) tend to show a greater preference for immediate rewards which would be quite functional in a natural setting. In keeping with this prediction, we have found that pigeons are less attracted to the gambling-like alternative when they are less food motivated and presumably less impulsive (Laude, Pattison, & Zentall, 2012).

Another variable that has been shown to affect the degree of suboptimal choice in animals is social enrichment (see Chapter 35, this volume). Pattison, Laude, and Zentall (2013) have found that pigeons given access to a large cage with conspecifics, compared with a typical, smaller individual cage that allows for limited social interaction, showed reduced choice of the suboptimal alternative. Thus, in this gambling-task, it may be that spending time in a socially enriched environment (a large cage with three other pigeons for approximately 4 hr daily) effectively reduced the attractiveness to the stronger conditioned reinforcer, consequently reducing choice of the suboptimal alternative. Whether environmental enrichment would have a similar effect on problem gamblers is not known, but if it did, it may have interesting implications for the treatment addictive gambling behavior.

Most of the animal research on gambling described here has involved pigeons, however, gambling-like research has also been conducted with other animals (see Heilbronner & Hayden, 2013; Paglieri et al., 2014; Zeeb et al., 2009). But as Heilbronner and Hayden (2013) have suggested, the variability in the designs of tasks used make it difficult to compare the results of these studies with human gambling behavior.

Base Rate Neglect

When judging the probability of an event (e.g., diagnosing a patient's disease) there are two types of information that may be available: generic information about the frequency of events of that type (e.g., information about the prevalence of the disease) and specific information about the case in question (e.g., information about the patient revealed by examination or test). The first type is called *base rate information*. People who have only generic information tend to use it to judge probabilities, which is the rational thing to do because that is all there is to go on. In contrast, when people have both types of information, they tend to make judgments of probability based primarily on the specific information (Tversky & Kahneman, 1985). This bias is known as *base rate neglect*.

An example of base rate neglect is the classic *taxi cab problem*. A taxi cab was involved in a hit and run accident at night. Two cab companies (green and blue) operate in the city. 85% of the cabs in the city are green and 15% are blue. A witness identified the cab as blue. The court tested the reliability of the witness under circumstances that existed on the night of the accident and concluded that the witness correctly identified each one of the two cab colors 80% of the time but failed to do so 20% of the time. Knowing that the witness identified the cab as blue, what is the probability that the cab involved in the accident was blue?

Most subjects who are asked this question give probabilities between 50% and 80%. The correct answer is 41% (see Table 15.1). Specifically, there is a 12% chance (15% times 80%) of the witness correctly identifying a blue cab. However, there is a

TABLE 15.1

The Phenomenon of Base Rate Neglect as Illustrated by the Taxi Cab Problem

Identification	**Frequency**	
	Green cabs	**Blue cabs**
Correct 80%	68%	12%
Incorrect 20%	17%	3%

Note. The probability of a correct identification =

$$\frac{12\%}{12\% + 17\%} = 41\%$$

17% chance (85% times 20%) of the witness incorrectly identifying a green cab as blue. Therefore, there is a 29% chance (12% plus 17%) that the witness will identify the cab as blue. This results in a 41% chance (12% divided by 29%) that the cab identified as blue is actually blue. That is, the chance that the witness is correct in identifying the cab as blue is less than 50–50.

Kahneman and Tversky (1973) explain this finding in terms of a heuristic (see Chapter 14, this volume) called *representativeness*. They argue that many judgments relating to likelihood, or to cause and effect, are based on how representative one thing is of another (or of a category). Kahneman (2000) considered base rate neglect to be a specific form of extension neglect (i.e., difference from a prototype) and Nisbett and Borgida (1975) argued that people underuse consensus information (the base rate) about how others behaved in similar situations and instead prefer simpler attributions.

To what extent is this heuristic unique to humans? To try to answer this question, Zentall and Clement (2002) trained pigeons on two matching to sample tasks (see Figure 15.8). For one task, pigeons matched red and green samples to red and green comparison stimuli. For the second task, pigeons matched red and white samples to vertical and horizontal lines. Thus, red was the sample on 50% of the trials and green and white were each the sample on 25% of the trials. Following acquisition, to introduce uncertainty into the task, Zentall and Clement inserted a delay between the sample and the comparison stimuli and we found that pigeons tended to neglect the 50–50 base rates associated with each pair of comparison stimuli and showed a strong bias to choose the comparison stimulus associated with the red sample (Figure 15.9). In this experiment, when the pigeons remembered the sample that was presented, they responded correctly but when it appeared that they were uncertain about the sample, the pigeons were influenced by the frequency of the samples. They did this in spite of the fact that half of the time the more frequently presented sample had appeared, it was not relevant to the comparison stimuli being presented (see also DiGian & Zentall, 2007; Zentall, Singer, & Miller, 2008).

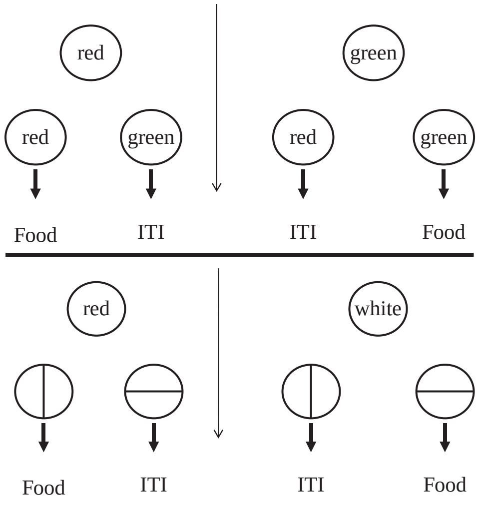

FIGURE 15.8. Design of the base rate neglect experiment (Zentall & Clement, 2002). Pigeons were trained on two matching tasks. Red and green samples mapped on to red and green comparison stimuli (in equal proportions) and red and white samples mapped on to vertical and horizontal comparison stimuli (in equal proportions). The pigeons were then tested with delays of variable duration between the offset of the sample and the onset of the comparison stimuli.

The results of these experiments with pigeons suggest that they too suffer from base rate neglect. Although it might be argued that humans show base rate neglect because they are told about the probabilities but do not have actual experience with them, when a base rate problem was given to doctors who should have actual experience with the probabilities

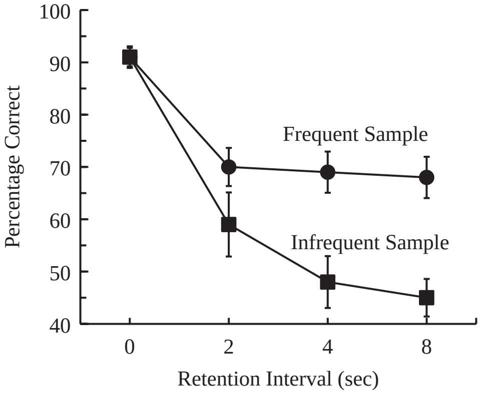

FIGURE 15.9. Results of the base rate neglect experiment (Zentall & Clement, 2002). After training on two matching tasks—red and green samples mapped on to red and green comparison stimuli (equal proportions of each) and red and white samples mapped on to vertical and horizontal comparison stimuli (equal proportions of each)—the pigeons were tested with delays of variable duration between the sample and the comparison stimuli. With increasing delay, the pigeons showed a bias to choose the comparison that in training had been preceded by the red sample, in spite of the fact that in the presence of each pair of comparison stimuli, the probability that the sample was red was the same as the probability that the sample was green, in one case, or white, in the other (i.e., not red).

they too showed base rate neglect (Eddy, 1982). Furthermore, the fact that pigeons show base rate neglect even after considerable experience with the contingencies of reinforcement suggest that the phenomenon of base rate neglect must reflect a basic behavioral process. That is, when it occurs in humans, it does not depend on a failure to understand the verbally provided probabilities.

The Nature of the Basic Behavioral Processes

The research presented in the section on irrational behavior suggests that animals show many of the same biases and suboptimal choices shown by humans. That a species as different from humans as the pigeon shows such suboptimal choices, suggests that these behaviors do not rely on cultural factors. But if these suboptimal choices are predisposed, it leads one to question in what ways these behaviors would not be suboptimal, were they to occur in nature. If this assumption is correct, one can speculate about the possible advantage of such behavior under natural conditions.

Justification of effort. In the case of level of food deprivation, food that is obtained after one has been without food for some time may have a greater effect on one's likelihood of survival and thus may have greater value. Similarly, if greater value is attributed to food that one has worked harder to obtain, it may encourage an organism to persist longer in looking further for food.

Sunk cost. Although task persistence in the face of a more efficient alternative would appear not to have adaptive value, in nature there is not only the relative probability of food in the current patch compared to the alternative patch but the fact that there is generally more information available about the current patch than about the alternative patch. Furthermore, there is often the added cost and uncertainty of the travel time to the alternative patch, not to mention the increased possibility of predation. All of those factors together may encourage the animal to stay longer than would be ideal. That this tendency to stay with a known task appears to persist even with a procedure in which, once the initial investment is made, the outcomes are no longer probabilistic (Pattison et al. 2012) is merely an indication that the predisposition to stay may be difficult to overcome.

The less-is-more effect. It may be that animals in nature do not often find themselves with encountered choices of this kind. More often, their choices are of the go/no-go kind in which comparisons between alternatives do not have to be made. When two-alternative choices do have to be made in nature, it is likely to be between two food patches that have discernable differences in the quality of the food items that they have. Thus, for example, a reasonable heuristic for the animals might be to approach the patch that has the higher quality of food, on average.

Gambling-like behavior. The behavioral basis of gambling behavior is of particular interest because of its pervasiveness in humans. It can be speculated that when humans choose to gamble several possible factors may be involved, including (a) the process itself is a pleasurable activity, (b) often humans do not experience it enough to learn that it is a suboptimal activity, and (c) the availability heuristic (winners get a lot of attention whereas losers do not). When it is demonstrated in animals, it suggests that something more basic may be involved. Research with pigeons suggests that the value of the gambling option is not the probability of reinforcement for gambling (which would take into account the probability of losing) versus not gambling, but the value of winning versus the value of not gambling. This was confirmed by showing that when the value of winning was held constant, the probability of winning played little role in pigeons' choice (Stagner et al., 2012). Interestingly, a similar mechanism has been proposed to account for gambling by humans (Barberis & Huang, 2008). But why is it that humans behave rationally under certain circumstances but irrationally under others?

One factor that distinguishes commercial gambling from more natural risk taking behavior is that in the gambling task, choice of the gambling alternative does not alter the probability of reinforcement. That is, each trial is an independent random event. Although the natural world is also probabilistic, it is not usually independent of previous events. For example, choice of a particular alternative may bring the animal into closer proximity of reinforcement thus, changing the probability of reinforcement. In humans, the disbelief in the independence of successive choices may result in the gambler's fallacy (Tversky & Kahneman, 1971). Knowing, for example, that in the long run equally probable events (such as a coin toss) will occur with equal frequency, humans will sometimes predict that if heads has come up on four successive tosses, the probability of a tail on the fifth toss will be greater than 50%.

Finally, for pigeons performing the suboptimal choice task, although the time between initial choice and reinforcement (when it occurred) was generally held constant, the immediacy of the strong conditioned reinforcer associated with 10 pellets or 100% reinforcement gave it greater value than the more frequent but smaller and largely uninformative conditioned reinforcer associated with the optimal alternative (no added information is provided following its choice).

Base rate neglect. Base rate neglect in humans may result from the complexity of the given information. When dealing with uncertainty, people rely on a limited number of simplifying heuristics rather than more formal and computationally extensive algorithmic processing. However, pigeons that have only direct experience with the probabilities associated with each of the outcomes show base rate neglect as well. This finding suggests that pigeons too place more emphasis on specific information (about the frequency of sample stimuli), rather than on generic information (the overall probability that each of the comparison stimuli is correct). It may be that this bias or heuristic to use specific information is more available and easier to use. Thus, it may have adaptive value to rely on specific information, especially in natural settings in which rapid decision making may be necessary.

CONCLUSION

The fact that it can be shown that many of the biases and suboptimal choices made by humans can also be found in other animals suggests that those choices are very likely not based on culture or language but are basic behavioral processes involving heuristics that allow for rapid responding in natural setting when delays might be detrimental, because of competition or predation. However, these heuristics appear to occur even under laboratory conditions where there is neither competition nor possible predation. But if these heuristics had adaptive value in nature, there may have been no need to have developed more optimal predispositions for use under the somewhat contrived laboratory conditions that we have established for animals or the complex cultural conditions in which we humans have found ourselves. Instead, if we value the ability to choose optimally, we must find a way to override those natural heuristics. Fortunately, humans have a remarkable capacity for learning, for modifying predisposed behavior, and when those approaches fail, for social intervention. For example, although we show unfortunate lapses in making optimal choices (e.g., in running up the charges on our credit cards), in other respects humans are capable of delaying gratification for long periods of time, as can be seen in our ability to plan for retirement, and when we have trouble doing so, social mechanisms may come into play (e.g., requiring that we make contributions to retirement funds such as social security).

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CHAPTER 16

DECISION MAKING UNDER UNCERTAINTY: PREFERENCES, BIASES, AND CHOICE

Alexandra G. Rosati

Imagine a choice between two potential jobs: a position that is stable but intellectually mundane, or one that is more exciting but offers only short contract with some chance of renewal. These kinds of decisions can be agonizing because they involve uncertainty. Although the first job option is a known quantity, the second job offers the possibility of being more fulfilling, but also the possibility of being let go in the near future. This uncertainty means that it is not possible to know the exact consequences of the decision in advance, making it difficult to judge the best course of action. Many important decisions involve this same sort of uncertainty—such as whether to invest in a new business, commit to a partner, or pursue a medical treatment. Yet uncertainty is not something only humans experience: It is pervasive in the natural world, and all animals must sometimes make decisions without complete information about the consequences of their actions. For example, foraging animals have to decide which patch of food to exploit, but will likely not know precisely how much food they will extract from different patches. Rather, this forager will have to decide where to go on the basis of some estimation of how much food different patches might provide, as well as the likelihood of that amount.

Uncertainty is a ubiquitous feature of animal and human lives. Consequently, illuminating how decision makers respond to uncertainty is a problem of interest across the social and biological sciences. Economists aim to predict patterns of choice in economic markets, where decisions often involve tradeoffs between the value earned and the risks incurred. Psychologists and neurobiologists aim to tease apart the mechanisms that humans and other species use to encode and evaluate uncertainty. Finally, biologists aim to understand the evolution of different behavioral strategies (often accounting for how psychological mechanisms may constrain possible behaviors), as uncertainty may influence the biological consequences that animals accrue from their decisions, including fitness benefits. This review will integrate theory across these fields to understand the psychological mechanisms that animals use to make decisions under uncertainty, as well as what biological function these mechanisms might have. I further argue that comparative research is a powerful tool for understanding the nature of economic decision making. Discovering that a particular decision making pattern is widely shared across humans and other species—or conversely, unique to humans alone—can provide important insights about the types of experiences that engender these psychological processes. For example, if many other animals also exhibit some human-like bias when faced with uncertainty, this would suggest that experience with economic markets or human culture is not necessary for this bias to emerge (see also Santos & Rosati, 2015).

This review is divided into three major sections. The first part examines different models of decision making under uncertainty from economics, psychology, and biology. This section will provide theoretical benchmarks for conceptualizing how

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and why decision makers account for uncertainty when they are making decisions. The second section will focus on empirical evidence concerning whether other species are sensitive to uncertainty, as well as what preferences they exhibit when making decisions. This section will focus on the psychological mechanisms that influence decision making: how animals detect variance in possible payoffs, learn about different potential courses of action, and ultimately evaluate options to settle on their preferred response. The final section will examine how these psychological mechanisms for thinking about uncertainty play out in the real world. This section will examine how an individual's state, the larger social context, or even differences in species-typical environment can influence the expression of risk preferences.

MODELS OF CHOICE UNDER UNCERTAINTY

Economics, psychology, and biology have all developed formal models of choice that reveal how decision makers can maximize their value (see Chapters 14 and 15, this volume). Such models can provide powerful tests of whether decision makers are acting in an optimal fashion—and can further help in revising our notions of optimality when actual behavior does not agree with the models. However, different fields often have quite different assumptions about what the optimal response to uncertainty is, as these disciplines diverge in terms of what value individuals are trying to maximize. Whereas economics and psychology often assume decision makers want to maximize some (internal or subjective) measure of "goodness" such as utility, biological models assume behaviors are designed to maximize long-term fitness benefits. These different expectations can lead to different predictions about decision-making strategies. Furthermore, whereas some models predict what an ideal decision maker should do (prescriptive models), other models rather aim to accurately describe what real-world decision makers actually do (descriptive models)—and different disciplines may have different focus in this sense as well. This section will therefore cover several diverse models of choice under uncertainty from across economics, psychology, and biology—which will guide later examinations of empirical evidence for patterns of animal decision making.

Classical Economics and Expected Utility

The challenge of deciding the best course of action when outcomes are uncertain was recognized even by early philosophers, predating modern economics as a field. Blaise Pascal (1670/1995) proposed his famous theological "wager," contrasting two possible courses of action: either living as if God exists, or living as if God does not exist. In Pascal's analysis—dated to the 1660s—acting as though God exists produces an infinitely high "payoff" if correct, but a small cost if incorrect. In contrast, acting as though God does not exist produces a small benefit if correct, but an infinitely high cost if incorrect. Pascal's treatment of this philosophical problem introduced several concepts that are now foundational to decision science. In particular, Pascal suggested that decisions involving uncertain outcomes should be based on the value of each outcome weighted by its likelihood. Whichever action results in the greatest expected value is thus the best course of action. In the case of this wager, the payoffs resulting from a belief in God are infinite—so even a very small possibility of being correct means that behaving as though God exists is the course of action with the highest expected value.

Pascal's wager highlights an important prediction of expected value theory: People should be willing to gamble on an infinitesimally small chance of winning an infinitely large amount reward. However, most people actually will not take this kind of extreme risk, suggesting that expected value approaches do not fully capture how people make decisions. Daniel Bernoulli (1738) formalized this violation as the St Petersburg paradox, arguing that the true currency of decisions under risk is not expected value. People do not decide only on the basis of probability of different outcomes alone, but rather weight the utility or goodness of those outcomes. The trick is that utility and value do not have a one-to-one relationship, because utility offers diminishing marginal returns. Consequently, a one-unit increase in a larger reward produces less utility to a decision maker than the same increase relative to a smaller initial reward. Bernoulli specifically conceptualized expected utility theory in terms of how the relative impact of some amount of money depends on the decision maker's wealth. That is, he suggested that winning some amount of money has less utility for a comparatively wealthy person than it does for a poorer person.

In the 20th century, Von Neumann and Morgenstern (1947) formalized this general approach with a set of four axioms describing the behavior of a rational decision maker. First, their hypothetical decision maker should have well-defined preferences (the *completeness axiom*): For any two options (e.g., apples and oranges), either one is preferred or they are equivalent. Second, these preferences should exhibit a consistent rank (the *transitivity axiom*): If apples are preferred to oranges, and oranges are preferred to bananas, then apples should be preferred to bananas. Third, these preferences exist on a common comparative scale (the *continuity axiom*): If apples are better than oranges, but oranges are better than bananas, then there should be probability where receiving an orange is thought to be equivalent to gambling on the likelihood of either winning the desired apple, or losing out and receiving only a banana. Finally, these preferences should not be impacted by irrelevant alternatives (the *independence axiom*): If someone prefers apples to oranges, apples should still out-rank oranges even if there is some broccoli lying around too. Von Neumann and Morgenstern showed that by following these principles, a decision maker would act to maximize his or her own personal utility function.

Behavioral Economics and Psychological Realism

The power of rational choice theory is that a few reasonable-sounding first principles can generate a wide-ranging set of predictions about how individuals should act. However, subsequent empirical research has revealed that humans (and other animals) often violate many of these predictions. Accumulating evidence of such anomalies led economists and psychologists to develop new theories that are more firmly grounded in the psychological processes supporting choice. These newer models aim to accurately capture real-world behavior, rather than reason about optimal behavior from first principles like rational choice theory. As there has been a subsequent explosion of models about decision making under uncertainty (Starmer, 2000), this section will address several broad developments in risky choice theory.

The first major attempt to synthesize several decision making anomalies came from prospect theory, developed by Daniel Kahneman and Amos Tversky. Prospect theory also assumes that decision makers act to maximize their utility, but proposes several major changes as to how utility is determined by real-life decision makers (Kahneman & Tversky, 1979; Tversky & Kahneman, 1981). First of all, people are not assumed to judge outcomes on the basis of their impact on total wealth (an assumption of classical theory). Rather, decision makers assess whether their choice results in a positive or negative change relative to a more local reference point. Second, this theory proposes that positive changes relative to the status quo (gains) are treated differently from negative changes (losses). In particular, people dislike a negative change much more than they like an equivalent positive change, a phenomenon called *loss aversion*. This means that the magnitude of how bad people feel about losing $10 from their pocket exceeds the positive feeling that results from finding $10 on the street. Third, people exhibit diminishing sensitivity to changes: The difference between winning $10 and winning $20 does not feel equivalent to the difference between $110 and $120, even though the absolute difference is the same. This results in a utility curve that is concave for gains, but convex for losses. More recent additions to prospect theory have further suggested that probabilities themselves might be weighted, not treated as equivalent to their actual magnitude as in previous work. In particular, people may overweigh the importance of outcomes that occur rarely, but underweigh the likelihood of outcomes that have a high probability (Kahneman & Tversky, 2000).

Overall, prospect theory successfully accounts for several major deviations between actual decision patterns and rational choice theory. One important example is the framing effect: People tend to be risk-averse for gains—trying to avoid variance in outcomes—but are actually risk-seeking for losses.

A classic study by Tversky and Kahneman (1981) illustrated this phenomenon by contrasting possible strategies to fight a disease outbreak. One strategy would certainly help a set number of people, whereas the other strategy was riskier: It might help everyone, or it might help no one. The twist was that people heard about these strategies either in terms of the number of people who would live, or the number of people who would die. The consequences of each strategy across situations were identical, except in whether the researchers described the outcome in terms of lives saved or lives lost. In fact, participants who made decisions about number of lives saved (the gain frame) were averse to taking risks. In contrast, participants who had to make decisions about the number of deaths (the loss frame) preferred the riskier option. That is, they gambled on the possibility of no deaths, rather than accept a certain number of deaths would definitely occur. Prospect theory accounts for this preference flip—called *the reflection effect*—because the utility curves for gains and losses have different shapes.

Broadly speaking, prospect theory and its descendants use expected utility theory as a general framework, but modify the utility computations involved to better align with real behavior (Barberis, 2013). More recent models of decision making from psychology have further deviated from expected utility theory by focusing other types of psychological substrates that are not obviously involved in such utility calculations. For example, people have mental states (e.g., knowledge) that can impact how they make decisions. Such knowledge states play an important role in how people response to distinct types of uncertainty: *risk*, where the likelihoods of potential outcomes are known; and *ambiguity*, where even the likelihood of different outcomes is not known in advance. Rational choice theory expects that people make decisions on the basis of expected value, regardless of their confidence in their knowledge (Savage, 1954). However, empirical research shows that decision makers' knowledge and confidence in their judgments can have a profound impact on preferences, such that people actually respond very differently to risk and ambiguity. The Ellsberg paradox is one illustration of this distinction. Imagine a decision maker faced with a choice between one urn known to contain 50% red balls and 50% blue balls, and another urn with an unknown distribution—there could be anywhere between 0% and 100% red balls. Which urn is more likely to produce a red ball? The expected value of these urns is actually identical, because the average chance of pulling a red ball out of the ambiguous urn (that could vary from 0% to 100% red balls) is also 50%, the same as the risky urn with the known distribution. However, people overwhelming prefer to bet on the risky option (Ellsberg, 1961). Although many situations conflate variation in known probability with ambiguity, studies that carefully tease them apart show that people strongly dislike choosing ambiguous options (Camerer & Weber, 1992). That is, people are biased against choosing the unknown.

Other models focus on other diverse aspects of psychological experience, such as emotional states. One prominent example is the risk-as-feelings model, developed by George Loewenstein and colleagues (Loewenstein, Weber, Hsee, & Welch, 2001). This theory proposes that people process risks at two psychological levels: by computing the costs and benefits provided by different options (as in expected utility approaches) and by evaluating their emotional responses to the available options. Such emotions may influence decision making via several complex pathways (Loewenstein & Lerner, 2003). For example, people may experience negative emotions after taking a risk and losing, including disappointment that they did not win, or regret that they did not choose differently (Coricelli, Dolan, & Sirigu, 2007). The mere anticipation of feeling such potent emotions can also shape decisions. For example, people may make choices that minimize the chance they will regret what they did—showing *regret aversion* even if their strategy reduces their total payoffs in the long run (Zeelenberg, 1999).

Finally, recent work in neuroeconomics aims to bridge economics and neurobiology by developing theories of how decision making is actually implemented in the brain (Loewenstein, Rick, & Cohen, 2008; Sanfey, Loewenstein, McClure, & Cohen, 2006). Research on decision making under uncertainty in particular has aimed to identify neural signals of value and probability, as well as to understand the interactions between neurobiological systems that influence choices (Platt & Huettel, 2008). In contrast to many theories from economics aiming to identify some unitary construct of value (e.g., utility), many neurobiological models of decision making suggest that more than one fundamentally different process can influence choices. Although there are several flavors of dual-process models, they often propose two distinct processes shaping choice: a more analytical system that is effortful and slow, as well as a more intuitive system that is automatic and fast (Kahneman, 2011). For example, the risk-as-feelings model discussed previously proposes that decisions about risk result from interactions between an analytical system that considers the rewards and probabilities in play, and an emotional system that reacts to this information (Loewenstein et al., 2001). These neuroeconomics models therefore try to decompose fairly complex decision-making behaviors into the underlying neural processes that represent or influence choice.

Behavioral Ecology and Biological Function

Theories from economics and psychology generally treat decision making as a process where individuals attempt to maximize their personal index of utility (see Chapter 15, this volume). Biological models also assume that individuals attempt to maximize some measure of value, but the "currency" in question is not utility, but rather biological fitness (Hammerstein & Hagen, 2005; Kacelnik, 2006; Krebs & Davies, 1978). Furthermore, biological models focus on a different type of prototypical decision-making situation: choices about food or caloric value that an animal obtains while foraging (see Chapter 14, this volume). Biological models therefore involve normative reasoning from first principles, much like classical economic theories. However, this approach has different assumptions about what decision makers aim to maximize.

The prevalent biological theory for decision making under uncertainty, called risk sensitivity theory, emphasizes that animals do not simply maximize mean foraging returns. Rather, animals also account for the potential variance in their payoffs—and the reason is because uncertainty in foraging returns can directly impact fitness above and beyond the mean returns. The key to understanding how variance in foraging returns can impact fitness is to consider an animal trying to acquire one additional unit of food. Although this additional amount of food clearly seems related to the decision maker's fitness, it does not have a one-to-one correspondence: The marginal gain from a given piece food depends on how much food the animal has already acquired. This idea therefore parallels approaches from economics and psychology arguing that the relationship between one additional unit of reward and one additional unit of subjective utility is not linear. However, risk sensitivity theory specifically proposes that the relationship between foraging returns and fitness depends on the animals' energetic state when they make their choice (Caraco, 1981; Caraco, Martindale, & Whittam, 1980; Stephens, 1981). Imagine one bird who is currently satiated, and one who is on the verge of starvation. The starving bird needs a greater payoff than the satiated animal to survive, because winning big is its only chance to meet its energetic needs. This type of analysis suggests that animals should shift their risk strategies across contexts: exhibiting risk-seeking behavior when energetic requirements exceed expected payoffs, but exhibiting more risk-averse behavior if the average expected payoffs will already meet these requirements.

Risk sensitivity theory therefore predicts that animals will generally be sensitive to variance in payoffs, but their particular preferences can flip across situations. This theory has been extremely influential, and the importance of variance is now a lynchpin of much work in behavioral ecology. However, the explanatory power of the specific predictions of this theory is currently unclear. Some early studies examining how animals respond to risk in different energetic states provided support for risk sensitivity theory. For example, when birds make decisions under conditions of relative food deprivation or when being maintained at cooler temperatures (i.e., birds needed more calories to meet their energetic requirements), they are more risk-prone then when making choices under better conditions (Caraco et al., 1980, 1990). However, a recent review pointed out that there have been few direct test of the specific predictions of risk sensitivity theory, and suggested that current evidence provides at best weak support (Kacelnik & El Mouden, 2013). Indeed, some research shows that animals may broadly account for risk, but nonetheless violate the specific predictions of risk sensitivity theory. In particular, energetic state may have different influences on risk preferences depending on the species in question. Although smaller animals may face a significant risk of starvation, larger-bodied animals do not face such a serious starvation threat and may respond differently to risk. In line with this idea, chimpanzees (*Pan troglodytes*) actually engage in riskier foraging behaviors resulting in more variable payoffs (such as hunting) when they are in a better state and therefore have the necessary energetic reserves to take risks (Gilby & Wrangham, 2007).

Regardless of support for the specific predictions of risk sensitivity theory, research examining the relationship between energetic state and risk preferences highlights another fundamental difference between economic and biological theory. Rational choice theory is premised on the idea that decision makers are internally consistent in their preferences, exhibiting the same preferences across contexts (Kacelnik, 2006). This is why situations where people act inconsistently across contexts, such as in response to framing, represent violations of rational choice theory. Biological models, in contrast, focus on how choices influence an animal's reproductive success, and natural selection does not necessarily prioritize consistency in preferences. Context may even provide important information about the fitness value of a behavioral strategy, so inconsistent preferences can maximize fitness in some situations (Fawcett et al., 2014; Houston, 1997). Therefore, context-sensitive decision making may be biologically optimal. The putative rationality of such context-dependent shifts in decision-making strategies therefore represent a major divergence between biological and economic theories of decision making under uncertainty.

PSYCHOLOGICAL MECHANISMS FOR UNCERTAINTY IN ANIMALS

Foundational theories from economics, psychology, and biology predict that decision makers will be sensitive to risk (although the reasons for this prediction are not necessarily the same). Research on humans decision making shows that humans are sensitive to risk, and generally exhibit a strong aversion to options with variable payoffs. Do other animals exhibit similar responses? This section will address the empirical evidence that animals are indeed sensitive to uncertainty, as well as explore the psychological processes that shape their responses. Some mechanisms for decision making under risk seem to be widely shared, including basic capacities to encode and detect differences in reward distributions. Yet many models of human decision making involve complex reasoning and emotional processes. Nonhuman studies can therefore address whether other species share these capacities, as well as help constrain interpretations of the psychological mechanisms that influence human choice (Santos & Rosati, 2015).

Methods for Probing Animal Decision Making

Human decision-making studies typically present linguistic descriptions of hypothetical one-shot choices, often concerning different payouts of money (Hertwig & Erev, 2009). For example, people might be asked, "Would you prefer a 50% chance of winning $20, or $10 for sure?" Animals, however, cannot answer such hypothetical questions (and are not particularly motivated to seek out money). Consequently, most animal decision making tasks measure behavioral responses to real choices, typically involving a series of iterated decisions about consumable rewards such as food or juice. Within this general methodological approach—iterated, experience-based decisions for real rewards—researchers have developed several paradigms to probe nonhumans' sensitivity to and preferences for uncertainty.

The most commonly used setup to probe animal decision making under risk involves decisions about quantitative uncertainty: distributions that provide different amounts of the same type of reward (much like human studies involving different monetary payouts). A typical experimental setup using this approach might contrast options that differ in the average payoff they provide, or the spread of possible outcomes that can occur. Importantly, in these paradigms, animals generally must initially learn that some cue (such as a color or location) signals the differences in reward distributions. For example, pigeons (*Columba livia*), starlings (*Sturnis vulgaris*), or rats (*Rattus norvegicus*) might learn that different rewards are associated with pecking different buttons or making nose pokes in different locations (see B. Marsh & Kacelnik, 2002; Paglieri et al., 2014; Zentall & Stagner, 2011). Similarly, rhesus macaques (*Macaca mulatta*) might learn that saccading their eyes to different visual targets will produce different volumes of juice rewards (McCoy & Platt, 2002). In other cases, primates such as chimpanzees, bonobos (*Pan paniscus*), or capuchins (*Cebus apella*) might learn that they can point at differently-colored containers, which reveal different reward distributions across trials (see De Petrillo, Ventricelli, Ponsi, & Addessi, 2015; Heilbronner, Stevens, Rosati, Hare, & Hauser, 2008). Finally, nectar- or pollen-feeding species such as rufous hummingbirds (*Selasphorus rufus*) or bumblebees (*Bombus* sp.) might learn that different artificial flowers vary in the volume or concentrations of nectar they contain (Hurly & Oseen, 1999; Real, 1991). Although these setups vary in terms of the cues that signal reward distributions, as well as the particular way that animals respond to make choices, they all share a commonality of presenting animals with decisions about options that vary in terms how much rewards they provide. Such studies of quantitative risk, therefore, provide a fairly equivalent metric to examine how difference species respond to payoff variation, and comprise the strongest comparative data of risk sensitivity in nonhumans.

However, by their nature these paradigms often require extensive training periods for animals to learn the predictive cues signaling reward distributions. Animals may have to complete hundreds or thousands of trials, including forced-choice or exposure trials (where only one option is available for the animal to choose, thereby ensuring they experience it) as well as trials that involve actual choices between different distributions. Even fairly simple tasks involving just one dyadic contrast between two options that provide the same average payoff but differ in variation across trials (e.g., a choice between a safe option that always provides four pieces of food and risky option that provides one or seven pieces with equal probability) may involve animals acquiring risk preferences over hundreds of trials (see Heilbronner et al., 2008, for such learning effects in apes). It is therefore important to note that differences in the training animals receive when initially learning payoff contingencies, as well as the number of trials and subsequent feedback that is experienced, can all shape how a given individual will respond to risk in the long run.

Given the long period of experience or learning that are typical of these risk tasks, some recent work has examined animals' more spontaneous reactions to uncertainty. The common premise of these sorts of paradigms is that animals can infer their chance of winning on a given trial (rather than learn some association between a given response and a given payoff distribution). Moreover, these setups also allow the rewards in play to vary on a trial-by-trial basis without training each new set of contingencies. One example of a risk paradigm using this approach tested how chimpanzees and bonobos make decisions when the risk involved variance in the type of food they received (Rosati & Hare, 2011, 2012, 2013). Apes saw an intermediately preferred food type (such as peanuts) placed under one container, whereas either a highly desirable (banana) or less-desirable (cucumber) type of food was placed under another container—the trick was that apes did not know which was there. In one study using this task (Rosati & Hare, 2013), apes were first introduced to the setup on one day, and then completed less than 20 choice trials on a second. In another inferential paradigm, chimpanzees, bonobos, gorillas (*Gorilla gorilla*), and orangutans (*Pongo abelii*) could infer the hiding locations of rewards that were distributed under different containers (Haun, Nawroth, & Call, 2011; see also Pelé, Broihanne, Thierry, Call, & Dufour, 2014). In this setup, a smaller reward would be placed under one known container, whereas a larger reward would be placed under one container from a larger set. Because the apes did not know which container in that set had the big piece of food, a selection of one of these containers represented a risky choice. This type of setup allowed the relative value and probability of winning to vary parametrically across trials, without new training on each decision contrast. Although these setups are more difficult to fit into traditional economic approaches focused on relative expected value of (quantitative) gambles, they do provide important information about how different species react to uncertainty in matched situations without such extensive training and experience.

Sensitivity to Expected Value, Variance, and Skew

Economic and psychological research shows that humans can use information about the distribution of payoffs when making decisions under uncertainty, responding to three aspects of a payoff distribution (see Figure 16.1): (a) the expected value, or mean payoff; (b) the variance, or spread of potential outcomes; and finally, (c) the distribution's skew, or asymmetry around the mean. These three characteristics of a statistical distribution can all vary independently, so some tasks will even pit them against each other to see which gets priority in the decision making process. For example, one piece of evidence that humans show an aversion to risk is that they are even willing to sacrifice some expected value to avoid variability in payoffs. Although most studies of risk involve gambles where payoff variance is distributed normally around the mean, another defining characteristic of a distribution is its skew. Current evidence indicates people do detect distribution skew, and are more risk-seeking when variance is negatively skewed such that better outcomes are more likely, with a small chance of very bad outcomes (Symmonds, Wright, Bach, & Dolan, 2011; Wright, Symmonds, Morris, & Dolan, 2013). That is, humans seem to prefer a gamble where choices generally result in a better-than-average outcome, but occasionally result in a much more undesirable one.

Can other animals detect uncertainty, and if so do they show the same sorts of preferences for risk that humans do? A wide body of research shows many diverse nonhuman species do detect variance in payoffs, and also tends to show an aversion to risk much like humans (see Kacelnik & Bateson, 1996, for a large review of comparative work). Species that exhibit some level of risk aversion include insects, such as bumblebees (Harder & Real, 1987; Real, 1991) and honeybees (*Apis mellifera*; Shafir, Wiegmann, Smith, & Real, 1999); birds, such as blue jays (*Cyanocitta cristata*; Clements, 1990), white-crowned sparrows (*Zonotrichia leucophrys*; Caraco, 1983), juncos (*Junco phaeonotus*; Caraco et al., 1980), hummingbirds (Hurly & Oseen, 1999; Waser & McRobert, 1998), starlings (Bateson & Kacelnik, 1995), and pigeons (Hamm & Shettleworth, 1987); rodents, such as rats (Logan, 1965); and primates, such as bonobos (Heilbronner et al., 2008), ringtailed lemurs, mongoose lemurs, and red ruffed lemurs (*Lemur catta, Eulemur mongoz, Varecia rubra*; MacLean, Mandalaywala, & Brannon, 2012). These results show that at least mild aversion to risk is a strategy spanning wide phylogenetic spaces, suggesting that risk aversion is a deeply conserved behavioral response. Consequently, human risk preferences in economic decision-making contexts are likely shaped by psychological mechanisms with deep biological origins.

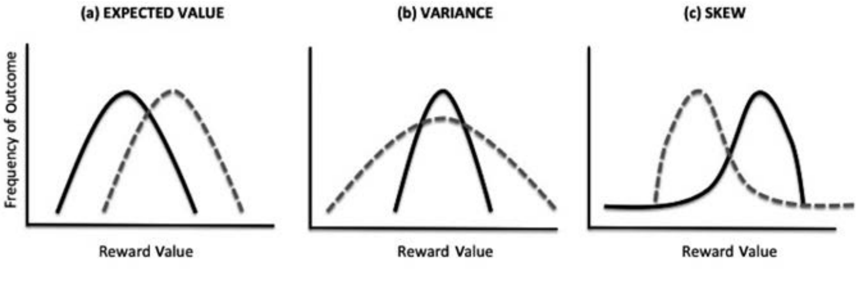

FIGURE 16.1. **Payoff distributions in choice under uncertainty. Distributions that vary in (a) expected value, or mean; (b) variance, or deviation; and (c) skew, or asymmetry.**

However, there are important exceptions to this general pattern. For example, although many bird species appear risk-averse in foraging tasks involving quantitative risk, grey jays (*Perisoreus canadensis*) are relatively risk-prone when tested in similar contexts (Ha, Lehner, & Farley, 1990). Several primate species also appear risk-seeking when faced with numerical variation in payoffs, including chimpanzees (Heilbronner et al., 2008), rhesus macaques (McCoy & Platt, 2002; Platt & Huettel, 2008), and capuchins (De Petrillo et al., 2015). Similarly, inferential paradigms (involving inferences about the location of different rewards) have also identified species differences in response to risk. For example, when faced with options that vary in the quality of reward type they provide, chimpanzees tend to gamble on winning the preferred food type, whereas bonobos prefer the reliable but intermediate-value reward (Rosati & Hare, 2012, 2013). Similarly, when larger or smaller rewards are hidden under different numbers of containers, chimpanzees and orangutans played the odds that they would find the larger reward, whereas bonobos and gorillas were more likely to go with the smaller reward in a known location (Haun et al., 2011). These species are therefore sensitive to risk—in that they discriminate between constant and variable options—but show a different pattern of preferences than humans and many other species.

Furthermore, current comparative research suggests that although animals can detect skew, they may show different preferences for asymmetrical variance than do humans. For example, white-crowned sparrows (Caraco & Chasin, 1984) and rhesus monkeys (Strait & Hayden, 2013) tended to prefer positively skewed risk. In this situation, smaller rewards are more likely, but there is a small chance of a very good outcome. One possibility is that this bias results from the differential salience of high-value and low-value payoffs for the animals. However, this is not the whole story, as rhesus monkeys' patterns of preferences for skew were actually fairly complicated: In addition to their preference for positive over negative skew, they generally preferred gambles with strong skew over weak skew or no skew, but also preferred normally distributed gambles over weak skew. This highlights that skew can have complex effects on risk preferences, and therefore that it is necessary to account for skew to characterize the computations that underlie decision making.

In all, current comparative evidence suggests that risk-aversion is generally a widely shared strategy, but that there are also some striking disparities given that some species may actually seek out risky gambles. When considering this sort of comparative data, it is important to note that payoff contingencies and task design can clearly influence risk preferences (see Heilbronner & Hayden, 2013, for a review). Moreover, the ways in which animals initially learn about payoff distributions can shape their responses to risk in fundamental ways, as explored in the next section. These sorts of contextual factors are critical considerations when comparing the performance of species tested in different setups (or setups that are designed to be analogous, but involve different learning acquisition periods). Moreover, these sorts of context-dependent shifts in risk preferences indicate that a given individual or species is unlikely to have a static strategy for dealing with uncertainty, such that they always avoid or always prefer risk regardless of context. Yet even given these caveats, some species seem to respond differently to variation in payoffs compared to other species—even when tested in broadly comparable or directly matched situations. The origins of such species differences in risk preferences is therefore an important issue for biological theories of decision making.

Learning About Payoffs

In many of the paradigms discussed previously, animals must first gain extensive experience with potential options, learning about the different reward distributions in play to make informed decision. For example, animals might sample all available options in an initial exposure phase involving forced choice or exposure trials, where only one option is available at a time to ensure that the individual has tried it out (see Zentall & Stagner, 2011). In other cases, animals might complete many hundreds or thousands of choice trials to learn about the distributions—with the main focus being on how animals perform after their patterns of choices have stabilized (see McCoy & Platt, 2002). Learning mechanisms can therefore have a big impact on how animals perform in decision making tasks. Moreover, foraging animals must often learn about payoff distributions by sampling different courses of action over time, for example by feeding on different patches (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005), so these learning mechanisms shape behavior in the real world as well. Consequently, illuminating the psychological mechanisms that animals use to learn about uncertainty and update their responses is critical to understanding how different species respond to risk.

What processes drive animal learning, and are there parallels between the psychology of humans and nonhumans? In fact, it is clear that experience-based learning can play an important role in the construction of risk preferences in humans (Hertwig & Erev, 2009), and in some contexts these same sorts of learning mechanisms shape other species as well. For example, when humans and pigeons are presented with structurally identical decisions and learn about their options through direct experience, they exhibit similar risk preferences (Ludvig, Madan, Pisklak, & Spetch, 2014; see also Weber, Shafir, & Blais, 2004). These kinds of direct comparisons between humans and nonhumans provide strong evidence for shared learning substrates across human and other species. However, animals and humans may show important differences in how they learn about more complicated distributions.

One example of a more complex task that had been implemented across species is the Iowa Gambling Task. In the original version of this task developed for humans (Bechara, Damasio, Tranel, & Damasio, 1997), individuals could choose between four decks containing cards, with each representing either a win or a loss of money. These decks differ in their average payoffs as well as their variance: Two decks produced losses on average over trials but occasionally result in a big payoffs, whereas the other decks did not have as much risk—and did not include very high-value cards—but resulted in average gains over time. Although people have no initial knowledge about the payoffs provided about these decks, most learn to prefer the higher-value, lower-risk decks as they sample the different options. Comparative adaptations of this paradigm, however, suggest that other species may not always be as sophisticated as humans at detecting the optimal response. For example, one study compared the responses of humans, chimpanzees, and capuchins to a simplified version of this task involving only two decks (Proctor, Williamson, Latzman, de Waal, & Brosnan, 2014). Across several conditions that differed in the relative variance and mean payoffs of the two decks, capuchins generally showed less evidence of learning the optimal response compared to humans or chimpanzees. Furthermore, several rodent adaptations of this setup involving operant tasks suggest that rodents may also fail to converge on the optimal response (see de Visser et al., 2011 for a review). For example, one adaption replaced the original monetary losses with time-out penalties, where choices could no longer be made. Although some rats could succeed at detecting the optimal option in this task, a significant portion persisted in choosing the option that provided a bigger immediate food reward but then imposed a longer, unpredictable time-out (Rivalan, Ahmed, & Dellu-Hagedorn, 2009). These results suggest that although other species can learn about reward variance by sampling unknown options, they may differ in how fast they learn or what aspects of the payoffs are most salient compared to humans.

The ability to flexibly update reward representations during learning may hold the key to a related question: Why do individuals sometimes make errors and choose suboptimally? Some evidence suggests that these seemingly maladaptive responses can stem from the mechanisms animals use to initially learn about rewards. One well-studied example involves a gambling paradigm with a choice between pecking two keys that differ in the variability and mean value of the rewards they provide (Zentall, 2011; Zentall & Laude, 2013; Zentall & Stagner, 2011). In this situation, pigeons can develop a preference for an option associated with lower average payoffs, but which sometimes provides a low-probability, high-value payoff. Indeed, humans tested in an analogous associative learning situation may show the same preference (Molet et al., 2012). What accounts for this counterintuitive selection of an option with lower expected value than the alternative? The trick is that this task involved two phases. Pigeons first choose between two key locations that differed in their reward distributions—but after their choice they then saw a discriminative stimulus (such as color) that differed in how well they predicted specific rewards. The initial associations that pigeons learned between color and rewards seem to drive their later risk preferences. For example, in one version of this task (Zentall & Stagner, 2011), pigeons chose between a risky option that provided an average of two pieces of food, and alternative that provided a constant three pieces of food. If the pigeons selected the risky-payoff key, there were two possible outcomes: On 20% of trials pigeons saw a red stimulus that was always followed by 10 food pellets, whereas on the other 80% of trials they saw a green stimulus that never produced a reward. That is, the red and green colors perfectly predicted their payoff on that trial and were highly discriminable given the big difference in reinforcement they produced. In contrast, the alternative option resulted in either a blue or a yellow stimulus, which both produced three pieces of food. Consequently, these color stimuli did not differentially predict subsequent reinforcement. A second experiment (Zentall & Stagner, 2011) showed that pigeons correctly preferred the higher-value option if the riskier option no longer produced a color cue that perfectly signaled a very large payoff. These findings suggest that the particular ways that animals (or humans) learn about reward distributions can impact the preferences they later show for different distributions—an important consideration when comparing decision making preferences across individuals or species that face different experimental setups.

Feedback and Outcomes

The previous examples dealt with situations in which animals receive extensive initial experience to learn about payoff distributions—that is, how animals acquire global information about their available options and develop a preference for a particular course of action. In most cases, however, animals show some stochastic variation in responses, rather than blindly choosing one option all of the time. For example, in situations where animals exhibit a strong preference (e.g., when rhesus macaques gamble for juice; McCoy & Platt, 2002), they still choose the alternative on some trials. Indeed, even tasks involving more inferential paradigms necessarily involve a series of iterated choices, during which time animals might adjust their strategies on a trial-by-trial basis. What information do animals use when choosing whether to play the odds on a given trial?

One important type of information that animals seem to use is what happened on their previous choice. In particular, many species exhibit a win-stay/loose-shift strategy across trials, showing a greater propensity to gamble again after a previous choice where they gambled and won, compared to those trials where they previously gambled and lost. Evidence for these sorts of trial-by-trial adjustments comes from diverse species, including monkeys (Barraclough, Conroy, & Lee, 2004; Hayden, Nair, McCoy, & Platt, 2008; McCoy & Platt, 2002), apes (Rosati & Hare, 2013), rodents (Stopper & Floresco, 2011), and humans in similar iterated tasks (Hayden & Platt, 2009; Worthy, Hawthorne, & Otto, 2013). However, it is important to note that not all species respond to feedback in the same way. For example, bonobos use a win-stay/loose-shift strategy like the previously mentioned species, adjusting their strategies depending on the outcome of their previous choice, but chimpanzees rather prefer to gamble regardless of their previous payoffs when faced with the same problem (Rosati & Hare, 2013). This suggests that even very basic mechanisms for adjusting responses on the basis of feedback can vary across species.

In more complex decision making paradigms, animals can use information beyond whether they simply won or lost. Imagine gambling at a slot machine. The goal is to match a set of outcomes, and on each trial it is possible to definitely win (all reels match), definitely loose (no reels match), or experience a near miss (some subset of the reels match, but not quite all of them). In fact, whereas clear losses in this situation reduce risk-taking behavior, these kinds of near misses actually seem to increase it. That is, the experience of almost winning makes people even more inclined to gamble again (Griffiths, 1991), possibly because people seem treat such near-misses as more like a true win than a true loss (Clark, Lawrence, Astley-Jones, & Gray, 2009). Do animals respond to this kind of feedback in the same way? In fact, some evidence suggests that feedback about near misses can also increase risk-seeking in rodents, much like in humans. In one study, rats could gamble in an adaption of a slot machine game (Cocker, Le Foll, Rogers, & Winstanley, 2014; Winstanley, Cocker, & Rogers, 2011). They first learned about a series of three flashing lights that were deigned to be similar to slot machine reels, such that a wining outcome was produced if all three lights were illuminated. On each trial, rats could decide whether to try to collect payoffs (a risky strategy, as they faced a time-out penalty if they lost), or start a new trial instead. Rats were more likely to try to gamble and collect the reward when three lights turned on (a win), but also showed increased risk-taking if only two lights were turned on—a near miss. This indicates that other species also respond to feedback about near misses, much like humans.

Finally, decision makers can consider not just feedback about their previous decision, but also integrate feedback about whole sequences of decisions over time to form expectations about future outcomes. In particular, humans seem to expect that winning will come in streaks—a phenomenon called the hot-hand bias, after the belief that sports players who have had success will continue to do so (Ayton & Fischer, 2004; Nickerson, 2002). More generally, people tend to perceive (illusory) streaks in sequences of random outcomes, and even form the expectation that they will continue to win big at a random event if they have won several times in a row. Indeed, people with a higher propensity to perceive such streaks are more likely to take risks in gambling contexts (Wilke, Scheibehenne, Gaissmaier, McCannet, & Barrett, 2014). Do other animals integrate information about sequences in this way, or even form expectations about their future winnings on the basis of such sequences? One study examined this question by presenting monkeys with sequences of visual stimuli (Blanchard, Wilke, & Hayden, 2014). To win, the monkeys had to correctly guess what symbol would occur next. In fact, monkeys tended to guess that the next symbol would match the previous one—and consequently faired worse at guessing the next image when faced with sequences specifically designed so that the outcomes did not occur in streaks. An open question, however, is whether animals merely predict that sequences of outcomes will match, or whether they form the expectations that their own behavior plays a critical role in shaping these outcomes, like humans.

Counterfactual Reasoning and Regret

There is robust evidence that many animals use feedback about the outcome of their previous choice to adjust what they do next. But humans do not only learn from what happened previously—we also account for what would have happened in the past had we acted differently (Bell, 1982; Loomes & Sugden, 1982). That is, in addition to learning the actual outcomes of their actions, people can also reason about hypothetical (or counterfactual) events that did not actually occur. This type of reasoning seems especially common when people receive a bad outcome (Byrne, 2002): Thinking about alterative courses of action may help people to learn to adjust their future behaviors appropriately. In terms of decision making under risk, this means that people tend to adjust their choices when they are given feedback about their forgone option, and discover that they could have won big if they had chosen differently (Coricelli et al., 2007). The critical difference from the examples of feedback explored in the previous section is that when people use information about counterfactual outcomes, they learn from events that they did not directly experience.

Can animals also consider what would have happened if they had chosen differently? Some recent evidence indicates that such learning mechanisms may be shared at least with other primates. For example, rhesus macaques played a computerized version of the game rock-paper-scissors in one set of studies (Abe & Lee, 2011; Lee, McGreevy, & Barraclough, 2005). On each trial, the monkey could choose one of three visual targets on the screen. They then found out whether they had won a juice reward by beating their computer opponent on that round. The trick was that the monkeys found out not only if they had made a winning move, but also whether they would have won if they chose a different target: The color of all three targets changed after the monkeys' choice to indicate how much juice they would have provided to the monkey, given the computer's choice on that round. The key question was whether the monkeys accounted only for the payoffs from the juice rewards they actually received, or whether they also learned about the alternative courses of action they did not take. In fact, the monkeys' choice strategies revealed that they accounted for realized payoffs and hypothetical payoffs. When monkeys lost on a given trial, they were subsequently more likely to choose what would have been the winning option—but they were not more likely to choose the second forgone target, indicating they specifically switched to the (counterfactual) winning target, as opposed to simply avoiding the loosing target they had directly experienced. That is, the monkeys learned about the value of their decision, as well as the value of a hypothetical alternative course of action.

Monkeys exhibit a similar sensitivity to counterfactual outcomes when making decisions in a more typical risky decision making context. In one example, rhesus monkeys played a computerized game where they could choose between eight possible options (Hayden, Pearson, & Platt, 2009). Seven consistently provided small juice rewards, whereas the final one sometimes provided a much larger reward, but sometimes provided a much smaller reward. The monkeys were given feedback about what the risky option would have provided, regardless of whether they had chosen it. As in the rock-paper-scissors task, modeling of the monkeys' behaviors showed that the monkeys adjusted their future strategies on the basis of what they would have received. If the risky option would have provided the high-value outcome, they were especially likely to seek this option out in future trials, rather than simply learning about the outcomes they had directly experienced because of their own choices.

In humans, counterfactual reasoning is often driven by a particular emotional experience: the feeling of regret. People feel regret when they realize that things would have turned out better had they acted differently, and this experience can cause people to shift their patterns of choice (Coricelli et al., 2007; Zeelenberg, Beattie, van der Pligt, & de Vries, 1996). Do nonhumans attend to hypothetical outcomes because they experience emotions like regret? Some evidence suggests that emotional responses may play some role in nonhuman decision making as well. When chimpanzees and bonobos could choose a risky gamble that delivered either a desirable food type or an undesirable food type, they were more likely to exhibit behavioral markers of negative emotions—including negative vocalizations, tantrum-like banging, and scratching (an arousal or stress response in primates) when they gambled and lost. These responses are analogous to disappointment at receiving the bad option. Furthermore, the apes seemed to realize they should have chosen differently: Both species spontaneously attempted to switch their choice after the fact after they gambled and lost. Importantly, apes rarely tried to switch their choice after choosing the safe alternative, even though it was also possible in this situation that a better outcome was available. Rather, apes made a selective attempt to correct their choice only after losing. Overall, these results from monkeys and apes suggest that at least some primates may consider counterfactual events when making decisions, and in some cases may even show some behavioral signatures of emotional experience.

Magnitude Biases

Most studies reviewed thus far have assumed that although decision makers might differ in their particular preferences for risk, they are generally accurate at detecting differences between reward distributions. However, there are good reasons to suspect that this is not the case. In fact, decision makers might find some forms of uncertainty to be easier to detect or more salient than others. These kinds of biases therefore have a potent impact of risk preferences because they shape the way information about risk is encoded. One such fundamental psychological biases shaping sensitivity to risk in humans are magnitude effects on perceptual judgments of numerical size. In fact, a long tradition of research in psychophysics suggests that animals and humans alike exhibit a fundamental bias in detecting differences between stimuli: The overall magnitude of the stimulus can change how easy it is to discriminate values. For example, it is relatively easy to glance at two items and tell they are a different amount than three items. However, it is more difficult to discriminate 102 items from 103 items. The absolute difference in amount is identical, but the overall higher magnitude makes the one-unit difference less salient in the second case. Known as Weber's law, this magnitude effect has been influential in understanding how a wide variety of species make perceptual, temporal, and numerical judgments (Brannon, 2006; Gibbon, 1977; see also Chapters 1, 14, and 25, this volume).

These same constraints may also apply to how decision makers detect differences in payoff distributions. Imagine a choice between taking $10 for sure, versus a gamble with an equal chance of winning either $20 or nothing. Now imagine a choice between taking $110 for sure, or a gamble resulting in either $100 or $120. The risk posed by the gamble in the first decision seems to loom larger than the risk posed in the second. Yet sensitivity to variance alone cannot account for this difference, because the risky option presents the same variance (or standard deviation) in both situations. One proposal suggests that this is because overall magnitude influences decisions under risk much like it does numerical judgments. Rather than being sensitive to variance alone, decision makers may be sensitive to the variance in outcomes divided by their mean, known as the coefficient of variance (Weber et al., 2004). As in the previous example, the coefficient of variance predicts that individuals will be more sensitive to changes in risk at lower reward magnitudes than at higher reward magnitudes.

This magnitude effect can have a potent effect on human risk-taking. Meta-analyses of studies involving different magnitudes of variance, as well as explicit empirical tests of this idea, have shown that humans are more likely to choose risky options when their coefficient of variation was low even when variance is held constant (Hertwig, Barron, Weber, & Erev, 2004; Weber et al., 2004). Do animals also exhibit this bias in encoding risk? Much like with humans, meta-analyses of animal data from a wide range of species indicate that nonhuman decision making under risk can differ across magnitudes in the same fashion (Shafir, 2000). Indeed, when humans and pigeons were presented with equivalent choices between a safe and risky option across two reward magnitudes, they showed similar increases in risk-seeking responses for choices at higher magnitudes, even when variation between potential options was held constant (Ludvig et al., 2014). This suggests that magnitude effects in decision making influence a wide variety of species, much like the finding that humans and animals alike follow Weber's law when making numerical comparisons—suggesting that this bias reflects deep-seated characteristics of the way organisms make such judgments.

These types of magnitude biases may have pervasive influences across many components of risk decision making. For example, there is some evidence that magnitude can impact animals' accuracy at detecting different probability distributions in the first place. In one study, chimpanzees faced a choice between two trays of containers (Hanus & Call, 2014). The trays differed in their number of containers, as well as how many cups within the array had been baited with a food reward: One tray might have two cups where only one was baited, whereas the alternative tray might have six cups where two were baited. They question was how well the chimpanzees could select a container from the tray with a higher likelihood of getting a reward. In fact, the apes were more successful at choosing a cup from the higher-probability tray when the difference in relative probability was bigger (e.g., 50% of cups were baited in one tray, versus 25% in the other) than when it was smaller (e.g., 50% versus 33%). This suggests that the same analog representational system that drives differences in sensitivity to magnitudes can also influence animals' sensitivity to probabilistic variation in outcomes.

Framing Effects

These perceptual biases impact how numerical differences in risk shape decision making preferences at a fairly basic level. But this kind of perceptual bias is not the only such bias shaping preferences for uncertainty. As reviewed previously, another potent bias with wide-ranging effects on human economic decision making concerns how options are presented, or 'framed.' In particular, humans treat decisions that appear to involve gains in resources as distinct from those that involve losses—even if the outcomes of these decisions are actually equivalent. As humans also psychologically overweight losses compared to gains, the result is that people respond quite differently to identical choices depending on whether they perceive them to improve or worsen the status quo. Do animals also evaluate their choices in this reference-dependent, loss-averse fashion?

One of the first studies to address whether animals judge options differently depending on whether they are perceived as a loss or a gain focused on how capuchin monkeys exchange tokens to receive treats (Chen, Lakshminarayanan, & Santos, 2006). In particular, monkeys received some allocation of tokens, and then could decide whether to trade those tokens with different experimenters who were offering food rewards. One experimenter initially showed the monkey one piece of fruit, but sometimes gave the monkey a bonus piece if the monkey chose to trade their token with them. A second experimenter always showed two pieces of fruit, but sometimes removed one if they were chosen. The average rewards provided by both experimenters was therefore identical, but the experimenters differed in whether they appeared to offer a relative gain or a relative loss compared to the initially presented amount. Despite the equivalent average payoffs, monkeys preferred to trade with the gain experimenter over the loss experimenter. Chimpanzees and bonobos also seem to evaluate equivalent options as more desirable when they are framed as a gain rather than a loss (Krupenye, Rosati, & Hare, 2015). This suggests that these evaluation mechanisms may be shared across several primate species.

Animals can therefore show a human-like bias in evaluating the desirability of losses versus gains. An important second question is whether this bias then shapes their preferences for risk: Are animals risk-averse for gains, but risk-seeking to avoid certain losses? Initial attempts to answer this question compared responses to variability in rewards with responses to variability in the delays to receive rewards. Here the rewards themselves are conceptualized as gains, whereas temporal delays to receive those rewards function as a cost or penalty and are therefore analogous to losses. One representative study compared starlings' responses to these two situations (Reboreda & Kacelnik, 1991). In the gain frame, they could choose between a safe food option that provided a constant amount of food, and a risky option that provided variable amounts, with the delays to receive the food always held constant. In the loss frame, they chose between a safe option that always provided food after a fixed delay, and a risky option that provided food after variable delays, with amounts held constant. As predicted by human framing results, the birds chose the safe option more often when the amount of food varied, but the risky option when the delay to receive food varied. Indeed, a variety of species show these patterns: mild risk-aversion for food rewards, but more risk-seeking responses toward the delays to receive those rewards (see Kacelnik & Bateson, 1996, for a review).

Of course, rewards and temporal delays are quite different, and the original demonstrations of framing effects on human risky choice involve responses to rewards that are themselves perceived as gains or losses. Thus, a stronger demonstration of human-like framing effects in nonhumans would use a more comparable situation. Several studies have developed novel paradigms to test just that. In the first such test, starlings were initially acclimated to receiving either a smaller or larger amount of food (B. Marsh & Kacelnik, 2002). Birds were then confronted with a decision about risk. In both situations this risky decision was identical, but the framing of the choice differed depending on the amount of rewards the birds were used to receiving: All of the potential outcomes represented a relative gain in payoffs if birds were acclimated to the smaller initial amount, but were relative losses for those acclimated to the larger amount. In fact, birds preferred to gamble on the risky option when they were used to receiving more food, whereas they favored the safe option when previously acclimated to the smaller amount. Capuchins show similar responses to risk in the token-trading paradigm described earlier (Lakshminarayanan, Chen, & Santos, 2011). Here, the monkeys preferred a safe experimenter who provided the same amount across trials when contrasted with a risky experimenter who varied the rewards they provided—but only when both experimenters tended to augment their initially proffered amount of food (gain frame). When both decreased their initial amount (loss frame), monkeys rather preferred the risky experimenter. Together, these comparative results indicate that several taxonomically diverse groups of animals exhibit human-like framing effects, suggesting that this bias is driven by widely-shared psychological processes.

Ambiguity and Information Seeking

The previous sections examined how animals encode and evaluate differences in known payoff distributions (i.e., risk). But what happens when animals do not have good knowledge about those distributions (i.e., ambiguity)? As discussed earlier, humans do not treat these situations as equivalent: We do not like choosing options where the potential range of consequences is unclear, showing a robust aversion to ambiguity. But the psychological underpinnings of this effect are not entirely clear—and several explanations for ambiguity aversion invoke complex forms of reasoning that seem unlikely to play a role in nonhuman choice. For example, people might avoid ambiguous options because they feel they cannot justify this choice to others (Curley, Yates, & Abrams, 1986), or people may actively try to assess their own competence or expertise (Heath & Tversky, 1991). More generally, ambiguity aversion involves some sensitivity to one's own knowledge, and the degree of metacognitive abilities possessed by nonhumans is a matter of current debate (Terrace & Son, 2009; see also Chapter 31, this volume). If these capacities are in fact necessary for the emergence of ambiguity aversion, nonhumans might not show this bias. Yet it is also the case that wild animals face decisions involving incomplete or unknown information (Dall et al., 2005), so perhaps the psychological tools for acting appropriately in this situation are widely shared. Comparative studies are therefore critical to understand not only how other species respond to ambiguity, but also to illuminate the mechanisms underlying human choices.

Current evidence suggests that at least some primates also distinguish between known and unknown probabilities, exhibiting a human-like aversion to ambiguity. For example, one computer-based task presented rhesus monkeys with a choice between a gamble with known probability of winning a high-value reward, and an ambiguous option with an unknown probability of winning (Hayden, Heilbronner, & Platt, 2010). Both options were visually represented as a bar with the probability of winning shown as a shaded portion, but part of the ambiguous bar was blocked from view such that the monkeys could not properly estimate the probability of winning on any given trial. Although these options were mathematically equivalent in terms of the payoffs they provided across trials, monkeys highly preferred the risky option with known probability—and even showed similar patterns of responses to human participants tested in an equivalent setup. These results suggest that exhibiting a human-like bias against ambiguity may not require the more complex forms of reasoning that have been proposed to underlie human behavior.

Other primate species also share this bias, and further highlight the importance of learning in shaping how individuals respond to ambiguity. Although most human studies of choice under ambiguity involve one-shot decisions (as is the case for human studies of risk preferences), animal work can provide insights into the learning mechanisms that influence responses to ambiguity under more real-world situations where decision maker must sample their available options. For example, one study examined chimpanzees' and bonobos' responses to four different types of choices (Rosati & Hare, 2011). In three types of choices, apes always saw the set of possible outcomes in advance, and therefore knew the probability of winning the high-value payoff: a 100% chance, a 0% chance, or a 50% chance. In the fourth type of choice, the apes' view of the potential outcomes was blocked, so they did not know the likelihood of winning. Although the average payoff from this ambiguous option was identical to the average payoff of the risky option (50% chance of winning), the apes were less likely to gamble on the ambiguous option. Importantly, the apes' initial bias against ambiguity later dissipated: Across trials, apes learned that the ambiguous and risky options were equivalent. Thus apes' experience with the ambiguous option shifted their strategies over time.

A final question is whether animals will take action to remedy their lack of knowledge when faced with incomplete information. That is, will animals seek out new information before making a choice if it is possible to acquire it? Most comparative research focuses on situations where animals learn by sampling and updating the knowledge about reward payoffs by simply participating in the task. In this kind of situation, it is not necessary to do anything special to gain information about the available options—animals simply acquire information by virtue of making a series of choices. However, humans will also actively seek out information to improve decision making (Loewenstein, 1994); indeed, gaining knowledge may even be pleasurable for humans (Loewenstein, 2006). In this way, a sense of curiosity may allow humans to resolve ambiguity before making decisions.

There is some suggestive evidence that some other species can also actively adjust their behavior so that they are also more likely to learn relevant information before making decisions. For example, apes engage in information-seeking behaviors (such as changing their perspective) when they lack knowledge about the location of a reward (Call & Carpenter, 2001). One study extended this metacognition paradigm to examine how apes respond to risky decisions (H. L. Marsh & MacDonald, 2012). Using a basic procedure similar to some previous decision making work (Haun et al., 2011), a treat was hidden under one of several containers out of the ape's sight, but they had to select just one. The trick was that in this setup, the ape could actually seek out more information about their likelihood of winning by peering under the containers from a different perspective to see which was baited. In fact, they were more likely to peer into the containers when their likelihood of selecting a baited container was low because more containers were present, than when it was higher because fewer containers were present. Importantly, there are species differences in the basic propensity to engage information seeking: whereas apes and rhesus monkeys (Hampton, Zivin, & Murray, 2004; Rosati & Santos, 2016) seem to engage in these targeted searching behaviors when they lack knowledge, capuchins do not (Paukner, Anderson, & Fujita, 2006). Thus, there may also be important differences in how animals seek information when faced with uncertainty as well (see Chapter 31, this volume).

UNCERTAINTY IN THE REAL WORLD

Nonhuman decision making is supported by a set of complex mechanisms that shape how animals encode, evaluate, and learn about uncertainty in their environment. As the previous sections showed, in many cases there are strong parallels between the cognitive mechanisms that humans and nonhumans use to make such decisions in many contexts. A critical issue is therefore how these strategies play out in more real-world situations where hungry animals must seek out food, sometimes in the company of others, and may even be pursuing different ecological "goals" in their foraging strategies depending on the particular environment with which they are faced. This final section will address how a decision maker's physiological state, their broader social context, and finally more persistent differences in cognition across individuals or populations can impact how animals think about and respond to uncertainty (see Figure 16.2).

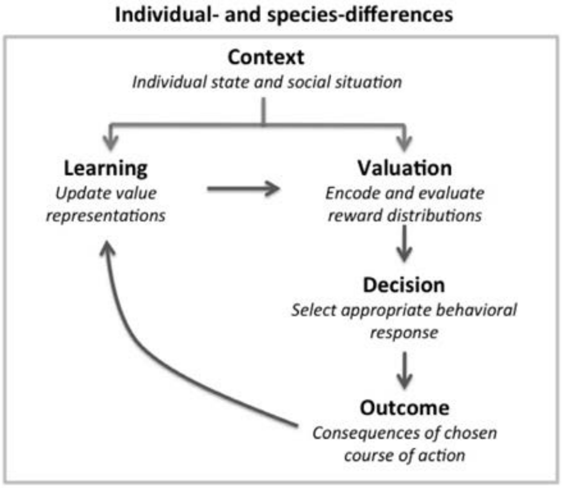

FIGURE 16.2. Psychological processes shaping choice under uncertainty. Context can flexibly influence how animals assign value to different options, as well as how they learn about payoff distributions in the first place. Individuals and species may also show more fundamental biases in how they generally respond to uncertainty.

Individual State

Risk sensitivity theory predicts that preferences for uncertainty should depend on a decision maker's state—in particular, their energetic status (see Chapter 14, this volume). This is a major difference between biological approaches to risk decision making and rational choice theory in economics, as classical economic theory assumes that individuals should exhibit consistent preferences across contexts. Indeed, human economic studies tend to use monetary rewards where these sorts of physiological considerations are less salient. In contrast, comparative studies of decision making typically involve foraging situations where animals seek out food rewards, so decision maker's energetic state or level of satiation is consequently of prime importance.

How does an individual's state interact with the psychological processes animals use to think about uncertainty? Although most work examining the influence of energetic state on decision making does not delve into the specific mental capacities in play, there are some hints concerning how physiology influences decision making from a mechanistic perspective. In particular, animals may encode the value of options differently depending on their energetic state when they encounter them. For example, some species treat rewards as having higher value if they initially experience them with lower energetic reserves, compared to when they encounter identical rewards in a higher energetic state (B. Marsh, Schuck-Paim, & Kacelnik, 2004; Pompilio, Kacelnik, & Behmer, 2006). That is, an animal's energy budget can influence how they encode the relative value of different options. The psychological mechanisms that animals use to encode value may therefore function as a rough heuristic for a reward's marginal benefit: higher when the reward is encountered in a low energetic state than a high state. Once the value of the reward is encoded, it can have an enduring impact on choices even if the individual is no longer in that low state.

These sorts of state-dependent learning mechanism can result in preferences that seem suboptimal. One such example is the sunk-cost fallacy, or valuing something more on the basis of past investment, even if it currently makes no sense to do so (see Chapter 15, this volume). This bias has been extensively explored in humans (Arkes & Ayton, 1999), and there is now compelling evidence that animals also overvalue options previously associated with greater effort or temporal costs to acquire (Pattison, Zentall, & Watanabe, 2012; Pompilio & Kacelnik, 2005). For example, in one study starlings could first experience two ways to acquire food: a high-cost route that required a lot of effort before the birds could peck an associated key to get food, and a lower-cost route that required less effort to access the associated key (Kacelnik & Marsh, 2002). Although both keys actually produced the same amount of food, when the birds were later given a choice between the keys (without having to do any work) they actually preferred the one associated with more effort. That is, the starlings assigned more value to the cue that (previously) involved greater cost. One possibility is that when the birds were initially exposed to the two routes of obtaining rewards, their learning hinged on the marginal value provided by each key: Given that they had to initially expend more energy to obtain a piece of food from the higher-cost route, that key was then associated with a larger relative increase in value than the alternative key.

These results suggest that energetic state can have potent effects on individual's decision-making preferences. The psychology of self-control suggests another pathway by which physiological state can impact decision making. Self-control is an important component of executive functions, allowing individuals to flexibly regulate their behavior and override undesirable responses. In fact, some evidence suggests that self-control is a limited resource that can be used up, so that it is more difficult to exert self-control in another situation (Baumeister, Vohs, & Tice, 2007). This phenomenon, called *ego-depletion*, may in fact be related to the physiological consequences of exerting self-control. For example, some argue that ego-depletion actually reduces metabolic stores of energy (Gailliot et al., 2007), or at least alter neurobiological systems influencing reward-processing and motivation (Molden et al., 2012). These same types of processes can play an important role in decision making under uncertainty. For example, suppressing unwanted emotional responses is effortful, and can make it more difficult to exert cognitive control in subsequent situations (Muraven, Tice, & Baumeister, 1998). Being placed in a situation where it is necessary to control emotional reactions—such as recollecting an embarrassing or anger-provoking episode from one's past—may subsequently increase risk-taking because self-regulation capacities are impaired (Leith & Baumeister, 1996).

This result highlights that energetic state and psychological state can be intimately connected. And although human economic decision-making research has focused less on energetic effects on risk task, there is strong evidence that mood states can shift responses to uncertainty in humans. For example, people experience negative states such as disappointment or regret as a consequence of unfavorable outcomes when making decisions under risk (Coricelli et al., 2007; Loewenstein & Lerner, 2003). Furthermore, altering psychological states such as anger, anxiety, or stress has a causal impact on human risk preferences (Isen & Patrick, 1983; Porcelli & Delgado, 2009; Raghunathan & Pham, 1999). It is currently unclear whether moods shift risky decision making in animals as well. However, many other species also show clear behavioral, physiological, and neurobiological signs of emotional processes (LeDoux, 2000; Panksepp, 1998; Phelps & LeDoux, 2005), and some primates even show human-like emotional responses specifically in risky decision making contexts (Rosati & Hare, 2013). Consequently, it is an important question for future research whether experimentally manipulating animals' psychological state can also shift their risk strategies, as in humans.

Social Context

Nonhuman risk preferences depend on context: Individuals make different decisions depending on their own physiological or psychological state. But no decision maker is an island. In fact, social-living species (including humans) must constantly make value-based decisions in the company of others. Mechanistically, there is increasing evidence that social context can shift a decision maker's goals or emotional state, influencing many of the psychological processes discussed in previous sections. For example, people are more likely to make risky choices if it improves their status relative to a hypothetical competitor (Ermer, Cosmides, & Tooby, 2008; Hill & Buss, 2010). Mechanistically, competitive social contexts may shift people's mood states (such as anger) and thereby facilitate risk-prone decision making (Fessler, Pillsworth, & Flamson, 2004). Competition may even impact the subjective utility people derive from payoffs: people weigh potential losses more heavily when alone, but focus on the possibility of winning more than others in social contexts (Bault, Coricelli, & Rustichini, 2008). Competition is an important component of social interactions in other animals as well, and there is some evidence that competition can shift other species' preferences in similar ways. For example, chimpanzees and bonobos both become more risk-seeking following a competitive interaction with a human, compared to a neutral context (Rosati & Hare, 2012). Importantly, this effect seems fairly specific to competitive interactions, as a more positive play interaction had no effect on their choices. More generally, these types of studies indicate that social context can influence economic decisions that involve individual-level strategies—possibly because social context can be an important cue as to the value of various resources in the current environment.

These studies show that social context can influence economic decisions unrelated to social interactions per se. But it is important to point out that many social interactions inherently pose problems involving risk, as decision makers must choose between courses of action where the variability in payoffs stems from another individual's behavior. For example, in situations involving competition between conspecifics that differ in their visual access to resources, animals can choose between relatively risky piece of food (that another individual can also see and therefore might approach) or relatively safe piece that the other individual cannot see and is therefore unlikely to pursue. This sort of sensitivity to "social risk" has been demonstrated in multiple primate species, including chimpanzees, rhesus macaques, and ringtailed lemurs (Flombaum, Santos, & Hauser, 2002; Hare, Call, Agnetta, & Tomasello, 2000; Sandel, MacLean, & Hare, 2011). Thus, animals seem equipped to respond to social risk when competing with group-mates for food.

Many cooperative interactions similarly involve payoffs that can vary depending on the partners' chosen action (see Volume 1, Chapter 44, this handbook). Nonhumans' responses to a variety of prototypical cooperative situations have been extensively studied, including the prisoner's dilemma (Stephens, McLinn, & Stevens, 2002), the stag-hunt game (Bullinger, Wyman, Melis, & Tomasello, 2011), the ultimatum and other negotiation games (Jensen, Call, & Tomasello, 2007; Melis, Hare, & Tomasello, 2009), the trust game (Engelmann, Herrmann, & Tomasello, 2015), as well as mutualistic interactions that involve simultaneous coordination of behaviors (Melis, Hare, & Tomasello, 2006). To take one example, in the stag-hunt game individuals can choose between pursuing a low-value resource (the hare) that can be acquired individually, or a high-value resource (the stag) that requires cooperation—but choosing to pursue the stag without anyone else joining results in a complete loss. In fact, chimpanzees seem quite risk-prone in this kind of situation, preferring to gamble on the possibility that their partner will also choose the high-value item (Bullinger et al., 2011). Similarly, chimpanzees in a modified version of the trust game tend to invest effort in giving their partner a high value resource—a risky strategy given that the partner might choose to keep all the food for himself (Engelmann et al., 2015). Importantly, humans not only respond to risk in social contexts, but also treat decisions involving social risks as distinct from equivalent nonsocial choices. For example, people are less willing to invest in their partner in the trust game, but more willing to gamble in a matched nonsocial risky decision with identical stakes (Bohnet & Zeckhauser, 2004). This phenomenon, called betrayal aversion, indicates people can be more averse to social risk where others may take taken advantage of them. Although animals clearly account for risk when making social decisions, it is currently unclear whether they also distinguish between social risk and nonsocial risk in this way.

Variation Across Individuals and Populations

The previous sections examined whether the same individual can flexibly shift their strategies when confronted with risky choices across different contexts. This evidence shows that humans and animals alike have flexible risk preferences that can be adjusted according to the particular situation at hand. However, despite the context-sensitivity of decision strategies, humans and animals may also exhibit relatively stable or trait differences in their responses. For example, one person may be generally more risk-prone than most others across contexts, even if their particular degree of risk-seeking behavior can be modulated. This final section will examine the possibility that there are also more stable differences in nonhuman risk preferences: Do some individuals or some populations generally exhibit different preferences than others?

One approach to answering this question is to examine individual variation in risk preferences within a species. In fact, there is significant individual variation in human responses to risk, and that propensity to take risks has an underlying genetic component. For example, twin studies indicate that degree of risk aversion is heritable, as monozygotic twins show more similar responses on economic risk tasks than do dizygotic twins (Cesarini, Dawes, Johannesson, Lichtenstein, & Wallace, 2009). Furthermore, some specific genetic variants in the serotoninergic and dopaminergic neurotransmitter pathways can predict an individual's propensity to gamble on risky prospects (Carpenter, Garcia, & Lum, 2011; Frydman, Camerer, Bossaerts, & Rangel, 2011; Kuhnen & Chiao, 2009; Zhong, Israel, Xue, Ebstein, & Chew, 2009). However, most nonhuman research examining the genetics risk-taking have focused not on economic decision making per se, but rather on related behaviors such as novelty seeking or physical risk taking (Kreek, Nielsen, Butelman, & LaForge, 2005; van Oers, de Jong, van Noordwijk, Kempenaers, & Drent, 2005; Watson et al., 2015). For example, variation in the D4 dopamine receptor predicts whether great tits (*Parus major*; Fidler et al., 2007), vervet monkeys (*Cercopithecus aethiops*; Bailey, Breidenthal, Jorgensen, McCracken, & Fairbanks, 2007), and horses (*Equus caballus*; Momozawa, Takeuchi, Kusunose, Kikusui, & Mori, 2005) engage in novelty-seeking (see Chapter 28, this volume). Although these results are therefore suggestive of shared genetic substrates underlying risk-taking in humans and other species, it is currently unclear if these results extend to value-based decision making contexts.

However, genetic variation is just one type of stable influence on individual differences in risky decision making. Humans also exhibit persistent gender differences in willingness to take risks: Men tend to be more willing to do so than women (Byrnes, Miller, & Schafer, 1999; Croson & Gneezy, 2009). This gender difference likely stems from a myriad of sources, including cultural norms of behavior, but there is some evidence that biological influences play a role as well. For example, risk taking can vary with levels of sex hormones such as testosterone (Apicella et al., 2008; Stanton, Liening, & Schultheiss, 2011; Stanton, Mullette-Gillman, et al., 2011). There are some hints that animals may exhibit similar variation in risk preferences. For example, one study examined framing effects in a large sample of chimpanzees and bonobos, finding that male apes were more susceptible to framing biases than were females (Krupenye et al., 2015). Given that nonhumans do not face the same norms of social behavior as humans do, these kinds of comparative studies can provide important insights into the contributions of social experiences and biological influences on the emergence of individual variation in human decision making.

For comparative psychologists, a final important question is whether there are stable differences in patterns of decision making across species. As discussed previously, risk preferences in animals generally seem to be strongly conserved, as the majority of species tested thus far exhibit at least mildly risk-averse for gains—a pattern that holds across many diverse insects, mammals, and birds (Kacelnik & Bateson, 1996, 1997). However, most research to date focuses on only one species in a given study, and there may be important differences in methodology across studies. Thus, the broad-strokes pattern of risk-aversion seen across many taxa may hide subtler differences in risk preferences between species. Indeed, there are some known deviations from this pattern. For example, rhesus macaques (McCoy & Platt, 2002; Platt & Huettel, 2008), capuchins (De Petrillo et al., 2015), and chimpanzees (Haun et al., 2011; Heilbronner et al., 2008; Rosati & Hare, 2012, 2013) have all been shown to be fairly risk seeking. Although preferences in any given study are clearly dependent on contextual variables, these species nonetheless are notable given that several other species show more risk-averse patterns of choice in similar or identical contexts.

What is the origin of these kinds of species differences in decision making? One possibility is that different species' cognitive capacities have a recognizable "psychological signature" of their typical socioecological environment—much like morphological characters such as body form or dentition can vary depending on different species' niche. That is, species with differences in their natural history might exhibit systematic differences in the cognitive skills that are central to decision making. Indeed, the use of the comparative method to relate differences in species' traits to differences in socioecological variables of interest is one of the most powerful tools in evolutionary biology (Mayr, 1982). This approach is therefore important for illuminating the origins of variation in cognitive abilities (MacLean, Matthews, et al., 2012).

Although there have been few studies comparing closely related species on matched tasks examining risk preferences, there are some hints that species facing different species-typical environments in the wild may show targeted differences in their decision making strategies. For example, chimpanzees and bonobos show such divergences in their risk preferences. Although these species only diverged from each other less than one million years ago (Won & Hey, 2004), they exhibit important differences in their socioecology (Hare, Wobber, & Wrangham, 2012; Kano, 1992). In particular, chimpanzees are thought to live in environments that display more seasonal variation in production, and chimpanzees also exhibit greater dependence on risky hunting than do bonobos (Boesch, Hohmann, & Marchant, 2002; Malenky & Wrangham, 1994). These differences in natural history therefore predict that chimpanzees may be more willing to accept risk compared to bonobos—and in fact, chimpanzees are more risk seeking than bonobos across populations and across several different experimental paradigms (Haun et al., 2011; Heilbronner et al., 2008; Rosati & Hare, 2012, 2013). These results provide some initial evidence that strategies for dealing with risk may be shaped by a species' ecological niche, such that variation in preferences for uncertainty across species reflect biologically rational responses to species-typical environments.

CONCLUSION

Humans and animals alike face uncertainty in their daily lives. Humans use complex, context-sensitive psychological mechanisms when making decisions about risk, and current comparative research suggests that many of these same mechanisms support animal choice behavior as well. Much like humans, various nonhuman species are sensitive to variation in their payoffs—and use similar psychological processes to encode payoffs, learn and update information, and evaluate the desirability of different options. Indeed, several species exhibit human-like economic biases, such as framing effects and the hot-hand effect. Some species also show human-like responses to decision problems often thought to recruit fairly sophisticated capacities in humans—capacities that are likely unique to our species. For example, several primates species show human-like aversion to ambiguity or incomplete knowledge—a bias previously attributed to high-level cognitive processes such as being able to justify one's choices to others. Given that animals show similar responses to ambiguity, this suggests that such processes may not be necessary. Overall, these comparative findings indicate that many of the psychological processes driving human economic behavior build on mechanisms that are widely shared with other taxonomic groups, in some cases ranging from primates to insects.

This is not to say that there are not important differences in how individuals or even species respond to uncertainty. Indeed, comparative evidence also shows that although many species may show human-like patterns of decision making under uncertainty, there are almost always important exceptions. Increasing evidence suggests that some species are more risk seeking (or risk averse) than are others, even when facing well-matched problems. Biologically minded approaches to decision making are therefore uniquely positioned to address questions about why these different decision making mechanisms emerged in the first place—that is, to illuminate the ultimate biological function of these psychological processes. In particular, comparisons of decision making across species that vary in socioecological characteristics can shed light on the evolutionary origins of different choice strategies. Moreover, comparative research has highlighted important facets of decision making that have not been the focus of human research, especially the importance of energetic state on decision making preferences and the learning mechanisms that drive these preferences.

Over the past four decades, behavioral economists and psychologists have developed new—and more nuanced—theories about how humans respond uncertainty. In many cases comparative research has drawn on theoretical advances from these fields to examine if other species also exhibit the defining characteristics of human economic behavior. But this collaborative borrowing goes both ways, as comparative research can inform and drive advances in psychology and economics as well. Indeed, some of the most pressing questions in the social sciences concern the origins of human economic biases: do they reflect human nature, are they learned, and if so what experiences engender their emergence? Comparative research with nonhumans is critical to address these questions precisely because animal lives have both continuity and discontinuity with our own. Evolutionary theory therefore provides a path to understand why this variation emerges in the natural world.

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CHAPTER 17

RELATIONAL THINKING IN ANIMALS AND HUMANS: FROM PERCEPTS TO CONCEPTS

Ed Wasserman, Leyre Castro, and Joël Fagot

"The power of abstraction has its germ in sense-experience." So wrote the famous comparative psychologist C. Lloyd Morgan (1894, p. 264) well over a century ago. At issue was how we progress from direct sense impressions to more abstract conceptual thoughts, a matter which still intrigues psychological scientists and about which we are concerned in the present chapter.

Morgan was especially interested in the abstract idea of sameness. He believed that the perception of similarity was basic to relational and conceptual thought—even to our appreciation of higher-order relations between relations. Morgan (1894) invites us into the realm of relational thinking in the following way:

> Suppose that we are looking over a series of coins or other similar objects. As we pass from one impression to another, we sense, or are marginally aware of, the similarity of each to each. We may then make the likeness of any two focal in consciousness and perceive the relation of similarity. We may go [even] further and perceive that the relation of this to that is similar to the relation of that to the other—we may perceive the similarity of the relations. But the relations that we perceive to be similar are particular relations. Not until the particular fades from view, and the relationship, as common to all the particular instances, becomes focal, do we reach the conception properly so-called. (pp. 263–264)

On the basis of the largely anecdotal evidence that was available to him, Morgan concluded that only adults are capable of such conceptual or abstract thought, that young children are initially incapable of abstract thought, and that animals altogether lack this cognitive capacity.

Morgan's (1894) views on the abstract idea of sameness were strongly shaped by the relationship between language and conceptualization.

> Our conception of similarity is indefinite from its very generality, and the moment we try and make it clear and precise to our mind's eye, we make it particular by thinking of an illustrative example. We exemplify the conception by reference to a particular perception. The symbolic name, however, serves to fix the general conception without particularizing it. (pp. 264–265)

Hence, Morgan deemed the final, critical step in the process of abstraction to be the complete uncoupling of perception and conception through analysis and synthesis.

> We find in a great number of particular cases, with which reflection presents us, the relation of similarity, and submitting these cases to analysis, we detach the relation from the related terms. But the relation is given in experience as a similarity now of colour, now of musical notes, now of pressures, now of tastes, now of scents,

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APA Handbook of Comparative Psychology: Vol. 2. Perception, Learning, and Cognition, J. Call (Editor-in-Chief)

> and so forth. Fusing these together, we reach the synthetic general conception of this relation as of universal application, and label it "similarity." (p. 265)

So, despite the fact that abstraction may have its germ in sense-experience, by virtue of symbolic labeling, Morgan proposed that perception and conception might no longer be coextensive.

Even today, we find Morgan's rich observations and incisive speculations to be particularly interesting and relevant. They serve as a fitting introduction to a view of cognitive processing which encompasses an exciting realm of contemporary psychological science, namely, the development and evolution of relational cognition.

In the present chapter, we explore the possible continuity in relational and analogical cognition between humans and nonhuman animals. Relational reasoning—particularly appreciating the relation between relations, as in analogies—represents what many theorists believe to be the pinnacle of human cognition. Nevertheless, recent evidence suggests that such abstract relational thought does not arise *de novo*; rather, it develops in humans and its evolutionary roots can be gleaned in the behavior of animals.

To embrace these exciting research discoveries, we outline an emerging theoretical perspective on the development and evolution of relational thinking, which proposes that perceptual and relational processes are intimately interrelated in humans and animals. The ultimate uncoupling that Morgan hypothesized may prove to be unattainable, as Goldstone and Barsalou (1998) suggested: "Concepts usually stem from perception, and active vestiges of these perceptual origins exist for the vast majority of concepts" (p. 232).

Specifically, we will review mounting evidence in the realm of animal cognition which undermines the common belief that same–different conceptualization is uniquely human. In fact, many species can discriminate first-order same–different relations ($A = A$ or $B \neq C$); and, possibly fewer species can discriminate second-order same–different relations (the relation between relations; $AA = BB$ and $CD = EF$ or $GG \neq HI$).

Evidence also suggests that relational control in animals does not emerge distinct from perceptual control: The processing of individual stimuli is foundational to and continuous with the processing that occurs between or among stimuli. This finding holds true for animals' processing first-order and second-order relations.

Critical to the comparative analysis of relational cognition, we further ask whether these findings are peculiar to animals. Here, the answer appears to be no. Although animals may not achieve relational thinking of the same versatility and complexity as do humans, striking behavioral similarities nevertheless emerge. Especially important is the observation that, during development, children too move from perceptually-based to relationally-based processing, owing to innumerable relevant experiences. Yet, even when human adults solve higher-order relational tasks, perceptual processes still may be involved (Kroger, Holyoak, & Hummel, 2004).

Finally, although animals and humans engage in perceptually- and relationally-based processing in complex judgment tasks, the role of symbolic language cannot be ignored. In this connection, we observe that linguistic encoding of higher-order judgment tasks may ease and promote relational thinking in children; nevertheless, language appears not to be mandatory for relational thought, as demonstrated by the success of nonverbal animals in mastering advanced relational tasks. We suggest that the contribution of language to relational thinking might best be seen to provide abstract symbols for humans to re-encode and simplify complex stimulus relations, thereby permitting us to solve higher-order relational problems that may be beyond the cognitive reach of animals which lack symbolic language.

FIRST-ORDER RELATIONAL PROCESSING IN ANIMALS

When learning or evaluating the relationship between two or more items, we talk about first-order relational processing. In first-order same–different discrimination learning, animals must in some way report whether two or more items are the same as or different from one another. The extent to which animals can learn and understand the relations of sameness and differentness has become a focal concern of comparative research, as we shall demonstrate in the sections that follow.

Comparative Evidence of First-Order Same–Different Discrimination Learning

Using a wide variety of experimental tasks, researchers have reported that several different species can solve first-order same–different discriminations. Chimpanzees (*Pan troglodytes*; Premack, 1976), rhesus monkeys (*Macaca mulatta*; Wright, Santiago, Urcuioli, & Sands, 1983), baboons (*Papio papio*; Wasserman, Fagot, & Young, 2001), rats (*Rattus norvegicus*; Wasserman, Castro, & Freeman, 2012), parrots (*Psittacus erithacus*; Pepperberg, 1987), honeybees (*Apis mellifera*; Giurfa, Zhang, Jenett, Menzel, & Srinivasan, 2001), and bumblebees (*Bombus impatiens*; Brown & Sayde, 2013) have all joined the growing list of species that are able to learn first-order same–different discriminations.

Yet, beyond all of these different animals, the pigeon (*Columba livia*) has proven to be the most comprehensively and assiduously studied species in the experimental investigation of same–different conceptual behavior. For that reason, the research that we will review in the next section was done with pigeons.

Evidence of First-Order Same–Different Discrimination Learning in Pigeons

Pigeons have mastered a broad range of discrimination learning procedures: two-alternative forced-choice training displaying a single array of items (e.g., Wasserman, Hugart, & Kirkpatrick-Steger, 1995); two-alternative forced-choice training displaying two or more successively presented arrays of items (e.g., Young, Wasserman, & Dalrymple, 1997); conditional same–different discrimination training displaying two or more simultaneously presented arrays of items (e.g., Castro, Kennedy, & Wasserman, 2010); and, go/no-go same–different discrimination training displaying a single array of items (e.g., Wasserman, Frank, & Young, 2002). We will further describe these and other discrimination methods as we consider a series of important substantive issues (see Chapter 15, this volume).

Influence of Item Information and Number of Items on Generalization Performance

It has become standard practice in the study of pigeons' same–different discrimination learning to begin an experiment by creating two sets of individual items from a common pool of visual stimuli: one set containing all possible training items and a second set containing all possible testing items. After discrimination mastery, a generalization test must be conducted to confirm that discriminative control by the familiar items in the training set effectively transfers to the novel items in the testing set. Successful transfer is the indisputable empirical hallmark of a same–different concept, because it requires relational control by untrained items.

No matter how many items are contained in each visual display—from two (the smallest possible number) to 16 items is typical—these items are customarily selected from a single training or testing set to create displays of identical items (same displays) and nonidentical items (different displays). This selection method guarantees that each individual item has an equivalent likelihood of appearing in same and different displays, thereby encouraging behavioral control by the same–different relations and discouraging behavioral control by the identities of the individual items. Figure 17.1 depicts a small sampling of such multi-item arrays originally used by Wasserman et al. (1995). Note that the individual items in the same and different arrays in set 1 do not overlap with the items in set 2. Also note that the individual items in the same arrays can also appear in the different arrays for set 1 (the locomotive and the compass) and set 2 (the brain and the music notes).

The effectiveness of these particular procedural practices is confirmed by reliable behavioral transfer from the training displays to the testing displays in most published reports of same–different discrimination behavior in pigeons and humans (*Homo sapiens*; reviewed by Wasserman & Young, 2010). Notwithstanding such successful behavioral transfer, discriminative performance to the novel testing displays frequently falls below that to the familiar training displays. This *generalization decrement* is believed to be because of the animals' remembering the individual training items during acquisition, despite the irrelevance of those individual items to the programmed demands of the discrimination task. Clearly, item and relational processing can co-occur in the mastery of same–different discrimination learning tasks.

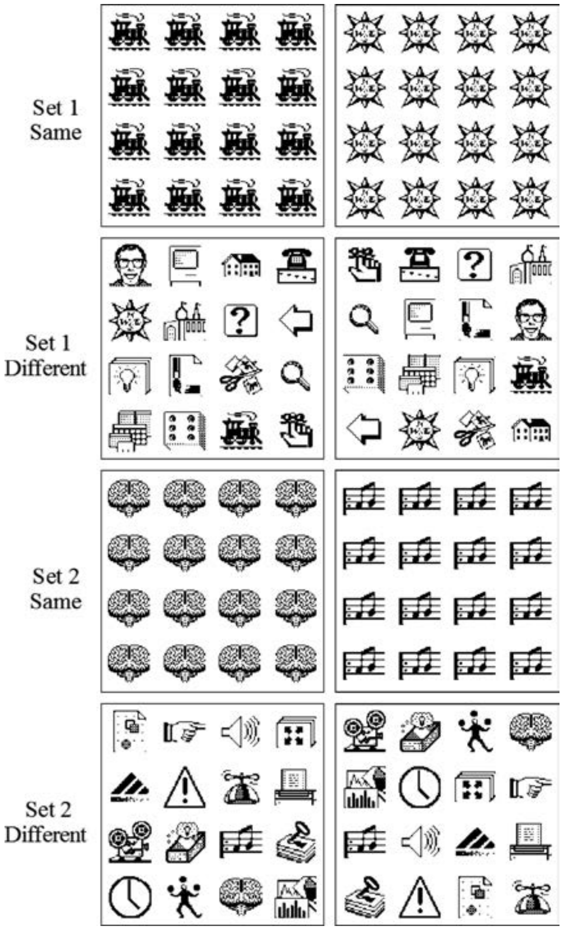

FIGURE 17.1. A sampling of the 16-icon same and different arrays used in Wasserman et al. (1995). Reprinted from "Pigeons Show Same–Different Conceptualization After Training With Complex Visual Stimuli," by E. A. Wasserman, J. A. Hugart, and K. Kirkpatrick-Steger, 1995, *Journal of Experimental Psychology: Animal Behavior Processes*, *21*, p. 249. Copyright 1995 by the American Psychological Association.

To take just one example of such joint item and relational processing, consider the study by Young and Wasserman (1997). These researchers first taught pigeons to peck one report button when they viewed a stimulus array comprising 16 copies of the same computer icon and to peck a second report button when they viewed a stimulus array comprising 16 different computer icons. Correct button responses produced food reinforcement; incorrect button responses failed to do so and led to one or more correction trials. Rather than placing the 16 icons of the same and different displays into a completely filled 4 × 4 grid (Figure 17.1), these investigators placed the 16 icons into an incompletely filled 5 × 5 grid (Figure 17.2) to weaken the role of stimulus "orderliness" in the pigeons' discrimination behavior, because arrays of identical items may otherwise appear to be more orderly than arrays of nonidentical items.

Despite deploying this method of upsetting the orderliness of the stimulus arrays, the pigeons' acquisition of discriminative responding was quite rapid and they showed strong transfer to displays of novel items. Over the course of postacquisition testing, discriminative performance to displays created from the training icons averaged 93% correct and discriminative performance to displays created from the untrained testing icons averaged 79% correct. Choice accuracy was much higher than chance to the training displays and to the testing displays, but accuracy was nevertheless lower to the testing displays than to the training displays.

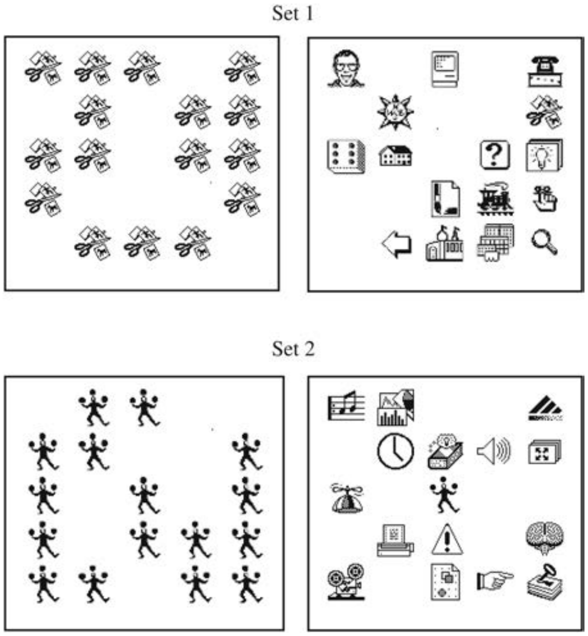

FIGURE 17.2. A sampling of the 16-icon same and different arrays used in Young & Wasserman (1997). The items in the arrays were randomly located in a 5 × 5 grid in order to avoid stimulus "orderliness." Reprinted from "Entropy Detection by Pigeons: Response to Mixed Visual Displays After Same–Different Discrimination Training," by M. E. Young and E. A. Wasserman, 1997, *Journal of Experimental Psychology: Animal Behavior Processes*, *23*, p. 158. Copyright 1997 by the American Psychological Association.

Considerable research has explored the nature of this generalization decrement. A key determinant of the disparity between training and testing performance is the number of items in the training set (e.g., Castro et al., 2010; Young et al., 1997) To illustrate the role of the number of training items on same–different discrimination behavior, consider the study by Castro et al. (2010). That project used a conditional discrimination task—introduced by Flemming, Beran, and Washburn (2007)—in which arrays of 16 identical and 16 nonidentical items were simultaneously presented on the pigeon's touchscreen. The birds had to learn a same–different discrimination conditional on the color of the background screen; each bird had to peck either the same array or the different array depending on whether the background color was pink or black. Two groups of pigeons were given this task: For one group the items came from a 24-item pool (group 24), whereas for the other group the items came from a 72-item pool (group 72). After training, all of the birds were tested with a common set of novel same and different stimulus arrays. Initial acquisition was faster for pigeons trained with stimuli from a 24-item pool than for pigeons trained with stimuli from a 72-item pool. However, transfer to arrays composed of novel stimuli showed the opposite trend. In group 24, accuracy on transfer testing trials (70%) was decidedly lower than on training trials (94%); yet, in group 72, accuracy on transfer testing trials (87%) was almost as high as accuracy on training trials (91%).

Prior basic-level object categorization studies with human adults (Homa, Cross, Cornell, Goldman, & Schwartz, 1973), human infants (Hayne, 1996), and pigeons (Wasserman & Bhatt, 1992) have also found that the more exemplars presented during the learning phase, the better the classification of novel exemplars during the transfer phase. Presumably, a large number of training stimuli enhances categorical control by increasing the salience of generic category features and/or by reducing the salience of features that are specific to each of the exemplars (Soto & Wasserman, 2010). The same pattern of results in same–different discrimination learning is consistent with the idea that pigeons initially attend to item and relation information, with more and more items increasingly taxing the birds' capacity for memorization; however, the transfer results may also reflect the pigeons' memorizing a larger number of stimuli, thereby attenuating any generalization decrement because of the sheer novelty of the testing items.

Relative Contributions of Item and Relation Information to Same–Different Learning

Several additional tasks have now been devised to assess the relative strength and speed of emergence of item and relation control in the course of same–different discrimination learning (Gibson & Wasserman, 2003, 2004; Wasserman & Frank, 2007; Wasserman et al., 2002). The invention of these tasks has been expressly guided by the plausible suspicion that item control might be stronger and emerge sooner than relation control.

For example, in Gibson and Wasserman (2003, 2004), item and relation information was arranged to provide redundant cues for discrimination mastery; this redundancy was accomplished by composing all of the same training displays from one set of 16 items (set A) and by composing all of the different training displays from a second set of 16 items (set B; see Figure 17.3, which further jittered the position of the items in the arrays to disrupt the pigeons' discrimination of item orderliness). Specifically, Gibson and Wasserman (2004) adapted the earlier methods of Gibson and Wasserman (2003) to train pigeons to discriminate displays of 16 same items from displays of 16 different items. The specific features of the items and the relations among the items could serve as discriminative features of the displays during training. Pecks to one report button were reinforced with food reinforcement in the presence of identical visual items from set A (same displays), whereas pecks to a second button were reinforced in the presence of nonidentical visual items from set B (different displays).

Gibson and Wasserman (2004) monitored item and relation control "online" with a low frequency of probe tests as the birds were acquiring the same–different discrimination. To assess the development of stimulus control by the relations among the icons, they tested the pigeons with displays of

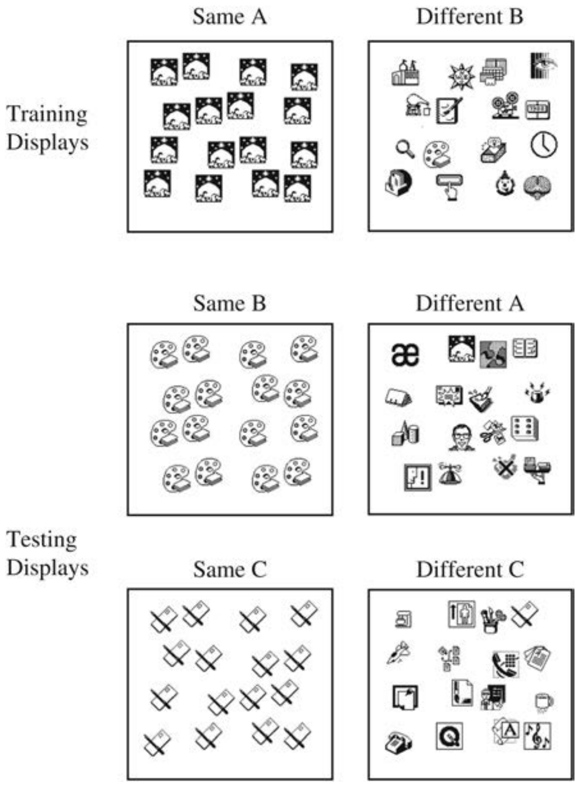

FIGURE 17.3. **A sampling of the same and different training and testing arrays used in Gibson & Wasserman (2003). The icon set (A–C) that was used to generate the items in the array is listed above each array. Reprinted from "Pigeons Learn Stimulus Identity and Stimulus Relations When Both Serve as Redundant, Relevant Cues During Same–Different Discrimination Training," by B. M. Gibson and E. A. Wasserman, 2003, *Journal of Experimental Psychology: Animal Behavior Processes, 29*, p. 86. Copyright 2003 by the American Psychological Association.**

identical and nonidentical stimuli from a third set of 16 items (set C) during each session. They also tested the pigeons with displays of identical items from set B and with displays of nonidentical items from Set A during each session; these "reversed" displays pitted relational control and item control against each other. This online monitoring procedure allows one to examine possible differences in the time-course of item and relation control during same–different discrimination learning.

The results of the Gibson and Wasserman (2004) study suggested that specific stimulus features and relational cues exerted equivalent behavioral control over the pigeons' initial choice behavior, with the specific stimulus features exerting stronger control during the final three-fourths of same–different learning. These findings thus replicated earlier research suggesting that pigeons encode the specific stimulus features and relational cues to which they were exposed, and for the first time documented the time-course of control by each kind of cue. The weaker relational control than item control in this study may be attributable to the fact that only 16 items were contained in each of training Sets A and B.

All of the research discussed so far suggests that, when they must do so to earn food reinforcement, pigeons learn to make discriminative responses to arrays of pictures that are either the same as or different from one another. But, is explicit training the only way for organisms to exhibit relational discrimination behavior? Or might other behavioral methods, that do not demand explicit same–different discrimination, disclose this cognitive capacity for abstraction? These questions inspired Wasserman et al. (2002) to devise another kind of discrimination learning method that might shed fresh light on same–different discrimination learning, in general, and on the interrelation between item and relation control, in particular. Figure 17.4 illustrates a small sampling of the many thousands of actual pictorial displays that they showed their pigeons. Pigeons saw stimulus arrays comprising 16 icons that were either the same as or different from one another. The stimuli for same and different arrays were selected from one of two sets of computer icons. Thus, there were four kinds of stimulus displays—same 1, different 1, same 2, different 2—where 1 and 2 refer, respectively, to two sets of computer icons.

Initially, the pigeons' pecks to all four kinds of displays produced food reinforcement. Later, pecks to only one of the four kinds of displays produced food reinforcement. For one illustrative pigeon (whose reinforcement contingencies are illustrated in Figure 17.4), same 1 arrays were positive discriminative stimuli (S+); hence, pecks to same 1 displays produced food reinforcement. Pecks to different 1, same 2, and different 2 arrays were negative discriminative stimuli (S–); so, pecks by this pigeon to any of these three displays did not produce food reinforcement. For different pigeons, other S+s and S–s were arranged, so that pecks to only one type of display produced food reinforcement, whereas pecks to all three of the other types of displays did not. All

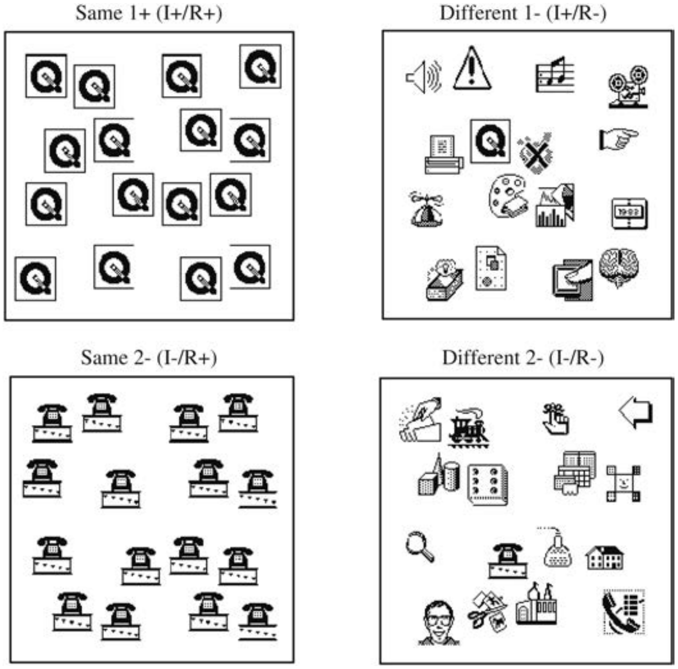

FIGURE 17.4. A sampling of the stimulus arrays used in Wasserman et al. (2002). For the illustrative pigeon, pecks to Same 1 arrays produced food (these arrays were positive discriminative stimuli), whereas pecks to Different 1, Same 2, and Different 2 arrays did not (these arrays were negative discriminative stimuli). For other pigeons, different positive and negative discriminative stimuli were arranged so that pecks to only one type of display produced food, whereas pecks to all three other types of displays did not. I = icons; R = relations; + = reward; – = nonreward. Reprinted from “Stimulus Control by Same Versus Different Relations Among Multiple Visual Stimuli,” by E. A. Wasserman, A. J. Frank, and M. E. Young, 2002, *Journal of Experimental Psychology: Animal Behavior Processes, 28,* p. 348. Copyright 2002 by the American Psychological Association.

four types of displays served as the S+ for different pigeons in the full experimental design.

Although the design of this study allowed pigeons to report same versus different relations among the items in visual arrays, it did not require the birds to do so for the receipt of food reinforcement. Nevertheless, pigeons did attend to and discriminate the relations among the 16 items as well as the individual items themselves. This conclusion is supported by the pigeons’ pattern of responding to the four categories of stimulus arrays. Responding to the S+ category was the highest of all four categories; here, the items came from the reinforced set and they exemplified the reinforced relation among those items (I+/R+). Responding to the I–/R– stimuli was the lowest of all four categories; here, the items and the relation among the items differed from the S+ category. And, responding was intermediate to the category containing items from the reinforced set, but exemplifying the nonreinforced relation among the items (I+/R–) and from the category containing items from the nonreinforced set, but exemplifying the reinforced relation among the items (I–/R+).

It is important to note that responding to arrays of items from a different set of icons that exemplified the same relation (I–/R+) as the reinforced arrays and responding to arrays of items from the same set of icons that exemplified a different relation (I+/R–) from the reinforced arrays each exceeded responding to arrays of items from a different set of icons that exemplified a different relation (I–/R–) from the reinforced arrays. The pigeons appear to have concurrently attended to the item and relational properties of these complex visual arrays on I–/R– trials. This finding suggests that the absolute salience of each of these different stimulus properties was high. Also note that by comparing the pigeons' responding to arrays of items from a different set of icons that exemplified the same relation (I–/R+) as the reinforced arrays to their responding to arrays of items from the same set of icons that exemplified a different relation (I+/R–) from the reinforced arrays, one can quantify the relative strength of item and relation control. As was true in Gibson and Wasserman (2003; 2004), the stimulus control exerted by the relation among the items was similar to that exerted by the items themselves.

We thus see that the two previous studies were quite successful in quantifying the strength and speed of learning about item and relation information. Clearly, pigeons do exhibit strong stimulus control by item and relation information even when they need not do so (see Chapters 5 and 15, this volume).

First-Order Same–Different Discrimination With Trial-Unique Stimuli

Finally, at what must surely be the set size limit, one can arrange for training arrays never to be repeated; each trial involves brand-new same or different items. This arrangement effectively means that each training display is also a testing display. Any learning must therefore go beyond the immediate processing of the training items, because those items never recur. Brooks and Wasserman (2008) reported pigeons' successful same–different discrimination learning under just these conditions using 4 × 4 arrays of trial-unique black-and-white mosaics, each mosaic comprising 8 black tiles and 8 white tiles randomly completing a 4 × 4 square. Each of four pigeons reached 80% correct choice responses on same and different trials under this two-alternative forced-choice training task involving single arrays of items that were never repeated, making every training trial also a transfer trial.

Of course, this impressive demonstration of relational learning in pigeons is likely to be limited to members of the single training class: 4 × 4 arrays of black-and-white mosaics. Shifting from these stimuli to others might very well prove to transfer little if at all, again implicating a perceptual basis to the pigeon's same–different conceptual behavior.

Conclusions on First-Order Relational Processing in Animals

Clearly, animals of several different species can reliably discriminate first-order same–different relations. The wealth of systematic data on pigeons suggests an important interplay between item and relational control, in which (a) each kind of information can control behavior when they are each relevant to the task, (b) relational control may be acquired at the expense of item control as the number of items in the training pool is increased, and (c) relational control can arise even in the absence of item repetition. The mechanisms of relational control have yet to be definitively determined, although there are strong indications that the variability or entropy of the displayed items is foundational to this cognitive behavior (Young & Wasserman, 2001).

SECOND-ORDER RELATIONAL PROCESSING IN ANIMALS

As we have discussed, animals can perceive and learn first-order same–different relations among stimuli. Even more challenging tasks require the organism to appreciate the relation between relations; these are second-order relations. In the latter case, if we have two identical apples and two identical lemons, then the relation between the apples (same) is the same as the relation between the lemons (same). Likewise, the relation between an apple and a lemon (different) is also the same relation as that between a cat and a mouse (different). Thus, learning a second-order relation requires the organism to appreciate how stimuli relate to one another and how that relationship is the same as or different from the relationship represented by other stimuli.

Initial Studies of Second-Order Relational Processing in Animals

Gillan, Premack, and Woodruff (1981) published the first paper on second-order relational processing in animals. This seminal study tested a single chimpanzee (Sarah) in a task which had the following conceptual structure: A is to A′ as B is to which of these two alternatives, B′ or C? In practice, Sarah saw three objects on a tray. The A–A′ pair of objects was presented on the left side of a tray and the B object was shown on the right side. Two other objects were presented below the tray and Sarah had to select the choice object (B′) that completed the analogy. Sarah was successful in a first version of this task (figural analogy) in which the objects were pieces of plastic varying in shape, color, and marking. She could also solve a more conceptual version of the task in which the objects were household objects and the relations were either spatial or functional (see Volume 1, Chapter 32, this handbook).

Of critical importance, Sarah was not naive at the start of the experiment. She had initially learned the symbolic meaning of pieces of plastic; she had also acquired the ability to communicate complex meanings by combining strings of plastic symbols in sentence-like structures (Premack, 1976). For that reason, Premack argued that language training was a prerequisite for Sarah's analogical reasoning; this language training may have provided the scaffolding for Sarah's symbolic encoding of the relation between relations (Premack, 1983).

Most later research on second-order relational processing in animals has used the relational matching-to-sample task (RMTS; e.g., Fagot & Thompson, 2011; Thompson, Oden, & Boysen, 1997), which can be more easily implemented with animals than Premack's analogical reasoning procedure. In this task, the subject initially sees a sample display composed of a pair of either same or different objects. Two comparison pairs are then presented after the sample display: One pair exemplifies the same relation as the sample pair, whereas the other pair exemplifies the alternative relation. Critically, these two comparison pairs are composed of items that are not common to the sample pair, thereby preventing correct relational matching responses from being based on perceptual similarity. The animal receives reward if it chooses the comparison pair instantiating the same relation as the items in the sample pair; the animal receives no reward if it chooses the comparison pair instantiating the different relation. In other words, the task can be conceptualized as "if AA then BB and if AB then CD." Success on this task has been taken to prove that the animal can reason about the relation between relations, because this task requires the processing of two sets of abstract relations and a comparison between these relations.

Thompson et al. (1997) used the RMTS task to reconsider Premack's original idea that language training is required for second-order relational processing in animals. The authors compared the performance of five chimpanzees on the RMTS task. Three had never received any form of language training, but had simply learned in a preliminary training phase to select a heart shape when they saw two identical objects in the trial, and to select an oblique line when they saw two different shapes. In other words, these "token-trained" chimpanzees had learned the meaning of two symbols—one for the identity relation and the other one for the nonidentity relation—but they never learned to combine these symbols in discursive sentences. Sarah, the "language-trained" chimpanzee, was also included as a subject in this study, as was another chimpanzee which had no preliminary token or language training and served as a control subject.

Thompson et al. (1997) found no reliable difference between Sarah and the other three token-trained chimpanzees, all of which were successful in the RMTS task, in sharp contrast with the fully naive chimpanzee which remained at chance level in this task. Thompson et al. concluded that experience with discursive string symbols is not required for solving second-order relational tasks. What might then be required for successful RMTS performance is a form of token training, in which such tokens could serve much like words in human language. These tokens might then promote a concrete encoding of the abstract relations of sameness and differentness, and further serve as anchors to retrieve and compare these relations, thereby providing the representational scaffolding for processing second-order relations.

Thompson and his collaborators wondered whether old world monkeys might also benefit from token (symbolic) training in the RMTS task, as these researchers had found was true for apes. Earlier studies had suggested that monkeys fail in the RMTS task without symbolic training. So, the RMTS task was given to rhesus monkeys which had previously been trained to associate geometrical symbols (circle or triangle shapes) with identity and nonidentity relations. In sharp contrast with the token-trained chimpanzees (Thompson et al., 1997), these token-trained macaques were unable to learn the RMTS task (e.g., Thompson & Oden, 2000; Washburn, Thompson, & Oden, 1997).

Confirmation that symbol training is of no help for monkeys was later provided by Flemming, Beran, Thompson, Kleider, and Washburn (2008), who compared humans, chimpanzees, and rhesus monkeys given two versions of the RMTS tasks. The first used nonmeaningful shapes; the second presented Arabic numerals as stimuli. Importantly, the chimpanzees and rhesus monkeys had learned the meaning of the numerals in previous studies.

Meaningfulness facilitated the acquisition of analogical matching for humans and to a more limited extent (in some subjects only) in chimpanzees. By contrast, the rhesus monkeys completely failed in the two versions of the RMTS task, suggesting that the symbolic meaning of the stimuli had no influence on their performance. Thompson and Oden (1995) concluded on that basis that a “profound disparity” exists between “analogical” apes and “paleological” monkeys. In their view, only the apes and humans would be capable of solving the RMTS task, albeit after symbolic training. Monkeys by contrast would be unable to do so, regardless of the form of prior training they received. More recent investigations of this issue in monkeys suggest that this idea should be reconsidered.

Relational Matching With Arrays of Same and Different Icons

Earlier in the chapter, we noted that abstract same–different discriminations can be established in pigeons (as well as baboons and humans) when arrays of several same and different icons, rather than pairs of same and different icons, are used as training and testing stimuli. Increasing the number of items in the training and testing arrays can decidedly enhance first-order same–different performance (e.g., Wasserman, Fagot, & Young, 2001; Wasserman & Young, 2010). Second-order relational processing has also been studied in the RMTS task with arrays of sample and comparison stimuli rather than with pairs of sample and comparison stimuli (Fagot, Wasserman, & Young, 2001).

Fagot et al. (2001) studied two baboons that had earlier received first-order same–different discrimination problems with arrays of 16 icons (e.g., Wasserman et al., 2001), but were initially naive with respect to second-order relational problems. These animals were tested in a computerized version of the RMTS task (see Figure 17.5), in which the relations of sameness and

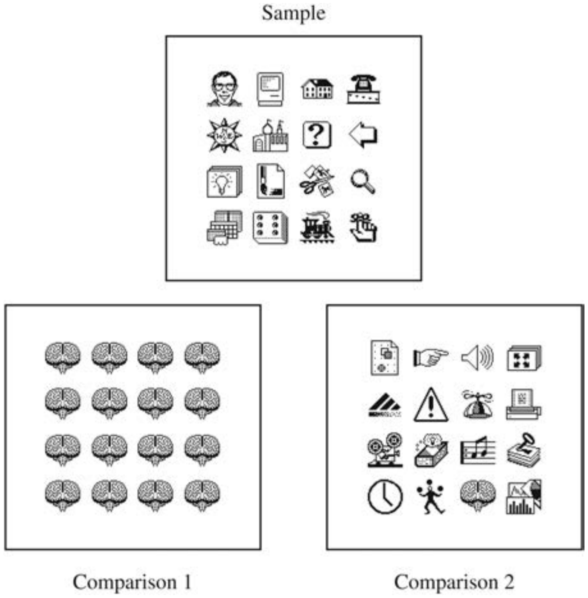

FIGURE 17.5. Relational matching task with arrays of icons. On top, the sample array, and on bottom, the comparison arrays. The animal has to choose the comparison array that matches the relationship depicted on the sample array. In this example, the relation among the items in the sample array is “different,” so the correct choice is the comparison array on the right, that also shows different items. Reprinted from “Discriminating the Relation Between Relations: The Role of Entropy in Abstract Conceptualization by Baboons (*Papio papio*) and Humans (*Homo sapiens*),” by J. Fagot, E. A. Wasserman, and M. E. Young, 2001, *Journal of Experimental Psychology: Animal Behavior Processes*, 27, p. 317. Copyright 2001 by the American Psychological Association.

difference were instantiated by arrays of icons. At the beginning of the study, the baboons were repeatedly trained with 16-icon sample and comparison arrays drawn from two independent sets of 24 icons, thereby eliminating the repetition of any items in the sample and comparison arrays on any given trial. Learning occurred slowly, but the two baboons eventually responded in excess of 80% correct.

After learning, the first critical test was to assess the generalization of RMTS performance to novel testing stimuli; here, the two baboons continued to perform at above chance levels (70% correct) with sample arrays drawn from a third pool of 24 icons that had never before been seen. Such reliable transfer across stimulus sets suggests that the baboons had indeed learned an abstract and generalizable concept. As in the case of first-order relational learning, the lower level of testing performance compared to training performance (84% correct) can be taken to reflect the baboons' effective processing and memory of individual stimuli despite the irrelevance of such information for solution of the RMTS problem. Fagot et al. (2001) concluded from their study that language or symbol training is not necessary for nonhuman primates to appreciate higher-order relations between relations, contrary to Thompson and Oden's (1995) initial theoretical position.

The possibly surprising success of the baboons in the RMTS task with arrays rather than pairs of sample and comparison items prompted Cook and Wasserman (2007) to replicate that procedure with pigeons. Cook and Wasserman trained four pigeons with the same general training procedure using 16-icon arrays as in Fagot et al. (2001). As was true for baboons, the pigeons' performance improved during training. After a great many training trials, the birds performed above 70% correct and transferred this discrimination to brand-new sets of stimuli, although at a slightly lower level of accuracy. Later tests further showed that perceptual changes in the sample displays—including, for instance, alterations in icon alignment, size, or orientation—produced little disruption in pigeons' RMTS performance, suggesting some measure of robustness in the pigeons' RMTS behavior.

Two-Item RMTS Task: Positive Consequences of Dogged Training in Monkeys

We noted previously that initial attempts to teach monkeys RMTS with pairs of items were utter failures, in sharp contrast to the studies with token- and language-trained chimpanzees (Thompson & Oden, 2000). We further noted that baboons and pigeons can solve RMTS tasks when same and different arrays containing several items, rather than stimulus pairs, are used as sample and comparison stimuli (Cook & Wasserman, 2007; Fagot et al., 2001). One interesting feature of the work of Fagot et al. (2001) and Cook and Wasserman (2007) is that success with the multielement RMTS task only emerged after what Premack (1988) labeled *dogged training* involving thousands of training trials. Later research explored the possibility that dogged training might promote the appreciation of relations between relations in baboons, even in the original version of the RMTS task involving pairs of stimuli as sample and comparison stimuli.

Extensive dogged training was made possible by the deployment of a new automated test system (see Fagot & Bonté, 2010; Fagot & Paleressompoulle, 2009), in which the test stations are available ad lib to a social group of monkeys for self-testing on a 24 hr schedule. This paradigmatic shift has had numerous positive consequences in comparative cognition studies, among them improved animal welfare (Fagot, Gullstrand, Kemp, Defilles, & Mekaouche, 2014) and the possibility of testing a large number of subjects voluntarily performing a massive number of trials (Fagot & Bonté, 2010; Fagot & Paleressompoulle, 2009).

Using this system, Fagot and Thompson (2011) tested a large number of baboons (N = 29) of various ages with a computerized version of the task shown in Figure 17.5, displaying only two items in each array. Continuous training was conducted over approximately 4 weeks. Many baboons did not learn, which is unsurprising given prior failures to teach RMTS to language-naive and even token-trained rhesus monkeys (Thompson & Oden, 2000). Nevertheless, six baboons ultimately did learn the RMTS task; their accuracy progressively rose, reaching or exceeding 80% correct after 17,000 to 30,000 training trials. Note that this number of trials is far larger than ever given to rhesus monkeys (e.g., 1,000 in Flemming et al., 2008; 10,000 in Flemming, Beran, & Washburn, 2007), which could explain why the baboons succeeded in learning this task. In addition, the gradual increase in accuracy suggests that no baboon suddenly comprehended the relational nature of the task. Such progressive learning implicates associative learning mechanisms and calls for additional tests to confirm the relational nature of the cognitive processes at work.

Two transfer tests were subsequently administered by Fagot and Thompson (2011) to investigate the nature of the cognitive processes used by the baboons. First, the animals were tested with stimulus pairs created from a pool of 90 novel stimuli. All of the baboons except one (incidentally, the oldest) continued to perform at above chance levels of accuracy with these novel stimuli, albeit at a lower level (65%) than with the original training stimuli. The second transfer test used a cross-mapping procedure. Cross-mapped trials followed the same design as in Figure 17.5, except that one of the stimuli of the sample pair was also used to create the nonmatching (incorrect) comparison pair. For example, if the sample pair was AA, then the correct comparison pair might be BB and the incorrect comparison pair might be AC. We reasoned that the baboons would (erroneously) select the nonmatching pair on cross-mapped trials if they gave priority to processing the items over the relations instantiated by the items. By contrast, the baboons should give priority to the matching pair if they attended to the relations shown by the stimulus pairs. The results were clear-cut. All five of the baboons that had demonstrated positive transfer to the new testing stimuli reliably selected the relational matching pair on 72% of the cross-mapped trials, thus confirming that their cognitive strategy was not strongly based on correspondence of individual items in the sample and comparison stimuli.

Truppa, Piano Mortari, Garofoli, Privitera, and Visalberghi (2011) published confirmatory data attesting to the fact that dogged training can support learning of the RMTS task. These authors studied capuchin monkeys (*Cebus apella*) which were trained with the RMTS procedure shown in Figure 17.5, displaying two, four, or 16 items in each array. One of the five capuchins learned the task and later showed positive transfer to new stimuli. This performance required a very substantial number of training trials, in the same range as the baboons in Fagot and Thompson (2011).

The studies presented so far have used pairs (Fagot & Thompson, 211; Truppa et al., 2011) or arrays of shapes (Fagot et al., 2001; Flemming et al., 2007; Truppa et al., 2011) as the sample and comparison stimuli in RMTS. Admittedly, this task has a conceptual structure which resides at a lower level of complexity than the gold standard of second-order relational processing: analogies in humans. Consider, for instance, the following verbal analogy: "I am to dancing what Roseanne is to singing." Here, the relation between the speaker and dancing remains unspecified until we have processed the relation between Roseanne and singing. Clearly, this task is different from the RMTS task, because the presentation of the sample in the RMTS task suffices to determine the relation (sameness or difference) to be processed in comparison step of the trial.

Fagot and Maugard (2013) devised a bidimensional version of the RMTS task to more closely approximate for baboons the complexity of human verbal analogies. In this research, the baboons first saw a pair of objects which were defined along two dimensions: color and shape. The sample pair could, for instance, comprise one yellow and one red object of the same shape or a square and a circle of the same color (see Figure 17.6). These bidimensional stimulus pairs were presented as samples on two kinds of trials. On *color* trials, the comparison pairs comprised vertical bars of identical shapes, but whose colors could vary. Because the shape of the bars was not a discriminative cue on the color trials, the baboons had to pay attention to the relations expressed by the color cues, and match the sample and comparison pairs accordingly. The same logic was followed for the second type of trials; on *shape* trials, the comparison pairs comprised stimuli of the same (white) color, but whose shapes could vary. Because the color of the comparison pairs conveyed no information on the shape trials, the baboons had to match the sample and comparison pairs in accord with the relations expressed by the shape dimension.

Fagot and Maugard (2013) observed accurate performance in this task by a total of four baboons. These

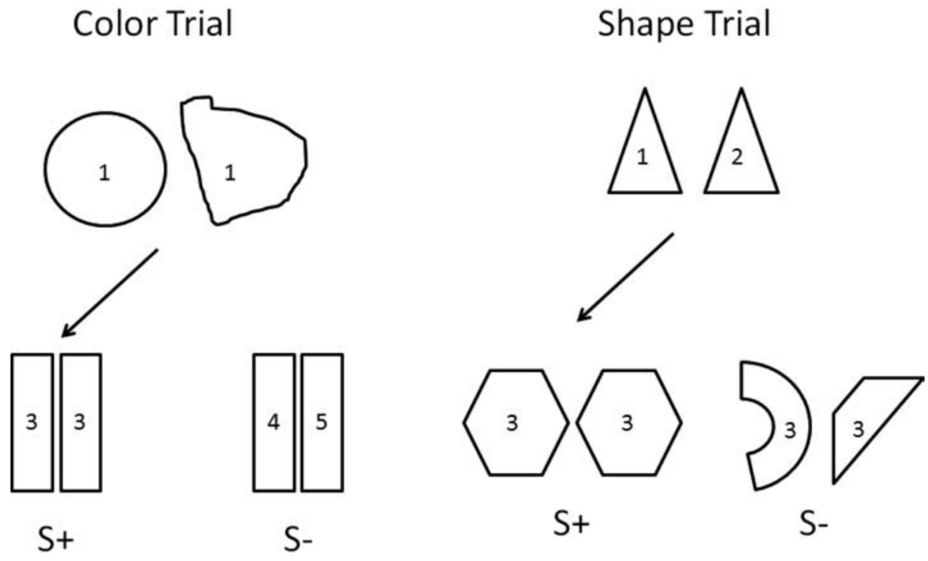

FIGURE 17.6. Illustration of the testing procedure of Fagot and Maugard (2013). These two panels illustrate testing trials in which color (left) and shape (right) were the relevant dimension. Colors are indicated by different numerals. The sample pair was shown in the middle of each panel and the comparison pairs were shown on the left and right sides (S+ = target pair, S– = foil pair) of each panel. Each pair comprised two items that might differ by shape, color, or both. On color trials (left), the comparison stimuli differed by color, not shape, thereby forcing the baboon to match the sample and comparison pairs on the basis of color. On shape trials (right), the comparison stimuli differed by shape, not color, thereby forcing the baboon to match the sample and comparison pairs on the basis of shape. This figure illustrates the procedure for Same trials, but the same logic was followed for Different trials.

animals achieved 80% correct or higher performance after training on color and shape trials. Moreover, one baboon's performance remained above chance when the two relations expressed by the sample were inconsistent, for instance when the sample pair contained two different shapes (expressing the different relation) both drawn with the same color (expressing the same relation). Finally, scores obtained on cross-mapped trials, in which the foil pair nevertheless shared one item with the sample pair, averaged well above chance (77% correct), but was slightly lower than on normal (non–cross-mapped) trials (79% correct). These two results suggest that the baboons processed the relations and the items in this task, with priority given to relational cues when perceptual and relational cues conflicted. Note that this level of performance could only be achieved after an average of 58,541 trials per monkey, and was therefore obtained after decidedly dogged training.

All of the previous studies underscore the importance of dogged training on animals' mastering the RMTS task. Two additional studies should be discussed for a balanced presentation of the literature. First, Vonk (2003) trained and tested four orangutans and one gorilla in a computerized version of the delayed RMTS task. These apes had earlier received identity matching-to-sample training with single stimuli, but they were initially naive with regard to the processing of relations between relations with pairs of stimuli. Four of the five apes demonstrated an immediate understanding of second-order relations; they could match, for instance, two blue shapes with two red shapes. Above-chance performance required only minimal training and was sometimes obtained in the first testing session.

Second, in a more recent project, Smirnova, Zorina, Obozova, and Wasserman (2015) tested RMTS performance in two hooded crows (*Corvus cornix*). Initial training with identity matching trials had already suggested that these animals might have acquired a general identity concept, but neither of the crows had been given the RMTS task. In sharp contrast with earlier reports (e.g., Fagot & Thompson, 2011; Truppa et al., 2011), but consistent with Vonk's (2003) ape work, the crows spontaneously displayed high levels of relational responding, and did so in several versions of the RMTS task requiring an appreciation of the relations expressed by stimulus size, shape, and color. This documentation of RMTS behavior is particularly noteworthy because the crows exhibited relational matching behavior (averaging 78% correct) that was as accurate as their identity matching behavior (averaging 73%) on trials in which one of the comparison pairs was identical to the sample pair. Although physical identity could have guided the crows' choice behavior on identity matching trials, physical identity could not have done so on relational matching trials, because no physical matches were possible between the sample pairs and the correct comparison pairs. These results suggest that physical identity contributed little or nothing to the crows' RMTS performance; relational processing seems to have been of prime importance to controlling the birds' choice behavior.

Why apes and crows were immediately successful in these latter two studies (Smirnova et al., 2015; Vonk, 2003) is unclear and remains a matter for future research. Part of the explanation may be due to the fact that these subjects had received extensive identity matching-to-sample training prior to RMTS testing. Such identity training may have enabled these animals to grasp a broadly applicable concept of sameness that could later be applied to RMTS testing. Nevertheless, animals in other studies (e.g., Cook & Wasserman, 2007) failed to exhibit immediate second-order transfer after having received first-order training.

Two-Item RMTS Task in Monkeys: Perceptual, Relational Processing, or Both?

Evidence suggests that language-naive baboons, rhesus monkeys, and capuchin monkeys all can achieve high levels of performance on the RMTS task after extensive training. Evidence further suggests the involvement of an abstract cognitive capacity, revealed by accurate responding even on cross-mapped testing trials (Fagot & Maugard, 2013; Fagot & Thompson, 2011), where stimulus identity should lead baboons to choose the incorrect comparison stimulus.

Are an animal's representational structures in RMTS purely abstract or are they also grounded on perceptual features, as already documented for first-order same–different discrimination tasks using visual arrays as stimuli (e.g., Fagot et al., 2001; Young & Wasserman, 1997)? The following results suggest that perceptual and relational processing contribute to performance on the RMTS task.

The first data on this issue come from the cross-mapped trials of Fagot and Thompson (2011). As noted earlier, the baboons achieved above-chance performance on these trials, thus implicating relational processing; however, a close look at the data divulged that accuracy on cross-mapped trials (72% correct) was lower than on normal, non–cross-mapped trials (77% correct). This small, but statistically reliable disparity indicates that the sharing of stimulus features between the sample pair and the incorrect comparison pair deleteriously affected the baboons' RMTS performance, suggesting that the processing of same–different relations is not completely independent of the processing of stimulus features.

Flemming, Thompson, and Fagot (2013) published even stronger documentation of the interaction between perceptual and relational processes. These authors tested baboons and humans with a version of the RMTS task involving arrays of 4 items as the sample and comparison stimuli. The subjects from both species were initially trained with arrays containing either four identical items (same relation) or four different items (different relation). After training with all same and all different displays, transfer was assessed using different *mixtures* of stimuli as samples (the comparison arrays continued to be composed of all identical or all nonidentical items). On probe trials, one of the shapes in the sample arrays was either repeated three times (e.g., AAAB or ABAA), two times (e.g., ABAB or AABB), or only one time (e.g., ABCD). The authors reasoned that the subjects should match all three of these types of sample arrays with the different comparison arrays, if the subjects based their responding on the abstract relations of sameness and difference. By contrast, the subjects might match the sample mixtures depicting mostly same items (e.g., BAAA) with the all same comparison arrays (e.g., AAAA) and complementarily match the sample mixtures depicting mostly different items (e.g., ABBC) with the all different comparison arrays (e.g., ABCD), if the subjects based their responding on the proportion of common individual items within the arrays. Matching this way can be construed as perceptual process, on the basis of the shared identity of the items in the arrays.

In this case, the baboons and humans exhibited highly similar response profiles, suggesting that both species adopted a common cognitive strategy in performing this task. The subjects from both species matched all of the various sample mixtures to the different comparison arrays, with the proportion of different response scores all exceeding .60. This strategy demonstrates that the relational structure of the sample arrays was the primary variable controlling subjects' choice performance. Still, the proportion of different responses increased as the sample mixtures increasingly contained more different items, suggesting that baboons and humans were primarily controlled by the relational structure of the sample displays, but that they were secondarily controlled by the perceptual variability of the sample displays.

A third project (Fagot & Parron, 2010) further confirmed the interplay between perceptual and relational processing in baboons. It used pairs of adjacent color patches as stimuli in the RMTS task. Because baboons have a bias for a local mode of visual processing over a global mode of visual processing (Fagot & Deruelle, 1997), the distance separating the two color patches was kept minimal (two pixels) from the onset of the RMTS training to facilitate the processing of the stimulus duos as pairs, rather than as independent items. Six baboons learned this RMTS task after extensive training and later showed positive transfer when new stimulus colors and sizes were introduced. Interestingly, the baboons' performance collapsed when the separation between the items was increased from two to 60 pixels, demonstrating that accurate performance could only be obtained under some perceptual constraints. Importantly, the effect of gap size was abolished when Fagot and Parron (2010) later arranged an extended training procedure (entailing from 6,400 to 8,600 training trials) to progressively increase the size of the within-pair gap.

Maugard, Marzouki, and Fagot (2013) further tested a subset of the baboons studied by Fagot and Thompson (2011) and Flemming et al. (2013). Its main innovation was to introduce another matching task between the presentation of the sample pair and the comparison pairs in the RMTS task. Specifically, the subject first saw the RMTS sample pair. The subject then saw the sample and comparison pairs of an identity matching-to-sample (IMTS) task, which served as the interpolated task; the subject had to match these single sample and comparison stimuli by shape. An incorrect identity matching response aborted the trial at this stage, but a correct response triggered the display of the comparison pairs of the RMTS task; the baboon now had to select the comparison pair instantiating the same relation as the initial RMTS sample pair to receive reward.

Introducing the interpolated IMTS task had a detrimental effect on RMTS performance compared to a control condition involving the same RMTS task with delays between the sample and comparison pairs matched to the time taken to complete the interpolated IMTS task. This interference effect accords with dual-task performance with human subjects, which implicates the contribution of working memory to the formation of analogies (e.g., Morrison, Holyoak, & Truong, 2001). Perhaps more interestingly, the negative effect of the interpolated task was more robust for different sample trials than for same sample trials (same trials: dual task = 74% correct, control task = 79% correct; different trials: dual task = 46% correct, control task = 81% correct).

Earlier studies with these same baboons had demonstrated that they do in fact process the relational structure of the RMTS task. This study involving IMTS and RMTS tasks further showed that processing of the different relation may be more demanding in terms of memory load than processing the same relation. A plausible account of this effect is that the different displays contain a richer set of perceptual information than the same displays. We interpret this selective effect of memory load on different trials as an additional argument supporting the idea that responses in the RMTS task result from the processing of perceptual and relational cues.

Conclusions on Second-Order Relational Processing in Animals

The studies reviewed here strongly suggest that apes (Thompson et al., 1997), baboons (e.g., Fagot & Thompson, 2011), capuchins (Truppa et al., 2011), crows (Smirnova et al., 2015), and pigeons (Cook & Wasserman, 2007) all have sufficient cognitive resources to accurately perform RMTS. Admittedly, the standard RMTS task does afford several perceptual cues (e.g., the identity of the individual stimuli in each display as well as variability in the number and proportion of each type of item in the sample and comparison stimuli) that animals might use in choosing the correct response. Some authors (e.g., Penn, Holyoak, & Povinelli, 2008) have contended that the availability of these perceptual cues precludes a definitive demonstration that animals use abstract reasoning to solve this task. However, considerable evidence has now been collected showing that priority is not always given to these perceptual cues (e.g., Fagot & Thompson, 2011; Flemming et al., 2013; Smirnova et al., 2015).

Another important point is that animals can be taught to apprehend the relations between relations by many means. The initial approach in the area was to contrive a symbolic representation of the RMTS task by way of language (Gillan et al., 1981) or token training (e.g., Thompson et al., 1997). (In the next section, we further consider the role of symbolic or language training in the developmental literature on children.) However, symbol training is surely not the only path to achieving a high level of responding to second-order relations, contrary to Premack's (e.g., 1983) original claim. Dogged training remains a slow, but effective option (e.g., Fagot & Thompson, 2011; Truppa et al., 2011). Finally, a rich prior history of first-order relational learning (including IMTS) may promote successful transfer to RMTS without any explicit RMTS being given (Smirnova et al., 2015; Vonk, 2003).

It might be the case that these different methods of training affect the cognitive processes at work in solving the RMTS task; further studies are needed to directly compare the cognitive consequences of these methods. Nevertheless, the findings reviewed here surely suggest that these diverse training methods effectively promote at least the basic cognitive substrates for second-order relational processing, in particular, the capacity to generalize relational responding to novel stimuli as well as to give priority to conceptual over perceptual cues, even when these cues conflict with one another.

DEVELOPMENT OF RELATIONAL LEARNING

Human relational and analogical reasoning capacities are often vaunted to be twin pinnacles of cognition (e.g., Hofstadter, 2001; Holyoak, Gentner, & Kokinov, 2001; Penn et al., 2008). But, these capacities appear to be limited and imperfect in infants and young children—much as they are in nonhuman species. And, as we shall see, several parallels can be drawn between the cognitive behavior of young children and nonhuman animals (see Volume 1, Chapter 20, this handbook).

Tracing the development of relational and analogical reasoning is critical for fully understanding the roots and mechanisms underlying these abilities. During development, children advance from perceptually based to relationally based processing, because of maturational processes as well as innumerable life experiences. Nonetheless, for children and adults, perceptual processes still seem to be intimately involved in advanced relational processing.

First-Order Relational Processing in Infants and Children

Compared to the extensive literature in animals, rather little research has investigated first-order same–different relations in human infants and young children. Tyrrell, Stauffer, and Snowman (1991) reported that 7-month-olds are sensitive to first-order same–different relations. Two groups of infants were first familiarized to either a pair of identical toys (identity group) or to a pair of nonidentical toys (different group). Tyrrell et al. were interested in documenting an early ability to detect same–different relations rather than in teaching infants to detect these relations, so only one pair of items was presented, twice, to each of the two groups. Later, all of the infants were given a novelty preference test in which they were simultaneously presented with two pairs of completely novel toys: one pair portraying identical objects and the other pair portraying nonidentical objects. If the infants were retaining the relation instantiated by the habituation pair, then they should show a preference for the testing pair instantiating the novel relation. Indeed, in both groups, infants' fixation times were longer for the relation that had not been experienced during habituation. Thus, Tyrrell et al. interpreted their results as evidence for infants' spontaneous encoding of abstract same and different relations.

However, Ferry, Hespos, and Gentner (2015) failed to replicate Tyrrell et al.'s (1991) findings. Specifically, these researchers did not find that 7-month-olds could distinguish between same and different relations after the presentation of just one pair of items. In their second experiment, Ferry et al. used a habituation–dishabituation paradigm in which testing was conducted with a single pair of objects, and again divided the infants into two groups: one familiarized with pairs of same objects and the second familiarized with pairs of different objects. Rather than presenting only one exemplar pair, the researchers showed infants four pairs of objects that were repeatedly presented until habituation occurred (on average, after seven trials). At testing, the infants looked significantly longer (that is, they dishabituated) at novel objects instantiating a novel relation than at novel objects instantiating the habituated relation. Ferry et al. concluded that the variety of exemplars experienced during the habituation phase allowed the infants to extract the common relational pattern and, thus, to form an abstract concept.

These findings closely accord with other results in the adult human (Gick & Holyoak, 1983; Homa & Vosburgh, 1976; Loewenstein, Thompson, & Gentner, 1999) and animal categorization literatures (Castro et al., 2010; Castro, Wasserman, Fagot, & Maugard, 2015; Katz & Wright, 2006; Maugard, Wasserman, Castro, & Fagot, 2014; Truppa et al., 2011; see also Chapter 5, this volume), in which multiple instantiations of a relational concept increase the salience of abstract properties of stimuli (see Chapter 6, this volume). According to Gentner and her colleagues (Christie & Gentner, 2010; Gentner & Namy, 1999; Markman & Gentner, 1993), presenting several exemplars promotes a comparison process from which stimulus commonalities are revealed. As we shall see, this comparison process is critical for perceiving second-order relations as well.

An interesting additional observation in Ferry et al. (2015) was that infants' looking times were the longest of all to novel items and novel relations. This finding suggests that, as in the animal studies reviewed earlier—especially that of Wasserman et al. (2002)—item and relational processing co-occur. Children perceived the common relation between the objects and they were also sensitive to whether those particular objects were familiar or novel.

In another study, which attempted to find the youngest age at which infants could discriminate same and different relations, Addyman and Mareschal (2010) used a standard habituation/dishabituation paradigm with infants who were 4 and 8 months of age. Half were habituated to the same relation, whereas the other half were habituated to the different relation. Up to a maximum of 19 pairs of unique photographic stimuli (a relatively large number) depicting either two same or two different items were presented during the habituation phase. In the testing phase, two novel same pairs and two novel different pairs were shown. Only the 8- month-olds who had been familiarized to pairs of either same or different objects showed a significant increase in looking when shown pairs of new objects portraying the novel relation.

In the second experiment, Addyman and Mareschal (2010) adapted the anticipatory eye movement paradigm developed by McMurray and Aslin (2004) to explore the understanding of same–different relations by the same 4- and 8-month-old infants who had participated in the first experiment. Their adaptation showed a pair of geometric shapes moving together behind an occluder and reappearing 3 s later on either the left or the right side of the occluder. If the shapes were the same as one another, then they moved in one direction; but, if the shapes were different from one another, then they moved in the opposite direction. If the infants could distinguish between same and different relations, then they should have learned to correctly anticipate the reappearance of the shapes. The 4- and 8-month-olds learned to anticipate the reappearance of the different pairs, but not the same pairs; likewise, they transferred their anticipatory behavior to novel different pairs, but not to novel same pairs.

For human adults, the concepts of same and different are assumed to be logical opposites of one another; if one knows what same means, then one necessarily knows what different means. Given Addyman and Mareschal's (2010) findings, an equivalent understanding of same and different does not appear to be true for infants nor, for that matter, for animals as well (Young & Wasserman, 1997). One possible reason, suggested by Smith et al. (2008), may be that, to establish that two items are the same, one must confirm that all properties of the objects are equivalent, whereas any single discrepancy establishes that two items are different. As we will discuss later, infants' ability to explore all possible alternatives is poor, perhaps because of their rather limited working memory (perhaps for pigeons too; Gibson, Wasserman, & Luck, 2011). Overall, Addyman and Mareschal's results disclose some sensitivity of infants to same–different relations, but they also reveal the absence of a fully-formed same–different concept equivalent to that of older children and adults.

Ferry et al. (2015) also found that attention to individual objects can interfere with same–different processing. If infants were allowed to play with some of the objects before the habituation/dishabituation task—possibly calling attention to the details of those objects—and those familiar objects were later presented in a new relation, then infants did not show dishabituation; that is, they did not respond on the basis of the relation between the objects. These results are not unprecedented. Young children make inferences about new objects from learned categories on the basis of perceptual similarity rather than on categorical information (Sloutsky et al., 2007). Also, when two matching choices are given—one based on the relations between objects and the other based on object similarity—young children strongly prefer object similarity over relational matches (Christie & Gentner, 2010; Richland, Morrison, & Holyoak, 2006).

Second-Order Relational Processing in Infants and Children

As we have seen, despite of some limitations, infants and young children do seem to be able to understand first-order same–different relations. However, analogical reasoning—requiring the appreciation of second-order relations—appears to take much longer to develop; although its rudiments may be seen at 2 years of age (Singer-Freeman, 2005), analogical reasoning does not approach adult-like performance until adolescence (Richland et al., 2006).

A formal analogy is commonly represented as A is to B as C is to D. In typical research projects, an organism must infer item D after being given pair A–B and being prompted with item C. Completing an analogy requires several prior steps: (a) the general relation represented by items A and B must be part of the subject's knowledge base, (b) the relation instantiated by items A and B must be inferred at the time when they are presented, and (c) that relation must be applied to item C to generate the correct answer.

Goswami and Brown (1990b) observed that studies reporting children's failures to solve analogies before the age of 12 were using quite complex relations to form the analogies. For example, children were asked to provide the completing term for "bird is to air as fish is to X" (Levinson & Carpenter, 1974) or "automobile is to gas as sailboat is to X" (Gallagher & Wright, 1977). Providing the solution to these analogies requires knowing the relation of animals to their ecological habitat or understanding the relation between mobile machines and the source of energy propelling them. The lack of knowledge of these relations rather than the capacity to solve analogies may be the real reason why young children failed in these tasks. Goswami and Brown suggested that using relations with which young children are actually familiar might yield decidedly different results.

Indeed, when Goswami and Brown (1990b) presented children with partial analogies involving familiar objects such as snow or apples and familiar actions such as melting or cutting, children as young as 3 years of age could successfully complete a large number of them. There was also developmental improvement, with 4-year-olds successfully completing more problems than 3-year-olds. This improvement appeared to be due, not to an age-related increase in the ability to reason by analogy, but rather to an increasing ability to understand the relations underlying the analogy. As children become increasingly familiar with such causal relations as melting or cutting, they become better able to transfer these relations to other domains. Because 4-year-olds tend to know more about these relations than do 3-year-olds, they can solve more analogies based on them.

Yet, even if a first-order relation is within their realm of knowledge, children may still fail to infer the correct relation that connects elements A and B. Singer-Freeman (2005) tested 30-month-old children using familiar objects and familiar relations. However, only when the relations connecting the A and B terms were explicitly demonstrated (for example, how yarn can be stretched) did children under 3 years of age solve the analogies. It seems that, up to that age, children have difficulty inferring the relation between elements; that difficulty then hinders their ability to solve formal analogies. This inferential difficulty may be due to young children's tendency to attend to the particular items instantiating the relation rather than to the relation itself. As a consequence, the objects' appearance or other irrelevant attributes can exert a strong influence on children's analogical reasoning behavior. Indeed, errors in young children's analogical reasoning are characterized by difficulty ignoring irrelevant properties of the stimuli involved in the analogy task (e.g., Gentner & Rattermann, 1991; Richland et al., 2006).

Addressing the developmental and attentional trends in the evidence, Gentner and Rattermann (1991; Rattermann & Gentner, 1998) proposed that a *relational shift* occurs between the ages of 4 and 5, from attention to common object properties to attention to common relational structure. They further suggested that the mechanism underlying this relational shift is not tied to the chronological age of a child, but is instead determined by the amount and kind of relational knowledge that the child possesses; so, until children acquire adequate knowledge, they will fail to reason analogically (Goswami, 1992, 2001; Goswami & Brown, 1990b).

In addition to the acquisition of knowledge, stronger executive functioning—in the form of increased working memory capacity (Halford, 1993)—and increased inhibitory control (Richland et al., 2006) for coping with relational complexity have been proposed as important mechanisms underlying developmental changes in analogical reasoning. Thibaut, French, and Vezneva (2010) studied analogy completion in 6-, 8-, and 14-year-olds. These researchers used abstract shapes, colors, and textures to avoid the influence of prior knowledge. The A–B pair could contain one specific shape and a similar, but transformed shape (e.g.,, a half ring and an elongated half ring), item C would be a completely different shape, and the children had to choose item D representing the same relation as the relation between A and B. Choices could include, in addition to the correct response, items sharing no perceptual features with A, B, or C, or items sharing perceptual features with A, B, or C. When choices contained perceptual similarities, particularly with item C, the number of errors was greater, especially in young children, than when no competing perceptual choices were presented, suggesting a poor capacity to inhibit attending to distracting information. Interestingly, 6-year-olds, who made many mistakes, were as fast to respond as 14-year-olds, who made very few mistakes. Thibaut et al. suggested that the reason for 6-year-olds' prompt responding is that they were not exploring all of the possible choices, but simply selecting the first salient item, probably because of a lack of inhibitory control, but perhaps also because of limited working memory that could not hold all of the possible solutions. According to Thibaut et al., this kind of hasty decision process speaks to poor executive control in young children, and cannot be explained by a lack of knowledge (e.g., Goswami & Brown, 1990a) or a shift in relational processing (Rattermann & Gentner, 1998). Richland et al. (2006) also found that relational complexity and irrelevant information can interfere with analogical reasoning, regardless of the child's knowledge of relations; therefore, limits in information processing during the early stages of development must be taken into account to fully understand the unfolding capacity for analogical reasoning.

Consensus holds that the prefrontal cortex is a critical brain area involved in executive control functions, such as working memory or inhibitory control. The human prefrontal cortex is much larger than in other primates, and birds do not even have a prefrontal cortex (although the avian nidopallium caudolaterale may serve analogous functions; e.g., Shimizu, 2009; see also Volume 1, Chapters 12 and 24, this handbook). So, it may be that poor working memory and inhibitory control, because of a lack of supporting brain structures, is also part of the reason for limited analogical capacities in nonhuman animals.

Facilitators of Second-Order Relations

In an attempt to encourage analogical reasoning in 2-year-olds, Singer-Freeman (2005) showed two examples of the same relation with different items (A_1–B_1 and A_2–B_2), before presenting the second term in the analogy completion task. Such increased exposure to the target relation probably helped the children solve the analogies; however, Singer-Freeman did not systematically manipulate this variable, so its influence is unclear.

Subsequently, Christie and Gentner (2010) examined the effect of including several examples of the first term of an analogy task. Arguing that the process of comparing two exemplars of the same relation would highlight their common structure, these investigators presented one group of children with two objects in a specific spatial configuration, followed by two other objects in the same spatial configuration; both pairs were placed next to one another and could be seen simultaneously, thereby encouraging the comparison process. Another group of children was presented with only one pair of objects. Then, 3- and 4-year-olds were given the choices of either a relational match (showing the same spatial relation as initially presented) or an object match (showing one or two of the same objects as initially presented). Regardless of age, children in the comparison group chose relational matches much more often than children in the no-comparison group. This result is consistent with the notion that the comparison process, prompted by the presentation of multiple exemplars, facilitates the extraction of common relations, as we have seen is true for first-order relations in young children and animals.

We should note that relational similarity involving spatial relations has also been studied in apes. For example, Haun and Call (2009) gave bonobos, chimpanzees, gorillas, and orangutans, as well as 3- and 4-year old children, a task in which two rows of three cups each were placed on an inclined platform: one above and one below, in such a way that each cup in one array had a corresponding cup instantiating the same relative position in the other array. The alignment between the upper and lower rows was not perfect: the cups in one row were distributed along the full length of the edge, whereas the cups in the other row occupied approximately two thirds of that distance, so that a simple proximity strategy would not necessarily lead to success. The subjects had to find a food reward (a small toy, in the case of the children) under one of the cups in one row after observing the reward being hidden under one of the cups in the other row. The baited cups in the two rows had the same relative position within the row, so that a relational mapping strategy (e.g., choose left if the observed baited cup was on the left) would always provide success, but no explicit training to teach this strategy was given.

Older children, bonobos, and chimpanzees, but not younger children, gorillas, or orangutans displayed performance consistent with the use of a spatial relational similarity strategy. Thus, Haun and Call concluded that relational similarity does not require symbolic training (as Premack, 1983, argued) or the use of language, although language and symbol systems may facilitate relational reasoning, as we shall see next.

Despite the noteworthy cognitive feats of animals reviewed earlier, we cannot deny that human adults' analogical reasoning behavior surpasses that of animals. It could be that there truly is a qualitative distinction between the cognitive processes of humans and nonhuman animals (Penn et al., 2008). Or it could be that, beyond sharing the fundamentals of cognition, behavioral differences arise because of the participation of human language and culture.

Christie and Gentner (2014) explored these possibilities by testing young children with a RMTS task, similar to the animal task described earlier. Two items (colored shapes) were presented that could be the same as or different from each other.

Children had to choose between pairs of novel items: one pair containing two same items and another pair containing two different items. The 2- and 3-year-olds failed this task; they did not spontaneously choose the matching relation. However, when children were given prior training with the words *same* and *different* (teaching a puppet the meaning of these words), 3-year-olds (but not 2-year-olds) could successfully solve the RMTS task, thus showing that verbal labels facilitate the acquisition of relational concepts.

Christie and Gentner (2014) also tested the role of verbal labels in a different way. In another experiment, the sample pair was given a novel label (e.g., truffet) and the children were asked which of the two choice pairs was also a truffet. Now, 2- and 3-year-olds succeeded in the RMTS task. Christie and Gentner suggested that the novel label invited comparison between the sample pair and the choice pairs: The task of finding the other truffet probably led children to compare the sample with each of the alternatives, and thereby to discover the common relational structure between the sample and the correct alternative, implying an interplay between linguistic symbols and comparison processes.

However, even if language and culture can facilitate and vault analogical reasoning to its highest levels, the research described earlier with baboons, apes, crows, pigeons, and prelinguistic infants suggests that language or symbol training is unnecessary for disclosing at least the basics of this cognitive capacity. Importantly, the baboons and pigeons in that earlier work had been trained to discriminate same from different collections of items before training on the RMTS task; this is normally the case for prelinguistic infants as well. Such prior learning of first-order relations may provide the scaffolding that facilitates the processing of second-order relations (although it may not always be necessary; see Haun & Call, 2009).

CONCLUSION

Relational reasoning, particularly appreciating the relation between relations that is central to forming analogies, represents what contemporary theorists deem to be the pinnacle of human cognition. Such relational cognition promotes our adaptation to complex and ever-changing circumstances; it also allows us to go beyond immediate sense experience to engage in abstract thought. The evidence that we have reviewed in this chapter suggests that such abstract relational thought does not arise *de novo*; rather, it develops in humans, and its evolutionary roots can be seen in nonhuman animals. To embrace these discoveries, we propose an emerging analytical perspective on the development and evolution of relational thinking, which suggests that perceptual and relational processes are inextricably interrelated in humans and animals.

From Perception to Conception

Although individual stimuli may be processed in terms of their constituent features, thereby supporting their identification and memorization, two or more stimuli invite comparative judgments. Primary among those comparative judgments is sameness and its complement difference. Evidence suggests that relational same–different control does not emerge distinct from perceptual control; the processing of individual stimuli is foundational to and continuous with the processing that occurs between or among stimuli. This finding not only holds true for processing first-order same–different relations, but for processing second-order same–different relations too, as in the case of analogies. Furthermore, there appears to be a reciprocal relationship between processing the identity of individual stimuli and processing the relations between or among stimuli. For infants and animals, comparing several different exemplars of a relation encourages abstracting the relations of sameness and difference; on the other hand, focusing on the identity of individual stimuli impairs relational processing.

From Animals to Humans

Although animals may not achieve relational thinking of the same complexity as do humans, striking similarities nevertheless emerge between humans and other species. Mounting evidence in the realm of animal cognition questions the common belief that same–different conceptualization is uniquely human. Evidence from animals as diverse as mammals, birds, and insects shows that they too can master first-order same–different relations. In addition, pigeons, crows, monkeys, and apes have successfully mastered cognitive tasks which require them to understand the relation between relations (second-order relations).

From Infancy to Adulthood

During development, children move from perceptually based to relationally based processing of stimuli, owing to innumerable relevant experiences. Nevertheless, for such higher-order abstract thinking, perceptual processes also seem to be intimately involved.

Although linguistic encoding of higher-order judgment tasks may ease and promote relational thinking in children, language seems not to be mandatory for relational thought, as shown by the success of nonverbal animals and preverbal humans learning advanced relational tasks. The contribution of language to relational thinking might better be seen to provide abstract symbols for humans to re-encode and thereby simplify complex stimulus relations, permitting us to solve higher-order relational problems that may be beyond the cognitive reach of animals.

Coda

Humans, no doubt, possess a powerful capacity for relational cognition, including analogical thought. This capacity appears to be continuous across development, with factors that affect relational thinking in adults and children also influencing infants as well. More broadly, considerable evidence suggests that there is phylogenetic continuity in the nature of relational and analogical thought. Initially, human infants and nonhuman animals may exhibit qualitatively similar relational and analogical abilities. However, adult humans come to dramatically outperform other animals in the complexity and intricacy of their relational and analogical thinking. Humans' experience with language and culture are likely to promote this advantage (see Volume 1, Chapters 15 and 20, this handbook), resulting in an ever expanding gap between humans and animals over the course of development. Nevertheless, we must appreciate that whatever heights of cognition may be attained by humans must have arisen via an evolutionary process about which we may gain key insights by studying the cognitive processes of our animal kin.

C. Lloyd Morgan would surely appreciate all that we have learned about relational thought since his fecund speculations over a century ago. We fully expect the next century to yield even more exciting revelations concerning relational thinking in animals and humans, with that progress critically leveraging contemporary computer and touch technology. It is no small matter that advances in our understanding of conceptual behavior have been significantly enhanced by technological innovations. These innovations have not only permitted better controlled experiments to be conducted, but for their conduct to translate to a broad range of animal species. Comparative cognition can thus properly come of age now that the longstanding interest in animal intelligence can fully exploit the power and precision of modern scientific methods.

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CHAPTER 18

SERIAL LEARNING

Greg Jensen

The term *serial learning* covers a broad range of phenomena, in no small part because different traditions in psychology disagree about the process and content of such learning. A comprehensive overview of the comparative study of serial learning is therefore best served by considering these many perspectives. This chapter first examines the two major approaches to serial learning used in comparative research. The first variety trains subjects to use *implicit serial orderings* (e.g., in the study of transitive inference), in which stimulus ordering must be inferred from feedback. The second form trains *explicit serial ordering* (e.g., the simultaneous chain), such that ordered stimuli remain available to the senses throughout a trial, permitting them to be processed in parallel. A comprehensive account of serial learning can only be accomplished through joint consideration of these two paradigms. In addition, a variety of other phenomena are reviewed that are thought to relate in fundamental ways to serial learning. These include (a) serial learning as a basis for social relations and dominance hierarchies and (b) the psychophysical sense of numerosity and the corresponding use of symbolic numbers. Not only are these domains informed by serial knowledge, but they are also revealing regarding the scope and utility of its cognitive mechanisms. Finally, an overview is presented of the contributions of comparative neuroscience to this topic, thanks to methodological innovations in recording and analysis.

Given this diversity of material, it is important to first define terms. This chapter takes serial learning to connote knowledge in which a subject's familiarity with a set of items includes a sense of their ordering. For example, although most people cannot recall the exact rank of each letter in the Latin alphabet, they nevertheless have an immediate sense that *R* is located later in that ordered list than *H*. Serial learning has been studied across a vast comparative literature precisely because it is widely believed that this aptitude for processing sets of related items with respect to order is a well-preserved cognitive aptitude with deep evolutionary roots.

Tables 18.1 and 18.2 provide a guide to the experimental studies cited by this chapter, organized by species. Although a handful of species have been studied extensively (particularly rhesus macaques [*Macaca mulatta*]), a diversity of species have nevertheless been sampled. These lists are not meant to be exhaustive; for additional studies, particularly older ones, refer to the reviews cited in each of the following sections.

IMPLICIT ORDER: TRANSITIVE INFERENCE

Transitive inference (TI) is one of the most extensively studied phenomena in comparative literature (see Volume 1, Chapter 32, this handbook and Chapter 29, this volume). Its premise is straightforward: A series of stimuli (A, B, C, etc.) have an ordering initially known only to the experimenter. On a series of trials, subjects are presented with subsets (usually pairs) of items, and told only if their choices are correct or incorrect, based on the rule that the correct item is the one appearing earlier (or,

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TABLE 18.1

Serial Learning Literature Overview (Nonhuman Primates)

Species	Papers	Transitivity	Explicit order	Social relations	Numerosities	Cardinal numbers	Electrophysiology	Surgery/ pharmacology
Squirrel monkeys (*Saimiri sciureus*)	McGonigle and Chalmers (1977)	X						
Cebus monkeys (*Cebus apella*)	D'Amato and Colombo (1988, 1990)		X					
	Judge et al. (2005)				X			
Chimpanzees (*Pan troglodytes*)	Gillan (1981)	X						
	Matsuzawa (1985)					X		
	Boysen and Berntson (1989)				X	X		
	Boysen et al. (1993)	X				X		
Cynomolgus monkeys (*Macaca fascicularis*)	Buckmaster et al. (2004)	X						X
Ringtailed lemur (*Lemur catta*)	Merritt et al. (2007)		X					
Ringtailed lemur (*Lemur catta*); Mongoose lemur (*Eulemur mongoz*)	MacLean et al. (2008)	X		X				
Brown lemur (*Eulemur fulvus*); Black lemur (*Eulemur macaco*)	Tromp et al. (2014)	X						
Rhesus macaques (*Macaca mulatta*)	Rapp et al. (1996)	X						
	Treichler and Van Tilburg (1996)	X						
	Treichler et al. (2007)	X						
	Treichler and Raghanti (2010)	X						

	Chen et al. (1997)		X					
	Brannon and Terrace (1998), (2000)		X		X			
	Orlov et al. (2000)		X					
	Terrace et al. (2003)		X					
	Subiaul et al. (2004)		X	X				
	Alvarado and Bachevalier (2005)	X						X
	Cantlon and Brannon (2006, 2007)				X			
	Nieder et al. (2006)				X		X	
	Diester and Nieder (2007)				X		X	
	Roitman et al. (2007)				X		X	
	Jordan et al. (2008)				X			
	Berdyyeva and Olson (2009, 2011)		X				X	
	Livingstone et al. (2010, 2014)				X	X		
	Merritt and Terrace (2011)	X						
	Scarf et al. (2011)		X					
	Gazes et al. (2012)	X						
	Jensen et al. (2013)	X	X					
	Jensen et al. (2015)	X						
Olive baboons (*Papio anubis*)	Barnard et al. (2013)				X			

TABLE 18.2

Serial Learning Literature Overview (Other Species)

Species	Papers	Transitivity	Explicit order	Social relations	Numerosities	Cardinal numbers	Electrophysiology	Surgery/ pharmacology
				Birds				
African gray parrot (*Psittacus erithacus*)	Pepperberg (1987)				X	X		
Chickens (*Gallus gallus*)	Hogue et al. (1996)			X				
	Daisley et al. (2010)	X						
Greylag geese (*Anser anser*)	Weiß et al. (2010)	X		X				
Hooded crows (*Corvus cornix*)	Lazareva et al. (2004)	X						
Pinyon jays (*Gymnorhinus cyanocephalus*)	Paz-y-Miño et al. (2004)	X		X				
	Bond et al. (2003, 2010)	X		X				
	Wei et al. (2014)	X						
Western scrub jays (*Aphelocoma californica*)	Bond et al. (2003, 2010)	X		X				
Azure-winged magpies (*Cyanopica cyanus*); Clark's nutcrackers (*Nucifraga columbiana*)	Bond et al. (2010)	X		X				
Pigeons (*Columba livia*)	Terrace (1991, 1993)		X					
	von Fersen et al. (1991)	X						
	Wynne (1997)	X						
	Lazareva and Wasserman (2006, 2012)	X						
	Reid (2009)		X					
	Daniels et al. (2014a, 2014b)	X						
				Rodents				
House mice (*Mus musculus*)	DeVito, Kanter, and Eichenbaum (2010); DeVito, Lykken, et al. (2010)	X						X

(*Continued*)

	Van der Jeugd et al. (2009)	X				X
Striped field mice (*Apodemus agrarius*)	Panteleeva et al. (2013)			X		
Rats (*Rattus norvegicus*)	Meck and Church (1983)			X		
	Davis (1992)	X				
	Roberts and Phelps (1994)	X				
	Dusek and Eichenbaum (1997)	X			X	
	Takahashi et al. (2008)	X				
Tree shrews (*Tupaia belangeri*)	Takahashi et al. (2008)	X				
			Miscellaneous			
Cichlid fish (*Astatotilapia burtoni*)	Grosenick et al. (2007)	X	X			
Bottlenose dolphin (*Tursiops truncates*)	Kilian et al. (2003)			X		
Honeybees (*Apis mellifera*)	Benard and Giurfa (2004)	X				

in some procedures, later) in the list. For example, in the pair AB, B would be incorrect because it appears later in the list, whereas in the pair BC, B would be the correct option as it appears earlier in the list. Given incomplete information (e.g., A > B and B > C), the question is whether subjects can infer relations between items that they have not yet experienced (e.g., A > C). If subjects can make this leap, they are said to have inferred the order of the new pair by exploiting the transitive nature of ordered relationships. Importantly, these inferences are made despite (a) never presenting the entire set of stimuli at once and (b) never explicitly indicating that the aim is to discover the ordering of that stimulus set.

The first nonhuman demonstration of TI was published by McGonigle and Chalmers (1977), who reported that squirrel monkeys (*Saimiri sciureus*) could perform TI for five-item lists. Many of the details of this study would go on to be archetypal. Animals were initially trained on the adjacent pairs (AB, BC, CD, and DE) until all such pairs yielded accurate performance. Under such a training scheme, A was always rewarded, E was never rewarded, and B, C, and D were each rewarded exactly half of the time. This detail is important because, according to associative/reinforcement learning models, the expected probability of reward is closely related to the associative strength of the stimulus, and such models therefore consider B, C, and D to be equal. Transitivity was subsequently tested by presenting subjects with the pair BD. Despite having reinforcement histories of 50% reward for B and D, the monkeys selected the correct stimulus 90% of the time, as though they had inferred the superordinate relationship from only the adjacent pairs. Another pair (AE) was constructed from the two terminal items; probe trials of this pair yielded perfect performance (see Figure 18.1).

This experimental design has since been replicated in dozens of species. Insofar as above-chance performance on BD is taken as proof of TI, then every vertebrate species that has been tested with this basic approach to date has displayed the

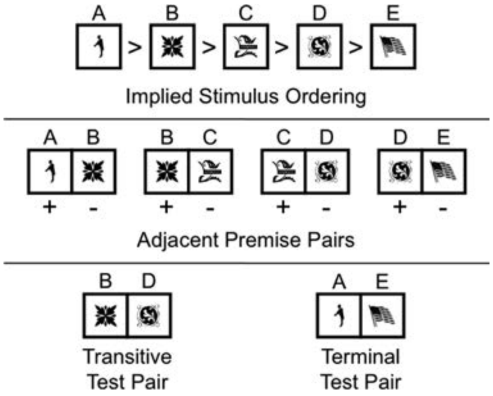

FIGURE 18.1. The classic transitive inference paradigm. (Top) Five distinct stimuli are assembled into an ordered list. This list is never presented in its entirety to subjects, who instead see pairs of stimuli, and are rewarded for selecting the stimulus that is positioned earlier in the list. Specifics of experimental apparatus and stimulus modality vary enormously across the literature. (Middle) Naive subjects are initially presented with the adjacent pairs, those that are adjacent in the implied list. Ordinarily, these adjacent pairs are presented with equal frequency, such that stimulus A is always rewarded, stimulus E is never rewarded, and stimuli B, C, and D are rewarded 50% of the time. (Bottom) If a subject's subsequent performance is only determined by the expected frequency of reward, then the pair AE should yield high accuracy, while the pair BD should yield chance levels of responding. If, on the other hand, subjects have inferred the ordering of the implied list, then BD performance should be high. Furthermore, if a symbolic distance effect is observed, BD should yield higher performance than the adjacent pairs, despite being a novel pairing.

aptitude. In keeping with McGonigle and Chalmers's (1977) pioneering study, other primate species tested included chimpanzees (*Pan troglodytes*; Gillan, 1981; Boysen, Berntson, Shreyer, & Quigley, 1993), cynomolgus monkeys (*Macaca fascicularis*; Buckmaster, Eichenbaum, Amaral, Suzuki, & Rapp, 2004), lemurs (*Lemur catta* and *Eulemur mongoz*; MacLean, Merritt, & Brannon, 2008; *Eulemur fulvus* and *Eulemur macaco*; Tromp, Meunier, & Roeder, 2015), and rhesus monkeys (*Macaca mulatta*; Jensen, Muñoz, Alkan, Ferrera, & Terrace, 2015; Rapp, Kansky, & Eichenbaum, 1996). TI has also been demonstrated in a wide range of bird species, including chickens (*Gallus gallus*; Daisley, Vallortigara, & Regolin, 2010), greylag geese (*Anser anser*; Weiß, Kehmeier, & Schloegl, 2010), hooded crows (*Corvus cornix*; Lazareva et al., 2004), pigeons (*Columba livia*; Daniels, Laude, & Zentall, 2014a, 2014b; Lazareva & Wasserman, 2012; Wynne, 1997), and other corvids (*Aphelocoma californica*, *Cyanopica cyanus*, *Gymnorhinus cyanocephalus*, and *Nucifraga columbiana*; Bond, Wei, & Kamil, 2010). Among rodents, demonstrations of TI have been made with mice (*Mus musculus*; DeVito, Lykken, Kanter, & Eichenbaum, 2010), rats (*Rattus norvegicus*; Davis, 1992; Roberts & Phelps, 1994), and tree shrews (*Tupaia belangeri*; Takahashi, Ushitani, & Fujita, 2008). Two other species are noteworthy: Fish were reported to perform TI (*Astatotilapia burtoni*; Grosenick, Clement, & Fernald, 2007), but honeybees failed to do so (*Apis mellifera*; Benard & Giurfa, 2004). Indeed, honeybees are the only invertebrates that have been tested on TI, and the only species that have failed the transitivity test. For further examples from this vast literature, see the review by Vasconcelos (2008).

Although BD performance is the most common TI result reported, other effects are arguably more theoretically compelling. One of these is the *symbolic distance effect* (D'Amato & Colombo, 1990), which is widely observed. If we assign ranks to an ordered list of items, then the symbolic distance is the difference in ranks between any two items. For example, the symbolic distance of the pair BD is two, because getting from B to D requires two steps along the list. Studies report that a symbolic distance effect has been observed if, as a function of increasing symbolic distance, (a) subjects' reaction times became more rapid (Scarf & Colombo, 2008) or (b) subjects' accuracy in correctly identifying the rewarding stimulus increased (Jensen, Altschul, Danly, & Terrace, 2013). Often, both effects are observed (Acuna, Sanes, & Donoghue, 2002; Merritt, MacLean, Jaffe, & Brannon, 2007; Merritt & Terrace, 2011).

However, symbolic distance effects are confounded with the widely-reported *terminal item effect* (Wynne, 1997), in which the first and last items in the list are correctly identified to a disproportionate degree. Thus, in pairings that include the first item, that item is more chosen than expected from symbolic distance alone, whereas in pairings that include the last item, that item is avoided more often than expected. Terminal item effects are consistent with associative accounts because those stimuli are differentially rewarded, so such effects are routinely taken to be evidence that low-level learning processes are at work. This explains the success reported by McGonigle and Chalmers (1977) on the pair AE: In a five-item list, A and E were terminal items. When trying to control rigorously for terminal items, a five-item list provided no means to test for a truly transitive symbolic distance effect, as BD is the only non-adjacent, non-terminal pair available.

In many cases, symbolic distance effects and terminal item effects are assessed in an ad-hoc manner. Most studies of TI do not, for example, test performance on every stimulus pairing, choosing instead to focus on critical test pairs. Despite this, it is desirable to be able to describe these effects quantitatively. Jensen and colleagues (2013) report that TI performance can be characterized succinctly using logistic regression. Doing so permits the effects of symbolic distance and of terminal items to be measured while controlling for one another. A simple model for doing so can be described thusly:

$$p = (1 + \exp(-(\kappa + \delta D + \alpha I_{bottom} + \omega I_{top})))^{-1}$$

Here, the probability p of a correct response on an item pair is a function of four parameters: an intercept parameter κ, a symbolic distance parameter δ, and two terminal item effects, α (for the item at the start of the list) and ω (for the item at the end of the list). The remaining symbols in the model represent the data themselves: D denotes the symbolic distance between the test items, whereas the pair I_{bottom} and I_{top} are indicator functions for whether each terminal item is part of the pair. For example, in a five-item list, the pair AE is considered to have $D = 4$ (because the symbols are 4 spaces apart) and $I_{bottom} = I_{top} = 1$ (because both terminal items are included). On the other hand, the critical test pair BD is considered to have $D = 2$ (marking it as a nonadjacent pair) and $I_{bottom} = I_{top} = 0$ (indicating that it is not confounded by terminal items).

Figure 18.2 displays group average performance, following adjacent-pair training, for six different studies testing six different species. In addition to including approximate standard errors (dark gray bands), the logistic model is also used to infer the expected performance on all pairs (dashed line), whether or not the study in question tested those pairs. The coefficients that best fit these group averages are included in each plot. Performance varies considerably from one study to the next, owing not only to species differences but also to differences in experimental procedure. In some studies (e.g., Lazareva & Wasserman, 2012), subjects underwent extensive training prior to test, whereas other studies used brief training periods (e.g., Jensen et al., 2015). Many studies did not clearly report the duration of training, instead proceeding to testing only when a criterion for adjacent pair performance was met (often, 80%). Furthermore, studies were different with respect to the order in which adjacent pairs were trained, which impacted performance at test (Daniels et al., 2014b). A consequence of this diversity of methods is that not all canonical TI effects are guaranteed to appear in every study. For example, McGonigle and Chalmers (1977) and Lazareva and Wasserman (2012) appeared to display negative symbolic distance effects once terminal items were taken into account (i.e., $\delta < 0$, implying the performance drops as distance between items increases). Similarly, Merritt and colleagues (2007) appeared to report reversed terminal items effects (because α and ω are negative). When trying to interpret results of this kind, it is important to keep in mind that comparative studies often work with small sample sizes, and that the test phase of an experiment is often relatively brief; these in concert, guarantee that precise performance estimates are often out of reach.

Despite the methodological differences between these studies and the likely volatility of their performance estimates, Figure 18.2 nevertheless shows the strength of the basic TI result. Critical test pairs (which are neither adjacent nor have terminal items) are shaded with a light gray backdrop, and performance exceeds chance in nearly every case. It is in this respect that TI has been described as ubiquitous.

One of the reasons symbolic distance is not reliably observed is that it is difficult to model using short lists, especially when terminal item effects are also under consideration. To test for symbolic distance without the confound of the terminal item effect, it is necessary to test TI using longer lists. For example, von Fersen, Wynne, Delius, and Staddon

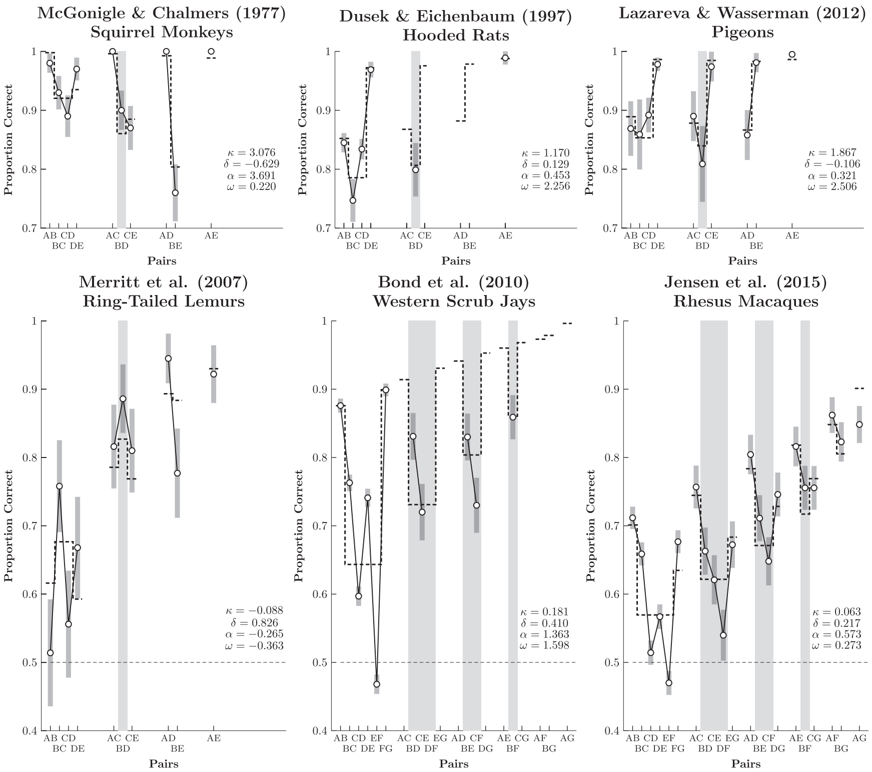

FIGURE 18.2. Group average performance on transitive inference tasks in six different studies. Each point represents performance, during a test phase that followed adjacent-pair training, for a particular stimulus pair. Pairs are grouped by symbolic distance. Dark shaded rectangles represent one standard error, based on reported summary statistics; because they were not derived from raw data, these should be treated as approximate, and are included to convey some sense of the reported variability. A logistic model was fit to these group averages, yielding a description that was used to infer performance on all pairs (dashed line), whether or not the study in question tested or reported performance on that pair. The light gray shaded regions identify critical test pairs: Those that are nonadjacent and do not contain terminal items.

(1991) used a seven-item list, which accords six unconfounded, nonadjacent pairs (BD, BE, BF, CE, CF, and DF). With a seven-item list, symbolic distance can also more easily be disentangled from terminal item effects when modeling behavior (as demonstrated by Bond et al., 2010 and Jensen et al., 2015 in Figure 18.2). A much more powerful method for training long lists, however, is the *list-linking paradigm*, which was introduced by Treichler and Van Tilburg (1996). First, they trained rhesus macaques on two five-item lists (ABCDE and FGHIJ) using traditional TI procedures. They then trained the pair EF, rewarding the selection of E, to link the two lists. Subjects were then tested on the resulting 10-item list, and showed a very robust symbolic distance effect across the full 10-item span. The logic of this experiment was later extended, in dramatic fashion, to link three 15-item lists, resulting in what was effectively a 45-item list, over which symbolic distance effects were observed (Treichler, Raghanti, & Van Tilburg, 2007). However, Wei, Kamil, and Bond (2014) attempted a replication of Treichler and Van Tilburg's (1996) procedure in pinyon jays, and found that the list linking did not arise as rapidly or as smoothly. Instead, accuracy within each of the five-item lists went down (and reaction time correspondingly went up), and transitive pairings across the linked gap were reliably below chance. This species difference is one of a number of important results suggesting that the ubiquity of TI aptitudes may in fact be the result of an array of different cognitive mechanisms, some of which transfer to other paradigms better than others (see also Moses, Villate, & Ryan, 2006).

Although a vast literature surrounding TI in animals has arisen, there is no clear consensus about the implications of the reported results. A central area of disagreement is whether animal performance is best explained by associative learning or by cognitive representation (see Chapter 31, this volume). Vasconcelos (2008) provided a detailed overview of the specific predictions of several associative models, including the venerable Rescorla–Wagner model (reviewed by Siegel & Allan, 1996), value-transfer theory (von Fersen et al., 1991; Zentall & Clement, 2001), the configural model (Wynne, 1995), and the Eta-Kappa model (Siemann & Delius, 1998). These models all have several features in common. First, they all assign a numerical value to each stimulus (or, in some cases, to combinations of stimuli). Second, they update these values only when the stimuli (or combinations of stimuli) in question are present during the trial. The associative tradition, as a rule, does not permit its models to update the value associated with a stimulus unless that stimulus is present during the current trial. For example, in a traditional five-item TI procedure, if the pair BC is currently being presented, then the associative strengths of A, D, and E are not modified as a consequence of the events of that trial. Associative models can, to varying degrees, display phenomena like the symbolic distance effect or the terminal item effect for typical task preparations, given specific parameters. However, all fall substantially short of being able to account for the full range of published findings.

Extant learning models routinely fail when presented with unusual experimental arrangements. For example, Lazareva and Wasserman (2012) trained subjects on the adjacent pairs of five item lists. Then, prior to testing for TI, they trained the pair DE for many additional trials. For any of the associative models previously mentioned, the expected effect should be a massive inflation of the value of D, causing it to erroneously overtake all other stimuli at test. Meanwhile, because A, B, and C are not presented on these trials, their values are not correspondingly adjusted. Although the simulated performance of associative models is consistently derailed by this procedure, pigeons are not: The learned ordering of all five stimuli were preserved despite the massed DE trials, such that performance on test pairs were not only accurate, but were indistinguishably so when comparing before and after the massed training on DE (see also a critique by Gazes, Chee, & Hampton, 2012, regarding macaques).

An even more difficult problem for extant learning models to account for is *transverse inference*. A transverse inference problem is structured like a TI problem, except that the stimulus rankings form a closed loop, as in the hand game rock-paper-scissors. For example, when trained on the adjacent pairs of the list ABCDE and presented with the pair AE, the correct answer given a TI is to select A, but the correct answer given a transverse inference is to select E (E > A > B > C > D > E > A). Only a handful of comparative studies have examined transverse inference (e.g., Alvarado & Bachevalier, 2005, in rhesus macaques; Couvillon & Bitterman, 1996, in pigeons; Gillan, 1981, in chimpanzees; Rodriguez & Levy, 2004, in rats), and these have found that animals are routinely able to learn adjacent pairings of items under these conditions (although such learning appears to be more difficult than ordinary TI). By contrast, any learning model that relies on comparisons of a global stimulus-reinforcer associative strength will fail at transverse tasks because all stimuli are expected to yield rewards with equal frequency.

At the opposite extreme from the associative models are cognitive models that suggest that animals solve the task through cognitive representation. The most common form proposed for such representation are spatial or quasispatial, as though stimuli were being placed along a number line and having their positions compared (e.g., Gillan, 1981; Jacobs, 2006; Jensen et al., 2013; Roberts & Phelps, 1994; Treichler & Van Tilburg, 1996). Under such a system, the model consists not only of a representation of the stimuli, but also a corresponding sample space. The advantages of representing the sample space are considerable. Symbolic distance effects, for example, arise naturally as a function of distance within the represented space (see Chapter 25, this volume). It is possible, for example, that success at transverse inference tasks can be achieved by representing the stimuli in a loop, rather than representing them in a line, as is presumed in the case of TI. Proposals of this kind typically are not sufficiently specified to permit rigorous simulation (although a recent exception is presented by Bouwmeester, Vermunt, & Sijtsma, 2012). It is also unclear how these representational spaces are selected and distorted as a function of task experience. If indeed transverse inference is achieved by twisting a line into a loop, how is this accomplished, and at what stage in learning?

Instead, experiments seeking to test spatial hypotheses typically rely on facilitative or disruptive effects of stimulus configuration. For example, Roberts and Phelps (1994) reported that TI in rats was facilitated when stimuli were arranged linearly (such that their position acted as a cue for their prescribed ordering). Contrastingly, Daniels and colleagues (2014b) found no difference in the acquisition of five-item lists in pigeons under various stimulus arrangements (see also Lazareva & Wasserman, 2006).

As the study of TI progresses, it may be necessary to acknowledge that it has become, to a degree, the study of a very specific experimental procedure. An exhaustive effort has been devoted to developing models suited to five-item lists, trained with adjacent pairs and tested with the pair BD. Some of the most dramatic demonstrations of TI (such as the list-linking procedures by Treichler & Raghanti, 2010; Treichler et al., 2007; Treichler & van Tilburg, 1996) were discovered by relaxing the procedural assumptions of traditional TI experimentation. Further broadening of experimental procedures will present existing models with challenging data, which can only serve to refine (and, where necessary, cull) extant models of TI.

EXPLICIT ORDER: THE SIMULTANEOUS CHAIN

Superficially, the demands of the simultaneous chaining procedure (SimChain; reviewed by Terrace, 2005) are very similar to those in TI. Subjects are presented with a set of pictorial stimuli that have a prescribed ordering, but this ordering must be discovered by trial and error. Unlike TI tasks, however, the SimChain task presents all stimuli in the list simultaneously, and only delivers a reward when each of the items has been selected in the correct order. Thus, unlike the TI task, in which list membership is implicit, but subjects never see the full stimulus set at once, SimChain makes the list explicit. No feedback is provided until (a) the last correct item is touched and a reward is delivered, or (b) an image is touched out of order and a timeout period is initiated, followed by a new trial. Subjects make progress by trial and error, progressing further into the list on successive attempts. The positions of the stimuli are scrambled from one trial to the next, requiring subjects to visually search for the items every time without recourse to motor memory (see Figure 18.3).

The SimChain was conceived as a reply to Lashley's (1951) critique of operant chaining theories of serial learning, and of radical behaviorism generally. In traditional operant theory, each response in a sequence must be initiated by a stimulus, resulting in some change in the environment that is then treated as a stimulus to motivate the next action

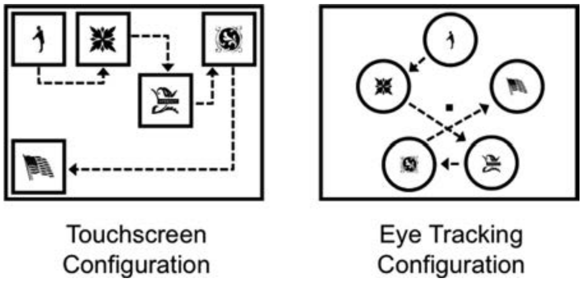

FIGURE 18.3. Experimental configurations for the SimChain. (Left) An example trial during a touchscreen version using the stimulus list from Figure 18.1 (Terrace, 2005). The five stimuli are presented simultaneously. The dashed arrows do not appear on screen; they instead indicate the sequence of touches that will result in reward delivery. If any stimulus is touched out of sequence, the trial ends immediately. Whether or not the trial yielded a reward, the arrangement of the stimuli is randomly scrambled on the next trial to prevent motor learning from facilitating learning. (Right) An identical SimChain, configured instead for an eyetracking paradigm (Berdyyeva & Olson, 2009, 2011). As before, the arrows are not presented during the trial, and instead indicate the correct sequence for the reader. In order to minimize spatial and motor confounds, eyetracking procedures usually require that subjects return their gaze to the fixation point after every response. Under these conditions, the arrangement of the stimuli can be scrambled following every response, forcing subjects to engage in a visual search for every step in the list.

in the sequence. The SimChain undermines this interpretation because the visual display is static throughout the trial. To perform such a task, the theorist must either acknowledge that subjects make use of their memory for their previous response as a stimulus (see Chapter 10, this volume), or else acknowledge that subjects must maintain a representation of the list ordering. When the reward is delivered, it is unclear under a reinforcement model which associations have been strengthened.

This general difficulty is now known as the *assignment-of-credit problem* (Staddon & Zhang, 1991), and persists in modern associative theories. A single trial of SimChain consists of a series of actions and judgments unfolding quickly over a few seconds, so reward delivery cannot be described as merely incrementing a single associative value. Furthermore, the reward rate from chance alone is typically very small (less than 1%), so when learning longer lists, behavior is maintained over many trials before any rewards are delivered, as if subjects are motivated either by the prospect of a future reward, or by their own subjective sense of making progress at figuring out the list order. Thus, although associative models can, under limited circumstances, approximate some TI behaviors, they struggle with SimChain (Reid, 2009).

SimChain performance has not been studied as extensively as TI, in part because the task's increased complexity is difficult to adapt to a wide variety of lab conditions. Nevertheless, a variety of labs have reported SimChain performance in a number of nonhuman species, including cebus monkeys (D'Amato & Colombo, 1988), lemurs (Merritt et al., 2007), rhesus macaques (Chen, Swartz, & Terrace, 1997; Jensen et al., 2013), and pigeons (Reid, 2009; Terrace, 1991). This provides a broad enough comparative sample to draw some general conclusions about serial learning.

Figure 18.4 presents performance on a five-item SimChain by three rhesus macaques (using data

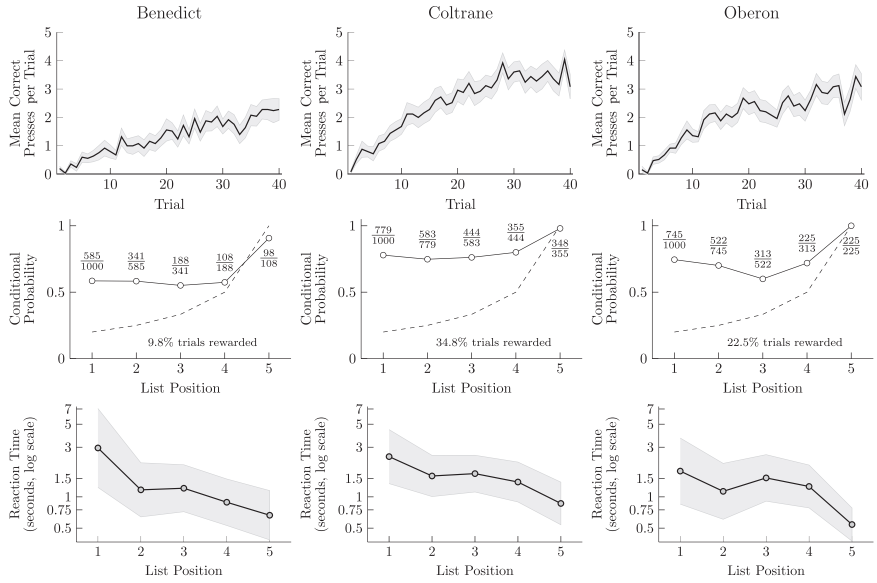

FIGURE 18.4. **Characteristic performance on a five-item SimChain by three rhesus macaques, derived from 25 novel lists collected by Jensen and colleagues (2013). These subjects had prior experience with serial tasks but were naive about the ordering of these specific lists. (Top) Mean number of correct responses per trial over the course of the first session of learning. The shaded area denotes one standard error of the mean. (Middle) Conditional probabilities of correct response as a function of progress during a given trial. The dashed line indicates chance performance (assuming no backwards errors). Also indicated is the overall proportion of trials that ended in reward. (Bottom) Mean reaction time as a function of trial progress. Values are depicted on a logarithmic scale. The shaded areas denote one standard deviation, and are included to convey the overall variability of reaction times.**

reported on by Jensen et al., 2013). In this case, the subjects in question have extensive experience with the SimChain procedure, but have never seen the specific lists of items presented before the first trial. A striking characteristic of these data is that subjects acquire new lists rapidly, reliably exceeding chance at each point in the chain within the first 40 trials. Another noteworthy characteristic is that reaction times are at once slower and more variable than is commonly seen in TI procedures. Several factors contribute to these slow reaction times, including visual search and motor planning (Scarf, Danly, Morgan, Colombo, & Terrace, 2011).

A common method for evaluating the content of learning following SimChain training is to present pairs of stimuli in isolation. A major conclusion from this work is that, among primates, most of the phenomena observed in the study of TI have analogous effects in SimChain. For example, tests on pairs of stimuli show symbolic distance effects for reaction time and accuracy: The wider the gap between the stimuli, the faster the reaction time and the more accurate the response. Comparable results were not observed, however, in pigeons. Instead, performance by pigeons was dominated by a terminal item effect, reliably selecting the first item in the list and avoiding the last item, but doing very poorly on the nonterminal pairs (Terrace, 1993). No appreciable distance effect was observed in either accuracy or reaction time (see also Scarf & Colombo, 2008). As in the case of the qualitative species difference in the list-linking TI studies previously mentioned, the varied SimChain results across species speaks to a need to examine one's comparative assumptions, rather than leap to the conclusion that similar behavior on a single task across species reflects a common cognitive mechanism. Unfortunately, as nearly all SimChain research has been done with primates, further discussion of the empirical findings must be undertaken with the understanding that the capacities revealed might be primate-specific.

One such result, observed in rhesus macaques, is performance on *derived lists*. Chen and colleagues (1997) presented macaques with four different four-item SimChains, training each to a high performance criterion. The stimuli were then reorganized into four new lists, each containing exactly one stimulus from the original four lists. For two of these new lists, the stimulus order was kept identical (both lists were ordered ABCD, such that a stimulus that was in the third position initially also remained in the third position in the new list). For the third new list, the first two and last two items were swapped (BADC). Finally, for the fourth new list, the order of the items was entirely reversed (DCBA). These four lists were then trained to a performance criterion (with a minimum of 120 trials). When presented with lists that preserved the original stimulus ordering, macaques rapidly acquired and were at or near criterion after the minimum number of trials had elapsed. The list BADC was not acquired as rapidly, taking roughly as long as an entirely novel list. Finally, the reversed list DCBA took substantially longer than a novel list to reach criterion. This result speaks to a learning whose membership is flexible (allowing items to be swapped from one list to the next easily) but whose geometry is relatively rigid (making operations like reversal of ordinal rank quite difficult).

A similar result was reported by Terrace, Son, and Brannon (2003), using 7-item lists. Because 7-item SimChains are quite difficult to learn (requiring multiple sessions over a number of weeks), the study examined derived *pairs* of stimuli, rather than entire lists. Consistent with the derived list result, subjects had no difficulty intermixing stimuli from multiple lists. Not only did these derived pairs show distance effects in reaction time and accuracy, but within-list versus between-list pairs were not statistically distinguishable on either metric of performance (see also Orlov, Yakovlev, Hochstein, & Zohary, 2000).

The similarity of the behavioral phenomena observed in primates performing SimChain procedures to those observed in more traditional TI paradigms suggests that both experimental paradigms tap into a common strategic framework. If so, then training on a particular set of list items using one task should enhance performance for the other task, provided the item ordering is consistent. Transfer in both directions (from SimChain to TI and from TI to SimChain) was demonstrated by Jensen and colleagues (2013). In each case, rhesus macaques were given a fixed amount of training using one paradigm before transitioning to the other, and the performance in each case was compared to acquisition using an entirely novel list. For TI-to-SimChain transfer, subjects learned five-item lists over the course of 120 trials (during which each of the ten pairs was presented 12 times). They then waited 24 hr before receiving the same set of stimuli in the SimChain task. Despite the brief duration of training and the delay before testing, transfer lists were nonetheless learned faster than novel lists. For SimChain-to-TI transfer, however, a more involved procedure was used. Subjects received 160 trials of SimChain training on a five-item list, over four days. Then, on the fifth day, subjects performed a TI task using a nine-item list consisting of the five familiar items interleaved with four novel items. Consequently, the TI transfer actually afforded a test of three kinds of stimulus pairs: those composed entirely of stimuli familiar from earlier training, those that were entirely novel, and those that mixed one familiar stimulus with an unfamiliar one. Familiar pairs were selected with near-perfect accuracy, and unfamiliar pairs were learned normally. Interestingly, analysis of the mixed pairs suggested that subjects had no difficulty incorporating novel items into the existing model.

Overall, the study of explicit list orderings suggests that serial learning is a general aptitude, rather than a specific strategy tailored to a singular experimental procedure. The consistency of phenomena between SimChain and TI, as well as the transfer of knowledge between paradigms, points to a common foundation. Consequently, future proposals for models of serial learning should aim to accommodate the performance observed in both styles of task, rather than restricting their focus to explaining one procedure or the other.

SERIAL LEARNING AND SOCIAL RANK

The aptitudes that animals display for highly abstracted serial learning tasks are, at first blush, difficult to justify from an evolutionary perspective. Consequently, many comparative studies seek to tie these aptitudes to problems more directly related to fitness and reproduction. Among the most widely discussed is the relationship between serial learning and social rank.

The hypothesis that one of the chief functions of serial learning is to permit animals to form and update dominance hierarchies has deep roots in comparative literature (e.g., Premack, 1983). According to this view, the vast evolutionary benefits of living in stable groups justifies the development of sophisticated cognitive machinery (see Volume 1, Chapters 12 and 17, this handbook). It has also been long apparent, however, that these aptitudes for social organization come very naturally to animals, whereas highly abstracted serial tasks sometimes require extensive training before animals show much facility with them (Cheney, Seyfarth, & Smuts, 1986). Recent analyses of dominance patterns in three-member groupings confirm that social dominance is predominantly transitive in a wide range of species (McDonald & Shizuka, 2013), so the premise that TI would be useful to social organization appears to be plausible. Nevertheless, “classical” comparative arguments of this kind were essentially rhetorical, and it has been difficult to collect evidence that permits the validity of the hypothesis to be evaluated directly.

Until recently, evidence linking the two has been limited to *animal observer experiments*, which demonstrate that animals are able to infer transitive relationships within linear dominance hierarchies through vicarious observation. For example, Hogue, Beaugrand, and Laguë (1996) performed an experiment in which hens were placed in an isolated pen from which they could observe other hens. The observer then watched as another hen, who the observer considered to be dominant, interacted with a stranger. When the stranger dominated the familiar hen, the observer subsequently treated the stranger as dominant without engaging with it directly. However, when the familiar hen dominated the stranger, the observer behaved as though the stranger was fair game and was subsequently likely to initiate challenges. A more elaborate version of this task was reported by Paz-y-Miño, Bond, Kamil, & Balda (2004), in which observers were presented with various pairings from multiple groups of pinyon jays.

These animal observer designs were further elaborated on in a clever study of transitive social judgments in *A. burtoni* fish (Grosenick et al., 2007). Rather than seeing a single challenge, subjects instead spent an extended training period observing five fish of known differing social rank. The experimenter allowed the observer to see only adjacent pairings (e.g., AB, BC, etc.), which reliably resulted in the dominant fish aggressing the lower-ranked individual. After training on this "five-item list" of fish, the observer was then placed in a large tank, once with the pair BD, and once with the pair AE. In both cases, the observer avoided the implied dominant member of the pair and instead spent time nearer to the implied subordinate, despite never having seen these pairings of fish previously. In this respect, the classic train adjacent, test non-adjacent approach from the TI literature was preserved.

It is important to acknowledge that animal observer studies such as these can support a number of interpretations. For example, it may be that rather than showing that serial aptitudes underlie social behaviors to some degree, it is instead social and observational aptitudes that facilitate serial learning. Experimental demonstrations of serial imitation show that proficiency for highly abstract experimental tasks can benefit from periods of observation prior to testing (e.g., Subiaul, Cantlon, Holloway, & Terrace, 2004, in rhesus macaques)

More recently, the appeal of convergent accounts of cognitive evolution have become more widely accepted, and it has been argued that serial learning is one of a number of cognitive tools that are likely to have evolved multiple times because the problems they solve are ubiquitous (Emery & Clayton, 2004; see also Volume 1, Chapter 12, this handbook). This prospect introduces a new means for thinking about serial learning in an evolutionary context: Although such reasoning may exist at a common baseline among vertebrates, one might hypothesize that gregarious species are under more selective pressure to refine those aptitudes than comparatively solitary species. Thus, rather than seeking a universal cognitive aptitude, the relative sophistication of species' serial cognition may be correlated with the social organization of which species make use.

The first study to test this hypothesis explicitly was reported by Bond, Kamil, & Balda (2003), comparing the pinyon jays (*Gymnorhinus cyanocephalus*) to western scrub jays (*Aphelocoma californica*). Although the two species are closely related and similar in many respects (size, diet, metabolism), pinyon jays live in large social groups of up to 500 individuals, whereas scrub jays live in the relative isolation of a breeding pair and its most recent offspring. Bond and colleagues showed that, under comparative levels of training, pinyon jays learned serial discriminations more rapidly, and achieved higher ceiling levels of performance, than did scrub jays. This result was later extended to include two other species: Clark's nutcrackers (*Nucifraga columbiana*) and azure-winged magpies (*Cyanopica cyanus*; Bond et al., 2010). In the four-species comparison, social complexity was a reliable predictor of serial aptitude. However, it was also the case that a species' reliance on cached food (and thus on long-term memory and spatial navigation) was independently correlated with serial aptitude. Thus, although it is reasonable to suppose that serial aptitude and social complexity are related, other evolutionary demands may have driven (or been driven by) this aspect of cognition as well.

A comparative study of this style was also performed with two species of lemurs (MacLean et al., 2008). Highly social ring-tailed lemurs (*Lemur catta*) were compared to relatively solitary mongoose lemurs (*Eulemur mongoz*) using a seven-item TI task (training on adjacent items and then testing on nonadjacent items). In the initial experiment, when subjects were task-naive, the ring-tailed lemurs significantly outperformed the mongoose lemurs, as predicted from the social-evolutionary hypothesis. However, in a follow-up experiment that added a correction procedure, the two species ultimately displayed similar aptitude. MacLean and colleagues (2008) argued that this demonstrates not a hardwired social-serial aptitude, but instead a difference in the predisposition to initially see problems as having transitive solutions.

This conclusion matters substantially in the ongoing debate over the evolutionary connection between serial learning and social rank, because it highlights the importance of expertise. Often, comparative studies present the accomplishments of extensively trained animals raise in lab environments, which does not reveal the aptitudes displayed by wild members of the same species living in their native habitat. Although some serial learning studies emphasize the importance of training, particularly when it is required for animals to display particularly impressive demonstrations of serial ability (e.g., Terrace et al., 2003), most minimize their coverage of training in favor of reporting the performance during the final test. Teasing biological predisposition apart from learned aptitude will require more extensive study of behavior in ecologically plausible environments.

SERIAL LEARNING AND THE NUMBER SENSE

A very different focus of study for serial learning is the quest to uncover the evolutionary roots of the human ability to mentally manipulate numbers. Although studies of numerical quantity have been studied in a variety of species (e.g., grey parrots [*Psittacus erithacus*]; Pepperberg, 1987; dolphins [*Tursiops truncates*]; Kilian, Yaman, von Fersen, & Güntürkün, 2003; striped field mice [*Apodemus agrarius*]; Panteleeva, Reznikova, & Vygonyailova, 2013), the vast majority of the recent work on this topic has been done in nonhuman primates. This is reflected in the following section (see also Chapter 25, this volume).

There is little doubt as to the ability of animals to make judgments regarding abstract psychophysical quantities (brightness, size, etc.), but there is also considerable evidence that nonhuman animals can make comparisons of *numerosities*, or the discrete count of the parts in a stimulus. For example, three blue dots on a green background can be interpreted as a numerosity of 3, regardless of the relative size of the dots (see Figure 18.5). Similarly, a burst of three discrete auditory tones can be interpreted as having a numerosity of 3, despite being presented in a different sensory modality. The independence of the numerosity from a specific modality suggests that it is a "supramodal" ability (Nieder, 2012), a claim supported by

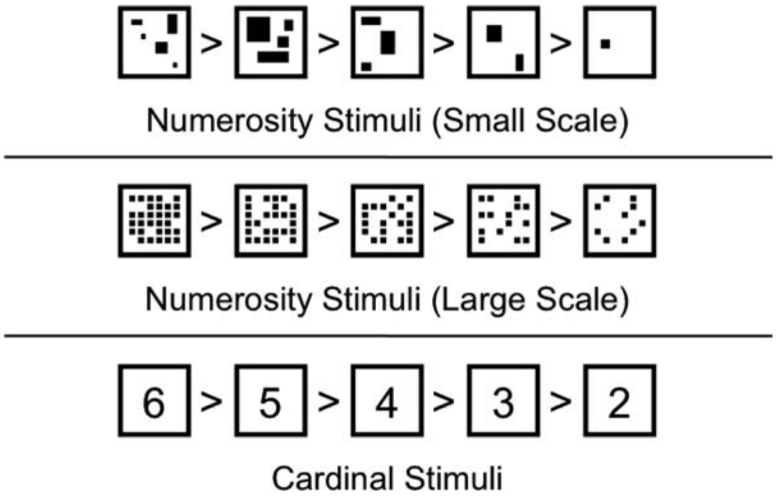

FIGURE 18.5. Examples of three different styles of stimuli related to the number sense. (Top) Numerosity stimuli on the order of small integers (e.g., Diester & Nieder, 2007). Individual stimulus units may be geometric shapes or clip art, and usually vary in size and shape to prevent those stimulus features from confounding the evident numerosity of the stimulus. For example, the four-box stimulus has a greater surface area than the five-box stimulus. (Middle) Numerosity stimuli on the order of large integers (e.g., Cantlon & Brannon, 2006). While stimulus units typically vary in these presentations, the dominant feature of clusters of large sets of units is their arrangement relative to one another. (Bottom) Cardinal numbers represented by lexical symbols (e.g., Livingstone et al., 2014). Unlike numerosity stimuli, which can be sorted immediately on the basis of the number sense, cardinal numbers must be trained extensively in no-human subjects before any serial characters of performance can be expected.

experiments in which counts in multiple modalities must be compared and manipulated (Jordan, MacLean, & Brannon, 2008; Meck & Church, 1983). Indeed, there is considerable evidence that numerosity itself can be understood as having a quasipsychophysical character. On this basis, it is widely agreed that subjects make use of a *number sense* that yields an approximate metric of the numerosity of a stimulus (Cantlon, Platt, & Brannon, 2009; for a developmental perspective, see Carey, 2010). This number sense displays many properties familiar to other psychophysical judgments (e.g., brightness, loudness), including reliable approximate conformity to Weber's Law (Dehaene, Dehaene-Lambertz, & Cohen, 1998; see also Chapters 1 and 25, this volume).

One of the implications of the number sense behaving like a psychophysical quantity is that it is continuous, and extends beyond the range of an organism's present training. For example, if subjects display aptitude in discriminating the numerosities 1, 2, 3, and 4 on the basis of their size, it follows that subsequent judgments of larger quantities (5, 6, etc.) should follow naturally with no additional training. This was tested in rhesus macaques using visual stimuli by Brannon and Terrace (1998, 2000). In both studies, the numerosities 1–4 were trained using the simultaneous chain procedure described previously. This was done either using a monotonic ordering (1→2→3→4) or a nonmonotonic ordering (3→1→4→2). Despite previous success with four-item SimChains and reliable acquisition of the ordered list, monkeys proved unable to learn the nonmonotonic list. This suggests that stimuli were not treated as discrete symbols, but rather as having a necessary and obvious ordering on the basis of their apparent counts (see also work on "patterned reinforcement"; Hulse, 1973). Once all monkeys had been trained on monotonic lists to a performance criterion, they were presented with pairwise tests of stimuli that included numerosities from 1 to 9. These pairwise tests yielded accuracy well above chance, as well as distance effects for accuracy and reaction time. Similar demonstrations also have been reported for cebus monkeys (Judge, Evans, & Vyas, 2005) and olive baboons (*Papio anubis*; Barnard et al., 2013).

This work was extended to stimuli with numerosities ranging from 2 to 30 by Cantlon and Brannon (2006), who not only extended the macaque work, but also replicated the procedure in humans to provide comparative data. Beginning with training on numerosities 1–9, their experiments culminated in an exhaustive comparison of all 105 pairings in that range, yielding psychophysical functions for reaction time and accuracy. Although humans consistently outperformed monkeys, they also consistently responded more slowly, suggesting that the two species favored different speed-accuracy tradeoffs. With this in mind, the authors describe both species as tapping into a shared system for their underlying number sense. This work was immediately followed up by Cantlon and Brannon (2007), in which subjects not only made judgments about numerosities, but also were required to performed mental addition of stimuli over a delay and report which probe stimulus corresponded to the resulting sum.

Although the study of numerosities is interesting from a psychophysical perspective, the aptitudes reported thus far are not sufficient to conclude that abstracted serial learning is taking place. A much more powerful demonstration of this kind of serial abstraction is the ability to connect the number sense to *symbolic representations* (such as cardinal numbers 1, 2, etc.). Until very recently, two bodies of work showed nonhuman primate facility with symbolic numbers. The first was an extensive case study of a chimpanzee named Ai, begun by Matsuzawa (1985; reviewed in Matsuzawa, 2009), who demonstrated aptitudes for pairwise comparisons and simultaneous chaining of the cardinal numbers. The second was work initiated by Boysen and Berntson (1989), also with chimpanzees (reviewed in Boysen & Hallberg, 2000). These studies emphasized operations performed on abstract quantities, such as comparison and arithmetic. In recent years, however, compelling cardinal results have been published with highly trained rhesus macaques. Livingstone, Srihasam, and Morocz (2010) gave juvenile rhesus macaques extensive training on a set of 21 symbols corresponding to the numbers 1 to 21. Following this training, subjects' ability to discriminate between numerals was comparable to their comparisons of numerosities, we well as perform well on trials that mixed numerals and numerosities. The resulting psychophysical functions relating accuracy to the ratio between stimulus values was also very similar for both stimulus types, and strikingly similar to the numerosity-driven functions reported by Cantlon and Brannon (2006; see also Jordan et al., 2008). This suggests that subjects had a relative feeling for the symbols that could be mapped with a high degree of correspondence to the number sense observed with numerosities.

An even more dramatic demonstration of this cardinal aptitude was reported by Livingstone and colleagues (2014). Rhesus macaques learned two different sets of numerical symbols (one alphanumeric and one consisting of symbols made from squares) that corresponded directly to the values 0 to 25 (as measured in terms of the number of drops of juice delivered as rewards). Not only were subjects then tested on pairwise comparisons of stimuli, but were also presented with stimulus addition problems. Performance on these cardinal tasks was then compared to numerosity evaluations using dot spreads. Remarkably, subjects made relatively reliable discriminations in all cases.

Many of the phenomena observed in numerical tasks resemble those observed in more abstract serial tasks (such as TI or SimChain), but the protomathematical account of serial learning is motivated by very different explanatory assumptions than the social rank account. Although the two are by no means mutually exclusive, it is important to keep these many accounts in mind when examining claims made about the utility of serial learning. Whether one account or the other seems more retrospectively plausible is a poor method for evaluating evolutionary history, compared to the more empirical approach of identifying which species demonstrate which aptitudes, and under what conditions.

COMPARATIVE NEUROSCIENCE OF SERIAL LEARNING

Although different theoretical interpretations have been put forward regarding serial learning, there is consensus with respect to the major behavioral findings. The same cannot be said of attempts to study how serial learning manifests in the brain, or the degree to which different brain regions are necessary for animals to display the appropriate behaviors.

The comparative study of serial learning in the brain has focused primarily on three regions of interest: (a) the network formed by hippocampus and parahippocampal gyrus (e.g., Alvarado & Bachevalier, 2005), (b) the prefrontal cortex (e.g., DeVito, Lykken, et al., 2010), and (c) the intraparietal sulcus (e.g., Nieder, Diester, & Tudusciuc, 2006). Each of these regions represents a somewhat different point of entry into the topic of serial learning, and as a consequence there has been no systematic harmonization of these different accounts. It is very likely the case, on the basis of data from humans, that serial learning tasks rely on complex networks active across brain regions (Prado, Mutreja, & Booth, 2013; Prado, Noveck, & Van Der Henst, 2010). However, because most nonhuman studies in awake behaving animals rely on localized recording, analysis of network activation during serial learning in animals remains an unexplored domain (see Figure 18.6).

Hippocampus and Parahippocampal Gyrus

When considering brain regions implicated in serial learning, the hippocampus has received the most extensive examination in nonhuman animals (see Volume 1, Chapter 25, this handbook). For the most part, the serial aspect of these studies was incidental to an overarching goal of understanding its role in memory and reasoning generally (reviewed in Eichenbaum, 2004). In this regard, serial tasks, such as the TI task, were taken to provide insight into basic mechanisms of cognitive reasoning. For example, Dusek and Eichenbaum (1997) trained rats using the classic five-item adjacent-training TI design, following one of two surgical preparations. In addition to a control group, one group underwent ablation of the perirhinal and entorhinal cortex, whereas another underwent transection of the fornix. All groups successfully learned the adjacent pairs, but both surgical groups failed to perform the TI needed to correctly respond to BD trials at test. Interestingly, all groups succeeded on a test of the terminal pair AE. This suggests that these regions of the parahippocampal gyrus are not integral to the terminal item effect (which may arise as a consequence of associative strength), but is otherwise needed to perform TI on nonterminal item pairs

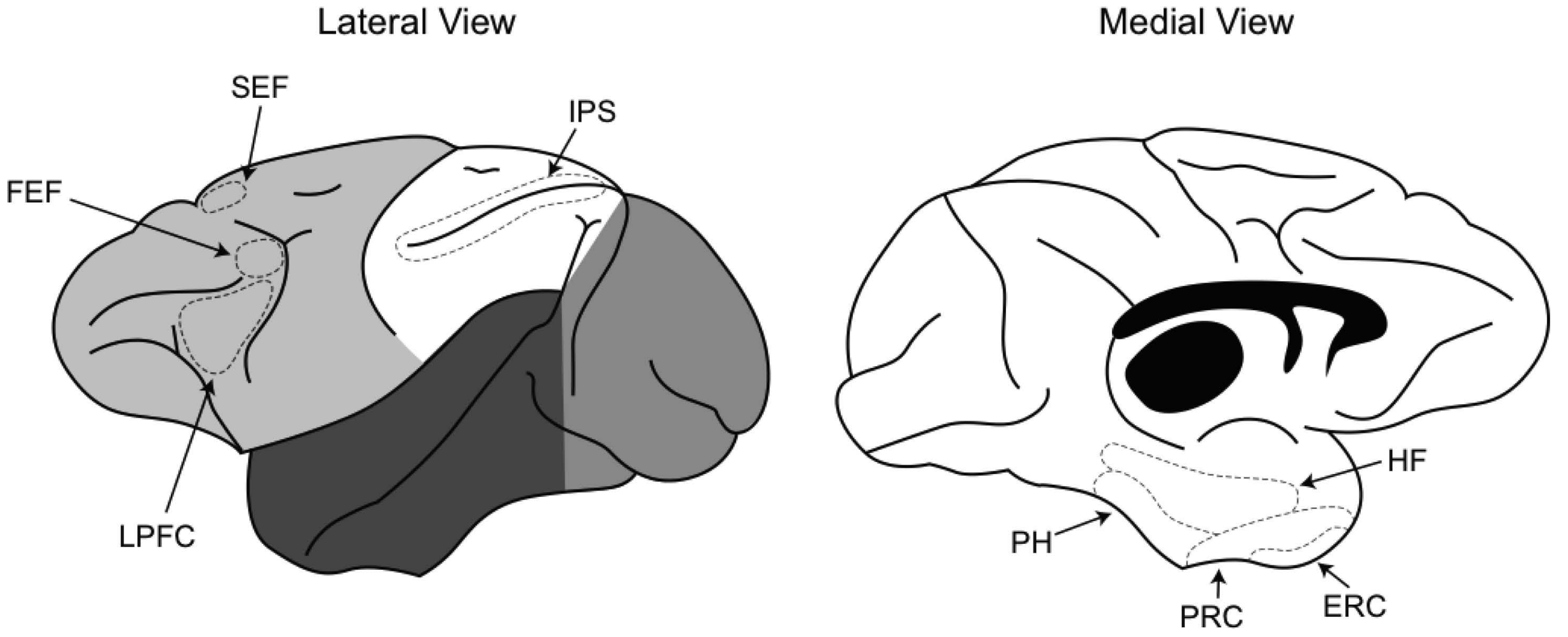

FIGURE 18.6. Diagram of a rhesus macaque brain depicting the regions most frequently targeted in the comparative neuroscience of serial learning. (Left) Lateral view of the brain, with the four lobes shaded. Regions of interest that have been implicated in serial or numerical reasoning include the intraparietal sulcus (IPS), the lateral prefrontal cortex (LPFC), the frontal eye field (FEF), and the supplementary eye field (SEF). (Right) Medial view of the brain. Shown is the extremity of the hippocampal formation (HF), as well as parahippocampal cortex (PH), perirhinal cortex (PRC), and entorhinal cortex (ERC).

(which cannot be accounted for by associative strength). Similar deficits were reported in monkeys with bilateral entorhinal lesions (cynomolgus monkeys; Buckmaster et al., 2004) and lesions of perirhinal or parahippocampal cortex (rhesus macaques; Alvarado & Bachevalier, 2005). These subjects showed systematic deficits in several assays of serial and relational learning.

Subsequent lesion studies of hippocampus itself, however, have yielded seemingly contradictory results with respect to when during learning the lesions occur. Van der Jeugd and colleagues (2009) also used the standard five-item protocol for TI with mice, with three different surgical preparations. A sham group received bilateral sham lesions, and acted as the control group. Meanwhile, a pretraining group received bilateral hippocampal lesions prior to adjacent-pair training, whereas a posttraining group had their hippocampi lesioned after training but before testing. All groups were able to acquire the individual adjacent pairs, and all performed above chance on the test pair AE in the final probe. However, although the pretraining lesion group performed at chance levels on the BD pair (consistent with the Dusek & Eichenbaum result), the posttraining group exceeded chance, doing nearly as well as the sham group. This suggests that the relational contributions of hippocampus take place during training, but are no longer essential in the subsequent testing period. This result was directly contradicted, however, by a study reported by DeVito, Kanter, and Eichenbaum (2010), in which bilateral hippocampal lesions were made in mice post-training, but BD performance was reduced to chance levels. Although these two studies differ in various particulars, it is not clear how to interpret this apparent contradiction.

Prefrontal Cortex

Whereas the hippocampus is a long-time area of interest for the study of memory, prefrontal cortex is predominantly an area of interest for the study of decision making. Most of the neuroscience on the contribution of prefrontal cortex to serial learning have been made with this focus in mind, and have been done using human participants (using fMRI; Acuna, Eliassen, Donoghue, & Sanes, 2002; Wendelken & Bunge, 2010; or in neurological patients with focal lesions; Waechter, Goel, Raymont, Kruger, & Grafman, 2013). Although these studies suggest an active role for prefrontal cortex in the completion of serial tasks, there has been relatively little work done on the topic with nonhuman animals. However, a handful of recent studies suggest that this is a fruitful area for future work.

Berdyyeva and Olson (2009) report that a population of cells in the supplementary eye field (SEF) of rhesus macaques showed differential firing as a function of the position of a stimulus in an ordered set, regardless of whether the information is conveyed spatially (in the case of a learned motor sequence) or symbolically (in the case of a SimChain). This study echoes an earlier result by Diester and Nieder (2007), who recorded from prefrontal and parietal areas of rhesus macaques. In their procedure, the numerosity of dot stimuli was tested using a match-to-sample paradigm. Additionally, they trained subjects to associate specific numerosities with the cardinal numbers 1, 2, 3, and 4. They found that 30% of cells in the prefrontal cortex that showed task-selective activity were selective for numerosities and cardinal symbols. By contrast, parietal cells tended to be selective for one type of stimulus but not the other. In response to the critique that these signals might be explained instead by mere passage of time or expectation of reward, Berdyyeva and Olson (2011) followed up on the result and found that although these confounds partially explained the observed pattern of activation, they were not able to entirely account for differential firing as a function of ordinal position.

Although these studies indicate activity correlated with serial learning tasks, they do not demonstrate the causal necessity of prefrontal cortex involvement. One demonstration of prefrontal importance was reported by DeVito, Lykken, and colleagues (2010). They made lesions to the infralimbic and prelimbic areas of medial prefrontal cortex in mice, which resulted in much slower learning of adjacent-pair relationships and chance performance on the transitive test pair BD. Performance on the terminal pair AE, however, was not significantly different from that of subjects who underwent sham surgeries. Unfortunately, it is difficult to assess precisely why performance was impaired in this study, as other factors unrelated to serial learning (such as motivation) may have been impacted. Nevertheless, the discrepancy between BD and AE performance at test suggests an active contribution by prefrontal cortex.

The Intraparietal Sulcus

As with prefrontal cortex, the study of the intraparietal sulcus (IPS) has been powerfully motivated by the study of numerosity judgments and the number sense. Motivated in part by an extensive literature of IPS activation during mental arithmetic in humans, studies were undertaken to examine the extent to which these mechanisms were also observed in nonhuman subjects (reviewed by Nieder & Dehaene, 2009). Nieder and colleagues (2006) performed one such study on rhesus macaques, using stimuli containing one to four circles on a monitor. These elements were either presented as clusters (as in the previously discussed studies on numerosity), or were presented one at a time over a span of time (making the stimuli temporally distributed and sequential, rather than spatial and simultaneous). They reported that a population of IPS neurons fire differentially as a function of the integer count of the dots, regardless of the modality (spatial or temporal) by which they were presented. Thus, they interpreted this neural code as reflecting a kind of protocounting usable in either problem domain (see also Diester & Nieder, 2007).

However, in contrast to this result, Roitman, Brannon, and Platt (2007) performed a study with rhesus macaques using a much larger range of numerosity stimuli, consisting of anywhere from two to thirty-two dots per cluster. They reported that cells in the lateral intraparietal area (LIP) displayed smoothly graded firing as a function of stimulus numerosity. Although all reported cells displayed increased activity following stimulus onset (rising from a background rate of 15 spikes per second to about 90 spikes per second), some displayed subsequent excitation as a function of increasing numerosity, whereas others displayed subsequent inhibition. Thus, in the prefer large cells, firing continued to rise to as high as 160 spikes per second for larger numerosities and remained elevated over the course of the trial, whereas the prefer small cells dropped off more sharply for the larger numerosities.

The discrepancy between integer-specific selectivity and an approximate number sense with a smooth grade is not necessarily contradictory (see Chapter 25, this volume). Instead, these may represent two complimentary numerical systems: one that deals with approximate number, and another that deals with precise quantities (Feigenson, Dehaene, & Spelke, 2004). However, although the relative independence of these systems is well-studied in human brain injury patients, the cost of lesion studies in primates, coupled with the possibility that low-cost animal models of these faculties may not be available, will make it difficult to confirm that these distinct systems (or their precursors) are evolutionarily well-preserved.

CONCLUSION

Serial learning is a rich area of comparative study with a long history. Because so many abstract problems can be efficiently solved using serial representations, it is unsurprising that so many species demonstrate a capacity for this kind of reasoning. That said, various lines of evidence point to considerable discrepancies in the aptitude and inclination of various species to treat tasks as having an ordered character. Consequently, it is important to reserve judgment regarding the universality of specific mechanisms. For example, although the phenomenon of TI is seen in one form or another among the vertebrates, this does not necessarily suggest that this widespread behavioral aptitude relies on identical cognitive machinery. The discrepancies between primates and corvids in TI and simultaneous chain procedures speak to the possibility that there may be multiple convergent solutions to these problems that have emerged at different times. Uncovering the specific mechanisms that permit serial learning to occur will greatly increase our ability to trace the evolutionary history of this widespread ability.

Vehement theoretical disagreements persist among those who study serial learning, particularly given the long-standing rivalry between the cognitive and associative camps. Three things are required to help the field come to a more robust consensus. First, theorists must formulate models that make specific predictions, particularly under conditions that differ from those for which the model was originally designed. Those of a cognitive persuasion have the most work to do in this regard, as many cognitive models are strictly conceptual or rhetorical, rather than being rigorous and formal. Second, those models that are able to yield specific predictions must be exposed to experimental designs that challenge them, rather than those for which they were optimized. Many of the rigorous associative models suffer from this shortcoming, in that papers are routinely published that "validate" a model using conditions similar to those for which the model was designed. Progress will be made more readily if theorists are willing to expose their models to conditions that might result in failure, as well as to be brave enough to acknowledge those failures when they materialize. Finally, stronger lines of communication must be forged between neuroscience, ethology, and comparative psychology, to bring together theory, mechanism, and consequent behavior. Until these different levels of analysis become more adept at persuading one another of their conclusions, the study of serial learning is likely to remain an archipelago of isolated research projects, rather than a unified body of knowledge.

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CHAPTER 19

THE COMPARATIVE PSYCHOLOGY OF SOCIAL LEARNING

Bennett G. Galef and Andrew Whiten

The last 3 decades have seen an extraordinary increase in studies of social learning in nonhuman animals and humans. The relevant literature is unusual in the range of backgrounds of authors making substantial empirical or theoretical contributions to our understanding of social influences on the acquisition of behavior. However, despite the diversity in the academic disciplines of those studying social learning, there has been general agreement as to the subject matter of the field. Indeed, we know of no one working in the area who would take exception to defining social learning as "learning that is influenced by observation of, or interaction with, a conspecific or its products" (Heyes, 1994, p. 207).

As might be expected given the breadth of interests of those studying social learning in animals and the resultant scatter of relevant publications across specialized journals in many disciplines, the need for reviews of work in the area was recognized early in its history, and assessments of progress in social learning in general and in subareas of the field have been frequent (see Appendix 19.1). The present discussion builds on its predecessors, but differs in that, consistent with the topic of this handbook, we explicitly consider the study of social learning as a branch of comparative psychology.

The first challenge to such an approach results from the considerable diversity of opinion concerning the defining features of this field of inquiry (reviewed in Demarest, 1980). Historically, the term *comparative psychology* has often been used in a rather general way to refer to the scientific study of behavior and cognition in nonhuman animals. This usage, however, led Konrad Lorenz to opine "I strongly resent it . . . when an American journal [the *Journal of Comparative and Physiological Psychology*] masquerades under the title of 'comparative' psychology, although to the best of my knowledge, no really comparative paper ever has been published in it" (Lorenz, 1950, pp. 239–240).

Lorenz and other more biologically oriented researchers (e.g., Hodos & Campbell, 1969) advocated a comparative psychology focused on studies of similarities and dissimilarities in homologous behavioral traits of closely related species. Indeed, when Romanes (1884), Darwin's protégé in matters behavioral, introduced the term comparative psychology into the modern scientific literature, he used the term in Lorenz's sense, proposing that comparative psychology should be modeled on comparative anatomy, focused on comparisons between closely related species and tracing the evolution of morphological traits:

> In the family of the sciences, Comparative Psychology may claim nearest kinship with Comparative Anatomy; for just as the latter aims for the scientific comparison of the bodily structures of organisms, so the former aims at similar comparisons of their mental structures. (Romanes, 1884, p. 5)

Romanes, however, recognized that comparisons of closely related species had to be preceded by examination of the "mental structures" of individual species. "When this analysis or dissection has been completed . . . the next object is to compare

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with one another all the structures which have thus been analyzed" (Romanes, 1884, p. 5). The results of such comparisons can be used "to [classify] all the structures thus examined . . . [though] in actual research these three objects are prosecuted not successively, but simultaneously" (p. 5).

In sum, in Romanes's view, comparative psychology involves three synergistic activities to be pursued simultaneously: (a) description of the mental structures of individual species, (b) comparison of such structures between closely related species, and (c) classification of similarities and differences. Although today we would be more likely to speak of cognitive processes inferred from behavioral observations than of mental structures and classification is seen as less central to scientific progress than it was in Romanes's day (when physics and taxonomy were considered to be the premiere sciences), the considerable diversity of current work on social learning in animals falls rather neatly into Romanes's scheme.

In the first part of this chapter, we use work on social learning published from January 2012 to December 2014 to determine whether students of social learning have overcome a suite of scientific "sins" of which the broader field of comparative psychology has, historically, been accused. Next, we briefly discuss classifications of social learning to provide a framework within which to consider teaching: A behavior that, like imitation, has been considered a uniquely human characteristic but is now viewed as part of the behavioral repertoire of nonhuman animals as well. Finally, we address Romanes's third goal, direct comparison of social learning in closely related species, focussing where the literature is richest, on comparisons of humans with other apes. This chapter is complemented by Chapter 20 of this volume, which focuses on the larger-scale phenomena of tradition and culture that are crucially dependent on social learning.

CONTRIBUTION OF STUDIES OF SOCIAL LEARNING TO COMPARATIVE PSYCHOLOGY

Classic comparative psychology has been criticized (see Lockard, 1971) for focusing on (a) a very limited range of species (Beach, 1950), (b) domesticated rather than wild animals, (c) too few and biologically irrelevant behaviors, (d) laboratory rather than field studies, and (e) the topic of learning at the expense of other factors important in behavioral development, as well as (f) working with a naive view of phylogenetics on the basis of the medieval *Scala Nature* rather than Darwinian evolution (Hodos & Campbell, 1969). We shall not elaborate on these criticisms here. Our review of the current literature on social learning clearly shows that today comparative psychologists studying social learning are far from guilty of these sins against biology, which were once attributed to the field.

We have examined all experimental papers on social learning cited in Web of Knowledge during the years 2012–2014 and listed the species and behaviors studied, as well the context (laboratory or field) in which research was conducted. A summary of the results of this overview are presented in Table 19.1. Citations of the reviewed publications, criteria for their selection, and the detailed table summarized in the text are available in Appendix 19.2.

As can be seen from Table 19.1, even in this snapshot of 36 months of publications, at least 104 research groups reported working with 66 species. Although amphibians, reptiles, and molluscs were clearly underrepresented, possibly because they do not often exhibit interesting examples of social influence on learning, a substantial number of vertebrate species and several different insects were subjects of study. Similarly, wild (55) and domesticated (11) species were well represented in the contemporary social-learning literature, with the standard laboratory rodents, so overrepresented in classic comparative psychology (Beach, 1950), playing a relatively small, though important, role.

Studies of social learning in avian species are more likely to be conducted in free-living than in captive populations, whereas terrestrial mammals and fish have been far more frequently studied in the laboratory than in the field. These data are consistent with the view that the relative ease of studying territorial, diurnal animals living in social groups, rather than intellectual bias, has played the major role in deciding whether to study social learning in laboratory or natural circumstances.

TABLE 19.1

Summary of Experimental Publications, 2012–2014

Class	Research groups	Species	Wild/domestic	Captive/free	Behaviors
Primates	29	10	10 wild	4 free, 4 both	16
Other mammals	31	20	15 wild	9 free, 1 both	22
Birds	17	15	13 wild	12 free	15
Fish	16	12	9 wild	0 free	7
Insects	7	5	4 wild	0 free	5
Other	4	4	4 wild	0 free	3
Totals	104	66	55 wild	25 free, 5 both	43

Note. Counting behaviors is necessarily somewhat subjective. The dependent variables used in the papers summarized in the table include preferences for foods, feeding sites, mates, and nest sites and the avoidance of predators, brood parasites, and biting insects.

Further, although work on social transmission of arbitrary laboratory operants (14 research groups) still occurs, primarily in mammals, the overwhelming majority of studies in all classes are of behaviors that animals might be expected to display in natural circumstances or are recognizable analogues of such behaviors adapted to captive study.

Because many research groups have become involved in studies of particularly promising phenomena, some areas, such as song learning in birds (for a recent review, see Catchpole & Slater, 2008; see also Volume 1, Chapter 26, this handbook), transmission of food preference in rodents, and imitation in chimpanzees (*Pan troglodytes*), have received inordinate attention. However, despite such focus, the number of behaviors investigated remains high. For example, studies of social influence on avian learning involved migration, homing (see Chapter 22, this volume), brood-parasite avoidance, nest-site selection, feeding-site selection, mate-choice, clutch size, tool use (see Chapter 30, this volume), social skills, and the spread of feeding innovations (see Chapters 20 and 28, this volume). In fish, social influences on predator avoidance, mate-choice (see Volume 1, Chapter 37, this handbook), and various aspects of foraging predominated, whereas insects were most frequently studied as sources of information on feeding-site selection, egg-deposition-site preference and predator avoidance (see Volume 1, Chapter 40, this handbook), though studies of laterality (see Volume 1, Chapter 27, this handbook) and spatial learning (see Chapter 21, this volume) in insects were also reported.

No simple enumeration of species and behaviors investigated can provide much insight into work in a field. Next, we describe four illustrative areas of research where progress has been particularly impressive, involving such subjects as a mammal, a bird, a fish and an insect.

Social Transmission of Information Concerning Distant Foods: Rats and Mice

Currently, the most heavily researched area in studies of social influence on the acquisition of behavior in nonprimate mammals involves the social transmission of food preference (STFP). The following is a now standard paradigm, originally developed as a laboratory analogue of a situation assumed to occur whenever a member of a central-place foraging species discovers and eats a food before returning to the harborage site it shares with others of its species (Galef & Wigmore, 1983): (a) A “demonstrator” animal first eats one of two diets, then, (b) in the absence of food, interacts briefly with a naive conspecific “observer” that finally (c) chooses, in isolation, between the two diets.

Invariably, the preferences of observer rodents (*Rattus norvegicus*) for the food that their respective demonstrators have eaten is substantially enhanced, and such effects are powerful and long-lasting, essentially undiminished a month or more after a demonstrator and observer interact (Clark, Broadbent, Zola, & Squire, 2002; Galef & Whiskin, 2003). STFP has been reported in many social, central-place foraging mammals from hyenas (*Crocuta crocuta*; Yoerg, 1991) to bats (*Carollia perspicillata*; Ratcliffe & ter Hofstede, 2005). Analyses of the sensory basis of such information transmission shows that the breath of a demonstrator rodent carries information allowing an observer (whether conspecific or human) to identify the food that the demonstrator had eaten (see Chapter 4, this volume), and equally important, a contextual cue that an observer has to experience at the same time that it experiences the diet-identifying cue, if exposure to the diet-identifying cue is to alter the observer's subsequent food preferences. Simple exposure to a diet by sniffing or eating has little effect on subjects' subsequent food selection.

Rodent breath contains several sulfur compounds, the most concentrated of which, carbon disulfide (CS_2), acts together with a food odor, as does the presence of a demonstrator, to produce changes in observers' food choices. For example, naive observer rats (*Rattus norvegicus*) or mice (*Mus musculus*) that interact with a piece of cotton batting dusted with food and moistened with CS_2 subsequently show as strong a preference for that food as do naive observers that interact with an anesthetized conspecific demonstrator dusted with the same food. Observers interacting with a piece of cotton batting dusted with a food and moistened with water showed no increase in preference for the food with which the cotton batting was dusted (Galef & White, 1988; Munger et al., 2010).

Much is now known of the sensory basis of sensitivity to CS_2. A small percentage of receptor neurons in the olfactory epithelium of mice (GC-D receptors) express guanylyl cyclase, and such GC-D receptors respond vigorously only to biologically relevant concentrations of CS_2 and a few related compounds (Leinders-Zufall et al., 2007). Homozygous gene-targeted mice with disruptions in the transmission cascades of their GC-D receptors fail to show an enhanced preference for foods, whether experienced on the breath of a demonstrator mouse or on a piece of cotton batting moistened with CS_2. By contrast, the STFP of heterozygous observer control mice with intact GC-D receptors are unimpaired (Munger et al., 2010).

STFP requires not only detection of olfactory stimuli, but also storage and utilization of memories of those stimuli. Work in several laboratories (e.g., Alvarez, Lipton, Melrose, & Eichenbaum, 2001) provided evidence that the hippocampus plays an important role in initial processing of STFPs, with longer-term memories residing in the orbitofrontal cortex. More recently, Lesburguères et al. (2011) used the absence of interactions among numerous STFPs in a single observer (Galef, Lee, & Whiskin, 2005) to further explore the interplay of hippocampus and cortex in early processing and later storage of STFPs. Contrary to the prevailing view that only the hippocampus is involved in early processing of memories (see Volume 1, Chapter 25, this handbook), Lesburguères et al. (2011) found that long-term memory was not established if the function of cortical structures was inhibited during the first week after an observer mouse interacted with a demonstrator. The finding was interpreted as showing that when an observer interacts with a demonstrator, specific neurons in hippocampus and cortex are allocated to that memory, and this subset of "tagged" neurons is necessary for later dialogue between hippocampus and cortex needed to establish long-term memory.

Perhaps the most surprising recent finding with respect to STFP is that it occurs even if observer and demonstrator are unconscious while interacting (Nicol, Sanchez-Andrade, Collado, Segonds-Pichon, & Kendrick, 2014). It has long been known that observers acquire a STFP from an unconscious demonstrator (Galef & Wigmore, 1983). However, the rather extraordinary finding that unconscious observer mice acquire a preference for a diet when exposed to an anesthetized demonstrator, but not when exposed to the diet alone (Burne, Johnston, Wilkinson, & Kendrick, 2010), promises extraordinary progress in understanding STFP and general effects of experience on preference development.

Advances in analysis of STFP have been ecological as well as neuroanatomical. For example, O'Mara, Dechmann, and Page (2014) working with a tropical, central-place foraging, frugivorous bat (*Uroderma bilobatum*) looked at individuals who had interacted simultaneously with two conspecific demonstrators, one previously fed a flavored food and the other with a different food placed on its fur.

When subsequently offered a choice between the two foods, observer bats preferred the food the demonstrator had eaten to the food on the demonstrator's fur. Discrimination between food cues carried on breath and on fur could lead bats to attend to particularly informative social cues. Ingested food has been eaten, whereas food on fur may have been contacted inadvertently.

Social Transmission of Experimentally Induced Behavioral Innovations: Great Tits

Two recent technical developments, the first statistical and the second a method for automatic, simultaneous tracking of the positions of members of free-living populations promise a revolution in field studies of social learning. Network-based diffusion analysis (NBDA), predicated on the assumption that propagation of behavior is more likely between individuals that spend time close to one another than between individuals that rarely associate, allows statistical detection of social learning in a population once its social structure has been determined (Hoppitt & Laland, 2013; see also Chapter 20, this volume). The combination of automated determination of association matrices using passive integrated transponders (PIT tags; Krause et al., 2013) and NBDA and other statistical methods (Hoppitt & Laland, 2013) for revealing correlations between network structure and the diffusion paths of behaviours through populations promises a revolution in field and laboratory studies of social learning.

NBDA can be used in either laboratory or field work (e.g., Hoppitt & Laland, 2013), not only to detect the involvement of social learning in the diffusion of behavior through populations, but also to identify particular learning mechanism involved in diffusion of a behavior, their relative strengths, and durations of action. Here, we discuss only a relatively simple application of NBDA. Aplin et al. (2014) have recently used an automated data collection system in conjunction with PIT tags and NBDA to describe the spread and persistence of behaviors introduced into populations of free-living great tits (*Parus major*), whose social network structure had been independently determined. Aplin et al. (2014) captured and trained two birds from each of five flocks of PIT-tagged birds to push the door of an automated feeder to either left or right to gain access to food. The authors traced the spread of introduced behaviors through these five populations and the three control populations without trained demonstrators.

Members of the five experimental flocks learned to open the puzzle box far more rapidly than members of the three control flocks and invariably used the same action (pushing the door to left or right) introduced into their flock. Year-long adherence to the introduced behaviors was seen in all five experimental flocks despite many individuals in each flock independently discovering the alternative action to acquire food and replacement of 60 percent of each flock by new recruits over the winter months. Most important, social structure predicted the path of diffusion of the introduced behaviors, with transmission rate between individuals linearly related to the frequency of association among individual flock members.

Social Influences on Mate Choice: Guppies and Mollies

Deciding which of several potential partners would make the better parent for one's offspring requires allocation of resources to evaluation of potential partners that might more profitably be directed to alternative activities. Copying someone else's choice ensures doing no worse than one's model without incurring the cost of evaluation and might be particularly valuable to young copying choices of older, more knowledgeable individuals.

A considerable literature indicates that female mammals, birds, and fish may show an increased preference for males they have seen court or mate with another female (for reviews, see Mery et al., 2009; Vakirtzis, 2011; see also Volume 1, Chapter 37, this handbook). In the first of such experiments, Dugatkin (1992) studied social influences on mate choices of female guppies (*Poecilia reticulata*), descendants of animals caught in the streams of Trinidad where wild guppies select partners and breed under conditions allowing observation and copying of one another's mate choices. In Dugatkin's laboratory, focal female guppies simultaneously watched one of two size-matched target males court another female (a model) while the other male remained alone. Each focal female was then released to choose between her target males. Seventeen of 20 focal females spent more time with the target male they had seen court a model female than with the target male they had seen alone.

Although such data are consistent with the hypothesis that female guppies copy one another's mate choices, they are open to alternative interpretations. For example, female guppies, members of a species that shoals in natural habitats, might prefer a location where they have previously seen two fish, to a location where they have seen only one (see Chapters 25 and 26, this volume). Also, the behavior or appearance of a male who has recently courted might be more attractive than those of a male who has not. Dugatkin's (1992) further experiments excluded a number of such plausible accounts of the increased affiliation of females with males they had observed courting, leading to the conclusion that focal females were copying the apparent choices of model females.

Evidence of mate-choice copying in fish is not confined to the laboratory. Witte and Ryan (2002) used a procedure analogous to that which Dugatkin (1992) had used to study social influence on the mate-choices of female guppies to investigate mate-choice copying in wild sailfin mollies. Witte and Ryan found that sailfin molly females (*Poecilia latipinna*) preferred to affiliate with males previously observed courting and that such enhanced association was, as Dugatkin found with guppies, not simply a consequence of mollies' tendency to shoal.

In natural environments sailfin mollies shoal with Amazonian mollies. Amazonian mollies (*Poecilia formosa*) are unusual in that although sperm is required to initiate their embryogenesis, inseminating males do not contribute genetic material to a female's eggs. Perhaps even more surprising, the sperm that initiates embryogenesis in female Amazonian mollies comes from mating with male sailfin mollies, although as noted previously, these males do not contribute genetic material to female Amazonian mollies' offspring.

It would seem a waste of time and energy for male sailfin mollies to court and inseminate heterospecific females who will not pass their genetic material on to future generations. However, Schlupp and Ryan (1996) have shown that a male sailfin molly becomes more attractive to conspecific females after they have seen him mate with an Amazonian molly. Thus, a superficially maladaptive behavior in male sailfin mollies is sustained by a tendency of female sailfin mollies to copy heterospecific females' mate choices. Social influences on mate choice are clearly more than a laboratory curiosity.

Social Influences on Choice of Feeding and Egg-Deposition Sites: Drosophila

Some of the earliest, and surely some of the strongest, evidence of social learning in any species is that provided by von Frisch (1967) and generations of students studying communication among honey bees (see Volume 1, Chapter 30, this handbook). Unfortunately, that work has not been well integrated into the literature on social learning, possibly because early in the 20th century, when von Frisch initiated his study of pheromonal and dance-language communication in honeybees (*Apis mellifera*), social learning did not exist as a coherent field of inquiry to which studies of honeybee communication could contribute. Consequently, work on honeybee communication, like work on bird-song learning (also well developed before studies of social learning had been integrated into a coherent field; see Volume 1, Chapter 26, this handbook), has proceeded not only very successfully, but also essentially independent of other contributions to the understanding of social learning in animals. Only in the last decade have studies of social influences on bumblebee (*Bombus terrestris*) foraging, orientation in ants (*Formicidae sp.*; see Chapter 22, this volume), and preferences of fruit flies (*Drosophila melanogaster*) brought work with insects into the main stream of the social-learning literature. (e.g., Leadbeater & Chittka, 2009; Dukas, 2010). Although studies of social influences on insect behavior are recent, intriguing findings, some with considerable potential for neurogenetic analyses of the physiological substrate of social learning are already available.

In natural environments, fruit flies aggregate in response to odors of ripe fruit and an aggregation pheromone released by adults at sites where they feed and lay eggs. In the laboratory, female fruit flies copy mate choices of others and are susceptible to social influences when selecting oviposition sites.

Reminiscent of STFP in Norway rats, Battesti, Moreno, Joly, & Mery (2012) have found that female fruit flies that have interacted in a neutral arena with a female that had laid her eggs on a scented medium subsequently preferred to deposit eggs on media with that scent. Preference acquisition required female flies to experience substrate cues on a conspecific; simple exposure to the substrate itself did not have a similar effect. Further, as in Norway rats (Galef & Aleen, 1995), socially transmitted preferences in fruit flies supported a local tradition with a socially learned preference passing from one generation to the next.

Sarin and Dukas (2009) showed that female fruit flies that experience a novel food together with other females that have laid eggs on that food subsequently show a greater probability of laying their own eggs on similar substrate than females that experienced the novel food alone. Further, female fruit flies are not only strongly attracted to food substrates previously occupied by larval fruit flies, but also subsequently prefer odors associated with such substrate. Increased duration of exposure to a substrate odor resulting from attractiveness of larval odor is entirely responsible for this change in preference (Durisko, Anderson, & Dukas, 2014).

Conclusion

The large corpus of recent studies enumerated in Table 19.1 and the sample of studies described previously involve a broad range of species, wild and domesticated, and biologically important behaviors studied in laboratory and field work. Gradual movement toward study of house mice, zebrafish (*Danio rerio*) and drosophila, species that for decades have served as model systems in the biological sciences, suggests that instances of social learning will soon be subject to sophisticated neurogenetic analyses and such integration of comparative psychological and biological approaches to studies of social learning promises a bright future for the field.

TEACHING: AN EXAMPLE OF ANALOGICAL CLASSIFICATION

Some outsiders to the field of social learning, especially those with a primary interest in functions rather than mechanisms of behavior, have found the schemes proposed by those seeking to classify the various instances of social learning not only irrelevant to their concerns, but also rather impenetrable. However, without such schemes, results of studies of social learning would provide little more than a collection of isolated facts about the development of adaptive patterns of behavior rather than the coherent body of work that has developed over the last few decades. Further, classification has played a critical role in discussion of the extent of overlap of the mental faculties (i.e., cognitive processes) of humans and other animals, an issue that has challenged comparative psychologists since inception of the field.

Over the years, resolving potentially incompatible portrayals of the relationship of animal to human cognition that date back to the origins of modern biology and a dispute between Darwin (1871) and Wallace (1870) as to the continuity of human and animal mind has motivated numerous studies of cognitive processes in animals and led to questions as to whether there exist cognitive processes unique to humankind. Because we will be considering imitation at considerable length later in this chapter, our discussion here focuses on teaching as an example of a behavior, that has emerged from consideration of taxonomies of social learning and, like imitation, was once believed to be uniquely human, but is no longer considered so.

Social Learning and Teaching

Recent reviews by Hoppitt and Laland (2008, 2013), Whiten, Horner, Litchfield, and Marshall-Pescini (2004), and Zentall (2011, 2012) provide extensive discussion of definitions and evidence related to all the principal categories of social learning differentiated in the core literature of the field. The list of categories of social learning is both long and hotly debated. It includes such widely used terms as stimulus enhancement, local enhancement, observational conditioning, response facilitation, emulation, contextual imitation, and production imitation. Space limits to the present chapter, together with the numerous excellent recent reviews of the vocabulary of social learning, have led us to provide here only brief definitions of 14 widely used terms and examples in Table 19.2. We direct interested readers to the reviews cited earlier for more extended analysis and discussion.

We focus instead on the definition and study of teaching, a different and recently topical example of the importance of categorization in organizing the multitude of empirical findings that constitute the foundation of discussions of social learning. To those not familiar with the social learning literature, it may come as a surprise that the reviews cited previously did not include teaching among their categories of social learning. The omission was no oversight. Teaching, although potentially important for social learning, is not generally regarded as a type of social learning as such. Rather, teaching is behavior that a knowledgeable individual performs that facilitates acquisition of some behavior by a naive pupil with whom the teacher interacts. Consequently, a teacher can in principle elicit or encourage any type of learning, whether exclusively social (e.g., imitation) or basically asocial (e.g., trial-and-error learning). For example, a teacher may teach by (a) simply focusing the attention of a potential pupil on some aspect of the environment (local enhancement), (b) exaggerating features of an action for a naive individual to copy (imitation), or (c) encouraging a pupil to persevere

TABLE 19.2

Categories of Social Learning

Category	Examples
Stimulus and local enhancement: Focus of model's behavior on an object or on a location causes learner to adopt a similar focus.	Female quail preferentially associated with males that had been in proximity to other females (Galef & White, 1998); bees focused their foraging on flowers visited more by other bees (Leadbeater & Chittka, 2007).
Observational conditioning: Response of model to a stimulus causes learner to direct a similar behavioral response already in its repertoire to similar stimuli.	Macaque monkeys showed fear responses to stimuli such as snakes after witnessing this in others (Cook et al., 1985).
Contagion/response facilitation: The probability that an individual will engage in a behavior already in its repertoire is increased when it sees another engage in that behavior.	Domestic fowl were more likely to perform preening when others in the flock preened (Hoppitt et al., 2007).
Affordance learning (a form of emulation): A naive individual learns from observing a model behave some operating characteristics (e.g., properties, functions, relationships) of objects or other elements in the environment.	Chimpanzees learned the raking function of a stick-tool from others (Tomasello et al., 1987).
Result and goal emulation: A learner achieves the same result that a model achieved or attempted to achieve but uses a different behavior to do so.	Chimpanzees that witnessed a model pouring water from a bottle into a container to make a peanut float within reach then spat water into their own container to achieve the same result (Tennie et al., 2010); chimpanzees that witnessed failed attempts to open an artificial food object opened the object but in a different way (Call et al., 2005).
Contextual and production imitation: Observing a model behave in a specific way causes an observer to act in the same way. In contextual imitation the observed behavior is already in the observer's repertoire; in production imitation the behavior is novel to the observer.	Pigeons stepped on or pecked a panel according to which of these options they saw a model perform (Zentall et al., 1996). Orangutan trained to "do this" with one set of actions performed full matches to 70% of a battery of 48 other actions, including many judged to be novel (Call, 2001).
Program-level imitation: Learner copies the structural organization of a model's behavior that is novel to the learner, even if component elements are not.	Chimpanzees copied whichever of two novel sequences of the same set of component actions they witnessed (Whiten, 1998); children copied whichever of two novel hierarchical organizations of the same set of component actions they witnessed (Flynn & Whiten, 2008).

Note. Major categories distinguished in the literature on social learning, largely on the basis of analyses by Byrne (2002), Byrne and Russon (1998), Galef (2012), Heyes (1994), Hoppitt and Laland (2008, 2013), Whiten and Ham (1992), Whiten et al. (2004), and Zentall (2012).

in individual trial-and-error learning (Hoppitt et al., 2008). Teaching itself is thus orthogonal to categories of social learning. Teaching has become increasingly important in recent discussions of social learning as a result of growing interest in the relationship between the traditions seen in human and animal populations. Some investigators have suggested that together with imitation, teaching is critical to social transmission of sufficiently precise copies of observed behavior to support the "ratcheting" necessary for the emergence of cumulative culture typical of our own species, and it is either absent (Tomasello, 1990; Galef, 1992) or minimal in other animals (Sanz, Call, & Morgan, 2009; Whiten, 2011).

The scientific study of teaching in animals developed late in the history of comparative psychology, in large part because early definitions of teaching focussed on the intention of a teacher to impart knowledge to a pupil. Some remain convinced of the utility of defining teaching in terms of teachers' intentions (Byrne & Rapaport, 2011). Others disagree (Thornton & McAuliffe, 2012) arguing that identification of instances of teaching and of the behavioral processes supporting such instances should be separated.

Caro and Hauser's (1992) redefinition of teaching provided an operational definition, on the basis of cost–benefit analyses already common in behavioral ecology, which led to a resurgence in the study of teaching in animals and humans. In brief, Caro and Hauser considered teaching to occur when a knowledgeable individual modified its behavior in the presence of a naive individual at a cost (or at least without any immediate benefit) to itself in a way that facilitated the naive individual's acquisition of some behavior.

When defined in this way, many potential instances of teaching were already in the literature. For example, the waggle dance that a successful honeybee forager performs in the hive to alert fellow honeybees to the location of sources of nectar or pollen (von Frisch, 1967), the tid-biting of gallinaceous birds leading their young to ingest nutritious foods (Sherry, 1977) or the mobbing and alarm-vocalizations that help naive individuals learn to recognize potential predators (Curio, 1988) all satisfy Caro and Hauser's (1992) criteria. Several interesting cases of teaching in animals meeting Caro and Hauser's criteria have been recently identified, perhaps most compelling among them is the adult provisioning of dangerous prey to young meerkats (*Suricata suricata*).

Learning to handle toxic prey: Meerkats. Young meerkats are largely dependent on provisioning by adults until 2 to 3 months old, when they begin to forage independently for insect prey, including potentially dangerous scorpions (Thornton & McAuliffe, 2006). Adult meerkats usually immediately consume prey they capture. However, in the presence of young meerkats, adult meerkats will often kill or disable, rather than eat, captured scorpions (in the latter case, removing the scorpions' stingers) so as to bring intact scorpions to juveniles.

Most spectacularly, adult meerkats modify their provisioning behavior in response to the perceived age of the young they are provisioning, increasing the frequency of bringing intact scorpions as the young mature and become increasingly competent to handle such dangerous prey. Playing recordings of begging calls of an older pup to an adult providing scorpions to a young pup causes the adult to increase the frequency with which it presents intact scorpions, even though the recipient is not yet ready to handle them. Conversely, playing the calls of young pups to adults provisioning older juveniles increases the frequency with which adults deliver disabled or killed scorpions that would normally be given to younger pups.

Further, as Caro and Hauser's (1992) definition of teaching requires, not only did provisioning adults incur a cost, providing prey to young they could have eaten themselves, but they also facilitate the development of prey-handling skills in the juveniles they provisioned. Young meerkats provided with disabled scorpions learned to handle intact scorpions more rapidly than pups artificially provisioned with either dead scorpions or a hard-boiled egg.

Learning the way to food and nest site: Tandem running in ants. Equally compelling evidence of teaching is available in *Temenothorax albipeenis,* a species of ant in which a successful forager that knows the location of a food source travels in an unusual way toward the food in tandem with a naive nest mate, pausing while the follower looks around, apparently examining landmarks along the route, and moving rapidly toward food only after its follower taps it with its antennae. As a consequence of this unusual behavior, the leader ant delays its return to food, taking four times longer to travel in tandem with a naive ant than it would if traveling the same path alone, whereas naive followers find food faster when following a knowledgeable leader than when searching for food on their own. Also, after following, naive ants return more directly to the nest site they share with their leader ant than the leader ant did after it first discovered the food (Franks & Richardson, 2006).

Teaching in chimpanzees and humans. Given the discovery in ants, bees, and various bird and mammal species of behaviors that met Caro and Hauser's (1992) criteria for teaching, it came as something of a surprise that many years of observation of chimpanzees in natural habitat provided essentially no evidence of teaching in this closest extant relative of humans (*Homo sapiens*), the planet's most accomplished teachers. (For an alternative view of teaching in chimpanzees, see Boesch, 2012.) Indeed, absence of evidence of teaching in chimpanzees led some to question the prevalence of teaching in preliterate human societies (Laland & Hoppitt, 2003).

The older ethnographic literature, in which formal verbal instruction of the sort common in the Western world served as the model of teaching, provided few reports of such instruction. However, more recent anthropological investigations relying on a definition of teaching consistent with Caro and Hauser's (1992) have provided compelling evidence that teaching is present in indigenous societies (for examples see Hewlett, Fouts, Boyette, & Hewlett, 2011; Kline, Boyd, & Henrich, 2013). The importance of teaching relative to other forms of learning (e.g., imitation, trial and error) in skill development in preliterate societies remains an open question.

The peculiar phylogenetic distribution of known instances of teaching in insects, gallinaceous birds, and humans, but not chimpanzees, raises important questions as to whether teaching is a single process or many different processes. As Premack (2007) indicated, animal teachers differ profoundly from their human counterparts in that the former always have a single domain in which they teach, whereas human teaching is a "domain-general competence" (p. 13862), with teachers facilitating acquisition of innumerable skills. Clearly, in discussing teaching as Caro and Hauser (1992) defined it, we are dealing with analogy not homology. The function of teaching is common across instances, the mechanism is surely not.

Constructing taxonomies of social learning requires attention to similarities in the behaviors of members of species that are only distantly related to one another, an approach to the analysis of behavior that some find hard to justify. If such an approach to behavioral comparison were all that the field of social learning had to offer, criticism of its contribution might well be valid. However, as our discussion will show, in harmony with the phylogenetically based comparative psychology that Romanes (1884), Lorenz (1950) and others advocated, comparative studies of social learning have involved investigations of similarities and differences in social learning in closely as well as distantly related species.

COMPARISONS OF CLOSELY RELATED SPECIES

Comparison of behavioral phenotypes of closely related species might be assumed to lie at the heart of any discipline calling itself comparative psychology. However, in attempting to review the relevant literature, we have found such comparisons remarkably rare, with the exception of comparisons between our own species and those with which we share our most recent common ancestry, the great apes, especially the most frequently studied of our closest primate relatives, the chimpanzee. Table 19.3 lists 25 articles comparing the behavior of humans with that of other apes. By contrast, our explorations of the literature revealed few comparative studies of social learning in two or more closely related nonprimate species.

Rationales for a Comparative Psychology of Social Learning

The rationales that authors offer for pursuing comparisons between closely related species vary in

TABLE 19.3

Comparative Social Learning Studies of (Other) Great Apes and Children, 1993–2015

Reference	Children	Apes	Model and actions	Overview
Direct comparisons				
Nagell et al., 1993	24 × 2 yr	15 chimps × 4 yr–8 yr	human models—flip over rake tool to more efficiently rake in reward, versus tool already flipped	Chimpanzees were no more likely to flip tool to its more efficient form having observed this modeled than having seen use of a tool already flipped. By contrast, children were more likely to flip tool in the observation condition.
Tomasello et al., 1993	16 × 1.5 yr–2.5 yr	6 chimps & bonobos × 3 yr–21 yr	human models—battery of 24 modeled actions incorporating specific, unusual acts on objects and their outcomes	Three human-enculturated apes showed levels of imitation (copying both actions and outcomes) similar to those of children tested. By contrast, three mother-reared apes were rarely judged to imitate.
Call and Tomasello, 1995	24 × 3 yr–4 yr	14 orangs × "juvenile and adult"	human + conspecific models—different sequences of pull, push, and rotate handle to release food; how sequence worked was opaque	Orangutans showed no evidence of learning the particular acts (e.g., rotate vs. pull) or sequences (e.g., rotate then push) they had witnessed, whether the model was a human or orangutan. By contrast, 37% of three-year-old children and 69% of four-year-olds matched sequence witnessed.
Carpenter and Tomasello, 1995	6 × 18 mos	6 chimps × 3 yr–21 yr	analyzed the joint attentional behavior of subjects	Amongst the apes, the extent of joint attentional behavior was positively correlated with imitative performance; enculturated apes were more like children in attentional behaviors.
Whiten et al., 1996	7 × 4 yr–8 yr	8 chimps × 4 yr–5 yr	human models—alternative actions on three components of artificial fruit, to extract rewards	Both chimpanzees and children matched the model's actions applied to one component whereas children matched for two components.
Call et al., 2005	48 × 2.5 yr	50 chimps × 4 yr–40 yr	conspecific models—for two alternative ways to open a tube, subjects saw (attempted) actions only, results only, both, or neither	Chimpanzees mainly reproduced only the results of alternative actions and tended to avoid the attempted but failed approach witnessed, whereas children often matched the latter.
Horner and Whiten, 2005; McGuigan et al., 2007, 2011	16 × 3 yr–5 yr	12 chimps 4 yr–6 yr	human models—causally relevant versus causally irrelevant actions; visibly so versus opaque	Chimpanzees tended to match sequence and type of actions in opaque condition but omit causally irrelevant actions in transparent condition. Children copied irrelevant actions in both conditions.
Tennie et al., 2006	201 × 1 yr–2 yr	14 chimps, 6 gorillas, 8 orangs × <5 yr and >15 yr	conspecific models—for two alternative ways to open a small door, subjects saw full action, only ("ghost") door movement, or no model	Apes did not match the alternative they witnessed in either condition (however, they succeeded in 7/8 of no-model condition, so had little need to learn by observation). By contrast, 1.5- to 2-year-old children tended to copy in both full model and ghost conditions.
Horner et al., 2006	31 × 3 yr–4 yr	22 chimps × 11 yr–42 yr	conspecific models—tool used to extract reward from two-action artificial fruit	Alternative methods of opening were faithfully transmitted along chains of 5 and 6 chimpanzees, and both chains of 8 children.

(*Continued*)

TABLE 19.3 (*Continued*)

Comparative Social Learning Studies of (Other) Great Apes and Children, 1993–2015

Reference	Children	Apes	Model and actions	Overview
Herrmann et al., 2007	105 × 2.5 yr	106 chimps × 3 yr–21 yr; 32 orangs × 3 yr–10 yr	human models—solutions to three problems chimpanzees did not display in baseline tests were modeled once (e.g., bang tube on ground to release reward inside)	Chimpanzees and orangutans never matched, whereas children always did. This was the most marked of all species differences in 6 tests of communication, theory of mind, and physical understanding.
Horner and Whiten, 2007	12 × 3 yr–4 yr	9 chimps × 2 yr–6 yr	human models—correct insertion of stick-tool to extract reward from tube with trap in it, versus initially incorrect move followed by correct approach, and a stimulus enhancement condition	Neither chimpanzees nor 3- to 4-year-old children benefited from viewing errors as well as correct and successful approaches. None gained an understanding of the nature of the trap problem. 5- to 6-year-old children were more successful but relied little on copying model behavior.
Hopper et al., 2008	40 × 3 yr–5 yr	32 chimps × 11 yr–44 yr	conspecific models—subjects saw door moved left or right by model, or only "ghost" door movement, or same with passive conspecific present, or no model	Chimpanzees matched the door direction witnessed only on first trial in the ghost condition (thus emulating) but did so consistently if viewing a conspecific perform the action. Children were the same except were also more likely to copy door movement when a passive conspecific was present.
Buttelmann et al., 2008	24–28 × 14 mos in each of 3 studies	16 chimps, 5 gorillas, 5 bonobos, 7 orangs, 3 yr–31 yr	human models—in three variations, subjects saw model use tool to obtain reward when unnecessary or when necessary because access blocked	In all three studies, infants were more likely to copy use of the tool when it was freely used rather than necessary, whereas apes did not, with the exception of the orangutans (cf. Buttelmann et al., 2007).
Tennie et al., 2009	27 × 4 yr	7 chimps, 6 gorillas, 8 orangs, 5 bonobos (no ages)	human models—either make a loop of wool and use it to lasso a peg on a board and pull it close to gain reward, or show the board movement only	No ape made a loop in any condition. One child made and used a loop after the object movement demonstration but 9/12 did so after seeing the act modeled.
Haun et al., 2012	16 × 2 yr–2.5 yr	15 chimps × 6-21 yr, 12 orangs × 6 yr–12 yr	Three conspecific models—placed tokens in one of three containers, versus one model posting in alternative container	Chimpanzees and children tended to match the majority choice, but orangutans did not.
Dean et al., 2012	35 × 3 yr–4 yr	74 juvenile and adult chimps, 22 capuchins	conspecific models—three-stage puzzle box permitting cumulative learning of solutions to obtain increasing rewards	Only children attained Level 3 in substantial numbers, evidencing superior imitative matching, teaching, sharing, and cooperation.
van Leeuwen et al., 2014	23 × 3 yr–4.6 yr	14 chimps × 7 yr–36 yr	conspecific models—participants received conflicting personal and social information on reward locations	Both children and chimpanzees favored personal to social information but when no personal information was available, children used social information whereas chimpanzees did not.
Haun et al., 2014	18 × 24 mos–33 mos	12 chimps × 6 yr–21 yr; 12 orangs × 5 yr–12 yr	conspecific models—individuals learned a reward location preference, then witnessed three conspecifics preferring another	Just over half the children switched to conform to the majority but only one chimpanzee did so and no orangutans did.
Vale et al., 2014	36 × 5 yr	32 chimps × 15 yr–44 yr	conspecific models—video of harvesting from resource rich (12 sec interval) or poor (84 sec) boxes colored differently	The two species displayed almost exactly the same tendencies to prefer (by approximately 2:1) the resource rich option.

TABLE 19.3 (*Continued*)

Comparative Social Learning Studies of (Other) Great Apes and Children, 1993–2015

Reference	Children	Apes	Model and actions	Overview
Claidiere et al., 2015	97 × 5 yr–7 yr	16 chimp adults; 14 adult + juv capuchins	conspecific models—individuals not acting prosocially, by choosing one of two options that would reward a conspecific, experienced prosocial responses	An increased propensity to choose a prosocial option was recorded in chimpanzees and older children (7 yrs) but not in capuchins and younger children (5 yrs).
Ape experiments with earlier (or later) child studies specifically compared to them				
Call and Tomasello, 1994	Nagell et al., 1993	16 orangs × 6 yrs–34 yrs	human and conspecific models—replication of Nagell et al. (1993) with orangutans	Like the chimpanzees in the Nagell et al. study, orangutans were no more likely to flip tool to its more efficient form having observed this modeled than having seen use of a tool already flipped.
Whiten et al., 2005	Flynn and Whiten, 2012; Hopper et al., 2010; Whiten and Flynn, 2010	3 groups of chimps, total = 40 × 6 yr–40 yr	conspecific models—two alternative ways modeled, using same tool to release food (plus no model control)	Unlike controls, 15/16 chimpanzees in each experimental group mastered task and adopted whichever of the two forms of tool use was seeded by the model in their group. Children also showed spread of the seeded alternatives, but more exploration of alternatives, so overall lower fidelity.
Tomasello and Carpenter, 2005	Bellagamba and Tomasello, 1999; Carpenter et al., 1998	3 chimps × 5 mo–4 yr	human models in all four studies—instrumental versus arbitrary acts; failed attempts; accidental versus intended acts; style of action done	One chimpanzee copied both arbitrary and instrumental acts; others copied or attempted to copy only the instrumental acts. All three chimpanzees showed evidence of completing intended but not achieved outcomes; did not mimic failed action attempt itself. Chimpanzees copied intentional more than accidental acts, similar to 16-month-old children (Carpenter et al., 1998). Unlike some 12-month-old human infants, chimpanzees copied outcomes but rarely matched style of action used.
Marshall-Pescini and Whiten, 2008	Whiten et al., 2009	11 chimps × 2–6 yr	human model—first shown use tool to extract honey, versus no model condition; then shown more complex use of tool to unlock top and gain greater reward	Chimpanzees learned the first fishing technique by observation but then did not learn the second, more complex approach. A majority of children did show cumulative learning of the second method.
Buttelmann et al., 2008	Gergely et al., 2002	8 chimps × 3 yr–8 yr	human model—touch panel to switch on light or sound using head, foot, or bottom, with hands occupied versus not occupied	Like human infants, enculturated chimpanzees were more likely to copy actions performed with the hands free, indicating a corresponding grasp of rationality in the actions of others.

detail, but at their core is the pursuit of evolutionary explanations for differences and similarities. Assuming that differences in social learning are manifest even when any two species being compared are exposed to similar rearing environments, then the root of any differences is attributable ultimately to genetic factors, which in turn are a result of selection by different ancestral ecological niches of the species compared. For example, Coolen, van Bergen, Day, and Laland (2003) showed that nine-spined sticklebacks (*Pungitius pungitius*) used the foraging behavior of other fish to identify the higher quality of two foraging patches, whereas closely related three-spined sticklebacks (*Gasterosteus* *aculeatus*) did not. The authors noted that the latter species has morphological features that protect against predatory attack that the former does not and that predatory fish preferentially target the relatively unprotected nine-spined species. Accordingly, nine-spined sticklebacks in Coolen et al.'s experiments tended to retire among protective vegetation and observe other fishes' foraging success, then later used those observations to decide whether to forage, whereas the more robust three-spined individuals would rapidly approach fish seen feeding, and were therefore less likely to learn by observation which feeding site was the more productive. The authors thus directly related differences in social learning to differences in predator-related habitat choices.

Because behavioral adaptations typically take the form of a complex of different components, their adaptive significance may not be related directly to habitat preferences, but to other central aspects of a species' adaptive behavioral profile. Thus, for example, Lefebvre, Palameta, and Hatch (1996) compared the propensity for social learning in the food finding behavior of a gregarious columbid (*Columba livia*) with that of a more solitary columbid (*Zenaida aurita)* to test the hypothesis that social learning might represent an adaptation to group living.

A similar hypothesis motivated a comparative study focused on mate-choice copying, in which individuals prefer to try to mate with partners they have witnessed others have already chosen. King, von Ende, and Moran (2013) predicted mate-choice copying would be stronger in a species of fish exhibiting parental care than one that simply hides its eggs, because it would be costlier for the former to make a bad mating choice. In fact, neither the study by King et al. nor Lefebvre et al. (1996) obtained data supporting the hypotheses tested. Nevertheless, both illustrate clearly a common rationale for conducting comparative studies.

Range and Virányi's (2013, 2014) comparisons of social learning in wolves and dogs illustrate a similar principle, although in dogs the "ecological niche" to which adaptations are predicted to have occurred is the cluster of features that characterise human domestication. In their first paper, the authors found that when the social learning tested was simple local enhancement (learning which alternative location was the more productive foraging site), the two species showed similar social learning, whether from conspecifics or human models. However, in the later paper, when dogs and wolves were compared on the possibly higher-level process of imitation (matching whether a paw or mouth was used to press a lever), wolf cubs were more attentive to conspecific models than were dogs, and only the wolves evidenced significant imitative learning. The authors suggested that the latter result reflects an adaptation for attending closely to actions of others necessary for the cooperativeness so important to wolf-pack life.

Examining the 100+ papers that cited the comparative studies reviewed previously, as well as the 1600+ articles on social learning cited in the recent monograph of Hoppitt and Laland (2013) suggested these rather meagre pickings exhausted the comparison of closely related, nonprimate species. In contrast, studies in which humans (typically children) are compared with other great apes (most often chimpanzees) have become numerous through the last 2 decades (Table 19.3).

Anthropocentric search for uniquely human characteristics has motivated many studies comparing children and chimpanzees. Possible similarities (allowing inferences about the phylogenetic history of social learning and culture from which present day humans' psychological capacities evolved) and possible differences (which may help to explain the yawning gap between us and "them" resulting in a human propensity for cumulative culture that has allowed us to dominate the planet; Whiten, 2011) are of interest. Still, fundamentally the rationale for comparisons among primates, like that for comparisons among nonprimates is to define similarities and differences and to explain them in evolutionary terms, elucidating their adaptive fit to the ecological niches humans and apes occupy. Apes live in tropical forests, whereas early human ancestors moved first into savannahs and ultimately far beyond. However, as noted earlier, social learning phenomena are likely to be adapted not only to physical environments, but also to other behavioral and psychological features, which in the case of humans includes hyper-cooperation (see Volume 1, Chapter 13, this handbook and Chapter 20, this volume), theory of mind (see Chapter 32, this volume), and other sophisticated sociocognitive features (Whiten & Erdal, 2012).

Methods and Pitfalls

A basic but powerful method of testing experimentally for social learning, exemplified in many nonprimate and primate comparative studies, is the *two-action method*. In such studies, observer animals are exposed to models performing either of two different actions directed toward the same object and the observers' tendency to perform the option they witnessed is evaluated. Ideally, a control group is included in which no model of any kind is available. Contrasts in task success between the two model conditions and the no-model control condition permit conclusions about the existence of some kind of social learning, whereas contrasts between the two different model conditions provide evidence about what is learned. For example, if the two different options available to subjects during testing involve simply feeding at one location rather than another, the conclusions drawn will concern the operation of local enhancement; if the two options are different acts (like moving a lever with paw versus mouth), the conclusions reached may concern imitation. However, several ape studies go beyond these simple contrasts in various ways outlined in Table 19.3 and are discussed in further detail following.

For example, in some studies the two-action approach has been extended to examine the potential for cultural transmission of initially seeded options, either along *transmission chains* of individuals in which each participant becomes a model for the next, or in *open diffusion* designs where an individual is removed from its group, trained, then returned and the question becomes whether the seeded behavior will spread (Whiten & Mesoudi, 2008). Alternatively, *ghost conditions*, in which the outcomes normally produced by a model's actions are made to happen without involvement of a model (e.g., Hopper, 2010), have been applied comparatively to determine whether observation of movement of an apparatus is sufficient for learning, or social learning occurs only when an agent is observed moving a portion of the environment.

Human–ape comparative studies have not only been particularly productive (Table 19.3) but also serve to illustrate several important problems in achieving effective comparisons. Ideally, to make valid interspecies comparisons in social learning, all variables other than species must be held constant. Assuring such equivalence is particularly problematic in the case of humans and chimpanzees. Because of the requirements for experimental control in studies of social learning, only a handful of experiments have been completed with primates living in their natural environments, and these studies have concerned lemurs and monkeys (e.g., Gunhold, Whiten, & Bugnyar, 2014; Schnoell, Dittmann, & Fichtel, 2014; van de Waal, Claidière, & Whiten, 2015) rather than apes. Relevant field experiments have begun with apes, but have yet to incorporate models and controls to rigorously test for social learning as have other primate studies (Gruber, Muller, Reynolds, Wrangham, & Zuberbühler, 2011; Gruber, Muller, Strimling, Wrangham, & Zuberbühler, 2009). Indeed, all studies listed in Table 19.3 have been conducted with captive apes typically housed in primate research centers.

The communities that captive chimpanzees live in are typically small compared to those of wild chimpanzees and captive environments, regardless of "enrichment," are impoverished compared with the wild or compared with the environments of human children with which captive chimpanzees are typically compared. Thus, species differences are confounded with environmental complexity.

Experimental tests lead to further difficulties in comparing like with like. In approximately half the cases in Table 19.3, the model for both species has been a human: A conspecific for children but an alien species for apes. Apes may find the shape and manipulative configuration of the hand of the model less easily identified with than children. Such difficulties may put chimpanzees at a disadvantage in revealing their true behavioral capacities, so failure of chimpanzees to express some capacity seen in children must be treated with caution. However, outcomes in which either apes or children exhibit a capacity the other species does not are at the very heart of a comparative approach that aspires to identify similarities and differences between species. Such difficulties in achieving valid comparisons have been recognized since the early days of comparative psychology, but are particularly significant in the case of human and nonhuman primates.

Humans and Other Apes Compared

Despite the hurdles to research discussed previously, over the last 2 decades, comparative studies have produced a rich literature comparing social learning in humans (typically children) and nonhuman great apes. A selection of the studies listed in Table 19.3 are discussed as providing evidence relevant to a series of significant questions.

Imitation versus emulation. Perhaps no issue has pervaded the human–ape social-learning literature more than that of the role of imitation and emulation. The discussion began when, in a study of chimpanzees' social learning of using a rake to acquire food, Tomasello, Davis-Dasilva, Camak, and Bard (1987) observed that, although most chimpanzees did not copy the particular motor act a model used to acquire food, they did apply the tool more successfully than could be accounted for by mere stimulus enhancement. The authors suggested that the chimpanzees observed "the relation between the tool and the goal" (p. 182) and learned "to use the tool in its function as a tool" (p. 182), a type of social learning that Tomasello (1990) later labeled *emulation*, noting that unlike the case of imitation, in emulation the observer may act "in any way it may devise" (p. 284) to achieve the goal it had seen attained.

A series of experiments comparing children's social learning with that of chimpanzees and focused on emulation followed. In the first, children copied a human model's trick of flipping over a pronged rake to pull in a reward and were described as imitating, unlike chimpanzees using the tool without replicating the flip action and therefore described as emulating (Nagell, Olguin, & Tomasello, 1993). Call and Tomasello (1994) found similar copying in orangutans (*Pongo pygmaeus*).

Using an ingenious and quite different approach, Call and Tomasello (1995) allowed orangutans to watch human and conspecific models operating a lever to release food from an opaque box which obscured the goals of the action, thus precluding emulation and leaving imitation of the demonstrator's action with the lever as the only method for observers to succeed. Various alternative actions like pulling, pushing or rotating the lever, and particular sequences of these were effective in releasing food. Young children had some success in copying such actions, but consistent with the hypothesis that orangutans are limited to emulation and cannot imitate, they failed miserably in the task.

However, this dichotomy between imitation and emulation subsequently proved an over-simplification. Sue Savage-Rumbaugh indicated that chimpanzees and bonobos (*Pan paniscus*) participating in her language learning studies appeared quite capable of imitation and a suite of formal tests soon confirmed her observations (Tomasello, Savage-Rumbaugh, & Kruger, 1993). However, imitation was seen only in chimpanzees that, like those in Savage-Rumbaugh's studies, had rich daily interactions with humans, not in other, mother-reared chimpanzees. The difference in capacity of these enculturated and mother-reared chimpanzees led to the hypothesis that enculturation could shape apes' attention to humans sufficiently to reveal human-like capacities for imitation.

Studies other than the comparative ones reviewed in Table 19.3 also demonstrate imitative responses in apes. Such studies in single species include "Do-as-I-do" experiments in which chimpanzees and orangutans were trained to match a series of actions and were then tested with a battery of more novel gestures and bodily actions (Call, 2001; Custance, Whiten, & Bard, 1995).

Other direct comparative studies took different approaches. Horner and Whiten (2005), for example, hypothesised that some degree of imitation and emulation might be present in the repertoires of children and apes (even if to a different extent), but are expressed differentially according to context. Horner and Whiten presented young children and wild-born chimpanzees with a model who used a series of tool-based manipulations to extract food from either an opaque or a transparent artificial fruit, in both cases incorporating some actions that were not causally necessary to complete the task (see Chapter 27, this volume). In the case of the transparent apparatus only, an observer could see that there was no connection between these extraneous acts and extracting the reward. It was anticipated that an intelligent imitator would imitate the whole series of actions observed to result in success in the case of the opaque apparatus that prevented determination of which actions were unnecessary, whereas those faced with the transparent version of the apparatus would omit unnecessary actions, taking a more emulative approach. The expected result was observed in chimpanzees, leading to the conclusion that chimpanzees possess a "portfolio" of alternative social learning capacities that includes imitation and emulation (as well as local enhancement) that may be expressed differentially according to circumstances (Whiten, Horner, & Marshall-Pescini, 2005). Surprisingly, and unlike chimpanzees, children did not act like the "intelligent imitator" sketched previously; instead children tended to imitate entire sequences including any causally unnecessary elements, even when working with the transparent artificial fruit that made the extraneous nature of some actions apparent.

Overimitation. Developmental psychologists quickly became fascinated with the discovery that children copied clearly irrelevant actions, labeling the phenomenon *overimitation* (Lyons, Young, & Keil, 2007). Further research has not only replicated the finding of overimitation in several cultures (Nielsen & Tomaselli, 2010; Nielsen, Mushin, Tomaselli, & Whiten, 2014), suggesting that overimitation may be a human universal, but also has led to the surprising conclusion that the tendency to copy even apparently causally irrelevant acts becomes stronger throughout childhood and into adulthood (McGuigan, Makinson, & Whiten, 2011; McGuigan, Whiten, Flynn, & Horner, 2007; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009).

Given that chimpanzees in the Horner and Whiten (2005) study could discriminate necessary from useless acts, whereas children copied both, a picture emerges of greater copying fidelity in humans than in apes and an ability to imitate in both primate species. Overimitation, by its very nature, suggests that our own species is prepared to copy what an intentionally acting model does, even when her acts appear bizarre. Chimpanzees, although more ready than children to emulate when a model behaves bizarrely, may nevertheless copy quite elaborate sequences when the relevant causal structure of the task is opaque. It is important to note, however, that although we now have a large corpus of overimitation studies in children, data on chimpanzees rests on only a single study (Horner & Whiten, 2005).

Why overimitation occurs in humans has become a subject of much debate and investigation. Possibly, we are such a thoroughly cultural species that it is simply a good rule of thumb to treat adults' intentional actions as generally worth copying, even when the relevance of aspects of those actions is mysterious, which is often the case given the opacity and complexity of the technologies about which children need to learn (Lyons et al., 2007; Whiten et al., 2005). Alternatively, overimitation may serve social functions, identifying and building relationships with others (Nielsen, Simcock, & Jenkins, 2008). Other explanations for overimitation have been proposed, but this is not the place to review this burgeoning literature; the reader is referred to Kenward (2012) for a review and further hypotheses.

Rational imitation. The concept of rational imitation originated in a replication by Gergely, Bekkering, and Király (2002) of an earlier study by Meltzoff (1988) that had shown young infants imitating the actions of an adult who used his head rather than his hands to contact a box and make it light up. The clever twist in Gergely et al.'s (2002) experiment was to add a condition in which the adult had a blanket round her arms, so only her head was free to contact the box. Infants were much less ready to imitate in this situation.

Gergely et al. (2002) concluded that infant imitation is guided by a sophisticated theory of action that discriminates a freely chosen act worth copying from an action constrained in some way and therefore to be ignored. Buttelmann, Carpenter, Call, and Tomasello (2008) completed a study with chimpanzees aiming to replicate and extend Gergely et al.'s (2002) study. Like the human infants, these human-reared enculturated chimpanzees, were more likely to imitate head-bobbing by a model with free hands, than by a model whose hands were occupied (e.g., holding a box).

Such context sensitivity in copying in chimpanzees is consistent with their lack of susceptibility to overimitation as context sensitivity and a failure to imitate irrelevant actions can be considered "rational" discriminations. In human children, however, the existence of rational imitation and overimitation presents a puzzle in need of resolution (Whiten, 2013). Perhaps the discovery that overimitation continues into adolescence (Nielsen & Tomaselli, 2010) and even into adulthood (McGuigan et al., 2011) provides evidence that overimitation is not so irrational after all, but most of the time serves members of our species well, on different occasions promoting acquisition of complex cultural skills, supporting social integration, facilitating social conventions, and various combinations of these.

Preferential copying of intentional acts. As part of a battery of experiments on the social learning capacities of three juvenile enculturated chimpanzees, Tomasello and Carpenter (2005) sought to replicate their earlier study (Carpenter, Akhtar, & Tomasello, 1998) showing that young children discriminated and preferentially copied intentional actions rather than equivalent actions engineered to appear accidental. Discrimination of intentional acts was also found in chimpanzees, so selectivity in chimpanzee imitation extends to the intentional/accidental distinction and that of rational choice previously discussed.

Moreover, in a related experiment, Tomasello and Carpenter (2005) found that, like human infants studied by Meltzoff (1995), young chimpanzees who witnessed a human model attempting, but failing, to complete an action (e.g., placing a loop over a stand), would successfully complete the action, rather than mimic the observed (failed) performance, thus achieving an appropriate outcome they had never witnessed. In both sets of experiments (accidental versus intentional, and failed attempts) young humans and young chimpanzees displayed an approach to imitation that was sensitive to the intent of the performer of an observed action (see Chapter 32, this volume).

Cultural transmission and diffusion. Some things that may be learned socially (e.g., which bush is fruiting today) have a limited window of existence, whereas other socially acquired information may be sustained and transmitted repeatedly, diffusing through a group or even across generations to become a tradition. Over the last half century, evidence for such cultural traditions has progressively accumulated from long-term field studies of primates.

Researchers studying chimpanzees and orangutans at multiple field sites have collaborated to identify scores of behaviors of different kinds (e.g., tool use, foraging, sexual and social habits) present at some sites but not at others and to exclude, insofar as possible, any ecological or genetic explanations for regional differences in behaviors (Krützen, Willems, & van Schaik, 2011; van Schaik et al., 2003; Whiten et al., 1999). Although such ape traditions are relatively insignificant in comparison with the vast cultural achievements of humans, field studies suggest that humans share with the apes an unusual degree of cultural complexity (Whiten, 2005, 2011).

To date, observational studies of ape traditions lack validation from experimental interventions carried out in the wild, an enterprise that, because of its logistic difficulties remains in its infancy in primatology (e.g., Gunhold et al., 2014; van de Waal, Borgeaud, & Whiten, 2013). However, several cultural diffusion experiments carried out with captive primates, some directly comparing the performance of children with that of other apes are now available. In the first such study, Horner, Whiten, Flynn, and de Waal (2006) established transmission chains in which a first individual was trained to open an artificial fruit using one of two techniques (sliding a hatch versus lifting a small door), then acted as the model for a second individual who became the model for a third, and so on for so long as each individual was successful (whichever method they used). Such chimpanzee chains were limited by participant availability. Nevertheless, chains of 5 or 6 individuals were achieved in which seeded alternatives were transmitted faithfully, thus simulating multiple-generation transmission. Children exposed to the same conditions faithfully transmitted alternatives along chains of 10 individuals. Transmission fidelity was sufficient in both species for multiple-generation transmission of distinct, if minimal, incipient traditions.

An alternative diffusion experiment with chimpanzees described as involving an open diffusion (Whiten et al., 2005) was subsequently matched with a child study using exactly the same apparatus (Flynn & Whiten, 2012; Whiten & Flynn, 2010). In all three studies, models were first trained to use a tool to either lift or poke a blockage to extract rewards from an apparatus. Each model was then reunited with its group (nursery groups in the case of children). In both species, different incipient traditions were established. Cultural corruption first appeared in the groups of children, with the difference between groups disappearing on the second day of the study. Children then copied the "corrupt" variants.

Fading of the initially established group differences in children was largely because of their greater tendency to explore and use the tool in as many ways as possible. Thus, the greater fidelity of transmission often claimed for humans, as compared with chimpanzees, was not evident in this study, which presently is the only direct comparison of children and apes of social transmission in an open diffusion experiment. The message, however, is not that humans are less capable of faithful copying, but rather the outcome of such experiments will depend on the fit between the challenges of the task and the intellects of the participants. In the present case, children were more likely to explore the affordances of the task, and their behavior highlights the difficulty of comparing like with like in comparative psychological studies of social learning.

Cumulative cultural evolution. It is frequently asserted that cumulative cultural evolution fundamentally separates our species from all others (see Volume 1, Chapter 15, this handbook and Chapter 20, this volume). However, experimental investigations of cumulative culture are rare. Marshall-Pescini and Whiten (2008) explored cumulative culture in chimpanzees, later applying the same experimental design to young children (Whiten et al., 2009). Participants in these studies first learned by observation a relatively simple method to extract honey from a foraging device (opening a small hatch with one hand while using the other hand to insert a probe to remove a small amount of honey). A familiar human caretaker then modeled a more complex procedure that incorporated and built on the first method in cumulative fashion (inserting the probe into an obscured hole to allow the whole top of the device to hinge open so all the honey and nuts inside became available).

Chimpanzees assigned to a group whose members had not learned the dipping technique discovered the more complex technique for themselves, yet surprisingly, none of those who had learned to dip shifted to the more complex, more productive second technique. By contrast, most children did shift to the more productive technique. The authors concluded that chimpanzees failed to evidence cumulative cultural learning because of a remarkable conservatism leading them to become "stuck" on the first, satisficing technique they learned (see Chapter 28, this volume). Subsequent studies have also highlighted such behavioral conservatism in the context of social learning in chimpanzees (Hopper, Schapiro, Lambeth, & Brosnan, 2011; Hrubesch, Preuschoft, & van Schaik, 2008).

Dean, Kendal, Schapiro, Thierry, and Laland (2012) took a different approach, presenting to capuchins (*Sapajus apella*), chimpanzees, and children a device that offered increasing rewards attainable in successive steps: Children were far more successful than primates at attaining the higher levels. The nonhuman groups, even when provided with conspecific models trained to attain the highest level, failed to advance beyond the first level where they received lesser rewards and provided further evidence of the conservative disposition found by Marshall-Pescini and Whiten (2008). Dean et al. (2012) pointed to children's tendency to copy witnessed acts, to overtly teach one another, and to share rewards as supporting children's cumulative progress (see Chapter 20, this volume).

Just what holds chimpanzees and other primates back remains mysterious, but work on the issue continues. For example, Vale, Flynn, Lambeth, Schapiro, and Kendal (2014) showed that chimpanzees, like children, recognize when others are gaining rewards superior to their own, so an inability to compare one's own success with that of others appears not to be a limiting factor (see Volume 1, Chapter 44, this handbook and Chapter 16, this volume). Others have shown some capacities in apes for cumulative learning (Lehner, Burkart, & van Schaik, 2011; Manrique, Völter, & Call, 2013; Yamamoto, Humle, & Tanaka, 2013), but only the last of these involved social learning and even there the evidence remains relatively qualitative.

Conclusion. The research outlined previously and in Table 19.2 has established a range of features of social learning shared by humans, other apes, and by inference our common ancestors. These features include a portfolio of context-sensitive social-learning processes including emulation and imitation that offer sufficient copying fidelity for the transmission of tool use and other behaviors within groups. Studies comparing social learning in children and apes have also sharpened our understanding of species differences in a capacity or motivation for high-fidelity copying, resulting at its extreme, in overimitation (see Volume 1, Chapter 20, this handbook). Possibly, such differences, along with other characteristics such as hyper-cooperativeness and sharing, support humans' special propensity for cumulative culture.

CONCLUSION

In the 19th century, when Romanes first proposed guidelines for a successful comparative psychology, he could never have imagined the diversity and richness of the field that was to develop from his pioneering work. Although study of animal social learning is a relative newcomer to the effort to understand the behavioral capacities of animals, in the last 40 years, the literature concerning animal social learning has grown at an astonishing rate and now makes a substantial contribution to our attempts to address the issues Romanes first raised.

The wealth of materials now available has required that any review of the comparative psychology of social learning be selective. Here, we have striven to provide readers with a first appreciation of the range and scope of this ever-expanding field. Those seeking greater engagement with the area should refer to the reviews listed in Appendix 19.1.

APPENDIX 19.1 RECENT REVIEWS OF SOCIAL LEARNING

Galef, B. G., Jr. (2012a). Social learning in rats: Historical context and experimental findings. In T. Zentall & E. Wasserman (Eds.), *The Oxford handbook of comparative cognition* (2nd ed., pp. 803–818). Oxford, England: Oxford University Press.

Galef, B. G., Jr. (2012b). Social learning, tradition, and culture: Data and debate. In K. Yasakawa & Z.-T. Martinez (Eds.), *Animal behavior: How and why animals do the things they do* (Vol. 1, pp. 115–150). Santa Barbara, CA: Praeger.

Garriepy, J.-F., Watson, K. K., Du, E., Xie, D. L., Erb, J., Amasino, D., & Platt, M. L. (2014). Social learning in humans and other animals. *Frontiers in Neuroscience*, *8*, 58. http://dx.doi.org/10.3389/fnins.2014.00058

Hopper, L. M., & Whiten, A. (2012). The comparative and evolutionary psychology of social learning and culture. In J. Vonk & T. Shackelford (Eds.), *The Oxford handbook of comparative evolutionary psychology* (pp. 451–473). Oxford, England: Oxford University Press.

Kendal, R. L., Galef, B. G., Jr., & van Schaik, C. P. (2010). Social learning research outside the laboratory: How and why? *Learning and Behavior*, *38*, 187–194. http://dx.doi.org/10.3758/LB.38.3.187

Laland, K. N., & Galef, B. G., Jr. (Eds.). *The question of animal culture*. Cambridge, MA: Harvard University Press.

Nielsen, M., Subiaul, F., Galef, B. G., Jr., Zentall, T. R., & Whiten, A. (2012). Social learning in humans and nonhuman animals: Theoretical and empirical dissections. *Journal of Comparative Psychology*, *126*, 109–113. http://dx.doi.org/10.1037/a0027758

Price, E. E., & Whiten, A. (2012). Social learning and culture in primates: Evidence from free-ranging and captive populations. In E. A. Wasserman & T. R. Zentall (Eds.), *Handbook of comparative cognition* (pp. 862–878). New York, NY: Oxford University Press.

Thornton, A., & Raihani, J. (2008). The evolution of teaching. *Animal Behaviour*, *75*, 1823–1836. http://dx.doi.org/10.1016/j.anbehav.2007.12.014

van Schaik, C. P. (2012). Animal culture. *Current Biology*, *22*, R402–R404.

Whiten, A., Hinde, R. A., Stringer, C. B., & Laland, K. N. (2011). Culture evolves. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences, 366*, 938–948. http://dx.doi.org/10.1098/rstb.2010.0372

APPENDIX 19.2

Animal Social Learning Articles, 2012–2014

Species	Type	Behavior	Relevant publications
African elephant	C	two-choice	Greco et al., 2013
African elephant	F	crop raiding	Chiyo et al., 2012
Ant	C	nest-site choice	Franklin and Franks, 2012
Baboon	F	foraging	Carter et al., 2014
Baboon	C	pattern recognition	Claidière et al., 2014
Big-eared bat	F	feeding techniques	Geipel et al., 2013
Black bear	F	feeding site	Hopkins, 2013
Blue tit	C	milk-bottle opening	Aplin et al., 2013
Bonobo	F	gestures	Halina et al., 2013
Bottlenose dolphin	F	tool use	Kopps et al., 2014; Mann et al., 2012
Bottlenose dolphin	F	feeding site	Donaldson et al., 2012
Bullfinch	F	feeding innovation	Ducatez et al., 2013
Bumblebee	C	flower choice	Dawson and Chitka, 2012; Leadbetter and Florent, 2014
Bumblebee	C	flower robbing/handedness	Goulson et al., 2013
California mouse	C	paternal behavior	Gleason and Marler, 2013
Chimpanzee	C	imitation recognition	Davila-Ross et al., 2014
Chimpanzee	C	foraging	Buttelmann et al., 2013
Chimpanzee	C	token deposition	Haun et al., 2013
Chimpanzee	C	multiple	Hecht et al., 2013
Chimpanzee	F	multiple	Kamilar and Atkinson, 2014
Chimpanzee	F	tool use	Koops et al., 2013; Luncz and Boesch, 2014; O'Malley, 2012
Chimpanzee	C	tool use	Rawlings et al., 2013
Chimpanzee	C	gesture	Taglialatella et al., 2012
Chimpanzee	C	bodily action	Tennie et al., 2012
Chimpanzee	C	foraging location	Vale et al., 2014
Chimpanzee	C	grass in ear	van Leeuwen et al., 2014
Chimpanzee	C	location choice	van Leeuwen et al., 2014
Chimpanzee	C	using straw to suck	Yamamoto et al., 2013
Chimpanzee	C	making moss sponge	Hobaiter et al., 2014
Chimpanzee	C	habituation to humans	Samuni et al., 2014
Chimpanzee, orangutan	C	foraging	Haun et al., 2014
Convict cichlid	C	predation risk	Barks and Godin, 2013
Cowbird	C	social skills	Gersick et al., 2012
Cuttlefish	C	fear conditioning	Huang and Chaio, 2013
Damselfish	C	predator avoidance	Manassa et al., 2014
Darter spp.	C	mate choice	Moran et al., 2013
Dog	C	do as I do	Fugazza and MiKlosi, 2014
Dog	C	two-action	Pongracz et al., 2012
Fairy wrens	F	brood parasite recognition	Feeney and Langmore, 2013
Fruitfly, adult	C	spatial learning	Foucauld et al., 2013
Fruitfly, larvae	C	food choice	Durisko et al., 2014
Galapagos pelicans	F	location for plunge diving	Brumm and Teschke, 2012
Goffin cockatoo	C	tool use	Auersperg et al., 2014
Golden hamster	C	dominance	Lai et al., 2014
Gorilla, orangutan	F	food choice	Gustafsson et al., 2014
Great tits	F	diversity of song	Feyet et al., 2014

(*Continued*)

APPENDIX 19.2 (*Continued*)

Animal Social Learning Articles, 2012–2014

Species	Type	Behavior	Relevant publications
Guinea dolphin	F	feeding	Oliviera et al., 2013
Guppy	C	foraging site	Franks and Marshall, 2013
Guppy	C	food richness	Trompf and Brown, 2014
Honeybee	F	foraging site	Balbuena et al., 2012
Horse	C	opening a drawer	Ahrendt, 2012; Krueger et al., 2014
House mouse	C	STFP	Choleris et al., 2013; Ervin et al., 2013
House mouse	C	STFP	Arakawa et al., 2013; Nicol et al., 2014
House mouse	C	food intake	Olszewski et al., 2014
House mouse	C	episodic memory	Lipina and Roder, 2013
Humpback whale	F	feeding technique	Allen et al., 2013
Hyena	F	feeding techniques	Benson-Amram et al., 2014
Japanese quail	C	foraging	Boogert et al., 2013
Killer whale	C	do as I do	Abramson et al., 2012
Lemon shark	C	target contact	Guttridge et al., 2013
Lemur	F	feeding technique	O'Mara et al., 2012; Schnoell et al., 2014
Locust	C	feeding/egglaying	Lancet and Dukas, 2012
Macaque	C	tool use	Macellini et al., 2013
Macaque	C	neonatal lipsmacking	Simpson et al., 2013
Macaque	C	food location errors	Monfardini et al., 2014
Mackerel	C	feeding site	Takahashi et al., 2014a, 2014b
Marmoset	C	foraging	Burkart et al., 2012
Marmoset	C	calls	Watson et al., 2014
Marmoset	F	feeding technique	Gunhold et al., 2014
Medaka	C	movement orientation	Ochiai et al., 2013
Meerkat	F	operate apparatus	Hoppitt et al., 2012; Thornton and Samson, 2012
Mexican guppy	C	mate choice	Bierbach et al., 2012, 2013
Mouse-eared bat	C	foraging site	Clarin et al., 2014
Norway rat	C	fear	Jones et al., 2014
Norway rat	C	fear conditioning	Yusufishaq and Rosenkrantz, 2013
Norway rat	C	drug self-administration	Peitz et al., 2013
Norway rat	C	STFP	Lindeyer et al., 2013
Octopus	C	operant	Tomita and Aoki, 2014
Orangutan	C	tool use	Gruber et al., 2012
Pied flycatchers	F	clutch size	Forsman et al., 2012
Pig	C	STFP	Figuera et al., 2013
Pigeons	F	homing	Pettit et al., 2013
Reed warblers	F	brood parasite recognition	Campobello and Sealy, 2011; Thorogood and Davies, 2012
Ring-billed gull	F	food location	Racine et al., 2012
Root vole	C	food choice	Li et al., 2012
Skink	C	association	Noble et al., 2014
Snake eagle	F	migration route	Panuccio et al., 2012
Sperm whale	F	codas (vocalizations)	Amano et al., 2014
Spider crab, juvenile	C	feeding site	Hanna and Eason, 2013
Squirrel monkey	C	feeding technique	Claidière et al., 2013
Stickleback spp.	C	feeding patch location	Atton et al., 2012, 2014
Stingray	C	operant	Thornhauser et al., 2013
Tent-making bats	F, C	STFP	O'Mara et al., 2014

APPENDIX 19.2 (*Continued*)

Animal Social Learning Articles, 2012–2014

Species	Type	Behavior	Relevant publications
Titmice spp.	F	nest-site preference	Slagsvold et al., 2013
Trout	C	prey identification	White and Gowan, 2014
Vervet	F	feeding technique	van de Waal et al., 2014
Vultures	F	foraging	Kane et al., 2014
Whooping cranes	F	migration route	Mueller et al., 2013
Wolf/dog	C	feeding site	Range and Viranyi, 2013
Wood frog tadpole	C	predator recognition	Chivars and Ferrari, 2014
Zebra finches	C	song learning	Deshpande et al., 2013
Zebra finches	C	mate choice	Rosa et al., 2012
Zebrafish	C	risk assessment	Zala and Maattanen, 2013
Zebrafish	C	escape aversive stimuli	Vital, 2013
Zebrafish	C	feeding-site preference	Riebel et al., 2012

Note. Where practicable, each research group/species/behavior combination has a single entry in this table, typically showing the most recent of any multiple relevant publications in this period.
F = free living; C = captive; STFP = social transmission of food preference.

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CHAPTER 20

ANIMAL SOCIAL LEARNING, CULTURE, AND TRADITION

Kevin Laland and Cara Evans

The fact that many animals, including humans, acquire valuable life skills and knowledge through copying others has been the focus of attention of animal behaviorists dating back to Darwin. In recent years the field of social learning has received massive attention, and experienced such growth that researchers have referred to an "explosion of interest" in the topic (Galef & Giraldeau, 2001; Shettleworth, 2001). Fueling this interest are a number of controversies within the field. These include the questions of whether social learning is dominated by context biases (e.g., copying the highest payoff behavior, conforming to the local norm) or acquired dependent on content; whether imitation is dependent on perspective taking, goal comprehension, or complex cognition; and whether traditions are constrained to be adaptive. Probably foremost amongst these debates is the issue of whether animals can be said to possess culture.

Historically, and still today, the attribution of culture to other animals rests largely on the answers to two important questions: First, is the candidate cultural behavior the result of social transmission between individuals, and can other explanations for the behavior, such as genetic influences or asocial learning, be ruled out? And second, should socially transmitted behavioral traditions in other animals be described as cultural, or should the accolade of culture be reserved for those socially transmitted behaviors that are considered uniquely human? Eastern but not western African chimpanzees *(Pan troglodytes*) use stalks to fish for termites, whereas western but not eastern chimps break open nuts with stone hammers (see Chapter 30, this volume). Capuchin monkeys in Costa Rica exhibit peculiar local social conventions, such as sniffing each other's hands and placing fingers in each other's mouths. Humpback whales and chaffinches from different regions sing different songs. If all of these, and other, animal traditions appear to be acquired through social learning, are scientists justified in speaking of animal "culture"? Many researchers would disagree. For instance, most anthropologists assert that human cultures are so imbued with meaning and value, so permeated with symbolism, and so reliant on uniquely human aspects of cognition, that it is ridiculous to liken them to more fleeting and technologically stagnant animal traditions.

Until recently, experimental investigations of social learning and transmission were largely restricted to behavioral investigations, typically conducted in the laboratories of comparative or developmental psychologists, and focused on very specific questions, such as whether animals can imitate (Call, Carpenter, & Tomasello, 2005; Nagell, Olguin, & Tomasello, 1993; Whiten, 1998; Whiten, Custance, Gomez, Teixidor, & Bard, 1996; see also Chapter 19, this volume). These approaches, although assessing the capability of nonhuman animals to transmit behavioral information socially in experimental settings, do not allow us to confirm or refute the

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existence of behavioral traditions occurring in the same species under more natural learning conditions. Meanwhile, and with the exception of some early experiments on birdsong learning (see Volume 1, Chapter 3, this handbook), biologists' interest in social learning was pursued almost entirely through behavioral observations and recordings of animals in their natural environment, especially by ethologists and primatologists. However, the observational data generated did not allow alternate explanations of the behaviors—that is, genetic or environmental explanations—to be irrefutably ruled out (Laland & Hoppitt, 2003; Laland & Janik, 2006).

In recent years, several new methodologies have been developed to address these challenges and controversies (Hoppitt & Laland, 2013). For example, the advent of rigorous new statistical approaches has provided unequivocal evidence that social learning can and does facilitate the rapid spread of behavioral innovation generated through a group of animals, leading to the establishment of intra-population behavioral traditions (Allen, Weinrich, Hoppitt, & Rendell, 2013; Hobaiter, Poisot, Zuberbühler, Hoppitt, & Gruber, 2014). At the same time, innovative field experiments have demonstrated that social learning allows vervet monkeys (*Chlorocebus pygerythrus*) to avoid toxic food (van de Waal, Borgeaud, & Whiten, 2013), meerkat pups (*Suricata suricatta*) to process and eat otherwise dangerous scorpions (Thornton & McAuliffe, 2006), great tits (*Parus major*) to "conform" to local feeding preferences (Aplin et al., 2015), and reed warblers (*Acrocephalus scirpaceus*) to mob nest-parasitic cuckoos (*Cuculus canorus*; Davies & Welbergen, 2009). Clearly the origin and social transmission of information potentially have major ecological and evolutionary consequences (Avital & Jablonka, 2000; Hoppitt & Laland, 2013). Regardless of whether the socially learned behavioral traditions of other animals should be awarded the accolade of culture, developing a deeper understanding of the evolutionary and ecological conditions that have given rise to them is central to understanding exactly how and why our own extraordinary cultural abilities have evolved (Rendell et al., 2011; van Schaik & Burkart, 2011; Whiten, 2011; see also Volume 1, Chapter 13, this handbook and Chapter 19, this volume).

DEFINITIONS

Certain terms, such as *social learning*, *social transmission*, *innovation*, *tradition*, and *culture*, appear repeatedly in the literature, in many cases with little consensus in their usage. In some instances, the terms themselves are the focus of debate. Accordingly, at the outset we specify what we mean by each of these terms, where we follow Hoppitt and Laland (2013; see Exhibit 20.1). Our chapter is complemented by Chapter 19 of this volume, which focuses on the psychological mechanisms thought to underpin social learning, tradition and culture from a comparative perspective.

In 2003, Fragaszy and Perry proposed a definition of a tradition on which our definition is based, characterizing it as "a distinctive behavior pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning" (p. xiii). Although having two individuals is the minimal requirement, the concept of tradition becomes of more interest when an idea or behavior pattern spreads by social learning across multiple individuals to become a population-level phenomenon, often with different populations developing different traditions. The "persists over time" stipulation may appear vague, yet this makes sense insofar

Exhibit 20.1
Definitions of Key Terms

- **Social learning** is learning that is facilitated by observation of, or interaction with, another individual or its products.
- **Social transmission** occurs when the prior acquisition of a behavioral trait T by one individual A, when expressed either directly in the performance of T or in some other behavior associated with T, exerts a lasting positive causal influence on the rate at which another individual, B, acquires or performs T.
- An **innovation** is a new or modified learned behavior not previously found in the population.
- A **tradition** is a distinctive behavior pattern shared by two or more individuals in a social unit that persists over time and that new practitioners acquire in part through socially aided learning.
- **Cultures** are those group-typical behavior patterns shared by members of a community that rely on socially learned and transmitted information.

as a continuum is possible, from mere fads and fashions (perhaps lasting only weeks or less) to those that pass down to many generations. No neat cut-off on this continuum will circumscribe traditions; rather, particularly robust evidence of traditions comes from those that are of long duration, or rely on multiple transmission events, whether between generations or within them.

The concept of culture is more challenging, and it has proven extremely difficult for social scientists to derive a consensual definition or operationalize; it is also sometimes portrayed as tautological, and as reinforcing an outdated nature–nurture dichotomy (Bloch, 2000; Durham, 1991; Kroeber & Kluckhohn, 1952; Kroeber, Kluckhohn, Untereiner, & Meyer, 1963; Kuper, 2000). In contrast, biologists and students of animal behavior have essentially ignored any such concerns, and appear to be broadly content with deploying the term culture as little more than a synonym for socially transmitted behavior. Amongst behavioral scientists, some authors essentially equate culture with tradition, and references to population-specific vertebrate traditions for singing particular songs, exhibiting specific feeding behavior, and the like as *cultural transmission* are common in the social learning literature (e.g., Slater, 1986). Our own definition of culture (see Exhibit 20.1) is also based on a broad and inclusive notion, only requiring evidence that group-typical behavior patterns rely on socially learned or transmitted information to be considered cultural; a pragmatic stance designed to foster exploration of the evolutionary roots of human culture in other animals (Laland & Hoppitt, 2003). On this perspective, a tradition is an element of culture.

Other authors interested in the evolutionary roots of human culture apply more stringent criteria to the use of the term culture, arguing that examples such as song and feeding traditions in other animals might be too readily assumed to be reliant on mechanisms homologous (i.e., sharing evolutionary ancestry) with human culture, when they might really be merely analogous (e.g., dependent on different forms of social learning; Boyd & Richerson, 1985; Galef, 1992; Tomasello, 1994). And some researchers maintain that culture might more usefully refer to that which comprises the exclusive domain of *Homo sapiens* (e.g., symbolic references, cultural norms), preferring instead to refer to all instances of socially transmitted behavior in other animals as behavioral traditions (Perry, 2009a). Still other authors have adopted the stance that the term culture should only be applied where an animal's behavioral repertoire is known to be comprised of multiple behavioral traditions (Whiten et al., 1999; Whiten & van Schaik, 2007).

Whichever definition of animal culture is adopted, there is clearly no suggestion that the culture of chimpanzees or chaffinches is identical to that of humans. All cultural species have their own distinctive species-typical modes of communication, learning and social interaction that render their culture unique. Nonetheless, these cultures also have defining properties in common (e.g., social learning, tradition), particularly at the functional level (e.g., homogenization of behavior within populations, source of differences between populations), which are of broad interest.

THE ANIMAL CULTURE DEBATE: A HISTORICAL PERSPECTIVE

Over the last century, field researchers have reported many cases of the spread of novel foraging behaviors in natural animal populations. Lefebvre and Palameta (1988) documented approximately one hundred examples spread across a variety of vertebrates, going back to 1887. Such behavioral innovations have spread too quickly to be explained by population genetic, ecological or demographic factors, and are thought to have spread through social learning. However, in general, researchers have rarely been able to substantiate the claim that such diffusions are actually the product of social (as opposed to asocial) learning, leaving open to criticism the assumption that the behaviors are spread socially (Laland & Galef, 2009; Laland & Janik, 2006). This concern cannot be casually dismissed, as there is now clear experimental evidence in fish and birds that the spread of a novel behavior through an animal population can occur without social transmission (Atton, Hoppitt, Webster, Galef, & Laland, 2012).

The modern debate over animal culture began when Japanese researchers began to document traditions in free-living, often provisioned, primate populations. The most famous among these is the washing of sweet potatoes by Japanese macaques (*Macaca fuscata*). Imo, an 18-month-old, female Japanese macaque, was seen washing a sweet potato in a stream in 1953. The diffusion through Imo's troop of washing dirt from sweet potatoes before eating them was described as *precultural* (Kawai, 1965). The term implied some correspondence between monkey and human behavior, be it homologous or analogous.

For several years after Kawai's publication, primatologists studying behaviors that observation suggested had been socially transmitted referred to the behavioral phenomena that they were interested in as precultural (e.g., Menzel, 1973), *protocultural* (Menzel, Davenport, & Rogers, 1972), or *traditional* (e.g., Beck, 1974; Strum, 1975). However, in 1978, McGrew and Tutin described a tradition involving an apparently arbitrary pattern of behavior, the grooming handclasp, prevalent in a troop of chimpanzees in Tanzania. McGrew and Tutin argued that handclasp grooming satisfied many of the criteria used to identify cultural patterns in humans. They asserted that the use of the term culture to refer not only to handclasp grooming, but also to other population-specific behaviors of chimpanzees, was justified. McGrew and Tutin's paper was the first to directly address the question of the relationship between the traditions of animals and the culture of humans, and initiated a shift to discussion of animal culture, particularly when speaking of chimpanzees (Boesch, 1993; Goodall, 1986; McGrew, 1992; Nishida, 1987; Whiten et al., 1999; Wrangham, McGrew, de Waal, & Helltne, 1996).

McGrew (1992) went on to investigate chimpanzee behavioral variation intensively, making detailed observational comparisons between sites, and reporting a number of different behavior patterns across a number of categories ranging from foraging to sexual, aggressive and medicinal behavior that varied across chimpanzee populations. The variation in chimpanzee behavioral repertoires, and McGrew's interpretation of this as cultural, received considerable attention and stimulated extensive debate. Shortly afterward, Whiten et al. (1999) expanded on the earlier work by McGrew in undertaking a major collaborative study, involving many leading primatologists, on which the case for chimpanzee culture is now largely based. Adopting a more systematic approach than McGrew's original analysis, Whiten et al. compiled behavioral information from seven long-term field studies across Africa, to generate 42 categories of behavior that exhibited significant variability across sites. Although some of this variation was attributed to differences in the availability of resources (e.g., absence of algae-fishing can be explained by the rarity of algae at some sites), most behavior patterns, including tool use, grooming and courtship behaviors, were common in some communities, but absent in others, and the authors claimed this distribution had no apparent ecological explanation. Whiten et al. titled their article "Cultures in Chimpanzees," and some of these authors went on to argue that chimpanzee and human cultures result from homologous processes (McGrew, 2005, 2009; Whiten, 2005).

Other researchers took issue with these claims of animal culture, by questioning the evidence that the putative traditions were indeed a consequence of social learning, and by suggesting that the parallels between animal and human culture rested on superficial analogies, rather than homologies, in cognitive processing (Galef, 1992, 2003; Tomasello, 1994, 1999). Some authors maintained that the observed behavioral differences between chimpanzee groups might be caused by factors other than social learning (Laland & Hoppitt, 2003; Laland & Janik, 2006), despite efforts by Whiten et al. (1999) to rule out alternative explanations. Genetic differences might have been contributing to some differences in behavior, for example, or behavioral differences between groups might have arisen because of individual learning in response to unmeasured ecological variables that the study authors missed. Likewise, Galef (1992) and Tomasello (1994, 1999) argued that human culture was supported by imitation and teaching; different psychological mechanisms than those that they envisaged underlay animal traditions.

Whiten et al.'s (1999) analysis triggered the application of similar observational methods to other species, including orangutans (*Pongo pygmaeus*), capuchin monkeys (*Cebus capucinus*) and bottlenose dolphins (*Tursiops sp.*; Krützen et al., 2005; Perry et al., 2003; van Schaik et al., 2003). Orangutan primatologists van Schaik and colleagues' (2003) use of the term cultural clearly implied homology with human culture. Capuchin researchers also published results of a major, long-term collaborative study of white-faced capuchin monkeys (*Cebus capucinus*) revealing behavioral variation in the social conventions of 13 social groups throughout Costa Rica (Perry et al., 2003). Several social conventions were reported, including hand sniffing, sucking of body parts, and placing fingers in the mouths of other monkeys.

These additional studies, also using behavioral comparisons between groups, are susceptible to the same criticisms leveled at the earlier chimpanzee work. Developmental approaches that seek to track an individual's acquisition of group-typical behavioral patterns, relative to their opportunities to observe and learn the behavior from others, would shed further light on these issues (Hoppitt & Laland, 2013). The debate remains unresolved, with a spectrum of views manifest in the literature (Laland & Galef, 2009; Laland & Janik, 2006).

Meanwhile, many biologists had started to use the phrase culture to describe animal traditions (e.g., Bonner, 1980). This particularly applied to birdsong (Catchpole & Slater, 1995; Mundinger, 1980), where geographical variation in the songs of many songbirds, notably, white crowned sparrows (*Zonotrichia leucophrys*) and chaffinches (*Fringilla coelebs*), had been documented since the 1960s (Catchpole & Slater, 1995; Marler & Tamura, 1964). From the 1970s, evidence began to appear for vocal traditions in mammals too, particularly bottlenose dolphins (*Tursiops spp.*) and humpback whales (*Megaptera novaeangliae*; Caldwell & Caldwell, 1972; Janik & Slater, 1997). Payne and Payne (1985) described how all males in a humpback whale population shared a song that changed gradually through the singing season, a change much too rapid to be explained by changes in genotype. Most striking, and providing some of the strongest evidence to date for vocal traditions in cetaceans, are studies by Noad, Cato, Bryden, Jenner, & Jenner (2000) and Garland et al. (2011) of humpback whale songs off the east coast of Australia. Noad et al. reported that a song recorded on Australia's east coast was observed to change unprecedentedly in just 2 years to one previously heard only off the west coast of Australia, probably as a result of movement of a few individuals from west to east (Noad et al., 2000). More recently, Garland et al., studying humpback whales in the same location, reported that multiple song types spread rapidly and repeatedly in a unidirectional manner, like cultural ripples, eastward through the populations in the western and central South Pacific over an 11-year period. Rendell and Whitehead's (2001) review described a wide range of traits that the authors claimed could be interpreted as cultural, including killer whales (*Orcinus orca*) beaching themselves during foraging and bottlenose dolphins using sponges to forage.

Until very recently, all claims of naturally occurring cultural behaviors in groups of animals have been vulnerable to counterclaims; students of animal culture were unable to prove that social transmission underpinned the spread of purported cultural traits. Innovative experimental procedures in the field (e.g., Aplin, Farine, Morand-Ferron, & Sheldon, 2012; van de Waal et al., 2013) and captive groups of animals (e.g., Whiten, Horner, & de Waal, 2005; Whiten et al., 2007) established that new behavioral traditions can spread through a group of animals via social learning, suggesting that at least some of the observed behavioral variation in the wild is an expression of culture. Skepticism has remained, however, as the demonstration of social transmission in experimental contexts does not equate to proof that those naturally occurring behavior patterns that appear cultural have also spread through social learning.

The first evidence that a naturally occurring behavioral innovation had spread through a population of wild animals through social learning, resulted from a detailed and long-term study of lobtail feeding in humpback whales (Allen et al., 2013). Using a pioneering new statistical methodology (network-based diffusion analysis [NBDA]) developed specifically to aid in the identification of socially transmitted behavior through animal groups, Allen et al. were able to track the emergence, social transmission, and establishment of this new feeding technique off the Gulf of Maine, using behavioral and social network data collected over 17 years. Following shortly, and using the same methodological framework as Allen et al., the first demonstration of a socially transmitted novel tool use behavior through a group of wild chimpanzees also emerged (Hobaiter et al., 2014). The significance of these findings is that they confirm the existence of a behavioral tradition in a species phylogenetically distant from our own, and that group-specific behavioral variants in other species can emerge through social transmission.

METHODOLOGICAL APPROACHES TO STUDYING ANIMAL CULTURE

The controversy over animal culture is to a large degree methodological in character. Disagreements have often occurred because researchers have lacked appropriate means of validating claims of culture according to mutually acceptable criteria. For example, where group-level differences in behavior have been identified, claims of culture have been vulnerable to the difficulty of ruling out alternative explanations, such as environmental or genetic variation (Laland & Janik, 2006). And even in cases where the spread and establishment of a behavioral trait can be observed directly, it is difficult (without use of the following methods) to distinguish socially learned behavioral acquisition from individual trial-and-error learning (Hoppitt & Laland, 2013). As a consequence, judgments about which species exhibit culture vary with differing assessments of the plausibility of circumstantial evidence (Laland & Hoppitt, 2003). With the advent of new tools for identifying culture in nature, a major part of the controversy should disappear.

Over the past decade great progress has been made in the development of conceptual and analytical tools that allow researchers to address these concerns. The tools provide means to ascertain when social learning and social transmission underlie a diffusion, or a distribution of traits, to identify the underlying mechanisms, and to determine the functional strategies deployed. Next, we describe three such new approaches that we believe are of particular utility in addressing the issues at the heart of the debate, namely NBDA, the option bias method, and the stochastic mechanism fitting model. The first two of which are starting to be used widely, whereas the third could be used much more. We end this section by drawing attention to the limitations of studying animal traditions based solely on identifying group-level differences in behavioral repertoires, and encouraging the application of complementary developmental approaches to studying animal traditions. (For a more comprehensive description of methodologies emerging and established in the field, see Hoppitt and Laland, 2013.)

Network-Based Diffusion Analysis

Many novel traits spread through animal populations by learning, a phenomenon generally described as diffusion. Although such diffusions often result from social learning, there are other types of social influence, as well as nonsocial processes, which can account for this spread. NBDA infers, and quantifies, the strength of social influence in a set of diffusion data by assessing the extent to which the pattern of spread follows a social network.

NBDA is of potential utility to any researcher interested in inferring social learning in natural populations, or captive groups of animals. It was invented by Franz and Nunn (2009), who assumed social transmission when the pattern of spread of a behavioral trait, as measured by the time to acquire a trait, followed the patterns of association in a social network. Hoppitt, Boogert, and Laland (2010) later extended NBDA to apply to order of acquisition data, now known as order of acquisition diffusion analysis, as well as time of acquisition, now known as time of acquisition diffusion analysis (TADA). They also extended the method to include individual-level variables that might influence the rate of acquisition, such as sex, age, and dominance, which can statistically control for the effects of these variables when testing for social transmission (Hoppitt, Boogert, & Laland, 2010). This is particularly important if such variables are correlated with the social network structure, as this can result in false positives for social transmission if such variables are not taken into account. More recently, a Bayesian NBDA approach has been developed (Nightingale, Boogert, Laland, & Hoppitt, 2015), which has the advantage that it provides a means of combining information arising from diffusions across different groups of animals (e.g., Webster, Atton, Hoppitt, & Laland, 2013). The expansion of NBDA to multiple diffusions is also valuable where researchers have repeated diffusions across the same group, or groups, of animals (e.g., Boogert, Reader, Hoppitt, & Laland, 2008), especially when they only have a limited number of animals, allowing them to obtain good statistical power.

For illustration, we briefly summarize the formal logic of the TADA model. However, we emphasize that statistical packages are now freely available that allow researchers to implement NBDA without requiring extensive knowledge of these technical details (see http://lalandlab.st-andrews.ac.uk/freeware.html). TADA is based on standard survival analysis models, and consequently the models are typically described using survival analysis terminology. For instance, they refer to the *hazard function* as giving the instantaneous rate at which an individual acquires a target trait, which in this case is the task solution. There are two parameters of interest in the basic *TADA* model: the rate of social transmission between individuals per unit of network connection (s) and the baseline rate of trait performance in the absence of social transmission $\ddot{e}_0(t)$. The hazard function for the model is expressed as

$$\ddot{e}_i(t) = \ddot{e}_0(t)(1 - z_i(t))R_i(t), \tag{1}$$

such that

$$R_i(t) = \left(s \sum_{j=1}^{N} a_{ij} z_j(t) + 1 \right), \tag{2}$$

where $\ddot{e}_i(t)$ is the rate at which individual i acquires the task solution at time t, $\ddot{e}_0(t)$ is a baseline acquisition function determining the distribution of latencies to acquisition in the absence of social transmission (that is, through asocial learning), and $z_i(t)$ gives the status (1 = informed, 0 = naive) of individual i at time t. The $(1 - z_i(t))$ and $z_i(t)$ terms ensure that the task solution is only transmitted from informed to uninformed individuals (Hoppitt, Boogert, & Laland, 2010). Different versions of TADA allow for an increasing or decreasing baseline rate $\ddot{e}_0(t)$ (Hoppitt, Kandler, Kendal, & Laland, 2010). The model assumes that the rate of social transmission between individuals is proportional to the connection between them, given by a_{ij}. It is used to generate a likelihood function, allowing it to be fitted by maximum likelihood or analyzed using Bayesian methods. Social transmission is inferred if a model including s is better than a model with s = 0, using Akaike's information criterion, if maximum likelihood fitting is used, or Bayes's factor if Bayesian methods are used. NBDA can be adapted to include other variables influencing the rate of social transmission or asocial learning that vary across individuals and/or time (see Hoppitt, Boogert, & Laland, 2010; Hoppitt, Kandler, et al., 2010; Nightingale et al., 2015, for further details).

Despite being a recently developed method, NBDA has already been used a number of times to analyze diffusion data from wild and captive animal populations, usually using an association metric to obtain the social network. For example, Aplin et al. (2012) found strong evidence that the time of and probability of discovering of novel food patches followed an association network in a wild population of great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), and marsh tits (*Poecile palustris*). A subsequent study revealed evidence for conformity (Aplin et al., 2015). Likewise, Allen et al. (2013) found strong evidence that the acquisition of lobtailing, a foraging innovation, followed an association network in a wild population of humpback whales. Kendal, Galef, and van Schaik (2010) also applied the method to analyze the diffusion of a novel foraging behavior in lemurs (*Lemur catta*), although there was no evidence that social transmission followed the network in that case.

The method can also be used to distinguish between social transmission and a nontransmitted social influence on the diffusion. For instance, Atton, Galef, Hoppitt, Webster, and Laland (2014) presented shoals of threespine sticklebacks (*Gasterosteous aculeatus*) with two identical foraging tasks and applied NBDA. They found strong evidence for a social effect on discovery of the foraging tasks with individuals tending to discover a task sooner when others in their group had previously done so, and with the spread of discovery of the foraging tasks influenced by groups' social networks. However, the same patterns of association did not reliably predict spread of solution to the tasks, suggesting that social interactions affected the time at which the tasks were discovered, but not the latency to its solution following discovery. The study illustrates how NBDA can lead to insight into the mechanisms supporting behavior acquisition that more conventional statistical approaches might miss. In this instance, it provides the first compelling evidence that the spread of novel behaviors can result from social learning in the absence of social transmission, a phenomenon that Atton et al referred to as an untransmitted social effect on learning.

Evolutionary theory predicts that natural selection will fashion cognitive biases to guide when, and from whom, individuals acquire social information, known as *social learning strategies*. Kendal et al. (2015) extended the NBDA method further to detect specific social learning strategies. This allowed them to reveal that common chimpanzees exhibit biases to copy higher-ranking and more knowledgeable individuals, and to copy others when uncertain of how to solve the task or when they are of low rank.

The Option-Bias Method

In many of putative cases of animal culture, it is often very clear that individuals in different groups perform different variants of a behavioral trait (e.g., chimpanzee ant dipping). In other cases, a group effect might be subtler, with individuals of the same group being more likely to perform the same variant, but with some stochastic variability within groups and within individuals. This pattern can be termed an *option-bias* (Kendal, Kendal, Hoppitt, & Laland, 2009), with each way of performing the trait termed an option. In such cases it is necessary to ascertain whether the observed option-bias could have arisen by chance, if individuals settle on a preferred option by asocial learning, independently of the choices of others in their group. The null hypothesis is that individuals in the same group are no more likely to choose the same option than those in different groups. A *prima facie* solution to this would be to apply a Chi-square test to a contingency table of the frequency of options performed in each group: However, this is not a valid approach, because multiple option-choices made by a single individual are unlikely to be independent, and therefore violate the assumptions of the Chi-square test. A solution is to use a randomization test on the data obtained from groups of individuals as follows:

1. Calculate the test statistic, T_{DATA}, for the contingency table (e.g., Chi-square) resulting from the original data.
2. Set N = 1, X = 1.
3. Randomly reassign individuals (i.e., the data obtained from each individual) to a group, maintaining the same number of individuals in each group as were originally present.
4. Recalculate the test statistic on the randomized group membership, T_N.
5. If $T_N \geq T_{DATA}$, increment X by 1.
6. Increment N by 1.
7. Repeat steps 3–6 until N is suitably large (e.g., 10,000).
8. The p value against the null hypothesis is X/N.

This option-bias test (Kendal et al., 2009) allows for the nonindependence of option choices by the same individual, because the randomization procedure ensures that the option choices made by an individual are always assigned to the same group. The logic underlying this procedure is that if the null hypothesis were true, the assignment of individuals to groups is arbitrary with respect to option choice, so T_{DATA} should be a typical value from the null distribution of T values. The p value quantifies the probably of getting a value of T_{DATA} that is at least as big as that observed, under the null hypothesis. For more details on the logic underlying randomization tests, see Manly (2008). Kendal et al. (2009) found that this randomization procedure had better power and more appropriate Type 1 error rates than alternative statistical tests, and was also typically more powerful than a Monte Carlo simulation approach. Huffman, Spiezio, Sgaravatti, and Leca (2010) used the option-bias method to infer that group-level differences in chimpanzee leaf swallowing, a self-medicating behavior associated with the expulsion of parasites, were spread and established by social transmission through two captive groups. Dean, Hoppitt, Laland, and Kendal (2011) also applied the option-bias method to data from groups of captive ruffed lemurs (*Varecia varigata* and *Varecia rubra*) presented with a food puzzle that could be solved in two alternate ways. There was no evidence that the method of puzzle solution was transmitted socially through the ruffed lemur groups, however, and therefore no option-bias was detected.

The option-bias test can be modified for groups that were seeded with demonstrators trained to perform a specific option, by constraining the demonstrators to remain in their groups during the randomization. Kendal et al. (2015) seeded chimpanzee groups with demonstrators trained to solve a novel food puzzle by sliding a door either to the left or to the right. Option-bias analysis later revealed strong evidence for the social transmission of the seeded method to naive group members, with the majority of door slides occurring to the left in the group seeded with the left variant and to the right in the group seeded with the right variant. The method could also be modified for noncategorical behavioral traits by replacing the test in step 1 with an appropriate test for group differences. For example, for a trait that varies continuously, one could apply an ANOVA with group as a factor in step 1, taking the F statistic as the test statistic.

The option-bias test only allows us to infer whether there is a group-level option bias that needs explaining, it does not, in itself, establish that this difference is a result of social transmission. To do so, a researcher needs to exclude or account for genetic and ecological hypotheses.

Stochastic Mechanism Fitting Model

Hoppitt, Samson, Laland, and Thornton (2012) proposed a stochastic mechanism-fitting model (SMFM) for inferring social learning mechanisms in the field or naturalistic circumstances in captivity. They applied the SMFM to data on groups of wild meerkats learning to solve a foraging task: two boxes containing food, both of which could be accessed using either a flap, or a tube, giving meerkats four “options” for solving the task (see Figure 20.1a).

The SMFM views individuals as moving between states of not interacting with the task and interacting with the task. Individuals can either terminate bouts of interactions successfully by solving the task, or abandon the task before succeeding. This gives a total of three transition rates (see Figure 20.1b).

The statistical model uses survival analysis methods (similar to those underlying network based diffusion analysis) to model the transition rates for each individual, *i*, as a function of both *i*’s previous manipulations (asocial learning), and *i*’s observations of other meerkats manipulations (social effects). The latter was split into direct social learning, where observations had a long lasting effect comparable to that of manipulations made by *i*, and transient social effects, where a transition rate was increased or decreased temporarily after each observation.

Hoppitt et al. (2013) expanded this model to estimate the effects of sensitivity to the observed outcome of the demonstrator’s actions: whether they were observed obtaining food and whether they were observed gaining entry to the task. They also expanded the model to estimate the extent to which social effects generalized between, or were specific to, options. This allowed them to estimate context specificity: Was each effect specific to an option (a highly specific location), a box (a less specific location), or to an option-type (a type of stimulus, a flap or a tube). The experiment was designed to tease this context specificity apart, but in other cases the options might be designed such that action specificity is also quantified, using a two-action test design.

They found a number of social effects in operation, affecting the rate of interaction and the rate of task abandonment. Indeed, they were able to identify nine separate learning processes underlying the meerkats’ foraging behavior, in each case quantifying its strength and duration, including local enhancement, emulation, and a hitherto unrecognized form of social learning, which we termed *observational perseverance*. The dominant social effect was a strong but short-lived (20s half-life) local enhancement effect, which attracted individuals to interact with the option they had recently observed being manipulated. This effect was strongest for younger observer meerkats (see Figure 20.2). The analysis suggested that a key factor underlying the stability of behavioral traditions is a high ratio of specific to generalized social learning effects. The approach has widespread potential as an ecologically valid tool to investigate learning mechanisms in natural groups of animals, including humans.

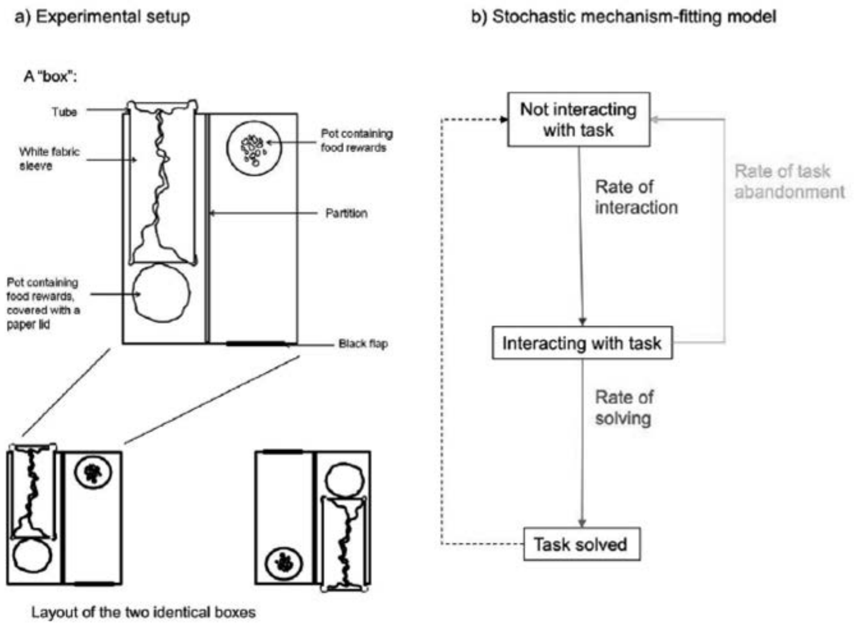

FIGURE 20.1. (a) The "box" apparatus used by Hoppitt et al. (2012) to investigate social learning mechanisms in groups of wild meerkats. The flap technique involved going through a black cat flap to obtain food from a pot; the tube technique involved pushing through a fabric sleeve on the tube and breaking a paper lid to obtain food. The experimental layout of the two identical boxes is shown below. (b) A diagrammatic representation of the stochastic mechanism-fitting model (SMFM) showing the three rates of transition that were modeled. Reprinted from "Identification of Learning Mechanisms in a Wild Meerkat Population," by W. Hoppitt, J. Samson, K. N. Laland, and A. Thornton, 2012, *PLOS ONE*, *7*, p. 3. In the public domain.

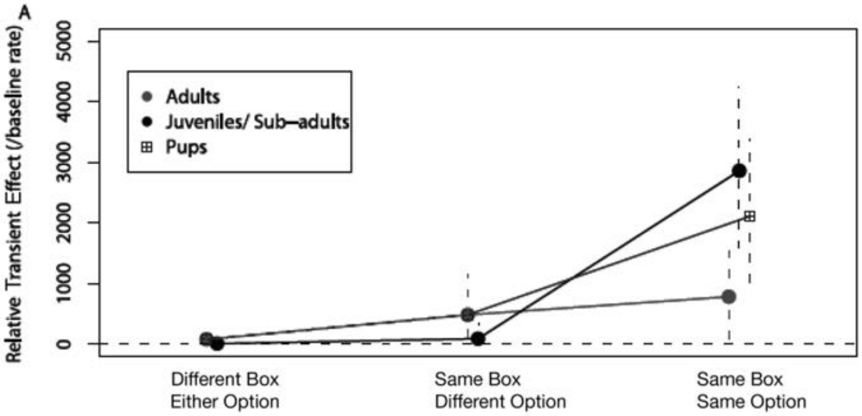

FIGURE 20.2. Hoppitt et al.'s (2012) estimates of the transient (short-lived) increase in rate of interaction at each option immediately following observation, for different age classes of meerkats. Reprinted from "Identification of Learning Mechanisms in a Wild Meerkat Population," by W. Hoppitt, J. Samson, K. N. Laland, and A. Thornton, 2012, *PLOS ONE, 7*, p. 6. In the public domain.

Developmental Methods

Although the methodological approaches previously outlined are of great utility in confirming or refuting social transmission on the basis of observable differences in animal behavioral repertoires, developmental approaches can also be extremely instructive (Biro et al., 2003; Fragaszy & Perry, 2003; Lonsdorf, 2006; Reader & Biro, 2010). To gain a deeper understanding of the processes determining how individuals acquire a group-level trait, researchers can seek to trace its emergence in individuals across the lifespan and in relation to their interaction with social and nonsocial aspects of their environment. Fragaszy (2011) maintained that behavioral comparisons across animal groups are inadequate in themselves to assess the role of social learning in the acquisition of behavioral traditions. She suggested that to evaluate how social learning shapes skill acquisition in individuals, researchers must try to relate individual differences in skill acquisition to individual histories of observing and learning from others. Developmental approaches complement approaches that seek to identify behavioral traditions on the basis of group-level and often snapshot comparisons of behavioral repertoires; they also potentially allow researchers to identify socially learned behaviors that exhibit no between group variability that would otherwise remain undetected using group comparison methods.

Following Hoppitt and Laland (2013), we define developmental approaches to the study of animal traditions broadly, including “any approach that aims to elucidate the role of social influences in the development of a behavioral trait” (p. 172). Developmental approaches can be further subdivided into two main research areas: observational methods and experimental manipulations (see Volume 1, Chapter 4, this handbook). We discuss each of these in turn.

Observational methods. The first type of developmental approach involves collecting data on the development of a given trait in naturalistic settings, along with information regarding developmental opportunities for learning the trait, such as interactions with other animals that perform it. This often requires detailed observations on a number of individuals, and a longitudinal study design. In using this approach, the researcher might identify the stages of development where social learning operates, and the types of social interactions that are necessary for the emergence of the trait.

This approach is exemplified by Biro et al. (2003; Biro, Sousa, & Matsuzawa, 2006), who studied the development of nut cracking and leaf folding behavior in chimpanzees at Bossou, a long-term field site in the Republic of Guinea. Biro et al. were able to identify a critical developmental window for the emergence of nut cracking behavior, finding that, although it did not appear before the age of 3 to 3.5 years, those animals that had not developed the skill by the age of 7 years were never seen to perform the trait. Leaf folding behavior was observed to develop in two stages: By 2 years of age the chimpanzees were able to use the discarded leaves that others had folded to drink water, but not until sometime after 3.5 years of age did they construct and drink from their own folded leaves. The data collected by Biro et al. also permitted an assessment of the role of social learning in the development of these two behavioral traits. It was noted, for example, that juveniles were not allowed the same opportunities as infants to scrounge from or interact with and observe adults engaged in nut cracking behavior, which might have contributed to the critical learning period for this behavior ending at age 7 years (Biro et al., 2006). Biro and colleagues (2006) also analyzed the pattern of observation of nut cracking and leaf folding behaviors between individuals of different age classes, finding that although the more proficient adults were more likely than juveniles or infants to be observed performing the behaviors, juveniles and infants were more likely to spend time observing other individuals performing the behavior than adults.

The data collected by Biro and colleagues (2003, 2006) fit expectations that individual chimpanzees tend to observe others who are more proficient at the target traits, and illustrated the merits of using longitudinal data to enhance our understanding of the role of social learning in naturally occurring traits. However, although Biro et al.’s data allowed the identification of opportunities for social learning, they did not identify whether trait acquisition occurs as a result of these opportunities, nor provided an estimate of the importance of social learning relative to other factors influencing development of the traits (Hoppitt & Laland, 2013).

Hoppitt and Laland (2013) described in detail a number of methodological approaches that have emerged in recent years attempting to link developmental variables to the emergence of the target trait in individuals. These approaches include (a) modeling the probability of acquisition relative to opportunities to socially learn, for traits that are not acquired by all individuals in a population (e.g., Sargeant & Mann, 2009, investigating foraging tactics in bottlenose dolphins); (b) modeling the time of trait acquisition relative to opportunities to socially learn (e.g., Lonsdorf, 2006, in relation to termite fishing behavior in chimpanzees); (c) modeling proficiency of trait performance relative to opportunities to socially learn (e.g., Humle, Snowdon, & Matsuzawa, 2009, studying the influence of maternal behavior on the acquisition of ant dipping behavior in chimpanzees); and, (d) modeling the factors affecting option choice in situations where a trait can be performed with two or more variants or options (e.g., Perry, 2009b, in a study of foraging techniques in white-faced capuchins).

Experimental manipulations. A concern that arises with observational data collected in naturalistic settings is that there might be unmeasured confounding variables influencing statistical assessments of the relationship between social interaction and target trait acquisition. Some of these difficulties can be overcome by implementing controlled field experiments. We describe three examples of field experimental techniques, namely diffusion experiments, manipulation of social experience, and translocation studies, that we believe are particularly complementary to observational methods (see Reader & Biro, 2010, for a complete review of field techniques).

Diffusion experiments are a relatively straightforward experimental approach to studying the spread and development of socially transmitted behaviors. In this approach, a novel artificial foraging task is introduced to a population of animals, and the behavioral acquisition of its solution traced as it spreads throughout individuals in the group. If the diffusion is seeded, a trained demonstrator is also introduced, whereas in unseeded diffusions all members of the population begin naive (Lefebvre, 1995). The former approach has the advantage that it is easier to infer social transmission from the resulting data if different groups are seeded with different methods of solving the task, although unseeded diffusions offer advantages to researchers also interested in behavioral innovation (i.e., who is most likely to first discover the task solution in a given group; Hoppitt & Laland, 2013). Diffusion experiments have been applied successfully in both captive facilities such as laboratories and zoos (e.g., Boogert et al., 2008; Day, Coe, Kendal, & Laland, 2003), and in the field (e.g., Biro et al., 2003; van de Waal, Renevey, Favre, & Bshary, 2010).

Another field technique that can be used to investigate the relationship between a type of social experience and development of a target trait is by experimental manipulation of the social behavior in question. This could be achieved by systematically removing naturally occurring experience of the social interaction proposed, although in practice it is likely to be more feasible and ethical to enhance it. This approach was used by Thornton and McAuliffe (2006) in their study of the development of teaching behavior in meerkats (see Chapter 19, this volume). Meerkats are a cooperatively breeding species, and it was suspected that adult "helpers" (i.e., nonbreeding adults who aid in bringing up the pups; see Volume 1, Chapter 36, this handbook) played an important role in the development of pup hunting skills, including presenting the pups with disabled scorpions such that they could practice their hunting technique. In a series of innovative experimental manipulations, in which pups' exposure to live stingless scorpions was systematically manipulated, Thornton and McAuliffe (2006) found that pups trained with live scorpions were indeed more successful and efficient at handling the prey following training, and in combination with other findings were able to make a strong claim that the behavior of the adult helpers constitutes a form of opportunity teaching.

Translocation studies are possibly the most elegant and compelling means of manipulating and investigating the role of social factors in the development of a target trait, but are also more likely to encounter logistical impracticalities or ethical objections than other methods. They involve the translocation of individuals between populations, and populations between sites, to critically test between ecological, genetic and social explanations for a naturally occurring behavioral tradition. The approach has been applied most successfully to the study of culture in fish. In one study by Helfman and Schultz (1984), French grunts (*Haemulon flavolineatum*) translocated between established populations adopted the same schooling patterns and migration routes as the local residents, suggesting that the behaviors were not determined by genetic factors. Likewise, control fish introduced into the same ecological regions after the residents had been removed did not adopt the same behavior patterns as the former residents, ruling out the possibility of ecological explanations. In ruling out genetic and ecological explanations for the observed differences in schooling and migratory behaviors between populations, the results obtained by Helfman and Schultz (1984) successfully demonstrate the existence of socially transmitted behavioral traditions in French grunts. Slagsvold and Wiebe (2007) have also applied the translocation approach successfully in birds by transferring eggs between nests, providing evidence that blue tits and great tits socially learn aspects of their respective foraging niches during early development. After translocating the eggs of blue tits (*Cyanistes caeruleus*) to the nests of great tits and vice versa, Slagsvold and Wiebe (2007) found that both species changed their foraging niches in the direction of the foster species, despite being raised in an environment that was otherwise natural to the birds.

Developmental approaches to the study of social learning and transmission have grown in use over recent years. Biro et al. (2003, 2006) demonstrate that the practical difficulties of conducting long-term observational studies in wild populations can be mitigated if data collection is restricted to manageable time windows and accessible locations. Similarly, researchers might be able to exploit data resulting from the natural movement of animals between populations and locations, where translocation studies would be impractical or unethical (Hoppitt & Laland, 2013; van de Waal et al., 2013). Although in the previous discussion we have restricted ourselves to techniques that can be applied in naturalistic learning settings, laboratory-based demonstrator-observer experiments would constitute a developmental methodology too (Hoppitt & Laland, 2013). Developmental approaches elucidating the factors affecting the emergence of traits in the wild, combined with experimental investigations of developmental processes in the field and lab, are a necessary complement to more traditional group-level approaches in the study of animal culture.

THE ANIMAL CULTURE DEBATE: WHERE DO WE STAND?

Methodological inadequacy is certainly not the only factor in the animal cultures debate, there is also a semantic battle. Whether or not we allow other animals the accolade of culture ultimately depends on where researchers etch culture's boundaries. At one extreme, culture becomes the exclusive domain of *Homo sapiens*, replete with language, teaching, and symbolism (e.g., Tuttle, 2001). At the other, culture might be any inherited group-level differences in behavior that are not attributable to genetic variation, a definition that encompasses a wide range of species, including some bacteria (Lumsden & Wilson, 1981). Some protagonists may wish to draw attention to the social complexity and diversity of their animals for conservation-related reasons (e.g., McGrew, 2004). Likewise, the persistence of Cartesian thinking, which perpetuates the belief of a divide between the mental abilities of humans and other animals, may have influenced many skeptics.

Historically, even where researchers have reached a consensus about which criteria should constitute culture, methodological difficulties—especially in ruling out genetic or ecological explanations for behavioral differences between groups—have prevented its confirmation in other species. However, assuming the broad and inclusive definition of culture previously deployed, there is now reasonable evidence for culture in the chimpanzee (Hobaiter et al., 2014; see Lonsdorf, 2006, for further support), humpback whales

(Allen et al., 2013; Garland et al., 2011; Noad et al., 2000), at least two species of birds (Slagsvold & Wiebe, 2007; see also Aplin et al., 2015) and fish (Helfman & Schultz, 1984; Warner, 1990). The two most recent findings rest on the application of novel and innovative methodologies developed specifically for detecting socially transmitted behavior in animal populations. We envisage a growing list of taxa that can be said to exhibit cultural behavior as these new methodologies are increasingly applied.

Some authors, also interested in studying the evolutionary roots of human culture, have taken issue with using the word culture to refer to socially transmitted behavioral traditions in other species (e.g., Hill, 2009; Perry, 2009a). For these authors, confirmation that a group-level behavior has been socially transmitted is not sufficient to warrant application of the term culture, as this might negate recognition that human culture is comprised of additional components not observable in other animals. Put another way, if other animals are increasingly awarded the accolade of culture, important questions still remain: How is human culture different? How do we explain the undeniable void between the cultural abilities of other species and the extraordinary cultural achievements of our own? Even if the cultures of other animals have some semblance to our own, understanding the extent to which this semblance can be attributed to homology or convergent evolutionary processes is paramount when we look to other animals for clues about the roots of human culture. We outline three broad areas—namely the mechanisms of culture, the existence of cultural norms, and symbolic culture—in which a definition of cultural transmission exclusive to human beings might prevail.

The first way in which human and nonhuman animal culture may differ involves the mechanisms of culture (or mechanisms of social transmission). There are those who assert that animal culture lacks some property (e.g., teaching, imitation, language) that they consider a key feature of human culture (Boyd & Richerson, 1985; Galef, 1992; Tomasello, 1994). Human and animal cultures are therefore perceived to be qualitatively different; analogs but not homologs (Galef, 1992; Tomasello, 1994). Tomasello (1994, 1999) has argued compellingly that imitation, teaching and language are in turn critical for cumulative cultural learning, because they alone afford high-fidelity transmission, and has suggested that humans alone exhibit cultural transmission with a "ratcheting" (cumulative knowledge-gaining) quality. Tomasello's argument has since received theoretical (Lewis & Laland, 2012) and empirical (Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Morgan et al., 2015) support. Humans alone appear to have stepped up from the technologically stagnant and often fleeting behavioral traditions typically characterized in other species (Laland et al., 1993), accumulating cultural improvements, generation on generation, that have allowed humans to live in societies overseen by complex governments, write books, engineer spacecraft, and drive cars, among other things. There have been claims of cumulative culture in a handful of animal species, most notably chimpanzees and New Caledonian crows (Boesch, 2003; Hunt & Gray, 2003). The evidence for these claims is circumstantial and equivocal, however, and the purported culturally accumulated behaviors are still rudimentary next to our own.

The second component of culture that might be exclusive to human beings is the existence of culturally transmitted norms and sanctions, prescribing how members of a cultural group ought to behave, and stipulating punishments for those who defy the rules (Hill, 2009). Norms, or social rules coordinating behavior within and between cultural groups, permeate all aspects of human life, regulating such areas as communication, exchange, courtship and marriage, and intergroup relations. Receiving much attention has been the role occupied by norms in explaining the perceived shortfall in standard gene-based evolutionary theories to account for our large-scale cooperation and enhanced prosocial tendencies (Chudek & Henrich, 2011; Fehr, Fischbacher, & Gächter, 2002; Gintis, Bowles, Boyd, & Fehr, 2003). According to this view, those societies that developed norms of cooperative interactions between distantly related individuals, along with sanctions for violations of these norms and a willingness among group members to engage in third-party punishment, likely outcompeted those less cohesive societies that did not. This uniquely human propensity to establish far-reaching and cooperative social ties has also served to amplify the spread of novel inventions and cumulative improvements in cultural knowledge (Hill et al., 2011). Empirical studies demonstrate that even young children appear equipped with a "norm psychology" or a suite of psychological mechanisms that facilitate adherence to cultural norms (Chudek & Henrich, 2011), including a propensity to conform to the behavior of peers (Haun, Rekers, & Tomasello, 2012; Haun & Tomasello, 2011), an ability to readily infer normative behaviors, and a willingness to sanction norm violators (Rakoczy, Warneken, & Tomasello, 2008).

Evidence of conformity to socially transmitted norms and sanctions is lacking in other species. Recently there have been claims that vervet monkeys (van de Waal et al., 2013) and wild birds (Aplin et al., 2015) conform to experimentally seeded and group-specific arbitrary feeding preferences, with migrating individuals readily switching their preference to the local feeding norm when entering a new group. But these claims are contested, the underlying motivations and mechanisms responsible for these patterns of behavior remain unclear, and there is no evidence that the adoption of the aforementioned feeding preferences were associated with any accompanying social pressures or sanctions. Perry (2009a) writes that despite numerous tales of differences existing between conspecific primate groups in certain types of social interaction, there is little published confirmation that behaviors such as sexual coercion, food theft or affiliative interactions differ between groups, and no unequivocal evidence of third-party punishment in response to group-level social behaviors being violated. Though it should also be noted that this is an area ripe for further research, and it is possible that evidence confirming these types of behaviors in other species, at least in rudimentary form, may emerge in the future (Perry, 2009a).

The final way that human culture appears to be set apart from the cultures of other animals is in its symbolic content. Across all human societies, arbitrary behavioral practices, rituals, artifacts, dress codes, culinary preferences, and other such traits frequently acquire an emotional saliency and moral significance associated with reinforcing and signaling group membership and adherence to a particular set of norms and rules (Hill, 2009; Perry, 2009a). This in turn helps to solve an important coordination problem: in signaling adherence to a given set of rules or morality, and evoking emotional responses toward others dependent on whether they bear the same or dissimilar markers, these arbitrary symbols enable their bearers to choose social partners who abide by the same set of cooperative norms and rules as they do (Efferson, Lalive, & Fehr, 2008; Hill, 2009). Other animals also exhibit evidence of group-level variability in arbitrary social behaviors or conventions. White-faced capuchins, for example, engage in behaviors such as hand sniffing, body part sucking, or inserting a partner's finger into one's own eye socket that vary from clique-to-clique (Perry et al., 2003). However, these social rituals most likely serve to test and cement dyadic bonds between social partners, rather than function as symbolic signals of group membership and norm adherence (Perry et al., 2003).

If culture is defined as comprising these three components—enhanced high-fidelity mechanisms of social transmission critical to ratcheting, culturally transmitted norms and sanctions, and symbolic content—then we currently have little evidence for claims of culture in other animals. However, the jury is still out. Common to all areas of research in the study of animal culture, researchers have often lacked the methodological tools to generate the kind of data that would confirm or refute the existence of these three cultural components in other animals. It remains possible that at least some of the aforementioned traits, currently regarded as being exclusive to human culture, will eventually be discovered in other species. Continued advances in our methodological tools for ascertaining the mechanisms and processes underlying animal social transmission are paramount to understanding whether the differences between their cultures and our culture are mostly of degree or kind.

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PART III

COGNITION AND EMOTION

CHAPTER 21

SPATIAL COGNITION

Ken Cheng and Kate Jeffery

Spatial cognition has been the target of an enormous amount of comparative psychological research in the past century or more, partly because of the ubiquity of spatial behavior across the animal kingdom, and partly because spatial cognition is an ideal model system for studying cognition more generally. Spatial cognition research has comprised ethological studies, mostly in the wild and involving a wide variety of vertebrate and invertebrate taxa (see Chapter 22, this volume), and behavioral and neurobiological studies in the laboratory, mostly on humans and rodents. Among rodents, the commonest subject has been the Norway rat (*Rattus norvegicus*) because of its conveniently small size, docility, and well-understood biology, but more recently attention has been switching to mice (*Mus musculus*) because of the opportunities afforded by genetic modification.

In this chapter we begin with some historical background about the study of spatial behavior and then review the variety of spatial behaviors that have evolved in different species, together with emerging findings about the brain circuits that support such behaviors. We examine how the differences and commonalities across taxa reveal some of the basic underlying properties of spatial representation and its biological substrate.

HISTORICAL PERSPECTIVE

Scientists have always been curious about animal behavior. Ancient Greeks, such as Aristotle, were keen observers of natural behavior, as were 19th century naturalists, such as Alfred Russel Wallace (1858) and Charles Darwin (1859, 1871). In psychology, the formal study of spatial cognition in animals began in the early 1900s in the context of research on animal learning, with an initial focus on association formation (see Volume 1, Chapter 2, this handbook). At first these associations were considered to be straightforward connections between stimuli or between stimuli and responses (Pavlov, 1927) or outcomes (Watson, 1913). By this view, spatial knowledge would be no different from any other kind. Early studies of maze learning in rats showed that they were adept at learning routes through even complex mazes like the Hebb–Williams maze (Hebb & Williams, 1946; see also Volume 1, Chapter 6, this handbook), suggesting a high-capacity memory, which could plausibly be supported simply by associations between local stimuli in the environment (e.g., particular junctions) and responses. However, a series of studies by Tolman and his associates in the 1940s suggested that the associations supporting navigational behavior may be more complex and involve internal constructs with specifically spatial content, such as the metric properties of distance and direction (Tolman, 1948), collectively creating something approaching a “map.”

Tolman’s biggest challenge to the then-dominant view of learning was his classic sunburst maze experiment (Tolman, 1948) in which rats were taught a dog-legged route to a goal and then offered the opportunity to take an alternative route to avoid a block in the usual one; the animals typically took

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the direct (shortcut) option, suggesting they knew where the goal was located in spatial coordinates, and possessed some internal representation, akin to an internal map, of the spatial layout of the maze. Although Tolman's experiment has been criticized on methodological and theoretical grounds (Bennett, 1996; O'Keefe & Nadel, 1978), his notion of an internal spatial representation, which he called a *cognitive map* (see Chapter 22, this volume), persisted and became more influential in subsequent decades, finally becoming accepted following the seminal discovery of the neural basis of spatial representation.

Tolman and his colleagues (Tolman et al., 1946) also showed that as well as learning the layout of the environment, rats can also use another more route-like strategy to locate a goal. They can, for instance, simply make a consistent body turn. This distinction between map-like and route-like navigation was echoed by O'Keefe and Nadel (1978), who formulated them as locale and taxon systems for navigation. This influential and important distinction has found support in the neurobiological evidence that the former kind depends on the hippocampal system (see Volume 1, Chapter 25, this handbook), whereas the latter is more habit-like and depends on the striatum (Gasbarri, Pompili, Packard, & Tomaz, 2014).

In other studies, Tolman and Honzik (1930) and Spence and Lippitt (1946) showed that spatial learning also occurs latently, without the need for explicit training or reinforcement. For example, Spence and Lippitt (1946) allowed satiated, hydrated rats to explore a Y-maze which had food located at the end of one arm and water at the end of the other. Because the rats were not hungry or thirsty they did not consume either the food or the water, but when subsequently returned to the maze when hungry they visited the food-containing arm, and when thirsty they visited the water-containing arm. Thus they had learned the location of these reinforcers even though these had not previously been reinforcing.

A separate tradition in research on spatial cognition emerged from ethological studies in other taxa. Nobel Prize winner Niko Tinbergen manipulated landmarks around digger wasps' nests, and showed that they used such landmarks to locate their nest (Tinbergen, 1932). Karl von Frisch, who shared the Nobel Prize with Tinbergen and Konrad Lorenz, famously showed that honeybees (*Apis mellifera*) were able to encode the vector (distance and direction) to a nearby food source (von Frisch, 1953), and communicate this to their hive-mates via the waggle dance. This set of experiments showed that vector encoding (a) is fundamental to navigation (perhaps unsurprisingly), and (b) need not require very many neurons. Subsequent research has indicated that honeybees encode far more than just a vector (Dyer & Gould, 1983; Menzel et al., 2005; Towne & Moscrip, 2008), leading some investigators to suggest that the representation may be actually more map-like (Menzel & Greggers, 2015; see also Chapter 22, this volume).

In mammalian spatial cognition, an important step forward came about in the 1970s following the discovery by John O'Keefe and colleagues (Moser, Kropff, & Moser, 2008; O'Keefe & Dostrovsky, 1971) of place cells in the rat hippocampus. Place cells are neurons in the rat hippocampus that are positionally selective, becoming active only when the rat enters a particular place in its environment. Each place cell prefers to fire in a particular place, or sometimes multiple places, its place field(s), with the population of neurons together encoding the whole environment (Geva-Sagiv, Las, Yovel, & Ulanovsky, 2015; Jeffery, 2010). O'Keefe and the neuropsychologist Nadel together proposed that place cells form the substrate for a cognitive map of the kind proposed by Tolman (O'Keefe & Nadel, 1978). This discovery, and the theory that followed, was a game-changer in cognitive psychology for several reasons. First, it indicated that rats (and, as was shown later, many other species including humans, Ekstrom et al., 2003) have an internal representation of location. Second, it showed that spatial cognition uses the same neural circuitry, comprising the hippocampus and related structures, which supports memory for life events (Scoville & Milner, 1957; see also Chapter 11, this volume). And third, it provided a model system for understanding how a cognitive representation can emerge from the synthesis of multiple incoming sensory signals.

Following O'Keefe and Nadel's (1978) proposal, laboratory studies of spatial memory in animals, mainly rats, were re-ignited and began to spread. One facilitating development was Olton's 8-arm radial maze (Olton & Samuelson, 1976), in which animals learn to retrieve food from the ends of spokes in a wheel-like arrangement of maze arms, without revisiting depleted arms or omitting baited ones. The term *learn* is used loosely because rats do this readily, and hardly require any training beyond familiarization with the novel environment. Rats solve this task by choosing arms in haphazard order, and thus seem able to remember which have food and which now (after being visited) do not. Interestingly, radial maze tasks in other species elicit more stereotypical behavior. Mice tend to choose neighboring arms in sequence, although they can also master a three-dimensional version of the maze, in which their behavior becomes much less sequential (Wilson et al., 2015). With some effort in training, pigeons (*Columba livia*) can solve this task (Roberts & Van Veldhuizen, 1985). Red-footed tortoises (*Geochelone carbonaria*) also proved able to perform on an analog of the radial maze at above-chance levels (Mueller-Paul, Wilkinson, Hall, & Huber, 2012; Wilkinson, Chan, & Hall, 2007; Wilkinson, Coward, & Hall, 2009), although when the task became difficult, the tortoises would also resort often to the stereotypical strategy of going consistently to the next arm (Mueller-Paul et al., 2012). Rats on the radial maze do this as well when the task becomes difficult (Roberts & Dale, 1981).

A long-running and continuing program of research on hummingbirds, mostly male rufous hummingbirds (*Selasphorus rufus*), showed that they too can solve an analog of the radial-maze task. Hurly, Healy, and collaborators have been investigating spatial cognition in hummingbirds in their natural habitat. These birds arrive in late spring at the study site in the foothills of the Rocky Mountains in southern Alberta. Males stake out territories to defend, so that within one bird's territory, the team knows that it is the owner that comes to the feeders provided. Artificial flowers containing sugar water lured the birds to experimental set ups. In analogs of the radial-maze task, multiple flowers in an array proffered reward. The group as a whole succeeded in minimizing repeat visits to already-depleted flowers, in two-dimensional (Healy & Hurly, 1995) and three-dimensional arrangements (Henderson, Hurly, & Healy, 2001).

Olton, Walker, and Gage (1978) went on to show that rats' performance on the radial maze task depends on the hippocampus, leading them to suggest that the hippocampus is a memory structure—a position that was inspired by the classic studies of the amnesic patient HM (Scoville & Milner, 1957). O'Keefe and Nadel (1978) argued, however, that the hippocampus-lesioned animals might not face a memory problem so much as a representational one: Perhaps the hippocampal-lesioned rats did not have an adequate cognitive map of the maze layout with which to identify the arms they had and had not visited.

The radial maze is a spatial task that could in principle be solved in a nonspatial way, by memorizing which environmental cues are related to each arm in a list-like, nonmetric way. Thus, the question of whether hippocampal lesions impair performance because of the spatial nature of the task or because of its memory component could not be answered with this apparatus. Resolution of this issue came from Morris's (1981) development of a most unmaze-like maze, the water maze, which consisted of a hidden platform in a swimming pool with turbid water. This task cannot be solved by cue memorization because no nearby cues reliably signpost the hidden platform. The Morris pool turned out to be exquisitely hippocampal-dependent (Morris, Garrud, Rawlins, & O'Keefe, 1982), and remains the gold standard for testing hippocampal function. With regards to the radial maze, it seems likely now that the map- and memory-accounts of the lesion deficit on the maze both have some truth, but the spatial component remains very important to researchers and the radial maze is still widely used in spatial cognition research, not least because it enables simultaneous investigation of working memory (of which arms have been visited to date on a particular trial) and reference memory (which of the arms ever contain food).

Uncovering of the neurobiology of spatial representation did not end with place cells—in fact, these cells were only the beginning. Subsequent studies that aimed to find out where place cells get their information from identified neurons in nearby brain regions sensitive to directional heading, which were thus named *head direction cells* (Taube, Muller,

& Ranck, 1990), and more recently another class of neurons, discovered in the Moser lab (Fyhn, Molden, Witter, Moser, & Moser, 2004; Hafting, Fyhn, Molden, Moser, & Moser, 2005), appear to combine signals for distance and direction to form something resembling a map grid, hence their name *grid cells* (see Figure 21.1; for reviews, see Geva-Sagiv et al., 2015; Jeffery, 2010; Moser et al., 2008). Other cells in the subiculum and entorhinal cortex, called boundary or border cells, may serve a role in encoding the geometry of space (Lever, Burton, Jeewajee, O'Keefe, & Burgess, 2009; Solstad, Boccara, Kropff, Moser, & Moser, 2008); they respond most intensely at particular, typically small distances from boundaries of space. These discoveries resulted in the award of the 2014 Nobel Prize in Physiology or Medicine to O'Keefe, Moser, and Moser, and are discussed in more detail later.

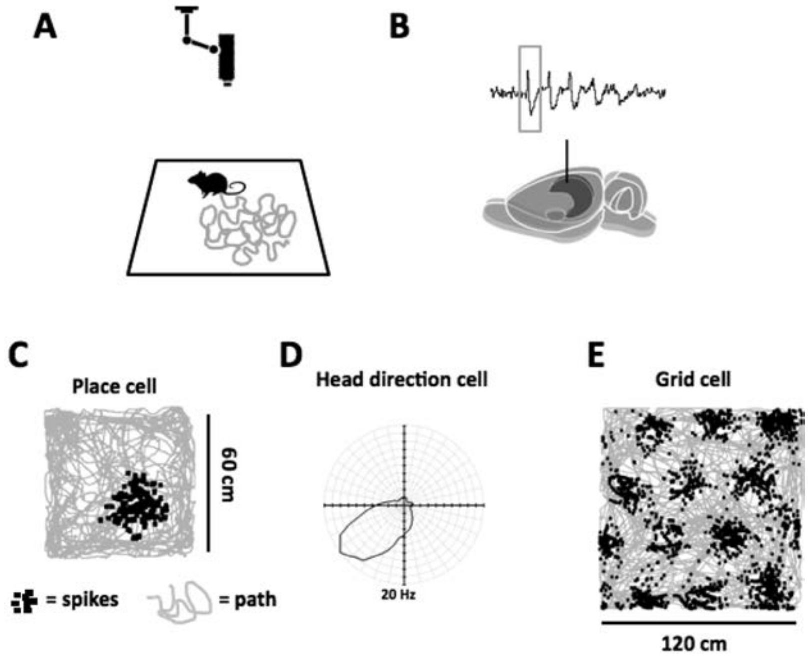

FIGURE 21.1. Recording spatially sensitive cells in the rat brain. (A) A typical experimental setup, with a rat exploring an open arena, monitored by an overhead video camera that tracks its path. (B) Schematic of the rat brain (below) with the hippocampus in dark gray. The black line represents a recording electrode located in the dorsal hippocampal area from which place cells are usually recorded. The oscilloscope spike trace of a place neuron (above) typically shows bursts of complex spikes, one of which is outlined in gray. (C) A *spike plot* showing that when spikes from a hippocampal neuron are overlaid onto the path of the rat they typically cluster in one place in the environment, hence giving rise to the name *place cells*. The spatially localized cluster of spikes is known as a *place field*. These neurons may function to signal current location. (D) Recording of a neuron from one of the head direction areas—these neurons fire everywhere in the environment (not shown) but their firing rate increases markedly when the rat faces in a particular direction (as shown by the polar plot of rate against direction). Head direction cells are thought to provide a compass signal for spatial computations. (E) Spike plot of a grid cell, depicted as in (C); these neurons show place fields, similar to place cells, but they are multiple, and recur at evenly spaced intervals across the surface of the arena, making a grid-like pattern of vertices of triangles; hence giving rise to the name *grid cells*. These neurons may serve to mark out distances, for use in spatial computation.

Attempts have been made to determine whether the spatially encoding neurons are also present in other taxa in the animal kingdom. Studies in monkeys revealed the existence of place-like activity that depends on where the animal is looking rather than (or as well as) where it currently is (Ono, Nakamura, Fukuda, & Tamura, 1991; Rolls & O'Mara, 1995). The *spatial view* cells have also been reported in humans, primarily in parahippocampal areas, along with place cells, mostly in the hippocampus (Ekstrom et al., 2003). Studies of bats have also revealed that place, head direction, border, and grid cells (big brown bats [*Eptesicus fuscus*]; Ulanovsky & Moss, 2007; Egyptian fruit bats [*Rousettus aegyptiacus*]; Finkelstein et al., 2014; Yartsev & Ulanovsky, 2013; Yartsev, Witter, & Ulanovsky, 2011; see Geva-Sagiv et al., 2015) are sensitive to three dimensions of space. In birds, observational and lesion studies of the avian hippocampus have suggested functional parallels to rodent hippocampus (see Volume 1, Chapter 25, this handbook). The avian homologue of the mammalian hippocampus has been shown to be important for spatial behavior, including food-caching (see Volume 1, Chapters 12 and 24, this handbook); in the food-caching species, its size increases during caching season (see Sherry, 2006). Recordings from hippocampus have been conducted on moving pigeons in the lab (Hough & Bingman, 2004, 2008; Kahn, Siegel, Jechura, & Bingman, 2008; Siegel, Nitz, & Bingman, 2005, 2006). Cells with spatially nonrandom firing have been found, called *location*, *path*, and *pattern* cells. Location cells differ from rodent place cells in having lower temporal reliability and stability, and they are usually found to be associated with goals such as places with food on a radial maze (Hough & Bingman, 2004; Siegel et al., 2005, 2006). Path cells fire the most when the bird is on a path connecting goals (Hough & Bingman, 2008; Siegel et al., 2006). The pattern cells were found in the open arena with unstable goals (Kahn et al., 2008) and fire at multiple places, albeit not stably. Their patterns superficially resemble those of rodent grid cells, but differ in showing very low rates of firing, low reliability, and the places where they fire do not form a regular grid.

Beyond the lab, many animals, including the bats, rats, and pigeons previously reviewed, travel great distances (see Chapter 22, this volume). Very little is currently known of the neurobiology underlying such ethologically natural journeys, which, aside from having much longer distances, also offer a potentially richer set of cues than a lab (Geva-Sagiv et al., 2015). The field awaits the technology of recording from the brain without using connecting wires.

These comparative studies have suggested that although there is some heterogeneity in hippocampal encoding, there is also an underlying commonality, and space seems to be a unifying theme. However, the variety of responses that are found within and between species add to a growing consensus that the hippocampus is about more than just space: it is also, almost certainly, about memory. On reflection this makes sense, because the most important thing about a place is the things that are found there and the events that happen there, including the time of such events, as well as planning where one should go from a current place (see Chapter 11, this volume). It thus seems that spatial encoding may be the foundation for a broader class of information processing (Gallistel, 1990). In what follows, we review the subcomponents of spatial cognition that have been uncovered over the last century.

HOMING AND PATH INTEGRATION

One of the most important and ubiquitous spatial behaviors for an animal to perform adeptly is returning to a home base, such as one's nest. This process of homing is widespread in the animal kingdom, particularly among central-place foragers that organize their excursions around a home base. An interesting feature of homing is that animals usually take a direct route, regardless of how tortuous the outbound path was. It is also actioned very quickly, particularly when danger threatens, and thus does not seem to require much thought. The directness of the return path together with the rapidity with which it is actioned led early investigators to propose that homing is supported by a process named *path integration*; so-called because it is supposed that during the outward journey the animal is constantly integrating each successive segment of its journey to update either a self-location with respect to home, or equivalently a homing vector (the inverse of home to self-location vector).

The earliest studies of path integration began with those of the desert ant (genus *Cataglyphis*) by Wehner (2003), who showed that these animals, after foraging across the desert sands, are able to execute homing vectors independently of local environment cues (see Chapter 22, this volume). They showed this by picking up the ant at the point where it was about to return home, and displacing it to a distant test site; the ants walked the direction and distance that would have returned them to the nest if they had not been displaced. The ants clearly had encoded direction and distance back to the nest.

Although insects use a suite of directional cues for path integration, the most important cue is the pattern of polarized light in the sky (Wehner & Müller, 2006). A specialized area of the compound eye at the top, called the dorsal rim area, contains the sensors for polarized light (Wehner, 1994). Neurobiological work has so far identified interneurons in the optic lobe in crickets (*Gryllus campestris*; Labhart, 1988, 1996) and neurons in the central complex in locusts (*Schistocerca gregaria*) sensitive to the direction of polarized light (Bech, Homberg, & Pfeiffer, 2014). The interneurons are excited by one direction of polarized light and inhibited by an orthogonal direction, this opponent-process property serving to give constancy to the system in the face of changing light levels (Labhart, 1996).

Path integration studies in mammals (see Etienne & Jeffery, 2004) began in earnest with the observation by Beritoff and Liberson (1965) that dogs (*Canis familiaris*) could return directly from an L-shaped outward journey, and were then formalized by the seminal studies by Mittelstaedt and Mittelstaedt (1980), who showed that gerbils (*Meriones unguiculatus*) could use inertial and other cues to maintain an internal representation of heading. They coined the term *idiothetic* to refer to such cues which include, as well as signals from the vestibular system, other cues to self-motion such as optic flow, proprioception, and motor commands. Following from these studies, Etienne's lab (Etienne, Boulens, Maurer, Rowe, & Siegrist, 2000; Etienne, Maurer, Boulens, Levy, & Rowe, 2004) explored, in golden hamsters (*Mesocricetus auratus*), how idiothetic cues interact with static positional information (mainly visual) from landmarks. Although idiothetic cues alone accumulate errors, these can be corrected by intermittent glimpses of landmarks. These studies revealed an important interaction between different sensory modalities and different classes of spatial information. The resetting of path integration by landmarks suggests that the landmark-based navigational system may well capitalize on the coordinate system provided by path integration (Etienne & Jeffery, 2004), giving the former one map-like characteristic. Such an interaction also provides a useful model system for studies of sensory integration in addition to revealing much about spatial cognition per se.

The terms path integration and homing are often used interchangeably; path integration and idiothetic processing are also often used as if they are synonymous. It is important to maintain awareness of the distinctions; homing may involve path integration but it may not; path integration may be used in homing but it may be used for other things (e.g., positional updating, as mentioned); and finally, path integration does require idiothetic cues but these are used for a computational purpose, in that idiothetic cues are necessary for path integration but do not equate to it. These distinctions may seem trivial, but become important when considering the underlying neurobiology.

Neurobiological studies of path integration in lab rats began in the 1990s, following the discovery of place cells, which encode current location. Studies by McNaughton and colleagues showed that place cells could update their locational signals on the basis of processing self-motion information alone (Gothard, Skaggs, Moore, & McNaughton, 1996), which suggested processing of the linear component of movement by the hippocampal place system. At around the same time, head direction cells were discovered (Taube et al., 1990), and early work showed that here, too, the cells seemed able to update their firing directions in the absence of landmarks (Yoder et al., 2011), suggesting, again, a processing of self-motion (idiothetic cues), this time in the angular domain. Skaggs, Knierim, Kudrimoti, and McNaughton (1995) and Zhang (1996) proposed an explanation for the idiothetic updating of head direction cells, on the basis of a convergence of self-motion cues and landmark cues on a ring attractor network, which is one in which the activity of each cell is informed not only by its own sensory inputs, but also by the activity of its near neighbors in head-direction space (that is, the cells configured to encode nearby directions).

A potential neural explanation for the linear component of path integration had to wait another decade: In the mid-2000s, researchers in the Moser lab discovered cells in entorhinal cortex (the main cortical projection to the hippocampus) which seem to encode distance as a function of direction (Fyhn et al., 2004; Hafting et al., 2005). These grid cells produce spatially focal patches of activity, like place cells do, but the patches are multiple and they are evenly-spaced across the environment, producing a grid-like array of firing fields that appears to integrate distance and direction. Thus, grid cells are a potential source of the path integration signal that helps place cells know where to fire (McNaughton, Battaglia, Jensen, Moser, & Moser, 2006). Currently, work is underway to determine whether animals are, as would be predicted, impaired in path integration if they lack grid cells.

An important outstanding question concerning place and grid cells is the extent to which they depend on environmental features such as landmarks, boundaries and other features; this question also pertains to spatial cognition at the level of the whole animal. We therefore turn next to the question of environmental feature-use, beginning with a simple form of feature-processing known as view-matching, and afterwards proceeding to object-processing and landmark use.

VIEW-BASED NAVIGATION

Navigation on the basis of views of the surrounding scene is well known in insects (see Chapter 22, this volume). In mammals, cells responding to views of scenes have been found in the parahippocamal area in humans (Ekstrom et al., 2003). But the cognitive and neurobiological bases concerning how scenes serve navigation remain currently as more theoretical constructions than empirical demonstration. In humans, Epstein (2008) suggested that the parahippocampal area serves to recognize scenes and set them in the broader context of one's spatial surroundings, whereas the retrosplenial complex uses such information to plan travel. In a neurocomputational model on spatial cognition in rats, Sheynikhovich, Chavarriaga, Strösslin, Arleo, and Gerstner (2009) took views of scenes to serve two fundamental roles in navigation, subserving taxon and locale systems first suggested by O'Keefe and Nadel (1978). Views may be directly linked to route instructions (e.g., head toward this part of the scene) in the taxon system, or they may serve to build up cognitive maps via the place cells, head-direction cells, and grid cells already reviewed.

OBJECTS AND LANDMARKS

Many animals use a set of objects (see Cheng & Spetch, 1998), or an entire scene as a whole (Sutton, 2009) to find a place (see Chapter 22, this volume). Use of a set of objects is often forced on the animals because the experimental set is shifted from trial to trial, with the desired target in a constant location with respect to the array. In some of these situations, it would be useful to recognize and identify objects and identify their locations.

A particularly useful laboratory task for studying object recognition has been the one-trial spontaneous recognition task (Ennaceur & Delacour, 1988), more recently recruited to test spatial recognition as well (Eacott & Norman, 2004). In a typical scenario, a rat explores two identical objects located in constant positions in a box; the rat is then removed from the box, the two objects replaced with copies, one of which is changed somehow (a different object, an identical object in a different place, etc.), and the rat then placed in the box again. If the rat recognizes that an object has changed it will explore it more; differential exploration duration of a spatially displaced object is thus a useful index of spatial processing. Experiments using such tasks have shown that spatial memory and context memory depend on the hippocampus, whereas object recognition depends on the perirhinal cortex (Eacott & Gaffan, 2005), and object-in-place memory depends on the perirhinal-hippocampal-prefrontal system (Barker & Warburton, 2015). Recent single-neuron studies have suggested that lateral entorhinal cortex may have a role in object/place memory, as neurons here respond to objects, with responses persisting even after the objects have been removed again (Deshmukh & Knierim, 2011; Tsao, Moser, & Moser, 2013).

Having recognized and localized an object, the next task is to use it for navigation. An object may act as a beacon that marks a goal; in beaconing, the animal needs to center the object in its field of view and head toward it. Beaconing requires object identification, and some animals may not have invested in the kind of visual system required to do that; for example, ants may use only the broad panorama without individuating objects (Wystrach, Beugnon, & Cheng, 2011). Another use of objects or the panorama is to define regions of space that are of importance to the animal. Studies of landmark use have taken place across many taxa, and landmark use appears ubiquitous in the animal kingdom.

Turtles (*Pseudemys scripta*) can learn to head to a place in a maze or open arena for a reward, on the basis of intra-arena cues plus landmarks all around the room (López et al., 2000, 2001). They can master the task when starting from different locations. Surrounding the arena or maze with curtains led to a deterioration in performance, as did re-arranging the cues around the room. The turtles could also learn to head to one particular beacon for a reward (a cue task), even when the cue shifted locations from trial to trial. Neurobiological lesions suggest that the medial cortex is essential for the place task, but not for the cue task (López, Gómez, Vargas, & Salas, 2003; López, Vargas, Gomez, & Salas, 2003; Rodríguez et al., 2002).

When it comes to lizards, evidence about landmark use is sketchy. However, two sets of studies from different labs provide clear recent evidence for landmark-based localization in side-blotched lizards (*Uta stansburiana*) in finding an escape hole (LaDage, Roth, Cerjanic, Sinervo, & Pravosudov, 2012) and in some Eastern water skinks of Australia (*Eulamprus quoyii*; 32% of those tested) in finding an accessible refuge in seminatural enclosures (Noble, Carazo, & Whiting, 2012).

In fish, Rodríguez et al. (2002) and López, Broglio, Rodríguez, Thinus-Blanc, and Salas (1999) found that goldfish (*Carassius auratus*) could learn analogous cue and place tasks to those given to turtles. Ablation of the lateral pallium of the telencephalon led to a deterioration in the place task, but not the cue task. The researchers suggested that the medial cortex of turtles and lateral pallium of teleost fishes serve homologous roles to the mammalian hippocampus (Rodríguez et al., 2002; Salas, Broglio, & Rodríguez, 2003).

Fish can move freely in three dimensions, which offers possibilities to explore spatial encoding in three dimensions (Jeffery, Jovalekic, Verriotis, & Hayman, 2013). Holbrook and de Perera (2011b) have shown that in a Y-maze having horizontal and vertical components, banded tetras (*Astyanax fasciatus*) processed these components separately, and prioritized the horizontal. The mechanisms of encoding in these two dimensions remain unknown, but the fish have swim bladders that are sensitive to changes in depth, and may even be able to provide information about absolute depth (Holbrook & de Perera, 2011a).

Birds move in three dimensions as well, but most studies have presented horizontal (in an arena) or vertical (on a monitor) displays. One exception is a study with rufous hummingbirds. Flores-Abreu, Hurly, and Healy (2013) presented a linear array to hummingbirds, with the array horizontal, vertical, or at a diagonal, varying vertical and horizontal locations across the array. The birds learned the horizontal array better than the vertical array. In case of a conflict between the horizontal and vertical components of the target locations, the birds favored the horizontal component. On the other hand, on a complex cubic maze consisting of numerous unit cubes, the birds moved equally in all three dimensions of space (Flores-Abreu, Hurly, Ainge, & Healy, 2014). Additionally, they were more accurate in the vertical component than in the horizontal component. The same study tested rats in the complex cubic maze as well. Rats moved more vertically than horizontally in exploration, and yet they were more accurate about the horizontal component of a location.

Although these studies on landmarks show the use of landmarks in a range of animals, they do not provide any indication of how landmarks are used. Some details of landmark use have emerged from studies of rodents and birds. One influential study on gerbils trained them to search for food in a large circular arena in which landmarks indicated the goal location (Collett, Cartwright, & Smith, 1986). Transformations of either the position or size of the landmarks revealed that the animals combined direction, distance, and landmark-identity information. In short, they appeared to use vectors from landmarks, which point from a landmark to a goal position (see Chapter 22, this volume). Such vectors differ from vectors in path integration, which point from self-location to a target (e.g., home). When two goal-defining landmarks were moved apart from their usual training distance the gerbils searched in two places, indicating storage of independent vectors to the two landmarks. Later, Pearce, Roberts, and Good (1998) showed that this kind of vector memory is not dependent on the hippocampus, because rats with hippocampal lesions were able to find a hidden platform in a water maze if this had a constant vector relationship to a visible cue. Nevertheless, place cells do show a sensitivity to landmarks (Rivard, Li, Lenck-Santini, Poucet, & Muller, 2004), suggesting that landmark information feeds into more than one spatial system and presumably plays different roles in each. More neurobiological work, however, needs to be done. As the research can take place in small arenas, such tasks are amenable to neuropharmacological manipulations and neurophysiological recordings.

Two research programs on birds have revealed some details of the cognitive mechanisms underlying landmark use. A program on pigeons has been well reviewed (Cheng, Spetch, Kelly, & Bingman, 2006; Kelly & Spetch, 2012); we will give an overview here. The program on hummingbirds, already introduced, will be reviewed here.

Pigeons were tested in arenas covered with sawdust in which food was buried at a particular location with respect to the arena and experimentally provided landmarks. After learning to find the buried food, tests with the food absent would be carried out, often with the landmark arrangement changed in what is known as the transformational approach (Cheng & Spetch, 1998). The program of research suggested that the birds encoded and used vectors to individual landmarks or perhaps to elements of landmarks such as an edge, as well as perpendicular distances to surfaces (Cheng et al., 2006).

Changing the width or height of nearby landmark objects produced no systematic effects on searching (Cheng, 1988). This suggests that the birds were not matching retinal images of such objects. For example, in matching image size, widening an object encountered in training (e.g., a stripe on the nearest wall) should drive the birds to search farther from the stripe. The birds did not do that.

Two kinds of data provide evidence that pigeons encode vectors from landmarks to the target location they are searching for, that is, landmark-goal vectors. The first line of evidence is that changing the location of landmarks on a test, by shifting them parallel to a wall, led to a shift in the peak place of searching in pigeons (Cheng, 1988, 1989). The pigeons shifted their search in the direction of landmark shift, with the extent of shift varying across birds. No systematic shift perpendicular to the direction of landmark shift was observed. The second line of evidence comes from experiments training pigeons to search in the midst of an array of isolated landmarks (cylinders in an arena or graphic landmarks on a monitor). When the array was expanded, the pigeons mostly searched at the correct distance and direction (i.e., at the correct vector) from a single landmark (on a monitor; Cheng & Spetch, 1995; Spetch, Cheng, & MacDonald, 1996; Spetch, Kelly, & Lechelt, 1998; Spetch & Mondloch, 1993; in an arena; Spetch et al., 1997). Work on other species suggested that common marmosets (*Callithrix jacchus jacchus*; MacDonald, Spetch, Kelly, & Cheng, 2004), capuchins (*Cebus paella*; Poti, Bartolommei, & Saporiti, 2005), orangutans (*Pongo abelii*; Marsh, Spetch, & MacDonald, 2011), as well as some young children (*Homo sapiens*; MacDonald et al., 2004; Marsh et al., 2011) also often show this pattern. Other studies suggested that the distance and direction components of vectors were separate, independently coded components in pigeons (Cheng, 1994), Clark's nutcrackers (*Nucifraga Columbiana*; Kelly, Kamil, & Cheng, 2010) and honeybees (Cheng, 1998).

In contrast, adult humans, tested in all these studies (MacDonald et al., 2004; Spetch et al., 1996, 1997), as well as some children (Marsh et al., 2011) tended to continue to search in the middle of the array on expansion tests. It is thought that humans are not matching a picture-like representation akin to insects in these cases, but actually applying something like a cognitive and more abstract "middle rule."

The evidence that pigeons also encoded and used the perpendicular distance to a surface comes from transformation tests in which the birds kept nearly the correct distance to the nearest wall despite other changes in landmark arrangement. Thus, if a landmark near the goal was shifted diagonally away from the nearest wall, pigeons would shift parallel to the wall in the direction of landmark shift, but shift little if any distance perpendicular to the wall in an arena (Cheng, 1990; Cheng & Sherry, 1992), and on a monitor (Spetch, Cheng, & Mondloch, 1992). The pattern of results in arenas has been replicated in a number of other bird species, the black-capped chickadee (*Poecile atricapillus*; Cheng & Sherry, 1992) and three species of corvids (Gould-Beierle & Kamil, 1998), the Clark's nutcracker, the pinyon jay (*Gymnorhinus cyanocephalus*), and the Western scrub jay (*Apheloma coerulescens*). Use of perpendicular distances is also consistent with findings that changing landmark height and widths typically has no systematic effect on search (Cheng, 1988). This component of perpendicular distance resembles a classic vector in having a distance and a direction (perpendicular to a surface), but differs in lacking a defined starting point.

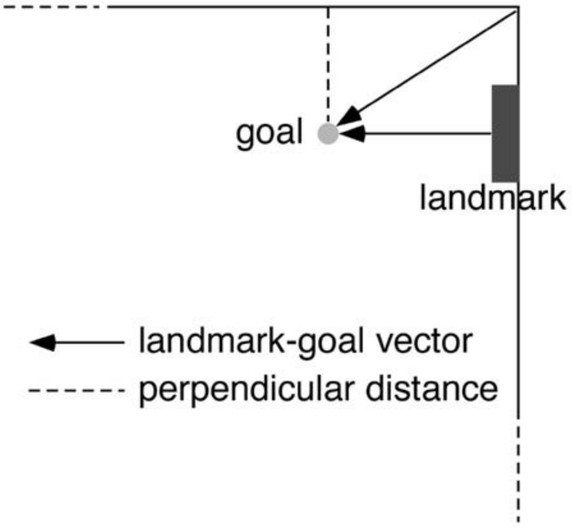

FIGURE 21.2. A schematic illustration of small-scale spatial representation in pigeons, a view advanced by Cheng et al. (2006). The bird is taken to encode vectors from particular points in space (landmark-goal vectors) and perpendicular distances from extended surfaces (vertical dashed line). The drawing depicts one corner of a rectangular arena.

Together, these two components of vectors from landmarks and perpendicular distances (see Figure 21.2) account for the behavioral data well. With some key behavioral mechanisms unraveled, it would be of interest to extend such behavioral research to other species, and to use such tasks to probe the neurobiology of landmark use in birds. Such expansions would enrich our knowledge of cognitive and neurobiological mechanisms of landmark use.

Like rats (e.g., Cheng, 1986), and the pigeons and other birds, nonhuman primates, and humans just described, hummingbirds can also learn to return to a rewarding location in a win–stay task (Hurly, 1996; Hurly & Healy, 1996). Birds that were shown that only one flower of an array contained food would return later to that flower to obtain more of the not-yet-depleted bounty. If the target flower was switched with another flower with different characteristics while the bird was away, location of flower and flower characteristics were put in conflict. Male rufous hummingbirds (Hurly & Healy, 1996), as well as female hummingbirds of three species (Tello-Ramos, Hurly, & Healy, 2014) favored the location rather than the flower characteristics on such tests. They can, however, also remember and use flower characteristics (Hurly & Healy, 1996), and flower characteristics facilitate learning in some circumstances (Hurly & Healy, 2002). More complex rules about the target flower can also be learned (Jelbert, Hurly, Marshall, & Healy, 2014). The hummingbirds could pick the correct flower even when which flower was correct depended on the nature of the background on which they appeared, or the order of presentation.

In comparison, results are variable for primates in such object-switch paradigms, across species and studies. An early study on two macaques (*Macacus cynomologus*) and two chimpanzees (*Pan troglodytes*; Tinklepaugh, 1932) found that spatial location dominated over objects in conflict tests. This pattern was also found across extant nonhuman great apes, orangutans, gorillas (*Gorilla gorilla*), bonobos (*Pan paniscus*), and chimpanzees in one study (Haun, Call, Janzen, & Levinson, 2006), but another study (Kanngiesser & Call, 2010) found a mix of using spatial and featural (object-based) strategies.

Other studies effected transformations of the flower array used in training. In one experiment (Healy & Hurly, 1998), hummingbirds were trained to feed from the middle flower in an array of five flowers. Interflower distance in training was varied across conditions. On the key (unrewarded) transformational test, the array was shifted by one interflower unit (the distance between flowers). This displacement pitted the absolute location of the target flower on Earth against the relative location with respect to the shifted array. Findings showed that at smaller interflower distances (up to 40 cm), the relative location dominated. At larger interflower distances (80 cm–320 cm), however, the absolute location was preferred. A later study also found that learning was faster if the rewarded flowers in an array were clumped rather than scattered (Hurly & Healy, 2002). The experimental manipulations used by Healy and Hurly (1998) echoed earlier work done on black-capped chickadees and dark-eyed juncos (*Junco hyemalis*; Brodbeck, 1994; see also Brodbeck & Shettleworth, 1995). These studies found that whereas the food storing chickadees favored spatial location over feeder characteristics on conflict tests, the nonstoring juncos showed no such bias.

Henderson, Hurly, and Healy (2006) trained the hummingbirds to choose the shorter or taller of two feeders/flowers. The flowers thus appeared at different heights. When a transfer test was given with two new heights, one of which matched one of the training heights, the birds displayed transposition (see Chapter 15, this volume). For example, if the training target flower was the taller flower, both flowers would be taller on a test, with the shorter flower now matching the training target height in absolute terms. The birds would continue to choose the taller flower.

Another study came closest to the hidden-goals approach used in pigeon research. A single flower was presented in the landmark-rich natural habitat of the rufous hummingbirds (Hurly, Franz, & Healy, 2010). After sufficient training, the flower was either displaced to a nearby location, 1.3 m to 1.7 m away, or removed, making it a hidden-goal test. Birds flew close to the training location of the flower in all tests. They flew closer to the fictive goal when the training flower was smaller. They did not fly directly to a displaced beacon. Any moves to a displaced flower followed the search at the original goal location. The results paralleled those found earlier by Devenport and Devenport (1994) in sciurids, least chipmunks (*Tamius minimus*), and golden-mantled ground squirrels (*Spermophilus lateralis*), when their usual feeder (beacon) was displaced. It seems common for a range of animals to rely on the panoramic natural scene for zeroing in on a spot rather than individual local beacons. This theme is echoed in insect navigation as well (Wystrach, Beugnon, & Cheng, 2011; see also Chapter 22, this volume).

Finally, one recent study probed what-where-when memory in hummingbirds, components of episodic-like memory (Marshall, Hurly, Sturgeon, Shuker, & Healy, 2013; see also Chapter 11, this volume). The birds succeeded at the task, but had most trouble with the “when” component. Other studies in this program, however, show that the hummingbirds learn interval timing in these natural conditions readily (Henderson, Hurly, Bateson, & Healy, 2006; Marshall, Hurly, & Healy, 2012; see also Chapter 23, this volume).

BOUNDARIES AND GEOMETRY

Another line of enquiry that has been influential in shaping spatial cognition research in a variety of species concerns geometry. Cheng (1986) found that rats prefer to use the shape of an enclosure as a guide to finding food, even when there are landmarks present that are more informative. Rats were trained to find food in a rectangular enclosure that had distinctive panels at the four corners, and in one case one distinctly colored wall (white instead of black). Despite these disambiguating features, the rats searched in a working-memory experiment, in which the goal location varied from trial to trial, equally often at the correct location and at the geometrically equivalent one, diametrically opposite at 180° rotation about the center of the arena. This finding led Cheng to propose that geometry is encoded in a cognitive module (Fodor, 1983), one that dominates over featural processing and forms the frame for coding where features are in the world (see Volume 1, Chapter 20, this handbook).

A substantial literature has now built up on the topic of geometry and features in a variety of species (Cheng & Newcombe, 2005). Recently tested species shown to use geometric and featural cues include toads (*Rhinella arenarum*; Sotelo, Bingman, & Muzio, 2015), ants (*Gigantiops destructor*; Wystrach & Beugnon, 2009; Wystrach, Cheng, Sosa, & Beugnon, 2011), and bumblebees (*Bombus terrestris*; Sovrano, Potrich, & Vallortigara, 2013; Sovrano, Rigosi, & Vallortigara, 2012). A fair summary is that in standard rectangular or even other rectilinear arenas, animals can learn geometric and featural cues. The story is more complex when it comes to cue conflicts and interactions, and isolated landmarks. Finally, although most studies have been conducted on level surfaces, slope information has proved to be a highly salient cue for pigeons. We review only some recent findings, as this topic has been thoroughly reveiwed (see Cheng, Huttenlocher, & Newcombe, 2013; Cheng & Newcombe, 2005; Kelly & Spetch, 2012; Vallortigara, 2009).

The geometric arrangement of a set of isolated landmarks often poses problems for animals. Chicks (*Gallus gallus domesticus*; Pecchia & Vallortigara, 2010a, 2010b), Clark's nutcracker (Kelly, 2010), and even young children (Gouteux & Spelke, 2001) have failed to use the geometry of a rectangular array of identical landmarks to locate a target corner defined by the arrangement of landmarks. With distinctive features, however, all these species succeeded. One intriguing finding from Pecchia and Vallortigara (2010b) is that when chicks always accessed the goal (one of the cylindrical landmarks) from the same direction (because of a restricted opening to a feeder), they succeeded in the task. Pecchia and Vallortigara suggested view-based matching as an explanation. Accessing the food always from the same direction meant that the view of the array was similar from trial to trial, facilitating view learning. Accessing the feeder from multiple directions, on the other hand, meant that the view at the goal varied too much from trial to trial for the chicks to learn.

The geometric cues that animals encode may well be less than the full suite of distances and directions of surfaces and objects as described by classic Euclidean geometry, but rather summary characteristics such as major axes. Cheng and Gallistel (2005) identified principal axes and medial axes as possible candidates. Principal axes comprise major axes of the entire space, whereas medial axes apply to sections of space, such as one arm of an L-shaped arena. Pearce's lab (McGregor, Jones, Good, & Pearce, 2006; Pearce, Good, Jones, & McGregor, 2004) identified local geometric cues as important for rats. Kelly, Chiandetti, and Vallortigara (2011) found local geometry and medial axes to play a role for pigeons. Sturz, Gurley, and Bodily (2012) found evidence consistent with the use of major axes of space in humans. The geometry that animals encode is decidedly metric, but may well consist of a panoply of summary measures and local measures rather than overall shape.

A key additional factor of importance is slope, examined in pigeons (Nardi & Bingman, 2009a, 2009b; Nardi, Mauch, Klimas, & Bingman, 2012; Nardi, Nitsch, & Bingman, 2010). Birds trained in a sloping terrain used slope information for locating a goal. In case the dictates of slope information conflicted with the dictates of geometric cues, they matched the dictates of slope rather than those of geometry. This work points out the importance of considering three spatial dimensions in research on spatial cognition, as much of the natural landscape contains slopes of various degrees of steepness and extents.

Studies of the responses of the spatially encoding neurons, the place, head direction, grid and border cells, can be informative in untangling some of these issues. For example, slope has been found to be an orienting cue for place cells (Jeffery, Anand, & Anderson, 2006), possibly because of an effect on the head direction system; this orienting effect may underlie the ability of animals and humans to use slope to aid navigation.

Studies of the spatially encoding neurons have also revealed the critical role of local boundaries in shaping the representation of local space. This was first explored systematically by O'Keefe and Burgess (1996) who showed that deforming a rectangular environment by stretching some or all of its walls had a deforming effect on place cell firing locations.

This suggested some kind of tension between the geometric cues provided by the walls and some other cues to distance, possibly idiothetic cues from path integration. O'Keefe and Burgess suggested that each place cell was configured to fire at a particular distance and direction from a given wall, with each cell having its own unique vector. By this view, deforming the environment would distort the cell's computation of its distance from the wall, by placing path integration cues in conflict with landmarks, with the cell adopting (in most cases) a compromise position for its firing field. The role of path integration in this process received later support from a related observation that grid cells deform their grids in a similar manner following wall-stretching, but only in a familiar environment (Barry, Hayman, Burgess, & Jeffery, 2007), suggesting that the system first learned the location of the walls (perhaps using grid cell grids as a metric reference, though this is far from proven) and then used the walls as one of the (now-distorted) inputs to the odometric system. Two recent studies suggest that the influence of boundaries on grid cells seems to be ongoing, as grid cells initially align their fields to a salient wall, but over time develop a slight angle as if the grid is being distorted (Krupic, Bauza, Burton, Barry, & O'Keefe, 2015; Stensola, Stensola, Moser, & Moser, 2015), raising the possibility that this might distort the animals' perception of space too. It is not yet known what attaches grids to the environment boundaries in this way; a candidate mechanism is the border cells, whose firing lies along environment borders (Solstad et al., 2008). However, changes in the nonspatial characteristics of the environment cause grids to shift (Marozzi, Ginzberg, Alenda, & Jeffery, 2015), whereas border cells do not shift, so the interaction may involve some other cell type.

Place cells also show sensitivity to changes in environment shape, such as between square and circle (Lever, Wills, Cacucci, Burgess, & O'Keefe, 2002) which may indicate detection of new features such as corners. Head direction cells, however, show only a very weak sensitivity to geometry (Knight, Hayman, Ginzberg, & Jeffery, 2011), using it only when the animal is disoriented and prone to making systematic misalignments with respect to the world (Golob, Stackman, Wong, & Taube, 2001). Interestingly, the misalignments of head direction cells by multiples of 90° in Golob et al.'s (2001) rats were not correlated with the rats' making errors in searching for a target corner.

Putting all this together, a tentative conclusion is that geometry used for navigation is decidedly metric in nature, as first proposed by Cheng and Gallistel (1984), but the characteristics used may be mostly a suite of local features (boundaries and corners) and summary statistics. It has yet to be shown unequivocally that animals encode the global spatial shape, or integrate spatial features on such a shape in a more holistic manner (see Minini & Jeffery, 2006, for a visual analogue of the geometry problem in a two-dimensional domain).

COGNITIVE MAP

One of the most contentious ideas in spatial cognition has been that one that Tolman advanced in the 1940s, which is that incoming sensory information from the spatial surround is "worked over and elaborated . . . into a tentative, cognitive-like map of the environment" (Tolman, 1948, p. 192). The difficulty that behaviorists had with this view is the map-like part of this proposal—that the associations between stimuli have, incorporated into them, some kind of additional, relational information.

In testing this idea behaviorally, it has been generally accepted that animals need to be able to demonstrate certain capacities for navigation that could not be achieved by simple stimulus–stimulus association (see Chapter 22, this volume). Tolman's (1948) own sunburst maze experiment, described previously, was the first example of such behavior, together with explicit demonstrations of short-cutting and detouring, both of which arguably require a map-like representation. Morris's (1981) water maze experiments showed clearly that rats are able to process spatial stimuli in a relational way. This is because navigation to the unmarked goal can only take place by referring to constellations of cues and the spatial relations between them. One can argue, however, that relational encoding in and of itself does not prove existence of a "map" as such. Indeed, much discussion focuses on the semantic issue about what characteristics a representation needs or does not need to be called a map (for some discussion, see Bennett, 1996; Menzel et al., 2005; Menzel & Greggers, 2015; see also Chapter 22, this volume). We simply note here that the existence of place, grid, border, and head direction cells has provided unequivocal evidence for encoding of spatial relationships, over and above nonmetric stimulus–stimulus associations, in the brains of rats and a number of other animals as well. A recent paper has reported neurons in the central complex of Drosophila flies (*Drosophila melanogaster*) with properties of head direction cells in mammals (Seelig & Jayaraman, 2015). The question now is whether these representations incorporate more elaborate, nonspatial details pertaining to places.

CONCLUSION

This chapter has attempted to summarize some of the key findings from comparative studies of spatial cognition across the past century. This is an enormous literature for which it is impossible to do justice in the limited space here, but we have attempted to synthesize some of the salient findings, and point out similarities and differences across species. Much about the evolution and nature of spatial ability requires further work, especially on a scale of travel that is ecologically realistic for animals outside the lab. Future work, we hope, will feature more close collaborations between ethologists, psychologists, and neurobiologists, to map the diverse spatial abilities seen in the wild to the underlying neural circuitry. Interdisciplinary synergy is needed to produce a deeper understanding of spatial cognition that stretches from genes through behavior to evolutionary perspectives and that ranges in scale from tethered animals in a lab to journeys across the globe.

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CHAPTER 22

HOMING AND NAVIGATION

David J. Pritchard and Susan D. Healy

Navigation can be defined in a number of ways. Most commonly, navigation is defined in terms of the movements of vertebrates, usually birds, over large distances (Able, 2001; Gallistel, 1990; R. Wiltschko & Wiltschko, 2003). Indeed, the word *navigation* conjures up images of epic journeys across vast, featureless expanses, transcontinental migrations, the crossing of great deserts, and circumnavigation of the globe. But navigation is also important in the more mundane, day-to-day life of many animal species. In this chapter we broadly define navigation as an animal's ability to make its way to a desired location and *homing* as the specific use of navigation to return home. Using these definitions, we can see examples of successful homing and navigation everywhere: Any animal returning to a location has to navigate in some way or another. For example, many bird species migrate enormous distances to breeding or to overwintering grounds, but microscopic zooplankton also migrate up and down the water column to feed while avoiding predation. Some species, such as chimpanzees, remember the locations of food and shelter within a territory that may exceed tens of square kilometers (Normand & Boesch, 2009). The territories of other animals, such as certain male fiddler crabs, may be much smaller (less than 1 m^2), but should a predator approach, a crab must be able to scuttle directly back to his burrow (Zeil & Hemmi, 2006). Whether traveling a meter or a thousand kilometres, successful navigation can mean the difference between life and death.

Given that the natural world is filled with animals navigating to and from important locations, it is no wonder that scientists have long been drawn to investigate the mechanisms that enable successful navigation. Despite the importance of navigation to so many species, however, most of what we know about how animals find their way around in the world is based on the intense study of only a handful of species. In this chapter, we begin with a summary of the wealth of data from two of the most intensively studied animal navigators: the homing pigeon and the desert ant. We then look beyond pigeons and ants to explore the wider world of animal navigation and the diverse sources of information that animals can use to find their way around. As cues are rarely used alone, in the final section we discuss the different ways multiple sources of information can be brought together to help animals navigate more flexibly. This leads to one of the most controversial and heavily debated topics in animal navigation: cognitive maps.

PARADIGMATIC SPECIES

Unlike many other fields within comparative psychology, humans are neither the main inspiration for research into the mechanisms underlying navigation, nor, in the absence of technological aids, are we considered particularly exceptional at finding our way around. While our propensity for learning from one another, understanding social and physical relationships, using tools, and communicating via language has stimulated the search for similar abilities in nonhuman animals (Shettleworth, 2009), the feats of navigation that have most intrigued scientists originate in the animal world.

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Homing Pigeons

Homing pigeons (*Columba livia*), released even hundreds of miles away in unfamiliar territory, reliably fly back to their home loft providing a valuable service for ancient generals and modern pigeon racers alike. This motivation to return at any time to a single, known location, from multiple distances and directions makes homing pigeons very amenable to simple but powerful experiments and therefore a very useful model for investigating avian navigation. Such investigations over the past 100 years have led to a wealth of data impossible to cover fully here (for a summary, see Wallraff, 2005), so we will cover the key components.

Maps in pigeon navigation. For pigeons, homing from an unfamiliar area appears to involve a two-step process (R. Wiltschko & Wiltschko, 2009; see Figure 22.1). The first step is the *map stage*, in which the bird determines its position relative to home (e.g., southwest of the loft). Pigeons are thought to do this by remembering the intensities of two or more different environmental gradients (e.g., odors from different factories; see Chapter 4, this volume) as perceived at their home loft as a set of home coordinates (Benhamou, 2003). When released at an unknown location, the pigeon establishes the coordinates of this new location by sampling the local intensities of the same cues, and, by comparing them to the home coordinates, can determine its position relative to home. Most research on the pigeon's map has involved identification of the cues that provide these coordinates and although there have been decades of disagreement over the relative importance of the cues used, it is clear that pigeons are very flexible in the cues they use to gain positional information. Those cues range from infrasound (Hagstrum, 2000) to gravity (Blaser et al., 2014) and from characteristics of the earth's magnetic field (R. Wiltschko & Wiltschko, 2003) to atmospheric odors (Wallraff, 2004). Such redundancy should not be surprising. High levels of redundancy may assist in robust navigation by making it more likely that the pigeon has experience of the cue gradients available at the release site.

Compasses in pigeon navigation. Positional information is not, however, sufficient for pigeons to home successfully and so, in the second step of the navigation process, known as the *compass stage*, birds determine the trajectory necessary to return home (R. Wiltschko & Wiltschko, 2009). Pigeons possess two different compasses, a sun compass and a magnetic compass, neither of which require familiarity with the animal's current position as they are based on the earth's magnetic field or on extraterrestrial cues (R. Wiltschko & Wiltschko, 2003).

The sun always rises in the east, and always sets in the west, a reliability that enables animals, including pigeons, to use the position of the sun in the sky as a compass (Guilford & Taylor, 2014). As the sun moves across the sky, however, animals must compensate for the time of day in order to use the sun compass for homing (W. Wiltschko & Wiltschko, 1998; see Figure 22.2).

Sun compasses can also be used to show the separate use of a map and compass, via an experimental manipulation known as *clock shifting*. Researchers

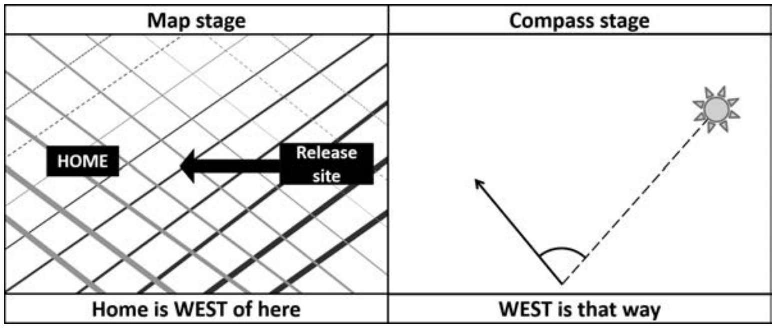

FIGURE 22.1. The map and compass model of navigation from an unfamiliar area.

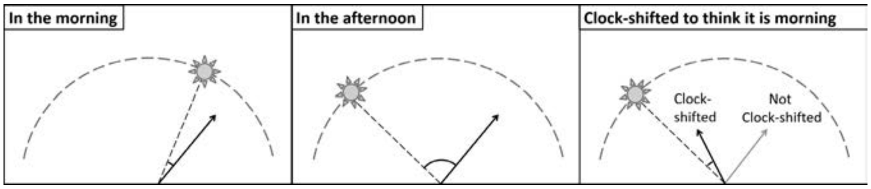

FIGURE 22.2. **Time compensation and clock shifting of the sun compass.**

influence the sun compass's time-compensation mechanism by changing when lights are turned on/off (or opening/closing shutters at the loft) altering when the pigeons perceive the day to begin and end. Changing when the day begins shifts the bird's internal clock, resulting in the birds compensating for the wrong time of day and shifting the direction that the birds fly after release away from the true direction of home (Figure 22.2). Clock shifting works because it interferes only at the compass stage. The pigeon still knows that it is southwest of the loft and that it must head northeast to get home but due to the clock-shift manipulation, its estimate of northeast is inaccurate.

As well as using a sun compass, pigeons can use the earth's magnetic field to orient (R. Wiltschko & Wiltschko, 2003, 2009). On cloudy days, when the sun compass is not available, pigeons released with coils around their heads to reverse the perceived magnetic field fly in the opposite direction to that of home. In addition to being a back-up system in the absence of the sun compass, the magnetic compass is thought to be involved in the development of the sun compass in young pigeons, providing a directional reference that the birds can associate with the position of the sun in the sky. As described in later sections, the mechanisms underlying magnetic compasses and which aspects of the magnetic field are used have been studied intensively in pigeons and other species.

Landmarks in pigeon navigation. Although pigeons use a map and compass system to return home from unfamiliar areas, when navigating over familiar terrain, they can use the features of the landscape (landmarks; see Chapter 21, this volume) that they have experienced on previous homing flights (Holland, 2003). Individual birds will pay attention to different landmarks, even when released from the same site, which can lead to the development of individually stereotyped routes (Guilford & Biro, 2014). Debate still rages, however, as to how pigeons use landmarks in the familiar area: whether they form a map similar to that used for longer distances or whether they rely on simpler mechanisms of landmark use (Guilford & Biro, 2014; R. Wiltschko & Wiltschko, 2009).

Desert Ants

The second group of paradigmatic navigators have also been studied primarily in their natural environment, due to the ease with which they can be experimentally manipulated *in situ*. Like the homing pigeon, desert ants of the genera *Cataglyphis* and *Melophorus* are central place foragers, primarily navigating to and from nests in the deserts of North Africa and Australia. Unlike homing pigeons, the distances that the ants cover are, at least to a human observer, fairly short, which allows a researcher to follow the movements of an individual with ease. Also, as desert ants are small and walk rather than fly, researchers can manipulate the path of an individual ant en route or by picking the ant up and moving her to a new location.

Path integration in ant navigation. Desert ants use a toolkit of several mechanisms for navigating to and from their nest (M. Collett, Chittka, & Collett, 2013). The first is *path integration* (see Chapter 21, this volume). By keeping track of the number of steps they have taken (Wittlinger, Wehner, & Wolf, 2006), as well as the direction they have traveled using a sun compass similar to that used by pigeons (Wystrach, Schwarz, Schultheiss, Baniel, & Cheng, 2014), ants can keep a running tally of their position relative to the nest (Müller & Wehner, 1988, see Figure 22.3A). This home-vector tethers the ant to the nest, allowing

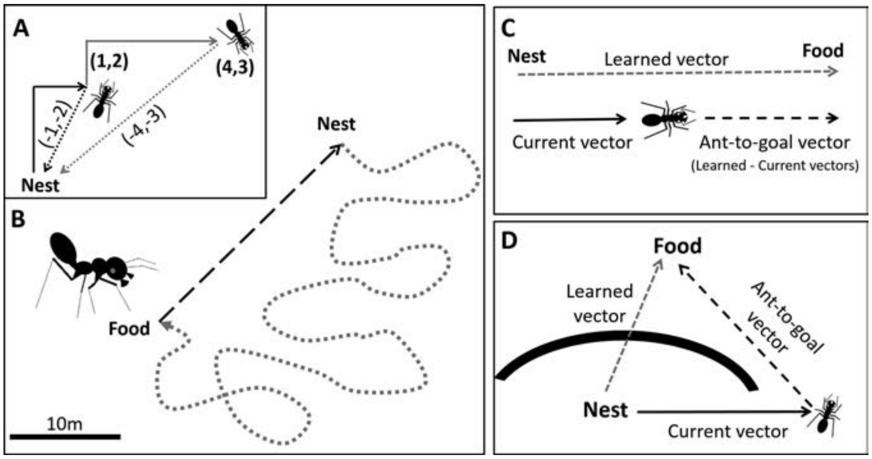

FIGURE 22.3. **(A) Path integration involves combining the distances and directions traveled to compute a constant vector back to home. (B) Desert ants can use path integration to travel straight home from considerable distances. (C) Ants can follow a remembered vector by subtracting the current position (as informed by path integration) from the remembered position of the goal. This system allows ants to keep on track to the goal, even when they must take a detour around an obstacle (D).**

the ant to head straight back to the nest once she has encountered food, even after a convoluted outward journey (see Figure 22.3B). The ant can also remember path integration vectors, which allows her to head directly to the food source on subsequent journeys.

Possessing an on-board set of current coordinates is useful for much more than just returning home directly. Ants can store the path integrator coordinates of important locations, which allow them to remember distances and directions away from the starting location. To return to these locations, ants can subtract their current coordinates (the home to current location vector) from the coordinates of the remembered location (the home to goal vector). Subtracting these vectors provides the ant with a constantly updated vector from their current location to the goal (see Figure 22.3C). Just as the current location to home vector automatically provided by the path integrator tethers the ant to her home, the current location to goal vector connects the ant to the goal location. The vector is updated as the ant moves, even compensating for detours the animal may experience, keeping her on course to the goal (M. Collett, Collett, & Wehner, 1999; Figure 22.3D).

Visual information in ant navigation. In addition to path integration, ants can also use visual information they have learned on previous journeys to guide their routes away from the nest (M. Collett et al., 2013). Although deserts might be thought of as featureless, even small differences along the skyline can result in the view in one direction differing from the view in another. During her journey, the ant attempts to align her current view of the surrounding landscape with the view she remembers from previous journeys. This remembered view acts as a visual compass to keep the ant on the correct path. Closer to the end of her journey the ant can use a remembered view from the position of the goal to return to the goal's location. By attempting to minimize the differences between the current view and the remembered view, the ant can move towards the goal's location until the current and remembered views match. Unlike the visual compass, which only provides route-specific directional information, ants can use the view from the goal to approach the goal from any location as long as they are not so far away that there is no shared information between the current and remembered views. Ants can also use a similar mechanism to return to their route if displaced by a strong gust of wind, predator, or pesky scientist.

Once back on route, the visual compass takes over and the ant resumes her journey (Wystrach, Beugnon, & Cheng, 2012).

Cue Use in Animal Homing and Navigation

Navigation involves traveling through the environment, but the information available to an animal in any environment will depend on their sensory systems. To human eyes, ears, and noses, the open ocean by day, for example, can be utterly disorienting. The constantly changing landscape of the waves robs us of any stable landmarks to tell us when currents are carrying us miles off course. Without a compass in hand most of us would become hopelessly lost. To ocean-navigating turtles and seabirds, however, there is a wealth of information available. While unavailable to humans without the aid of technology, both magnetic fields (Lohmann, Cain, Dodge, & Lohmann, 2001) and atmospheric odors (Gagliardo et al., 2013) can guide these oceanic navigators over considerable distances. Under water, we can see further examples of the diversity of sensory information that animals can use to navigate. Fish may use the change in water pressure to remember where in the water column to find food (Holbrook & Burt de Perera, 2011; Holbrook & Burt de Perera, 2013; Taylor, Holbrook, & Burt de Perera, 2010), while electric fish can sense their surroundings using an electric field produced from a specialized muscle in their tail, which allows them to find their way around in total darkness (Cain & Malwal, 2002). Although species can differ dramatically in the sensory information they have available, many species have converged on useful ways to use this information to navigate.

Compass Guidance

Sometimes successful navigation only requires travelling in the correct direction. Indeed, most animals have and use an internal compass to maintain a heading over unfamiliar territory. Such a strategy is probably the cornerstone to genetically inherited navigation systems, such as the clock and compass strategies of juvenile starlings (*Sturnus vulgaris*) and blackcaps (*Sylvia atricapilla*), where first-time migrants follow an inherited compass course for a set duration (Thorup, Holland, Tøttrup, & Wikelski, 2010). An inherited preferred compass direction allows juveniles to migrate in the absence of experienced individuals, which may occur if adults and their young migrate at different times in the season or if adults die after breeding.

Time-compensated sun compass. Sun compasses that compensate for the movement of the sun over time, are found in a wide range of species, from the homing pigeons mentioned earlier, to coral fish larvae finding their way home (Mouritsen, Atema, Kingsford, & Gerlach, 2013), and food-storing birds relocating their caches (Balda & Wiltschko, 1991; Duff, Brownlie, Sherry, & Sangster, 1998). In addition to using the actual position of the sun in the sky, many animals, including honeybees (*Apis mellifera*; Kraft, Evangelista, Dacke, Labhart, & Srinivasan, 2011), cuttlefish (*Sepia officinalis*; Cartron, Darmaillacq, Jozet-Alves, Shashar, & Dickel, 2012), bats (*Myotis myotis*; Greif, Borissov, Yovel, & Holland, 2014), and birds (*Oenanthe oenanthe*; Schmaljohann, Rautenberg, Muheim, Naef-Daenzer, & Bairlein, 2013), can also perceive the pattern of polarized light that the sun casts across the sky and use this pattern to orient. The information from polarized light may be used alongside, or as part of, the time-compensated sun position compass. For example, migratory birds that use polarized light to orient themselves at dusk also respond to clock-shift manipulations, which suggests that even though, the polarization compass is used only at the same time of the day, this information is still time-compensated (Able & Cherry, 1986).

Time compensation involves an animal building an internal representation of the sun's movement through the sky over time (Guilford & Taylor, 2014). For pigeons this representation is formed through the association of the magnetic compass and the position of the sun in the sky but is restricted to only working at times of day when the bird has seen the position of the sun (W. Wiltschko & Wiltschko, 1998; but see Budzynski, Dyer, & Bingman, 2000). For example, if a pigeon has seen the position of the sun in the morning, but never in the afternoon, it can compensate for the movement of the sun during the morning, but not during the afternoon. Other animals can generalize beyond their own experience of the sun's position (Wehner & Müller, 1993). Bees, for example, which had only ever experienced the movement of the sun during the morning, were trained to visit a goal in the afternoon when the sun was obscured by cloudy skies (Dyer & Dickinson, 1994). When later communicating the direction of the goal to their sisters via the waggle dance, the bees could compensate for the unseen movement of the sun from east to west between morning and afternoon.

Star compass. While time-compensated sun compasses correct for the rotation of the earth, star compasses take full advantage of it. Over the course of the night, the stars in the sky appear to rotate around the earth's rotational axis. The center of rotation in the night's sky can therefore provide directional information: north in the northern hemisphere, south in the southern hemisphere (Emlen, 1970). But waiting all night to get a compass reading is an inefficient method of orientation, so nocturnally migrating birds (Mouritsen & Larsen, 2001) and seals (Mauck, Gläser, Schlosser, & Dehnhardt, 2008) learn to identify constellations and prominent stars around the center of rotation, allowing them to get a quick directional fix (Figure 22.4). Unlike the sun compass, this star compass is not time compensated, even though the constellations and stars move through the sky over the course of the night. This was shown in an experiment in which pied flycatchers (*Ficedula hypoleuca*) and blackcaps, which can use the position of the stars in a planetarium to orient themselves, were kept under a stationary sky of stars for a whole night. If the birds used a time-compensated star compass, the time spent under a stationary sky should have lead the birds to change the direction in which they tried to travel over the course of the night. But they did not. It appears, then, that the bearing that they took from the stars was independent of the time of night (Mouritsen & Larsen, 2001).

Magnetic compass. Many of the man-made compasses with which people are most familiar use the earth's magnetic field to provide directional information. The magnetic compasses that animals use are based on one of two different properties of the earth's magnetic field: polarity and inclination. Magnetic polarity describes the direction of the magnetic field, which travels from north to south. The magnetic compasses of bats (*Nyctalus plancyi*; Wang, Pan, Parsons, Walker, & Zhang, 2007), naked mole rats (*Heterocephalus glaber*; Marhold, Wiltschko, & Burda, 1997) and lobsters (*Panulirus argus*; Lohmann et al., 1995), are all based on magnetic polarity, as are the hand-held compasses used by human hikers and explorers. Magnetic inclination, on the other hand, does not discriminate between north and south, but describes the angle at which the magnetic field intersects the planet's surface. The inclination of the magnetic field changes from being perpendicular to the earth's

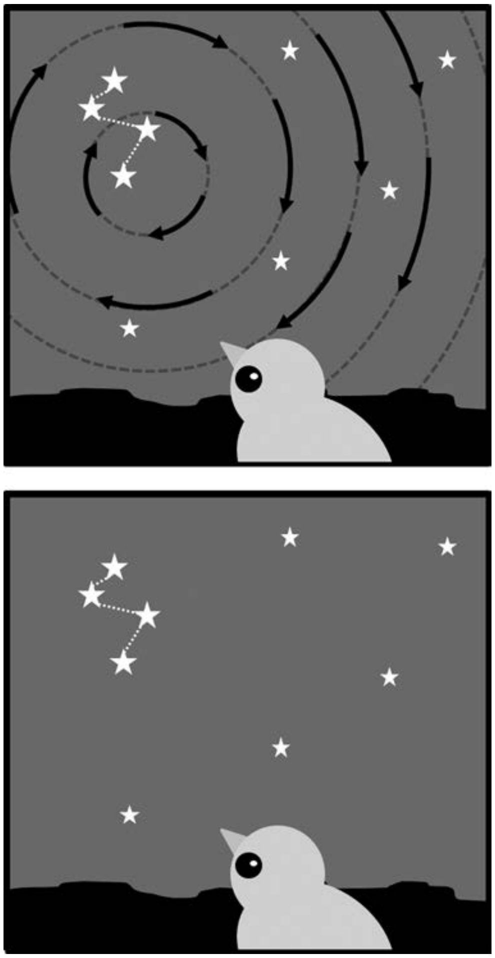

FIGURE 22.4. The star compass. (Top) Birds are able to use celestial rotation to identify the direction of the north or south poles. They then learn constellations in this direction. (Bottom) Learned constellations provide a quick directional fix.

surface at the poles to being parallel to the surface at the equator. An inclination compass, such as those possessed by birds and turtles, provides direction in terms of toward pole and toward equator rather than in terms of north and south (W. Wiltschko & Wiltschko, 2005). This poses a problem for transequatorial migrants, such as garden warblers (*Sylvia borin*) whose journey south takes them first toward the equator from Europe, then toward the pole to Southern Africa. To compensate for limits of the inclination compass, garden warblers at the equator change their preferred compass course from toward equator to toward pole, using the horizontal magnetic inclination at the equator to trigger this change (W. Wiltschko & Wiltschko, 1992).

A lot of research has gone into unravelling how animals detect magnetic information, an ability known as *magnetoreception* (W. Wiltschko & Wiltschko, 2005). As we might expect, the mechanisms underlying magnetoreception differ between animals with an inclination compass and those with a polarity compass. The inclination compass depends on low wavelength light entering the eye, leading to suggestions that the compass is based on quantum interactions between molecules in the eye following absorption of a photon. The polarity compass, in contrast, is thought to be the based on the presence of magnetite particles.

Path Integration

Given the focus of path integration on a set "starting point" it is unsurprising that path integration has been well studied in several central-place foraging species, including bees (*Apis mellifera*; Srinivasan, Zhang, Lehrer, & Collett, 1996), golden hamsters (*Mesocricetus auratus*; Etienne & Jeffery, 2004) and fiddler crabs (*Uca sp.*; Layne, Barnes, & Duncan, 2003; Zeil, 1998). The fiddler crabs, in particular, use path integration not only to keep track of their position from their burrow but also to keep their body perpendicular to the direction of the burrow. Fiddler crabs run sideways, and so keeping their burrow constantly to their side, even when the burrow is out of view, allows the crabs to scuttle home rapidly without wasting time turning around. In addition to work on central place foragers, path integration has also been described in humans, dogs, and geese (Etienne & Jeffery, 2004; Von Saint Paul, 1982; see also Chapter 21, this volume), suggesting that an animal does not need to have its entire life revolve around a single location to benefit from path integration.

Path integration requires animals to assess the distance and direction they have traveled continually. Although path integration is taxonomically widespread, different species sense this distance and direction information in different ways (Etienne & Jeffery, 2004). Bees and ants both use a celestial compass to estimate direction but while ants use the movement of their legs to estimate the distance walked, bees estimate distance via the *optic flow* of visual information going past their eyes. Spiders and some species of fiddler crabs, however, rely only on the movement of their legs to estimate distance and direction, in terms of steps and turns, respectively. Finally, mammals use visual landmark information to estimate direction but they can also use a combination of self-motion cues, such as leg movements, as well as the inertial cues caused by the angular motion of turning. These same self-motion cues are also used to estimate distance travelled: humans are more like spiders than many realize.

Landmarks

When animals learn to associate some environmental information, such as objects or smells in the environment, with a route or location, and use that information to navigate, that information is labeled a landmark (see Chapter 21, this volume). While the term *landmark* usually refers to discrete, visual features, an all-encompassing definition seems more appropriate because landmarks should be defined by how they are used and not by the sensory system used to detect them. The animal world is diverse, and many species sense and experience the world very differently to humans. Concomitantly, there are many ways that animals can use landmarks, few of which are exclusive to discrete visual features.

Beaconing. The simplest strategy for using a landmark is to move directly towards one. Beaconing is the use of a prominent landmark, often near or at the goal location, to move directly to the goal (T. Collett, 1996; Redhead, Roberts, Good, &

Pearce, 1997). But beacons are not always visual. For example, nocturnal petrel species, including thin billed prions (*Pachyptila belcheri*) and Wilson's storm petrels (*Oceanites oceanicus*) use the odor plume emanating from their nest burrow to relocate it when they return at night (Bonadonna & Bretagnolle, 2002). Using an odor plume as a beacon does, however, present some challenges. While the direction of a visual beacon may appear obvious, detecting the direction of the origin of an odor involves determining the direction in which the odor increases in intensity, the direction of the gradient. Beaconing is then a process of moving up that gradient, until the source is reached. Similarly, an animal heading towards a visual beacon moves to decrease the perceived distance between themselves and the beacon.

Beacons also do not have to be at the goal or to be stationary to be useful. In some species, such as storks and geese, young or inexperienced individuals follow more experienced individuals on migratory journeys (Mueller, O'Hara, Converse, Urbanek, & Fagan, 2013). To the first-time migrator, the experienced individual acts as a beacon and by continuing to head towards this social beacon, the inexperienced bird can make its way to the wintering ground, and learn the route in so doing.

Landmarks en route. Most beacons placed at the goal, particularly visual beacons, probably have a limited range. Storks and geese can follow the beacon of an experienced individual across distances that often exceed hundreds of miles only because the beacon is constantly moving ahead of them. Animals that use stationary beacons over long distances may need to combine beacons into chains, with each beacon bringing the animal within view of the next until they reach their goal. To find their way home, they can simply repeat the process, reversing the order of the beacons so they travel toward home rather than toward the goal. This hopping from beacon to beacon, sometimes referred to as *serial beaconing*, *steeplechasing*, or *piloting*, is a simple way whereby animals can use landmarks to remember the route home (Able, 2001; T. Collett, 1996; see Figure 22.5). Pigeons appear to use such a sequence of landmarks when flying stereotyped routes home to their loft. Overlaying the multiple routes by a pigeon on top of one another shows that some points of the route are more conserved than others,

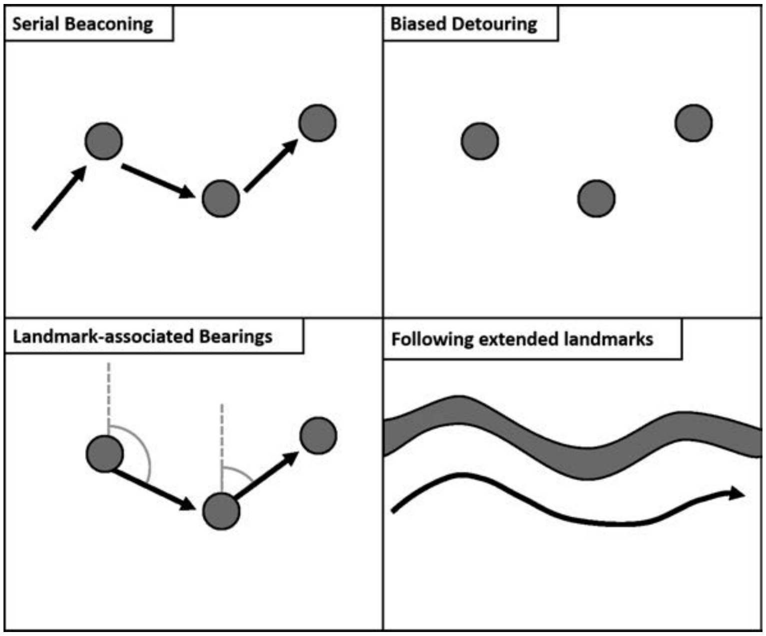

FIGURE 22.5. **Different ways of using landmarks along a route.**

which are often points associated with particularly prominent landmarks (Mann et al., 2011).

Serial beaconing is not the only way that landmarks can be used to remember a route. Rather than just heading towards a beacon, animals could keep a landmark to their left or right as they pass it by, a strategy known as *biased detouring* (T. Collett, 1996; Figure 22.5). Alternatively, prominent landmarks could be associated with a compass bearing indicating the direction of the next landmark in the chain, or even the goal itself shown by some effect of clock-shifting on pigeons flying within their familiar area, even when they are within view of the home-loft. Finally, as well as using discrete landmarks, animals may follow extended landmarks, to return to a goal (Figure 22.5). Pigeons follow the course of roads and rivers as part of their routes home (Biro, Meade, & Guilford, 2004), while ants can learn to follow a wall as part of a visual route (Graham & Collett, 2002). Migrating birds will follow coastlines and mountain ranges as part of their migration route but this might also be due to favorable wind conditions or a hesitancy to head out over the sea. As tracking technology progresses, the role of landmarks in migratory routes will become more accessible to investigation (Guilford et al., 2011).

Landmarks to fix a position. At the end of a journey, animals need to find their goal. For some, such as digger wasps, this is an inconspicuous hole leading to their nest, for others, such as the marsh tit, the goal is a seed hidden under some tree bark. To remember the location of the goal, many species therefore use landmarks around the goal to encode the goal's location (Gould, Kelly, & Kamil, 2010; see Figure 22.6).

View-matching. There are multiple ways to use landmarks to encode a location. One such is view matching, in which an animal does not have to even identify individual landmarks in order to use them to return to a location. Insects, such as ants, bees, and crickets, as well as possibly spiders, learn the visual panorama as seen at the nest or goal location, and return to the goal by trying to match this remembered view (Zeil, 2012). Similarly, pigeons remember the view of their surroundings at release sites, homing faster when they are provided with the same view as during training, than when they are provided with a novel view of their surroundings (Biro, Guilford, & Dawkins, 2003).

Views contain a lot of spatial information. For examples, a simple snapshot of the view from a goal includes the relative positions of surrounding visual features, as well as their distance from the goal in the form of their apparent size on the retina. Some of this information may be more salient than others: Although ants and bees will both often search further from a landmark after it has increased in size (Cartwright & Collett, 1983), ants tend to prioritize matching the relative position of features over matching their apparent size when the two are put into conflict (Durier, Graham, & Collett, 2003). This can make testing whether animals match views difficult, as increasing or decreasing the size of a landmark might have little effect if more salient properties of the view remain stable. Additionally, a remembered view does not need to be in the form of a two-dimensional snapshot (Wystrach & Graham, 2012a). Three-dimensional remembered views

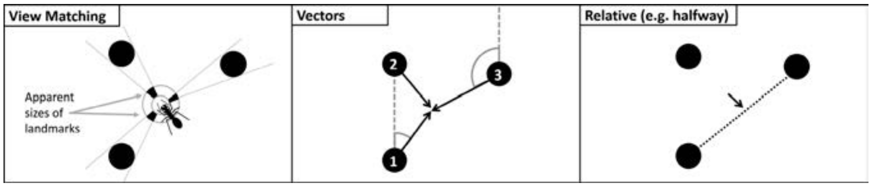

FIGURE 22.6. **Different ways of using landmarks to fix a position: view matching, vectors (including relative bearings from landmarks 1 and 2, and absolute bearings from landmark 3), and relative distances (halfway).**

can incorporate depth, either through stereopsis via binocular vision, or by recording the degree to which different components of the view move relative to one another as the animal moves, a phenomenon known as *motion parallax* (Dittmar et al., 2010; Kapustjansky, Chittka, & Spaethe, 2010; Zeil, 1993). Given the potential complexity of remembered views, investigation of the use of remembered views often requires detailed analysis of the sensory information available to the navigating animal, and of their behavior during the task (Wystrach & Graham, 2012a, 2012b).

Vectors. Some species do not rely on apparent size to estimate distances. Gerbils (*Meriones unguiculatus*), for example, trained to search for food at a set distance from a landmark, do not search further away when the landmark is made larger or closer when it is made smaller (T. S. Collett, Cartwright, & Smith, 1986). Like pigeons (Cheng, 1988) and Clark's nutcrackers (*Nucifraga Columbiana*; Kamil & Jones, 1997), the gerbils appear to use absolute distance (e.g., meters) from a landmark rather than the apparent size of that landmark. As well as learning the distance of the goal from the landmarks, gerbils and pigeons also learn the direction of the landmarks from the goal, essentially learning a vector to the goal from each landmark (see Chapter 21, this volume).

Direction from a landmark can be remembered either as an absolute bearing, taken from an external compass reference, or as a relative bearing, where the direction of the goal is determined by the angle between the goal and more than one landmark. In some cases, the difference between these two frames of reference is clear. Chickadees (*Parus atricapillus*), Clark's nutcrackers, and several species of North American jays all use a sun compass to remember the absolute bearing of a goal from a landmark (Balda and Wiltschko, 1991; Duff, Brownlie, Sherry, & Sangster, 1998; Wiltschko, Balda, Jahnel, & Wiltschko, 1999). In the lab, however, the sun compass is unavailable, and so when animals continue to search in the same absolute direction after the landmark array has been rotated, it is unclear whether animals are truly using absolute bearings (Gould-Beierle & Kamil, 1996; Jones & Kamil, 2001), or relative bearings using prominent boundaries as extended landmarks (Cheng & Sherry, 1992; Kelly, Kamil, & Cheng, 2010). Regardless, the use of absolute or relative bearings appears to be flexible and dependent of previous experience. In most cases, animals that prefer absolute bearings can be trained to use relative bearings when the former are unavailable or unreliable (Gibson, Wilks, & Kelly, 2007; McGregor, Good, & Pearce, 2004).

Relative distance. As well as using comparatively concrete spatial information such as distances and directions, some animals can also learn more abstract relationships between landmarks and a goal. For example, Kamil and colleagues (Jones, Antoniadis, Shettleworth, & Kamil, 2002; Kamil & Jones, 2000; Spetch, Rust, Kamil, & Jones, 2003) investigated whether birds could use abstract rules to guide their use of landmarks. Over several experiments, Clark's nutcrackers, pigeons, and jackdaws (*Corvus monedula*) were trained with two landmarks, presented at various distances from one another to prevent the birds learning vectors, and the location of the goal was determined by a relative rule: halfway between the landmarks, a quarter of the distance between the landmarks, at a constant distance from the landmarks, and at a constant bearing from the landmarks. In almost all cases, the birds learned the rule underlying the location of the landmarks to the goal. While the pigeons were able to learn the constant distance and constant bearings conditions equally well, the nutcrackers performed best in the constant-bearing condition, suggesting that these food-storing birds may be particularly sensitive to the direction of landmarks from a goal (Kamil & Cheng, 2001; Kamil, Goodyear, & Cheng, 2001).

BRINGING IT ALL TOGETHER: INTERACTIONS BETWEEN MECHANISMS

One of the problems with identifying cues that animals can use to navigate is that many species may use multiple different cues to find their way home. Attempts to remove individual cues thought to be important to navigation, either by attaching magnets to an animal's head, removing their sense of smell, or, in a particularly bizarre yet classic experiment, covering a pigeon's eyes with frosted contact lenses to obscure their vision, all had unexpectedly little effect on how well the animals were able to navigate (R. Wiltschko & Wiltschko, 2003). Yet there was good evidence that animals did use these cues. The take-home message is that just because animals can use a particular cue does not mean that that cue is the only cue they do use.

Competition Between Different Cues

As described above, many animals have multiple sources of information available for finding their way around. Often, different sources will indicate similar information: A vector from one landmark to a goal essentially provides the same information as the vector from another landmark to that goal. Similarly, a prominent beacon and a path integration vector both provide the same heading to a location.

In some cases, animals appear to choose between redundant sources of information. A rat in a water maze, and a hummingbird in the wild, for example, may learn to attend to either a beacon or the surrounding landmarks to return to their goal (a platform for the rat, and a sucrose reward for the hummingbird), with the choice of each depending on their experience (Flores-Abreu, Hurly, & Healy, 2012; Redhead et al., 1997). This suggests that beacons and landmarks compete with each other to be learned by the animal. In other circumstances different sources of information are learned side by side, resulting in animals having multiple ways to find their way to the same location.

Having a Back-Up: Hierarchical Strategies

An animal that relies on a single source of information for navigation runs the risk of being unable to navigate if that source disappears. Even the most stable of cues, such as the sun or the earth's magnetic field, can be unavailable some of the time. Animals passing through magnetic anomalies or traveling on cloudy days still need to find their way around, and so different cues are organized hierarchically. When a preferred cue is not available, the animal focuses instead on the next preferred, and so on. For example, black-capped chickadees when learning to visit one of four distinctly colored feeders learned not only the location of the rewarded feeder on the wall, but also the location of the rewarded feeder relative to the other feeders, as well as the color of the rewarded feeder. In the test, the birds used each of these cues in order (Brodbeck, 1994).

The order of a hierarchy can be based on the perceived reliability of the different cues. Rats that could use both path integration and a beacon to find a goal, for instance, searched using one and then the other when the two predicted different locations. When the beacon was moved 45° around the arena, the rats' first choice, that is to say the preferred option in the hierarchy, was the beacon (Shettleworth & Sutton, 2005). When the beacon moved 90°, then the rats switched to preferring path integration. This dynamic weighting of the different components of the hierarchy could explain why some wild animals prefer certain cues to others. Nectarivorous bats, for example, first search for a reward on the basis of its location, before changing to a beaconing strategy on the basis of the echolocation profile of a flower (Thiele & Winter, 2005). Many flowers of the same species look the same but an individual flower is only ever in one location. Given that the bat's goal is to return to a particular flower and not to just any flower of a certain species, perhaps such a cue hierarchy makes sense.

Structuring Learning: Scaffolding

Attending to multiple sources of information could allow animals to use one mechanism to navigate, while acquiring information for a different mechanism. In such a situation, by using the first navigation mechanism the animal structures the learning of the other information, ensuring that only information relevant to the navigation task is acquired. This process is known as scaffolding. Juvenile starlings, for example, undertaking their first migration reach their destination by following an inherited preferred compass direction for a predetermined duration or distance. While following this endogenous navigation program, however, the birds also learn environmental information about their route, such that on subsequent journeys the now adult starlings rely more on their experience than on their inherited preferred compass direction. This change in strategy was famously demonstrated by Perdeck in the 1950s when he displaced migrating starlings from the Hague in the Netherlands to Switzerland, hundreds of kilometers from their normal migratory route (Perdeck, 1958). Adult starlings compensated for the displacement and flew to their usual wintering grounds, but the juveniles continued to fly in the direction in which they had been flying when caught and subsequently spent the winter hundreds of kilometers from the adults. The juveniles learned about the route to this new destination, and the following year, the now-adult birds returned to their new overwintering grounds.

Increasing Accuracy: Calibration and Weighting

Weighting multiple options. In the section on desert ants, we discussed how ants have a toolkit of different mechanisms available to use during navigation, including path integration and forms of visual guidance. Although path integration and visual information are thought to be processed independently of one another (M. Collett & Collett, 2009), navigating ants can use both systems simultaneously by combining the predicted headings from each mechanism. This is no problem when path integration and visual information indicate the same direction, but if they disagree, the final heading the ant takes will depend on the weights she gives to each mechanism (M. Collett, 2012). This collective decision making by different navigational systems allows desert ants to use multiple sources of information efficiently to find their way around, without having to combine this information into a single representation.

A similar averaging process is used to increase the accuracy of the sun compass, a mechanism that is essential for path integration by insects. If the sun compass is inaccurate, then each of the accumulated vectors of the insect's outward journey is also inaccurate resulting in a massively inaccurate home vector. To mitigate this accumulation of error, desert ants can combine multiple pieces of information from the sun, including polarized light, UV, and the sun's position, to orient (Wystrach et al., 2014). When all this information does not align fully, the ants head off in an intermediate direction.

Animals can also average together information from different landmarks. Pigeons, for example, average the direction element of their landmark-to-goal vectors when using multiple landmarks to return to a goal (Cheng, 1994). Flying squirrels (*Glaucomys volans*) having learned to find a goal based on three criteria (absolute position, relative position, and color), preferred to search at the location that preserved any two of those criteria, averaging equally without a hierarchy (Gibbs, Lea, & Jacobs, 2007). Not all landmarks are necessarily equal, and so animals can weight landmarks according to how informative they are. Clark's nutcrackers, for example, weight landmarks closer to the goal higher than those further away (Vander Wall, 1982).

Compasses calibrating compasses. A navigational strategy based on following a set compass direction is only as accurate as its compass. Several species, therefore, rely on multiple sources of compass information and either average the outputs of multiple compasses, or, occasionally use other compasses to calibrate the compass they actually follow.

Although animals that navigate nocturnally, such as bats and some bird species, cannot use the sun compass during navigation itself, they do use it to calibrate the other compasses on which they rely. Visual cues from the sun at sunset reset the magnetic compass so that it corresponds with the direction of the setting sun (Muheim, Phillips, & Deutschlander, 2009). Animals that are experimentally manipulated with a rotated magnetic field at sunset are, therefore, stuck with a miscalibrated magnetic compass for the continuation of the night, continuing to fly in the rotated direction until the sun can once again re-calibrate the magnetic compass to normal (e.g., Cochran, Mouritsen, & Wikelski, 2004; see Figure 22.7). When the sunset is not visible, the magnetic compass acts as the primary compass, recalibrating the star compass to correspond with a perceived magnetic direction. This system of multiple back-ups and interactions enables nocturnal migrants to maintain a useful bearing regardless of the cues available at any one time.

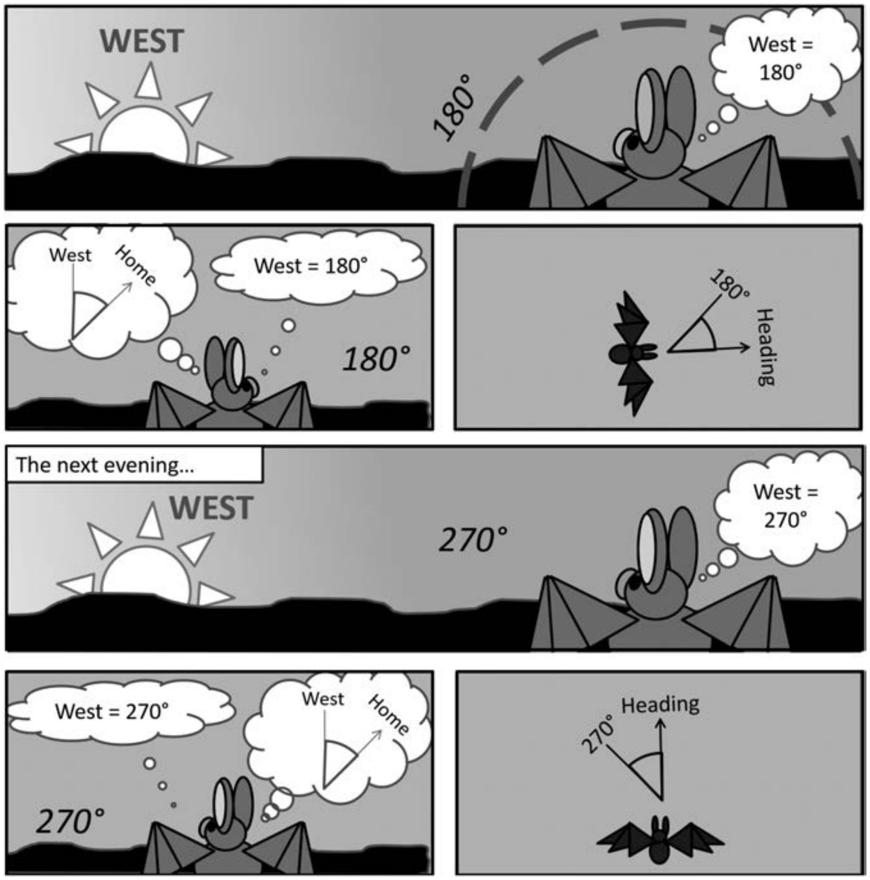

FIGURE 22.7. **Calibration of the magnetic compass by sunset cues. In the top panel, the magnetic field surrounding the bat has been shifted by 90°, so that true west reads 180° rather than 270°. On seeing the sun setting in the west, the bat incorrectly recalibrates its magnetic compass so that 180° equals west. As a result, the bat travels in the wrong direction. The next evening the bat is able to experience the true magnetic direction alongside the setting sun, recalibrates its magnetic compass back to true west (270°), and heads off in the correct direction.**

Landmarks calibrating path integration. Path integration involves continual calculations about the distance and direction of an animal from their starting point, each of which involves a small error that accumulates over the course of an animal's journey. For first-time travelers, this is tough luck, but experienced travelers may be able to correct for accumulated errors by remembering the path integration (PI) coordinates of a location from previous experience. Hamsters, for example, can use the view of the landmarks at a familiar location to recalibrate the path integrator, resetting their PI coordinates to match the remembered coordinates of that location (Etienne, Maurer, Boulens, Levy, & Rowe, 2004). Ants, on the other hand, can learn the PI coordinates of locations they have previously visited, as well as visual information at these familiar locations, but do not recalibrate their path integrator to match the coordinates at the remembered location, suggesting that these two sources of information, views and coordinates, are kept separate (M. Collett & Collett, 2009).

COGNITIVE MAPS

Animals can bring together different sources of information to navigate more effectively. As seen in the previous section, this interaction between cues has been demonstrated in many different species. A longstanding argument in the study of animal navigation, however, is whether these different cues are integrated into something larger—a cognitive map. First introduced in 1976 by O'Keefe and Nadel in their classic book *The Hippocampus as a Cognitive Map*, the cognitive map was proposed to be a single internal representation of space that fills in with information as an animal explores its environment (see Chapter 21, this volume). The book was a sensation, stimulating a vast swathe of work, from behavioral neuroscience to animal behavior. And yet, cognitive maps remain one of the most fiercely debated and controversial aspects of animal navigation: Some researchers remain deeply skeptical of the concept of cognitive maps (Shettleworth, 2009), and call for the abandonment of the term "cognitive map" (Bennett, 1996; Mackintosh, 2002), while others happily describe the study of animal navigation itself, as the study of cognitive maps (e.g., Jacobs & Menzel, 2014).

What Is (and Is Not) a Cognitive Map?

A major challenge for the study of cognitive maps is the specification of what a cognitive map is and what it is not. At its most basic, a cognitive map could refer to any internal spatial representation, for example, between a goal and some landmarks (Gallistel, 1990). More often a cognitive map refers to a representation of distances and directions between all known locations so far experienced, often referred to as a metric or Euclidean map (Jacobs & Schenk, 2003; Wiener et al., 2011; see Figure 22.8). The existence of Euclidean maps in animals is usually at the center of the cognitive maps debate. For this reason, when we refer to "cognitive maps" in this section, it is these Euclidean maps to which we are referring.

Cognitive maps in the sense we are using here, therefore, resemble the properties of physical maps with which many of us are familiar, such as providing distances and directions between points. They can be used to provide positional information, as well as plan routes and journeys. Other forms of spatial representation have also been referred to as maps, and can be used by animals to determine their position and guide behavior (Figure 22.8). Unlike cognitive (Euclidean) maps, these maps do not represent the distances and directions between different locations, as would a paper map. Indeed some of these "maps" barely resemble a map as we know it at all.

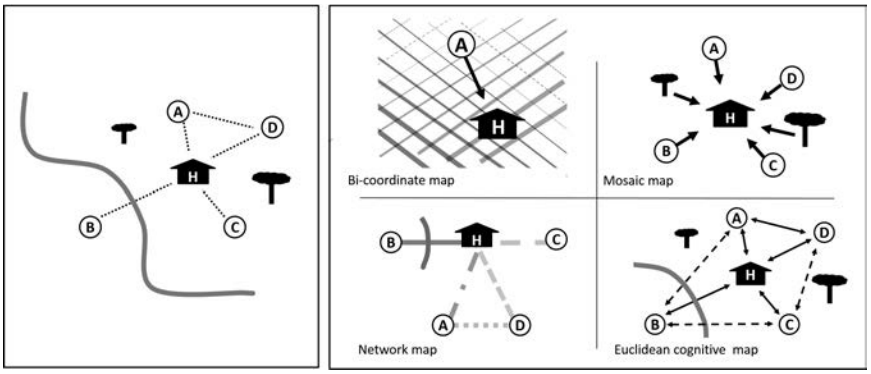

FIGURE 22.8. An animal who has traveled through the environment can represent the space it has explored in several different ways. The diagram on the left shows a habitat, with dashed lines showing which routes an animal has taken between home (H) and four different sites (A–D). The animal has traveled between home and each site, as well as between A and D. The diagrams on the right show different kinds of maps the animal may have constructed. Bicoordinate maps only provide the direction of home from a current location (see Figure 22.1). Mosaic maps provide the direction home from many points in the environment, but not the distance or the spatial relationships between other sites. Network maps represent the known routes between locations, but not their distance and direction from one another. Euclidean, or metric, cognitive maps represent the distances and directions of all known sites to each other, allowing animals to take shortcuts and detours that they have never previously experienced (dashed arrows).

Bicoordinate maps. In a *bicoordinate map*, such as is thought to be involved in map and compass navigation by birds, the animal uses the comparison between remembered and currently perceived values of two or more known gradients to estimate its position relative to a particular location, usually home (see Figures 22.1 and 22.8). The term *position* here might be a bit misleading. While animals can use a bicoordinate map to determine their direction relative to home, birds at least, require a separate compass system to travel towards home. The map cannot provide directional information, which is why clock-shifted birds follow their inaccurate compass despite knowing their position relative to home. In addition, there is little evidence that a bicoordinate map encodes the distance of an animal from home (Able, 2001). When close to the loft, pigeons appear to switch from a bicoordinate map to a using familiar landmarks, which makes encoding distance in the bicoordinate map unnecessary, but also difficult to experimentally test.

A bicoordinate map is, therefore, not much like any map with which we might be familiar. The arrangement of environment features on a paper map, for example, can provide us with some sense of direction, even in the absence of a compass. In contrast, while a bicoordinate map can provide a bearing to get you home from your current location, it cannot by itself provide any means to follow that bearing. This does not mean that bicoordinate maps are not useful. The map and compass model, which includes bicoordinate maps as a major component, is one of the most successful models of long-distance navigation, with its influence reaching far beyond the data from pigeons and migratory birds for which it was originally developed. For example, juvenile salmon (*Oncorhynchus tshawytscha*) imprint on the combination of magnetic intensity and inclination at the river in which they hatched, and use these coordinates to return to their natal river in subsequent years (Putman, Jenkins, Michielsens, & Noakes, 2014). Young sea turtles do the same (Brothers & Lohmann, 2015), as well as using the magnetic coordinates of their position in the Atlantic Ocean to keep themselves safely in the North Atlantic gyre during their formative years (Lohmann et al., 2001). If all you need to know is what direction in which to swim or fly, a bicoordinate map is for you.

Mosaic maps. A map constructed by associating landmarks with the appropriate compass bearings to indicate home is termed a *mosaic map* (Figure 22.8). Mosaic maps collect together the combination of landmarks and bearings we described in the section on landmark-defined routes in a single representation. They are also typically thought to make up the map component when birds use map and compass navigation in a familiar area. However, unlike the role of bicoordinate maps, on which most researchers agree (even if they disagree as to the sensory basis of such a map), the importance of mosaic maps continues to be disputed. Most of the evidence in favor of mosaic maps comes from experiments in which homing pigeons have been clock-shifted and the released within a familiar area, but the data from these experiments are mixed: Not all pigeons respond to such shifts in the same way. Some show a smaller deviation than would be predicted, while others show no deviation at all (Holland, 2003). We do not currently understand the cause of this variation.

Like bi-coordinate maps, mosaic maps appear to provide only the direction of home relative to the animal's current position. There is no evidence that mosaic maps include the distance of different landmarks to home, or even the direction of landmarks from one another. At their most basic, mosaic maps may resemble less a map, and more a bicycle wheel, with home at the center and bearings from different landmarks spreading out radially.

Network maps. Wild chacma baboons (*Papio ursinus*) prefer to stick to known routes when traveling between sites, only significantly detouring when in view of their goal or prominent surrounding landmarks (Noser & Byrne, 2007). This behavior has been suggested as evidence that the baboons use *network maps*. These maps contain the relative locations of different locations, as well as the routes that connect them, but do not contain information about distances and direction, as do cognitive maps (Figure 22.8). Network maps might, then, be thought of as similar to subway maps or circuit diagrams, representing all of the connections in the habitat rather than the absolute locations.

Do Animals Have Cognitive Maps?

In theory, many species "have what it takes" to build and use a cognitive map (T. S. Collett & Graham, 2004; Gallistel & Cramer, 1996; Jacobs & Schenk, 2003). Path integration, for example, provides a framework for establishing the distance and directions of locations from a set starting point, such as when hamsters store the path integration coordinates of visually defined locations (Etienne et al. 2004). If these locations can also be encoded in relation to one another and not just to the starting point, this, in theory forms a cognitive map. So far, so good. The problem is determining whether an animal ever actually creates and uses such a map. To test this, one must examine what it is that a cognitive map allows an animal to do that other forms of navigation do not. The disagreement over cognitive maps is partly born from the vague, and continually evolving, concept of what exactly constitutes a cognitive map, but also from legitimate disputes as to whether the current evidence supports the possession and use of cognitive maps by animals during navigation (Jacobs & Menzel, 2014; Shettleworth, 2009). One common expectation of a cognitive map is that it should allow the animal to perform certain feats of navigation that are impossible without such a map.

Integrating experiences. A cognitive map should fill in as an animal explores its environment. As an animal discovers new information, this information should be integrated into the map. One testable prediction of cognitive mapping, therefore, is that animals with a cognitive map should be able to knit together different experiences of the same environment into a single representation. Alternatively, animals could learn to associate landmarks, or other cues, with a location, but keep this memory separate from other memories of other locations.

The evidence for integration is mixed. Rats can integrate two different landmark arrays, which they have only previously experienced separately, only if there is a landmark common to both arrays (Chamizo, Rodrigo, & Mackintosh, 2006). Although this might suggest that rats can build up a cognitive map, experiments in which navigating rats were tested with novel views to those they experienced during training, would suggest otherwise: despite having seen the majority of the experimental room, presumably providing sufficient opportunity to construct a cognitive map, when the rats were faced with a novel view of their surroundings, they appeared totally disoriented (Benhamou, 1996).

Integration could be thought to occur across sensory modalities as well. Bats, for example, may use both echolocation and vision to find their way around. It is surprising, then, that bats previously trained to locate a perch using vision showed no advantage over naive bats when trained to the same location in the dark (Holland, Winter, & Waters, 2005). Based on these experiments, at least, it is not clear that animals do integrate spatial information across experiences and sensory modalities into a single cognitive representation of their environment. Or, if animals do build cognitive maps over multiple experiences, then it would seem that this process is more complicated than previously thought.

Planning. One of the advantages of a cognitive map is that it permits animals to plan journeys (see Chapter 27, this volume). Animals can choose the most direct route between different locations, saving time and energy, or prepare for a journey they are yet to take. The behavior of male Poison dart frogs (*Allobates femoralis*) that carry their newly hatched tadpoles to various nursery pools in their territory would appear to fit this bill. Before heading off to a distant pool, a frog will place more tadpoles on its back than before heading to a closer pool (Ringler, Pašukonis, Hödl, & Ringler, 2013). This behavior could be the result of the frogs using a cognitive map to anticipate the distances they are about to travel, and planning their cargo accordingly. Alternatively, the frogs may not be planning their journeys at all but, rather, tend to walk further when carrying more tadpoles. This second explanation does not require a cognitive map, and pulling apart these different explanations can be very difficult.

An ingenious study on bees provides one example of how clever experiments can use planning to more directly test for cognitive mapping. Bees in a hive were provided with information about a rewarded location via a waggle dancing robotic bee, a location in the middle of a lake. Despite the implausible direction of the dance, the bees did not reject this information and headed out anyway, suggesting that they did not recognize the implausibility of the location (Wray, Klein, Mattila, & Seeley, 2008).

Planning may also be considered as evidence of a cognitive map, if the planning implies knowledge of the distances and directions of different locations relative to one another. When faced with the task of visiting multiple different locations, primates and pigeons can travel the most efficient route (Gibson, Wilkinson, & Kelly, 2012; Janson, 1998), even when that means not heading to the nearest location first. Such planning may require an internal representation of the distances of all of the locations from one another but the mechanism underlying this planning is not well enough understood for us to conclude that cognitive maps are key to such behavior.

Planning a route does not necessarily require a cognitive map. A wonderful series of experiments by Tarsitano and Jackson (1994, 1997) provided jumping spiders of the genus *Portia* with two possible routes, only one of which would lead them to their prey. Not only could the spiders choose the correct route on their first choice, even when that route was more distant, they could distinguish between useful routes and routes that were impassable. To plan their routes, the spiders looked along the full length of each route before heading off, spending more time on the more useful route, suggesting that the spiders could use relatively simple rules to plan their journeys (Tarsitano & Andrew, 1999).

Detours and shortcuts. A key prediction of cognitive mapping is that a cognitive map should allow an animal to navigate flexibly (Jacobs & Menzel, 2014). By knowing the distances and directions between different locations, the bearer of a cognitive map should not be limited to fixed routes but should be able to calculate novel routes, such as detours and shortcuts between locations. Observations of flexible navigation from the laboratory and the wild have often been used as evidence that animals use a cognitive map (e.g., Jacobs & Menzel, 2014; Normand, Ban, & Boesch, 2009). Such observations include seeing that an animal approaches a goal from more than one direction or that it travels in a straight line from a novel to a familiar location. The problem is that this interpretation is based on the assumption that cognitive mapping is the only way that an animal could perform such behaviors, an interpretation that either ignores other possible sources of information or rules them out as unlikely. In his influential critique of cognitive mapping, Bennett (1996) set out a couple of alternative explanations for researchers to rule out before they conclude that the observed flexible navigation is evidence for a cognitive map.

First, researchers must exclude the possibility that the animal used path integration to reach its location. As described for desert ants, the use of path integration alone can allow animals to detour through unfamiliar areas on their way to a goal (M. Collett et al., 1999; Etienne et al., 1998), to approach a goal from different directions, and may allow animals to shortcut between locations without a map (Cruse & Wehner, 2011). As a path-integrating animal stores a direct vector between its starting location and the goal, if that an animal is forced to take a circuitous route to that goal on its first outward journey, it should be able to travel directly to the goal in subsequent trials. Fortunately for researchers interested in cognitive maps, path integration should be easy to manipulate as it requires animals to keep constant track of their position. Picking an ant up and dropping it in a new location will sever her path integration tether to home and, therefore, prevent her from using path integration to detour or shortcut her return. Unfortunately, because hamsters (Etienne et al., 2004), and probably some other animals, can remember the path integration coordinates of familiar places, controlling for path integration in these animals is much more difficult. In addition, if path integration is used in the construction of a cognitive map (Collett & Graham, 2004; McNaughton et al., 2006), then it might be expected that disrupting path integration would affect how well animals can use their cognitive map. Although path integration does provide a clear, alternative explanation for "flexible" navigation, demonstrating that animals are using path integration without a cognitive map can be far from simple.

Bennett's second alternative to cognitive mapping is another feature we might associate with a map: landmarks. Although animals could use landmarks as part of a cognitive map, landmarks can also be used to take novel routes without the aid of a map.

If an animal can see landmarks at one location that it recognizes as having seen at another location, it could take a novel shortcut between the two locations by simply heading towards the familiar landmarks. The animal could do this either by beaconing to discrete landmarks or by trying to match their view to that that they experienced at the second location. Controlling for the effect of familiar landmarks is often at the crux of debates over evidence of cognitive mapping. Honey bees released at an unfamiliar location, for example, can travel directly to either a feeding site or to home, but only if cues visible from the familiar route either to home or to the feeding are also visible from the release site (Dyer, 1991). Other experiments that have also purported to show evidence of cognitive maps in bees (e.g., Cheeseman et al., 2014; Menzel, Geiger, Joerges, Müller, & Chittka, 1998; Menzel et al., 2012, 1998), have suffered the same criticism that there might be familiar visual information available at the release site (e.g., Cheung et al., 2014). Such criticisms of shortcutting experiments focus less on discrete landmarks, which may appear more obvious to human eyes, and more on view matching as an alternative explanation. Experiments purporting to show novel shortcuts therefore need to analyze the information available at a release site, not just in terms of individual landmarks, but also potentially subtle visual gradients (Wystrach & Graham, 2012a, 2012b).

So, despite its apparent simplicity, Bennett's critique of cognitive mapping is difficult to disprove. Truly novel shortcuts must involve no path integration information and no familiar visual information associated with the goal. Unsurprisingly, there are very few experiments supporting cognitive mapping that meet these criteria. And those that do meet these high standards are often matched by those that don't. For instance, one experiment in the laboratory has shown that rats can take novel shortcuts (Roberts, Cruz, & Tremblay, 2007), but another that rats will only take shortcuts that they have previously traveled (Grieves & Dudchenko, 2013). Some have suggested that the scale and sterility of the lab prevent animals from acquiring cognitive maps or being motivated to use them and that animals should be tested on larger scales with more available sensory information (Jacobs & Menzel, 2014). But doing so would also make it harder to isolate cognitive mapping from alternative methods of navigation. Although Bennett's criteria may be strict and may underestimate the prevalence of cognitive mapping in animals, there is currently no clear alternative to these criteria, short of uncritically accepting the existence of cognitive maps.

The study of cognitive maps, then, is fraught with contradictions. On one hand, there appears to be clear evidence for cognitive maps when animals navigate flexibly. Animals can take multiple routes to a goal, compensate for detours, and plan efficient routes. On the other hand, when specific properties of cognitive mapping are put to the test, such as integration and shortcutting, the results more often than not suggest that animals do not possess a cognitive map. Part of the disagreement over cognitive maps comes from how to interpret this discrepancy. To supporters of cognitive mapping, it could be that the criteria for cognitive maps are too high, or that animals have not been tested under the necessary conditions for mapping to develop (Jacobs & Menzel, 2014). After all, even in humans, much of the evidence for cognitive mapping comes from asking questions to participants, rather than monitoring their behavior without them knowing. Detractors of cognitive maps might conclude that the term is not useful, that the concept is in contraction to the evidence, and the idea that animals navigation by reference to an internal map is overly anthropomorphic. Alternatively, it could be argued the strict Euclidean definition of cognitive maps at the center of these debates, represents only one of many possible spatial representations, each with different abilities and computational limitations (Fagan et al., 2013). In this case, maybe the question should move on from "do animals have a cognitive map" to, more generally, "how do animals represent space"? Regardless, after almost 40 years of debate, it is unlikely cognitive maps are going anywhere soon.

CONCLUSION

At its heart, the study of homing and navigation concerns the interaction between animals and their environments, and how animals can extract and use the information necessary to travel to where they need to go. Animals possess multiple strategies for navigating, and can combine different sources of information in a number of different ways. Different species may rely on different information, as may different individuals, in different environments, or with different experiences. Even within a single category of cues, we see diversity: there is no single way to use landmarks, for example.

Animal navigation brings together biologists and psychologists, ecologists and neuroscientists, computer scientists and mathematicians. Studies range from observations, including using the latest in tracking technology, to carefully controlled laboratory experiments. And yet there is still much we do not know about how navigation mechanisms select and acquire information from the environment, how multiple sources of information do or do not interact with one another and why. These questions remain for the next generation of scientists eager to understand how animals find their way through their world.

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CHAPTER 23

TIMING IN ANIMALS: FROM THE NATURAL ENVIRONMENT TO THE LABORATORY, FROM DATA TO MODELS

Marco Vasconcelos, Marilia Pinheiro de Carvalho, and Armando Machado

The capacity to adjust to temporal regularities in the environment is widespread in the animal kingdom. Animals are able to tailor their behavior and physiology to a variety of periodic regularities spanning from very high to very low frequencies (i.e., from seconds to years).

One of the most obvious regularities is the daily light–dark cycle. An animal able to anticipate daily environmental changes and fine tune its behavior and physiology to them would certainly benefit in the struggle for survival and reproduction. Thus, from a functional perspective one would expect natural selection to have favored sensitivity to the correlates of the 24-hr rotation of the earth. In other words, natural selection should have engendered (as it did) what are known as *circadian rhythms* at the physiological and behavioral levels (see Volume 1, Chapter 29, this handbook). Such rhythms are generated by internal clocks set or entrained by regular environmental cues, with the daily light–dark cycle having the dominant role (e.g., Panda, Hogenesch, & Kay, 2002; Reppert & Weaver, 2002). Biological and social stimuli, though, may also entrain circadian rhythms (e.g., Davidson & Menaker, 2003; Mistlberger & Skene, 2004).

In animal research, the periodic nature of feeding activities has been given much of the spotlight. Circadian regulated feeding was found in a variety of species including, among many others, honeybees (*Apis mellifera*; Beling, 1929; Frisch & Aschoff, 1987; Pahl, Zhu, Pix, Tautz, & Zhang, 2007), garden warblers (*Sylvia borin*; Biebach, Falk, & Krebs, 1991), pigeons (*Columba livia*; Saksida & Wilkie, 1994), and rats (*Rattus norvegicus*; Bolles & Moot, 1973). Circadian clocks also seem to modulate sensory (e.g., Krishnan, Dryer, & Hardin, 1999) and cognitive performance in a variety of tasks and species (e.g., Cain, Chou, & Ralph, 2004; Kyriacou & Hastings, 2010), as well as a variety of physiological variables such as temperature (Refinetti & Menaker, 1992) and heart rate (Massin, Maeyns, Withofs, Ravet, & Gérard, 2000), to name a few.

Another periodic regularity is afforded by the 23.48° axial tilt of the earth as it makes its annual elliptical orbit around the sun. This tilt leads to the environmental periodicities called seasons, each raising its own challenges and opportunities to animal adaptation. Here too, natural selection sculpted organisms able to adjust behaviorally and physiologically to the many season-specific ordeals, thus allowing them to cope with the annual changes (Gwinner, 2012; Lincoln, Clarke, Hut, & Hazlerigg, 2006; Zucker, 2001). Adaptations to these long-term cycles include not only the well-known cases of hibernation (e.g., Kondo et al., 2006; Pengelley & Asmundson, 1974), migration (e.g., Gwinner, 2001), and reproduction (e.g., Karsch, Robinson, Woodfill, & Brown, 1989), but also, among many others, pelage growth (e.g., Martinet, Mondain-Monval, & Monnerie, 1992), timing of pupation in

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some insects (e.g., Nisimura & Numata, 2001), and food intake and body condition (Loudon, 1994).

These fine tunings to the daily and annual regularities of the environment are, to some extent, unsurprising considering their ubiquity and stability, as well as their daily impact in the animals' ecosystem. Perhaps more unexpected is the animals' ability to adjust to or display temporal regularities of seemingly arbitrary durations. Periodical cicadas of the genus *Magicicada* (Homoptera: Cicadidae) provide one of the most fascinating examples of long temporal regularities: Every 13 or 17 years, depending on the species, they emerge from the ground, develop into adults, mate, lay eggs, and die, all within an interval of 4–6 weeks (Williams & Simon, 1995). Most of the fascination with these long-lived insects comes from their prime-numbered life cycle and their synchronous emergence in staggering numbers (up to 3.5 million ha^{-1}). Several hypotheses have been put forward to explain this behavioral synchronicity, from the avoidance of long-lived parasitoids (Lloyd & Dybas, 1966a, 1966b) to predator avoidance (Hoppensteadt & Keller, 1976) and hybridization avoidance (Cox & Carlton, 1988, 1991), but the issue remains controversial (see, e.g., Grant, 2005).

What about arbitrary short durations? Do animals adjust their behavior when the environment imposes temporal regularities in the range of seconds to minutes? Animals are generally able to perform an action for a specific duration; anticipate an event once a particular interval has elapsed; retrospectively judge which of two intervals was shorter; or choose which of several cues signals the shortest delay to reward. This capacity is called *interval timing*, or timing, and it is the main topic of this chapter.

In what follows, we briefly underscore the relevance of interval timing in the natural habitat and then focus our discussion on laboratory research. We describe the most relevant experimental procedures, the typical pattern of results obtained with them, and two of the theoretical models that have been proposed to explain such results and generate novel predictions.

THE RELEVANCE OF SHORT INTERVALS

In the natural world, animals can use a multitude of cues to regulate their behavior. The time elapsed since a particular event is one of them, but one cannot be sure whether it is indeed used or if it interacts or is even confounded with other available cues. The assumption that timing regulates some behavior in the wild is to some extent risky given the lack of controls, but the abundant evidence for timing in carefully controlled laboratory experiments mitigates the risk. Be that as it may, there are several domains of animal behavior that would ostensibly benefit from interval timing in natural circumstances.

Any animal foraging on a renewable food source faces a natural timing task. Assuming the animal is sensitive to the inter replenishment intervals, it can forage more efficiently not only by avoiding recently visited food sources but also by visiting each particular resource at or close to the moment of its new replenishment. This behavior is known as cropping and has been observed in a variety of species. Cody (1971), for example, observed various species of finches in the Mohave Desert moving to different foraging sites each day and revisiting each site according to its replenishing interval. Similar behavior has been observed in pied wagtails (*Motacilla alba*; Davies & Houston, 1981) and many other species. Henderson, Hurly, Bateson, and Healy (2006) reported a particularly relevant field experiment with territorial rufous hummingbirds (*Selasphorus rufus*). The experimenters replenished eight artificial flowers at different intervals, four flowers 10 min after the bird emptied them, and the other four 20 min after being emptied. As Figure 23.1 shows, hummingbirds matched their return visits to the refill schedules, with the frequency distributions of intervisit times peaking at the appropriate intervals.

Closely related to these examples is time–place learning (for a review, see Thorpe & Wilkie, 2006), wherein animals change their foraging site according to predictable temporal patterns. Typical demonstrations include the anticipation of tidal rhythms by wading oystercatchers (*Haematopus ostralegus*) to match foraging bouts with the time mussel beds become exposed (Daan & Koene, 1981) and the increased visits by krestels (*Falco tinnunculus*) to a previously seldom visited field around the time mice were now regularly released (Rijnsdorp, Daan, & Dijkstra, 1981). This type of temporal regulation

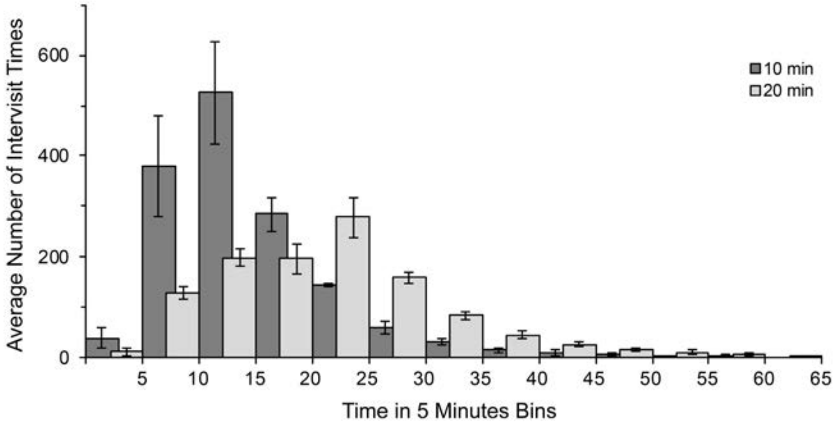

FIGURE 23.1. Average frequency distributions of intervisit intervals (n = 3 rufous hummingbirds). From "Timing in Free-Living Rufous Hummingbirds, *Selasphorus rufus*," by J. Henderson, T. A. Hurly, M. Bateson, and S. D. Healy, 2006, *Current Biology, 16*, p. 513. Copyright 2006 by Elsevier. Adapted with permission.

has been observed in many other species, including garden warblers (Biebach et al., 1991; Biebach, Gordijn, & Krebs, 1989), starlings (*Sturnus vulgaris*; Wenger, Biebach, & Krebs, 1991), eight small passerine species (Stein, 1951), honeybees (e.g., Beling, 1929; Wahl, 1932), a variety of fish (Barreto, Rodrigues, Luchiari, & Delicio, 2006; Delicio & Barreto, 2008), rats (e.g., Carr, Tan, & Wilkie, 1999; Carr & Wilkie, 1997; Pizzo & Crystal, 2002; Thorpe, Hallett, & Wilkie, 2007; Thorpe & Wilkie, 2005), and pigeons (e.g., Saksida & Wilkie, 1994; Wilkie, Saksida, Samson, & Lee, 1994).

Many of these time–place situations are amenable to circadian regulation, but interval timing is also involved in some of them, either exclusively (Wilkie et al., 1994) or in combination with circadian timing (e.g., Pizzo & Crystal, 2002). The length of the interval seems to be a key factor determining which timing mechanisms is deployed: Interval timing for relatively short durations and circadian timing for longer durations (Wilkie et al., 1994). Overall, time–place learning tasks may be solved on the basis of circadian and/or interval timing, depending for example on the discriminability of the time intervals, but also on many other relevant cues (e.g., in the oystercatchers' case, multiple visual cues that correlate with tides; see Crystal, 2006; Thorpe & Wilkie, 2006).

Optimal foraging theory (Stephens & Krebs, 1986) also presupposes suitable temporal perception. Assuming that resource distributions are unstable, thus precluding the evolution of stable strategies across generations, animals must develop foraging strategies on the basis of experienced distributions (McNamara & Houston, 1985). One of the best studied foraging scenarios is the marginal value theorem (MVT; Charnov, 1976; Parker & Stuart, 1976) as applied to central place foraging. Because the benefit of foraging in a particular patch increases less than linearly (the more food is found, the harder it is to obtain the next piece of food), at some point the local capture rate is lower than the average rate of the environment. The question then becomes, when should the animal abandon the patch? The answer is at the precise time when the local rate equals the overall rate (for a detailed treatment, see Chapter 14, this volume). Importantly, as the average travel time to a patch decreases so should the optimal residence time because the less time is spent traveling the higher the capture rate. To our knowledge this prediction was met in every test (e.g., Kacelnik, 1984).

It should be clear from the previous discussion that the MVT requires sensitivity to various time intervals such as travel time and interprey capture. In a laboratory task emulating the less than linear increase in benefit, Brunner, Kacelnik, and Gibbon (1992; see also Kacelnik & Brunner, 2002) showed that starlings seem to use interval timing to solve the task.

Communication is also, by definition, temporally structured: The sender must be able to transmit a message composed of signals in a particular sequence and duration such that the receiver is able to understand it. Songbirds, for example, learn songs and sometimes specific dialects by listening to other individuals (conspecifics or not; Baptista & Morton, 1988; Beecher & Brenowitz, 2005; Beecher, Campbell, & Stoddard, 1994; Marler & Tamura, 1964; see also Volume 1, Chapters 26 and 30, this handbook). This requires learning the frequencies and durations of each song component. Similarly, a variety of insect species including brush-legged wolf spiders (*Schizocosa ocreata*; Gibson & Uetz, 2008), field crickets (*Teleogryllus oceanicus*; Rebar, Bailey, & Zuk, 2009), and fireflies (*Coleoptera: Lampyridae*; Lewis & Cratsley, 2008) extract information used in mate choice from the interpulse intervals and other temporal properties of the signals sent by potential partners.

This small tour illustrates the adaptive contributions that interval timing may have in countless naturally occurring behaviors. But to understand the precise properties of interval timing, understood as the control of behavior by arbitrary periodicities shorter than 24 h, we need to resort to the controlled conditions of the laboratory.

THE PSYCHOPHYSICS OF TIME: PROCEDURES AND DATA

The control of behavior by relatively short intervals has been evident since early laboratory experiments in classical and operant conditioning. Even though we will focus our discussion in operant preparations, some of the first examples were reported by Pavlov (1927). For example, when a delay conditioning procedure is used (i.e., the learned cue, the conditional stimulus, is presented on its own and ends with the presentation of the biologically relevant stimulus, the unconditional stimulus), animals show a conditioned response only toward the end of the interval. This phenomenon is called *inhibition of delay* and suggests the animal is timing the learned cue.

The field of interval timing has produced some of the most elegant experimental procedures and explanatory models in the field of experimental psychology. We describe next some of the typical procedures, including concurrent timing tasks, in which animals respond as the critical interval elapses (e.g., fixed-interval schedule, mixed fixed-interval schedules, peak procedure) and retrospective timing tasks in which the animal responds only after an interval ends (e.g., temporal generalization procedure, bisection task). We will then use some of them to illustrate how the models handle different tasks.

The Fixed-Interval Schedule and the Mixed Fixed-Interval Schedule

The operant equivalent of the delay conditioning procedure that led to the discovery of inhibition of delay is the fixed-interval (FI) reinforcement schedule. In a FI T-s schedule, a time maker such as the previous reinforcer or the onset of a tone or a light initiates the to-be-timed interval. Responses during the T-s interval are not reinforced and the first response after T-s elapse is reinforced and terminates the trial.

Clearly, optimal performance in such a schedule requires a single response immediately after T-s have elapsed. But as we will see in the following sections, timing mechanisms are not sufficiently accurate for such a pattern of behavior to emerge. Instead, as training proceeds, animals start to temporally differentiate their behavior, with little or no responding early in the interval, followed by one of two possible patterns: (a) a gradual acceleration of responding peaking near the end of the interval (the scallop pattern; Dews, 1978) or (b) a sudden transition from a low rate of responding to a high and constant rate that persists until the end of the interval (the break-and-run pattern; Schneider, 1969). Which pattern is observed seems to depend on the length of the interval, with longer intervals engendering the former. Regardless of the pattern observed on each trial, when a number of such trials are aggregated, the response-rate function resembles and is well fitted by the left limb of a normal distribution. Figures 23.2a and 23.2b show data from pigeons and rats trained in FIs ranging from 30 s to

300 s and from 3 h to 7 h, respectively. For a comparative analysis of fixed-interval performance in several species, including pigeons, rats, woodmice (*Apodemus sylvaticus*), domestic turtle doves (*Streptopelia risoria*), tilapia (*Sarotherodon niloticus*), and freshwater turtles (*Pseudemys scripta elegans*), see Lejeune and Wearden (1991). Boisvert and Sherry (2006) reported similar findings in an invertebrate, the bumble bee (*Bombus impatiens*).

Through the years, a flurry of research has attempted to identify the variables that influence responding in FI schedules, including the interval length, the amount of training, and the magnitude of the reward on several dependent variables such as the duration of the initial pause, the overall pattern of responding (break-and-run versus scallop), and the rate of responding, among others (e.g., Dews, 1978; Guilhardi & Church, 2004; Lejeune & Wearden, 1991; Lowe & Harzem, 1977; Lowe, Harzem, & Spencer, 1979; Richelle & Lejeune, 1980; Schneider, 1969; Wynne & Staddon, 1988). Undoubtedly, the most relevant finding was that the response rate functions superimpose when both axes are scaled; the *x*-axis with respect to T and the *y*-axis with respect to the maximum response rate observed during the interval (e.g., Dews, 1970). Figures 23.2c and 23.2d show examples of superimposition of rate functions. Superimposition across different FI values means that, regardless of the absolute FI value, the same proportion of the maximum response rate occurs at a particular proportion of the interval. Known as the *scalar*

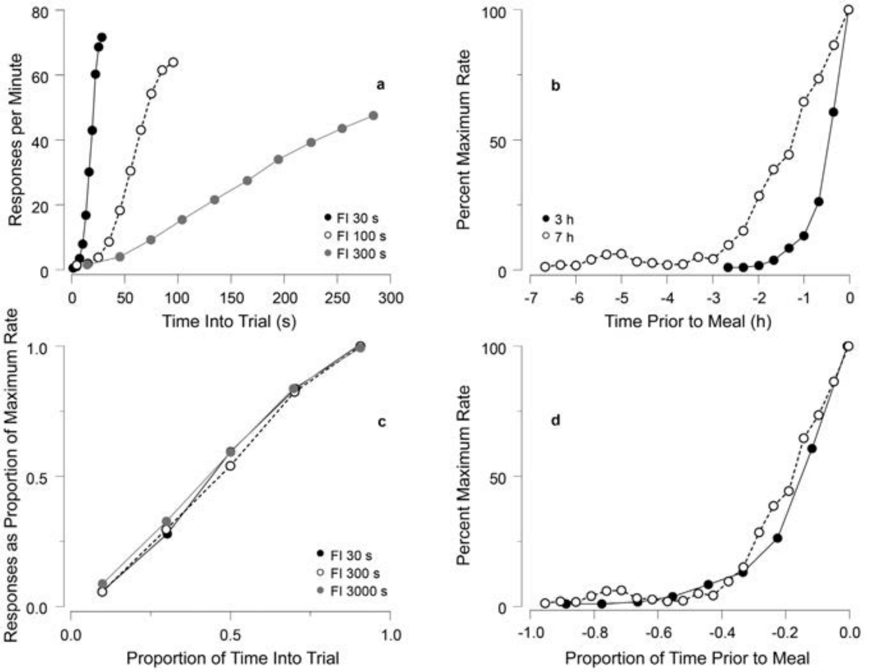

FIGURE 23.2. Average response rates in different FI schedules as a function of time into the trial. (a) Average response rates (n = 3 pigeons) in three FI schedules. Adapted from "Arousal: Its Genesis and Manifestation as Response Rate," by P. R. Killeen, S. J. Hanson, and S. R. Osborne, 1978, *Psychological Review, 85*, p. 574. Copyright 1978 by the American Psychological Association. (b) Average response rates (n = 6 rats) in two modified FI schedules. Adapted from "Circadian Time Perception," by J. D. Crystal, 2001, *Journal of Experimental Psychology: Animal Behavior Processes, 27*, p. 70. Copyright 2001 by the American Psychological Association. (c) The superposition of data from three FI schedules as predicted by the scalar property. From *The Theory of Reinforcement Schedules* (p. 48), by W. N. Schoenfeld, 1970, New York, NY: Appleton-Century-Crofts. Copyright 1970 by Appleton-Century-Crofts. Adapted with permission. (d) Data from Crystal (2001) plotted as relative response rate as a function of relative time.

property, this is the quasiuniversal hallmark of short interval timing (for discussions of its violation, see Lejeune & Wearden, 2006; Staddon & Cerutti, 2003; Zeiler & Powell, 1994).

To observe the scalar property, the standard deviation of the measured behavioral variable should increase linearly with its mean, yielding a near-constant *coefficient of variation*. If we define timing accuracy by the coefficient of variation, then the scalar property means that timing accuracy remains constant across different intervals. The scalar property is thus the equivalent of Weber's law in the time domain (see Chapters 1 and 16, this volume). Given its ubiquity, the scalar property has imposed a significant constraint to timing theories as it must be accommodated in some fashion. This property gives the name to one of such theories, the scalar expectancy theory (Gibbon, 1977, 1991; Gibbon, Church, & Meck, 1984).

One issue that remains poorly understood is the effect of reinforcement at T on durations longer than T. The few studies and observations that omitted the reinforcer and prolonged the interval indicate that the response rate either remains high (Ferster & Skinner, 1957; Machado & Cevik, 1998; Monteiro & Machado, 2009) or oscillates between pauses and periods of responding (Crystal & Baramidze, 2007; Kirkpatrick-Steger, Miller, Betti, & Wasserman, 1996; Machado & Cevik, 1998; Monteiro & Machado, 2009), depending on how long the interval is prolonged. In other words, reinforcement at T seems to have different effects on responding before and after T. This asymmetry challenges the inference that because the maximum response rate occurs at T, the animal is timing the interval. Hence some researchers prefer to analyze the time of the first response (known as waiting time) in FI schedules. The general finding is, however, that the steady-state duration of the average waiting time is indeed a linear function of the programmed FI (Catania, 1970; Ferster & Skinner, 1957; Richelle & Lejeune, 1980; Wynne & Staddon, 1988).

The FI schedule is also often used in mixed schedules. In one of the simplest, the *mixed FI* T_1-*FI* T_2 *schedule*, on a proportion of trials, *p*, the first response after T_1 s have elapsed is reinforced; on the remaining trials, reinforcement is contingent on the first response after T_2 s have elapsed, with $T_1 < T_2$ (Catania & Reynolds, 1968; Ferster & Skinner, 1957; Leak & Gibbon, 1995; Lima, 2010; Whitaker, Lowe, & Wearden, 2003, 2008). Because both FIs are signaled by the same cue, when the FI T_1 is in effect, the average response pattern is similar to the one observed in the single FI schedule of reinforcement. However, when the FI T_2 is in effect, a bimodal response pattern emerges. Figure 23.3 shows the response rate function obtained by Whitaker et al. (2003) using a mixed FI 30 s-FI 240 s. The function shows an increase in response rate toward a peak located close to 30 s into the trial, a subsequent decrease to low levels, and a final increase reaching a peak at 240 s.

The mixed FI-FI schedule of reinforcement is particularly important to understand timing mechanisms, for it shows that animals are able to learn to time two intervals to food signaled by the same cue. Moreover, some models assume the existence of separate memory stores for each reinforced interval (i.e., concentrated memories), whereas others assume that temporal memories are distributed. The response patterns observed in the longer components of a mixed FI-FI schedule are consistent with the latter and raise serious challenges to the former.

The Peak Procedure

Intimately related to the FI schedule, the *peak procedure* (Catania, 1970; S. Roberts, 1981) allows us to directly assess temporal memories. In some cases, it also illustrates the ability of animals to time at least two different intermixed durations sometimes signaled via different sensory modalities (e.g., S. Roberts, 1981). Formally a mixed schedule, the peak procedure is composed of two types of trials signaled by the same cue: regular FI T-s training trials interspersed with longer trials (say 3T s) ending without reinforcement, and known as *peak* or *empty trials*. Typically, after sufficient training, the average response rates on peak trials increase from $t = 0$ to $t = T$ and then decreases again as t surpasses T. Figures 23.4a and 23.4b show average response rates from rats and humans in peak trials. As for relatively short FIs, these smooth functions are usually an averaging artifact, given that performance on individual peak trials usually follows a break-run-break

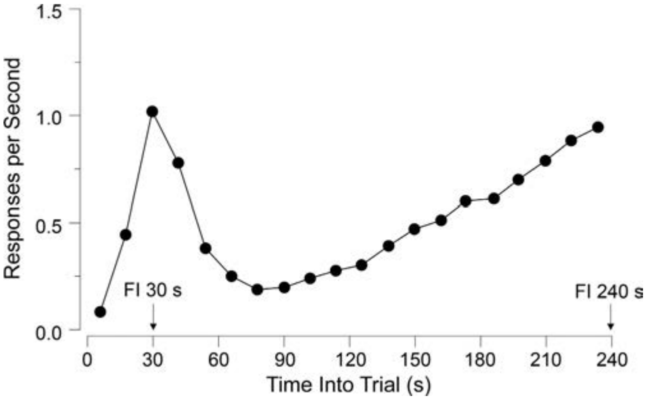

FIGURE 23.3. Average response rate as a function of time into the trial in a mixed FI 30–FI 240 s schedule (n = 4 rats). Adapted from "Multiple-Interval Timing in Rats: Performance on Two-Valued Mixed Fixed-Interval Schedules," by S. Whitaker, C. F. Lowe, and J. H. Wearden, 2003, *Journal of Experimental Psychology: Animal Behavior Processes, 29,* p. 280. Copyright 2003 by the American Psychological Association.

pattern (e.g., Cheng & Westwood, 1993; Cheng, Westwood, & Crystal, 1993; Church, Meck, & Gibbon, 1994; Gibbon & Church, 1990, 1992; Zeiler & Powell, 1994).

The response rate function typically observed in peak trials has been extensively studied, including the location of its mode (peak time), the height at the mode (peak rate), its symmetry around T, how it changes with different time markers, and how it evolves throughout training (e.g., Balci et al., 2009; Gibbon et al., 1984; Kaiser, 2008; S. Roberts, 1981, 1998; W. A. Roberts, Cheng, & Cohen, 1989). Still other studies have examined the effects of sudden interruptions of the stimulus signaling trial onset (e.g., Cabeza de Vaca, Brown, & Hemmes, 1994; Kaiser, Zentall, & Neiman, 2002; S. Roberts, 1981, 1998). When relatively long empty trials are used sometimes response rate increases again toward the end of the trials (e.g., Kaiser, 2008; W. A. Roberts et al., 1989) and may even show a cyclic pattern (Crystal & Baramidze, 2007; Kirkpatrick-Steger et al., 1996; Machado & Cevik, 1998; Monteiro & Machado, 2009). But for our purposes, two findings are particularly noteworthy. First, as for the fixed interval schedules, the curves for different values of T superimpose when plotted in a common scale (i.e., they follow the scalar property); Figures 23.4c and 23.4d show the same data of Figures 23.4a and 23.4b plotted in scaled axes. Second, to observe the decrease in response rate for intervals longer than T, the animal must repeatedly experience those intervals in extinction.

The Temporal Generalization Procedure

The temporal generalization procedure is a conditional discrimination task in which the sample duration signals whether a response will be reinforced. In its simple form, it is the retrospective analog of the FI schedule: Each training trial involves the presentation of a stimulus with one of two possible durations, T_S or T seconds, with $T_S < T$. At the end of the stimulus, a response key is illuminated or a lever is inserted to allow the animal to respond, but only responses that follow T are reinforced; those that follow T_S are not. After learning this discrimination, unreinforced generalization trials with intermediate durations are interspersed amongst the training trials. Typically, the response rate or probability increases from T_S to T, with the gradients obtained with different values of T following the scalar property.

If instead of two, the stimulus has three possible durations (T_S, T, and T_L; with $T_S < T < T_L$) and responses are reinforced only after T, we obtain the

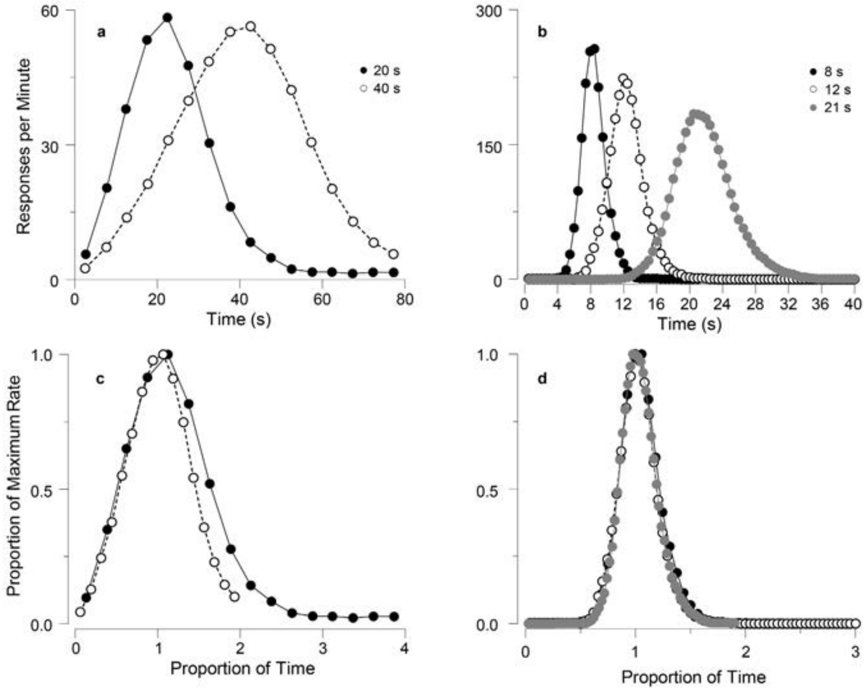

FIGURE 23.4. Average response rates as a function of time into the trial in peak trials. (a) Average response rates (n = 10 rats) in peak trials (the corresponding FIs were 20 s and 40 s). Adapted from "Isolation of an Internal Clock," by S. Roberts, 1981, *Journal of Experimental Psychology: Animal Behavior Processes, 7,* p. 245. Copyright 1981 by the American Psychological Association. (b) Average response rates (n = 7 humans) in peak trials for participants tested with 8 s, 12 s, and 21 s signal durations. Adapted from "Scalar Expectancy Theory and Peak-Interval Timing in Humans," by B. C. Rakitin, J. Gibbon, T. B. Penney, C. Malapani, S. C. Hinton, and W. H. Meck, 1998, *Journal of Experimental Psychology: Animal Behavior Processes, 24,* p. 21. Copyright 1998 by the American Psychological Association. (c) Data from (a) plotted as relative response rate as a function of relative time. (d) Data from (b) plotted as relative response rate as a function of relative time.

retrospective timing task equivalent to the peak procedure. Because now the animal experiences reinforcement at T and extinction at shorter and longer intervals, the gradient becomes Gaussian-like, peaking a T. Also, the longer T is, the broader the generalization gradients are and, when different values of T are compared, these gradients conform to the scalar property, superimposing when plotted with rescaled axes. Figures 23.5a and 23.5b show the response probability functions obtained by Church and Gibbon (1982) with T = 2 and 4 s, $T_S = 0.8$ s, and $T_L = 7.2$ s. As in previous procedures, the curves superimpose in relative time (Figure 23.5c).

One outstanding issue concerns the shape of the generalization gradient outside the trained range. Few studies have analyzed systematically the issue with durations shorter than T_S or longer than T_L (see Church & Gibbon, 1982), but the issue is theoretically relevant given that different timing models either predict or assume particular patterns outside the experienced ranges.

The Bisection Task

The bisection task is one of the procedures most extensively used to understand timing in general and the properties of the generalization gradients in particular. In this task, a trial begins with one of two samples differing only in duration: the short sample, S_S (e.g., a 2 s light or tone), or the long sample, S_L (e.g., an 8 s light or tone). After

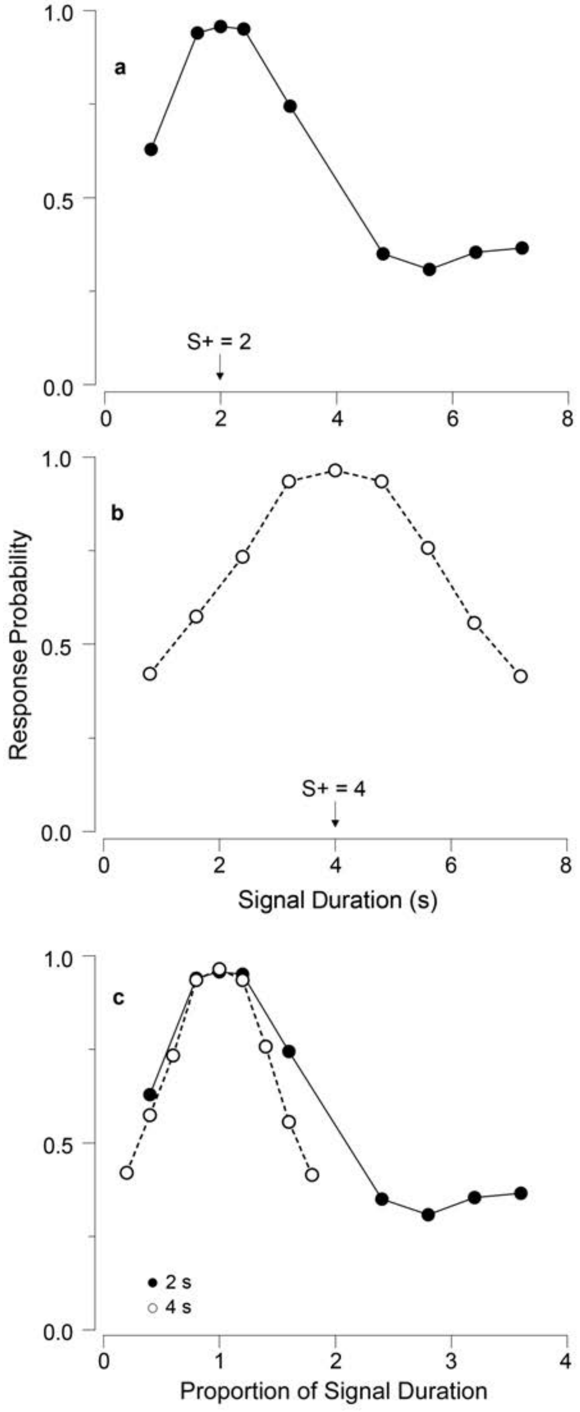

FIGURE 23.5. Median response probabilities as a function of signal duration. Reinforced durations were (a) 2 s (n = 7 rats) and (b) 4 s (n = 10 rats). (c) Data from (a) and (b) plotted as relative response rate as a function of relative time. Adapted from "Temporal Generalization," by R. M. Church and J. Gibbon, 1982, *Journal of Experimental Psychology: Animal Behavior Processes, 8,* p. 172. Copyright 1982 by the American Psychological Association.

the sample, two *manipulanda* are simultaneously made available—two levers may slide into the operant chamber when studying rats or two response keys may be illuminated when studying birds. For simplicity, we refer to responses on these manipulanda as R_1 and R_2. The task of the subjects is to learn an arbitrary mapping. For example, choices of R_1 following S_S and of R_2 following S_L are reinforced, but not otherwise. Once they learn this task, the experimenter presents new samples of intermediate durations and measures the choices of, say, R_2. The function relating the proportion of R_2 responses to the sample duration is the *psychometric function*. Figure 23.6a shows typical psychometric functions from the seminal work of Church and Deluty (1977).

In this task animals are required to classify the just experienced interval (the sample) as relatively short or long. As Figure 23.6a suggests, the transition from a *short* to a *long* classification is rather smooth, not abrupt. In effect, the typical gradient is ogival, with few or no long responses at S_S and reaching its maximum at S_L. Of particular interest is the duration at which they choose R_1 and R_2 equally often, called the *point of subjective equality* (PSE) or the bisection point, for it is interpreted as the duration perceived as halfway between the short and the long samples. The PSE tends to be at the geometric mean of the trained durations ($GM = \sqrt{(S_S{*}S_L)}$; Catania, 1970; Church & Deluty, 1977; Platt & Davis, 1983; Stubbs, 1976). Moreover, as Figure 23.6b illustrates, gradients obtained with sample pairs with the same ratio (e.g., $S_{S1} = 1$ vs. $S_{L1} = 4$, $S_{S2} = 2$ vs. $S_{L2} = 8$, and $S_{S3} = 4$ vs. $S_{L3} = 16$), superimpose when plotted in relative time (e.g., test duration / long duration).

THEORIES OF INTERVAL TIMING

The field of interval timing has been a vibrant area of research for the last 40 years, yielding a plethora of research findings to which the previous section can barely do justice. The empirical developments were accompanied by hefty advancements on the theoretical front. What are the mechanisms underlying

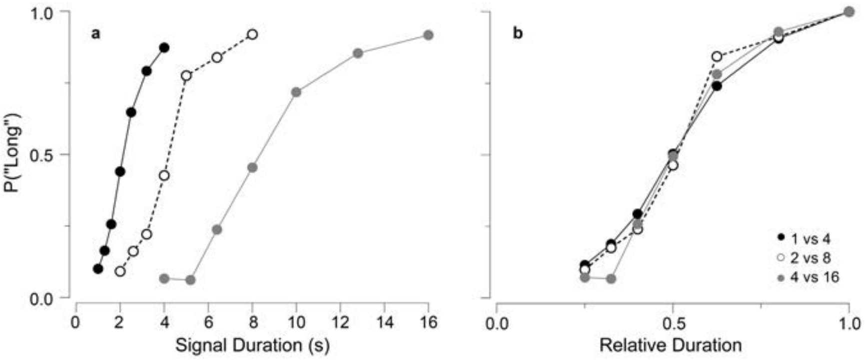

FIGURE 23.6. Temporal generalization gradients obtained in three bisection tasks (n = 8 rats). (a) One s versus four s samples, two s versus eight s samples, and four s versus 16 s samples. (b) Data from (a) plotted as relative response rate as a function of relative time. Adapted from "Bisection of Temporal Intervals," by R. M. Church and M. Z. Deluty, 1977, *Journal of Experimental Psychology: Animal Behavior Processes, 3,* p. 220. Copyright 1977 by the American Psychological Association.

interval timing? How do those mechanisms engender Weber's law in the time domain (i.e., the scalar property)? These are two of the unavoidable questions that any theory of timing must tackle. We will focus our discussion in two models: the scalar expectancy theory (SET; e.g., Gibbon, 1977, 1991; Gibbon & Church, 1984; Gibbon et al., 1984) and the learning-to-time model (LeT; Machado, 1997; Machado, Malheiro, & Erlhagen, 2009). The former, a cognitive, information processing model, is arguably the most influential model of animal and human timing. The latter emerged from the behaviorist tradition and has proved to have broad generality. Many other models could be discussed; a non-exhaustive list includes the multiple oscillator theory of timing (Church & Broadbent, 1990; see also Gallistel, 1990), the behavioral economic model of timing (Jozefowiez, Staddon, & Cerutti, 2009), the behavioral theory of timing (Killeen & Fetterman, 1988), packet theory (Kirkpatrick, 2002) and its modified version, modular theory of learning (Guilhardi, Yi, & Church, 2007), the multiple-time-scale timing model (Staddon & Higa, 1999), the spectral model (Grossberg & Schmajuk, 1989), the diffusion model (Staddon & Higa, 1991), and the active time model (Dragoi, Staddon, Palmer, & Buhusi, 2003) among numerous others, some neurobiologically inspired. We focus our attention on only two, not only in the interest of space but also for theoretical reasons: SET is intuitively clear at first glance and highly influential whereas LeT proposes entirely different timing processes that have been studied extensively in the laboratory.

The Scalar Expectancy Theory

SET (e.g., Gibbon, 1977, 1991; Gibbon & Church, 1984; Gibbon et al., 1984) is unquestionably a hallmark in our understanding of timing processes. It has inspired highly creative research and several generations of researchers as well as alternative approaches from those disagreeing with its assumptions or unease with its inconsistencies.

SET is a steady-state pacemaker-accumulator model with the structure shown in Figure 23.7a: A pacemaker generates pulses at a high rate, an accumulator adds the pulses when a switch is closed, a long-term memory store saves the counts from the accumulator at the end of each reinforced interval, and a comparator keeps track of the relative discrepancy between current (i.e., accumulator) time and target (i.e., memory) time. When the discrepancy is small enough, the animal starts responding.

It is known that animals' temporal judgments vary from trial to trial and that such judgments usually follow the scalar property. This implies that the timing mechanism must have at least one source of variance. For SET, variance can arise at the clock, the long-term memory, the comparator,

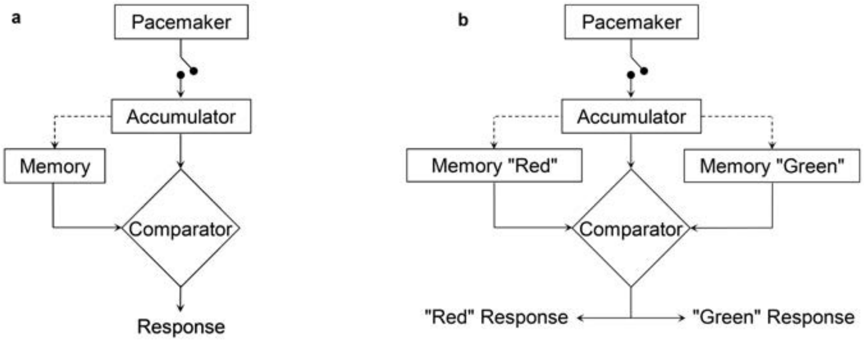

FIGURE 23.7. **The structure of SET. A pacemaker generates pulses which are added to an accumulator and stored in one or more long-term memories stores at the end of the to-be-timed interval (dashed lines). The animal compares the number of pulses currently in the accumulator with samples extracted from the memories to decide when and where to respond. (a) In FI schedules, only one long-term memory store is formed. (b) In the bisection procedure, two long-term memories are formed.**

or the switch latency. The pacemaker is usually conceived of as a Poisson emitter, that is, a device that generates pulses at a constant rate on average, but random, exponentially distributed interpulse intervals (Gibbon, 1977, 1992). Mathematically, a Poisson timer leads to the opposite of what is usually seen, relatively more accurate timing with larger intervals because, in Poisson processes, the variance (not the standard deviation) increases proportionally with the mean, and the coefficient of variation decreases instead of remaining roughly constant. SET has addressed this issue in several ways, but typically it is assumed that the pacemaker emits pulses at a rate that remains constant within a trial but varies from trial to trial according to a normally distributed random variable (Gibbon et al., 1984). This generates scalar variance. Still within the clock subsystem, the switch may have variable latencies to close and open thus adding variability to the system, but such variability should be independent of the stimulus duration.

Long-term memory can also introduce variability at the moment of storage and retrieval. For example, is has been assumed that under some circumstances the counts in the accumulator are multiplied by a Gaussian random variable, *k*, when transferred to long-term memory. Finally, variance can also arise in the decision phase if we assume that the point at which the relative discrepancy between elapsed and target time is small enough varies from trial to trial (for a detailed discussion of sources of variance, see Gibbon, 1992; Gibbon et al., 1984).

To grasp the dynamics of SET, we will assume only one source of variance, that of the pacemaker, with its rate varying from trial to trial according to a normal random variable. Consider, for instance, a FI 10 s. At the onset of a to-be-timed stimulus four important events occur: (1) one sample is drawn from a normal distribution determining the pacemaker rate, λ; (2) the accumulator is reset to 0; (3) the switch is closed and the pulses from the pacemaker start flowing into the accumulator, the accumulator then tracks the duration of the signal via the number of pulses it contains, and; (4) a sample from the long-term memory store is retrieved. Because this is a steady-state model, it is assumed that this store is already populated with previously reinforced subjective durations. As time elapses, the comparator continuously compares the elapsed time (i.e., number of pulses in the accumulator) with the remembered time. When the relative discrepancy between the two is lower than a given decision threshold, *b*, the animal starts responding at a constant rate until the end of the trial. The typical decision rule for a FI schedule is

$$\frac{N-\lambda t}{N} < b \tag{1}$$

where N is the number of pulses in the sample extracted from long-term memory, λ is the rate of the pacemaker in the trial and t is the elapsed time (λt is therefore the current number of pulses in the accumulator), and b is the threshold value. This mechanism generates the aforementioned break-and-run pattern. Finally, when the signal terminates and the response is reinforced, the switch opens and the number of pulses in the accumulator is transferred to long-term memory.

The pacemaker rate and the sample extracted from long-term memory will almost certainly be different on different trials, and therefore the moment the relative discrepancy falls below the threshold will also vary across trials. The effect of this variation are shifted break-and-run patterns that, when averaged, yield a smooth sigmoid response rate function similar to the average data shown in Figures 23.2a and 23.2b. Figure 23.8 illustrates the dynamics of a FI trial according to SET.

The extension of SET to the peak procedure is straightforward. At stimulus onset on a given peak trial, a random sample sets the pacemaker rate (λ), the switch is closed allowing the pulses to be transferred to the accumulator and a sample from long-term memory is retrieved. As the value in the accumulator increases, the relative discrepancy between the number in the accumulator and the number retrieved from memory decreases. When

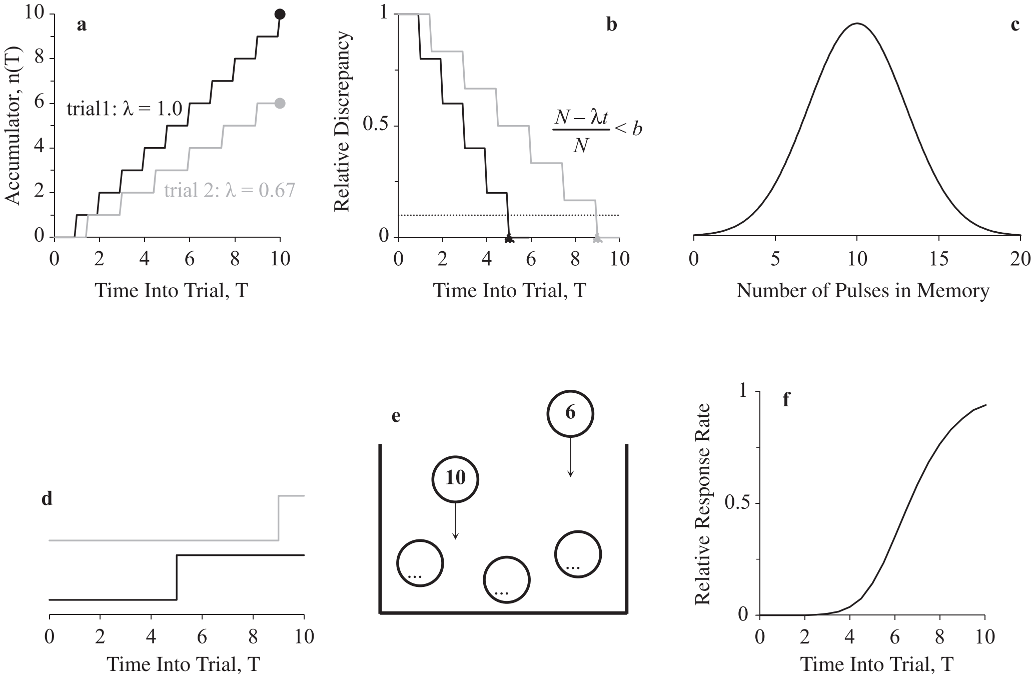

FIGURE 23.8. The dynamics of SET in a FI 10 s schedule. (a) As time into the trial elapses, the number of pulses in the accumulator increases at a rate λ pulses. Two trials are shown, one with $\lambda = 1.0$ and the other with $\lambda = .67$, with λ sampled at the beginning of each trial from a normal distribution. (b) To decide when to respond, the animal compares at each moment the number of pulses in the accumulator (λt) with the sample extracted from long-term memory (N). When the relative discrepancy between the two crosses the threshold, in this case $b = .1$, the animal starts to respond. The decrease in relative discrepancy is shown for $\lambda = 1.0$ and N = 5, and for $\lambda = .67$ and N = 6. The inset shows the decision rule. (c) The long-term memory store from where N is retrieved contains the number of pulses reached in previous reinforced trials. (d) once the threshold is crossed, the response rate is high and constant. Two functions are shown, one with a start point at 5 s (when $\lambda = 1.0$ and N = 5) and the other with a start point at 9 s (when $\lambda = .67$ and N = 6), each with a break and run pattern. (e) When the final response is reinforced, the number of pulses in the accumulator is transferred to the long-term memory store, 10 when $\lambda = 1.0$ and 6 when $\lambda = .67$. These counts are now included in the long-term memory distribution shown in (c). (f) Averaged across many trials, the break and run pattern generated in individual trials yields a smooth sigmoid response rate function.

the discrepancy falls below the threshold, *b*, the animal starts to respond at a relatively constant rate. As time elapses, the discrepancy reaches 0 and then increases because on peak trials the reinforcer is omitted and the trial is extended well past the usual reinforcement time. When the discrepancy exceeds the threshold, *b*, the animal ceases to respond. The net effect is a break-run-break pattern on a trial by trial basis and an average Gaussian-like function similar to the average data shown in Figures 23.4a and 23.4b.

Detailed analyses, however, suggest that to explain some experimental findings two independent thresholds, b_1 and b_2, may be necessary. Moreover, it seems that the two thresholds should be sampled from random variables with different means and variances (Church et al., 1994). In a two-threshold SET model, b_1 and b_2 determine the start and stop times, respectively, according to the modified decision rule

$$-b_2 < \frac{N - \lambda t}{N} < b_1 \tag{2}$$

For the bisection task, further elaborations are needed. Recall that in this task each trial involves one of two intervals, S_S or S_L, say 2 s or 8 s, respectively; once the interval elapses, the animal has to classify the sample as short or long depending on its duration. Testing involves the presentation of unreinforced intermediate durations. To clarify the description, let us assume that the correct responses after the 2 s and 8 s samples are red and green, respectively. Because the task involves two intervals, SET assumes that two long-term memory stores are formed during training, containing the counts from previous experiences with the 2 s and 8 s samples. Figure 23.7b shows the structure of SET for this task. As usual, at stimulus onset a randomly drawn sample determines the pacemaker rate, λ, and the switch closes allowing the pulses to flow into the accumulator. Once the sample ends, the switch opens and the animal then compares the number of pulses in the accumulator (λt) with, not one but two samples, a sample retrieved from the 2 s long-term memory store (N_R), and a sample retrieved from the 8 s long-term memory store (N_G). If λt is more similar to N_G, the animal tends to classify the sample as long, otherwise it tends to classify the sample as short. Formally, the probability of choosing green is given by

$$P(G) = P\left(\frac{\lambda t}{N_R} > \frac{N_G}{\lambda t}\right) \tag{3}$$

Detailed analyses show that SET predicts the superimposition of psychometric functions when the ratio of the samples is held constant and the PSE at the geometric mean of the trained durations (see Gibbon, 1981). Figure 23.9 illustrates the dynamics of a 2 s sample and an 8 s sample trial according to SET.

As it can be surmised from the previous descriptions, SET is not a unitary model but a family of models. Modifications can be implemented at each of its main components (the clock, the long-term memory, and the comparator) to accommodate the specificities of a particular timing task, but caution is recommended. On the one hand, coherence requires that similar tasks should be tackled with similar if not equal models. On the other hand, noticeably different tasks may grant modifications to capture their distinctiveness (Wearden, 1999). Of course this distinction is not always clear and the proliferation of "family members" has prompted harsh critiques (e.g., Staddon & Higa, 1999) and ultimately alternative models. We turn to one such model next.

The Learning-to-Time Model

LeT (Machado, 1997; Machado et al., 2009) is a dynamic account of how time comes to control behavior, using as raw ingredients well-known principles of learning. Specifically, it relies on reinforcement, extinction, and generalization operationalized in fairly simple ways (e.g., linear learning rules) to predict and explain the temporal differentiation of behavior during acquisition and steady state. Because LeT does not appeal to specialized timing mechanisms but merely uses general and widely studied principles, we believe it sets the standard for those proposing complex and dedicated timing mechanisms.

Metaphorically, LeT spatializes time and the task of the animal is to learn through trial and success where relevant events (such as food) occur. The model has three components, whose basic structure

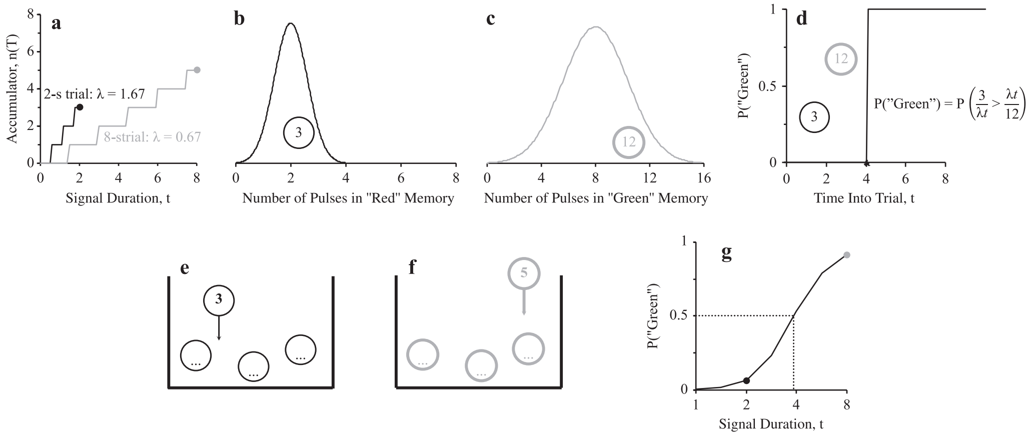

FIGURE 23.9. The dynamics of SET in a bisection task with a short sample of 2 s and a long sample of 8 s mapped onto red and green, respectively. (a) In all trials, the number of pulses in the accumulator increases at a rate λ pulses per second. Two trials are shown, a 2 s trial with λ = 1.67 and an 8 s trial with λ = .67, with λ sampled at the beginning of each trial from a normal distribution. When the signal terminates, the animal compares the number of pulses in the accumulator (λt) with two memory samples, one retrieved from (b) the 2 s long-term memory, $N_R = 3$, and (c) the other from the 8 s long-term memory, $N_G = 12$; the long-term memory stores from where N_R and N_G are retrieved contain the number of pulses reached in previous reinforced trials. (d) If the number of pulses in the accumulator is more similar to N_G, the animal tends to choose green, otherwise it is more likely to choose red. The inset shows the decision rule. If the animal chooses the correct response and receives food, the number of pulses in the accumulator is transferred to either (e) the 2 s long-term memory store or (f) the 8 s long-term memory store, depending on the chosen response. These counts are now included in the long-term memory distributions shown in (b) and (c). (g) when the animal learns to correctly classify the two samples, new intermediate durations are introduced. Averaged across many trials, a smooth and ogival psychometric function is obtained, with a Point of Subjective Equality at the geometric mean of the trained durations.

is represented in Figure 23.10a: a set of behavioral states (n = 1, 2, . . .), a set of associative links connecting the states to the operant response, and the operant response itself. At the onset of a time marker, the states are activated serially, one at a time. With training they become differentially associated or coupled with the operant response. From these two features, temporal regulation emerges: As time passes, different states become active; active states strongly coupled with the operant response occasion that response, whereas active states weakly coupled with the operant response do not occasion it.

LeT describes performance in FI schedules as follows. Once a trial starts, the behavioral states activate serially, one at a time. The speed of activation, λ, is a Gaussian random variable, with mean μ and standard deviation σ sampled at the beginning of each trial. The first state is active from 0 to 1/λ seconds, the second from 1/λ to 2/λ, and so on. In a FI 10 s schedule, for example, assume that λ = 1 state/second at trial onset. Hence state n = 10 will be active at 10 s when the subject responds and receives food. On another trial, λ might equal 0.8 states/second and state n = 8 will be active at 10 s. In other words, the state active at 10 s or shortly thereafter varies from trial to trial. The model's response rule states that although state n ≥ 1 is active, the animal responds if the strength of the link of that state, W(n), is greater than a threshold θ. To mimic undifferentiated responding at the beginning of training, the initial strength (W0) of all links is greater than θ.

Finally, when the subject responds and receives food, the link between the active state, n*, and the operant response increases by the amount $\Delta W(n^*) = \beta[1 - W(n^*)]$, where $\beta > 0$ is a reinforcement parameter, and the links from the earlier states (n < n*), active during extinction,

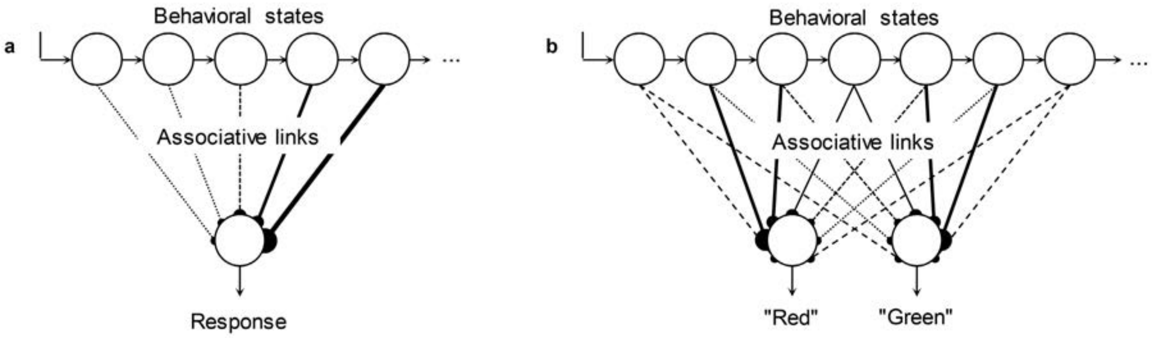

FIGURE 23.10. Components of the LeT model. A time marker initiates the activation of the behavioral states. Each state is associated with the operant response via the associative links. (a) In FI schedules, only one vector of associative links is formed coupling the behavioral states to the operant response. (b) In the bisection procedure, two vectors of associative links are formed connecting each state to each available response.

decrease by the amount $\Delta W(n) = -(\alpha/n^*)W(n)$, where $\alpha > 0$ is an extinction parameter. The links of all inactive states ($n > n^*$) do not change their current strength. To summarize, the link strength of the reinforced state, n^*, increases; that of all previous states, decreases; and that of all subsequent states does not change. Figure 23.11 illustrates the dynamics of a FI trial according to LeT.

The cumulative effect of reinforcement is to increase the links of the states more likely to be active at 10 s; conversely, the cumulative effect of extinction is to decrease the links of the states more likely to be active before 10 s. In particular, the links of the initial states decrease below θ and, hence, the subject ceases to respond at the beginning of the interval (the post-reinforcement pause). At the steady state, the link strengths express the cumulative effects of reinforcement and extinction—the animal's learning history—and form a distributed temporal memory.

The model predicts a break and run pattern for relatively short FIs and a scallop-like pattern for longer FIs (Dews, 1978; Machado et al., 2009; Schneider, 1969); the average response rate function will be sigmoidal, similar to the data shown in Figures 23.2a and 23.2b. Interestingly, the model also predicts that if we extend the trial well beyond T, responding should persist unabated for a long time, for the states that become active after T will have remained inactive during training and therefore will have preserved their initial links at $W0 > \theta$.

The model accounts for the scalar property by means of its state activation dynamics and its extinction rule. Parameter λ, the random variable that governs the speed of state transition, induces scalar variability in the active state at time t (i.e., if $n(t) \approx \lambda t$, $\text{avg}(n(t)) \approx \mu t$, and $\text{var}(n(t)) \approx \sigma^2 t^2$). Moreover, the decrease in the links of states active in extinction is inversely proportional to the number of the reinforced state (α/n^*). The rule means that the effect of extinction decreases with T—the longer the FI value, T, the higher $n^* \approx \mu T$, and the smaller the effect of extinction, $\alpha/(\mu T)$, a result akin to the partial-reinforcement-extinction effect. As Machado et al. (2009) showed, this learning rule ensures that the scalar variability present in state activation transfers, as it were, to measurable response rate.

The extension of LeT to the peak procedure is straightforward. Because the states active past T have rarely been active during the FI training, the strength of their associative links is preserved above θ. On peak trials, however, these states become active and lose their initial strength because of extinction. The net result is a Gaussian-like function similar to those displayed in Figures 23.4a and 23.4b.

To account for performance in the bisection task, we add to LeT's basic structure a second operant response and a new set of links between the behavioral states and that response. Figure 23.10b shows the structure of LeT for this task. Thus, each state has two sets of links, one to R_1 and the other to R_2. The learning and decision rules also change because the animal does not respond during the sample and, when it does, it must choose between

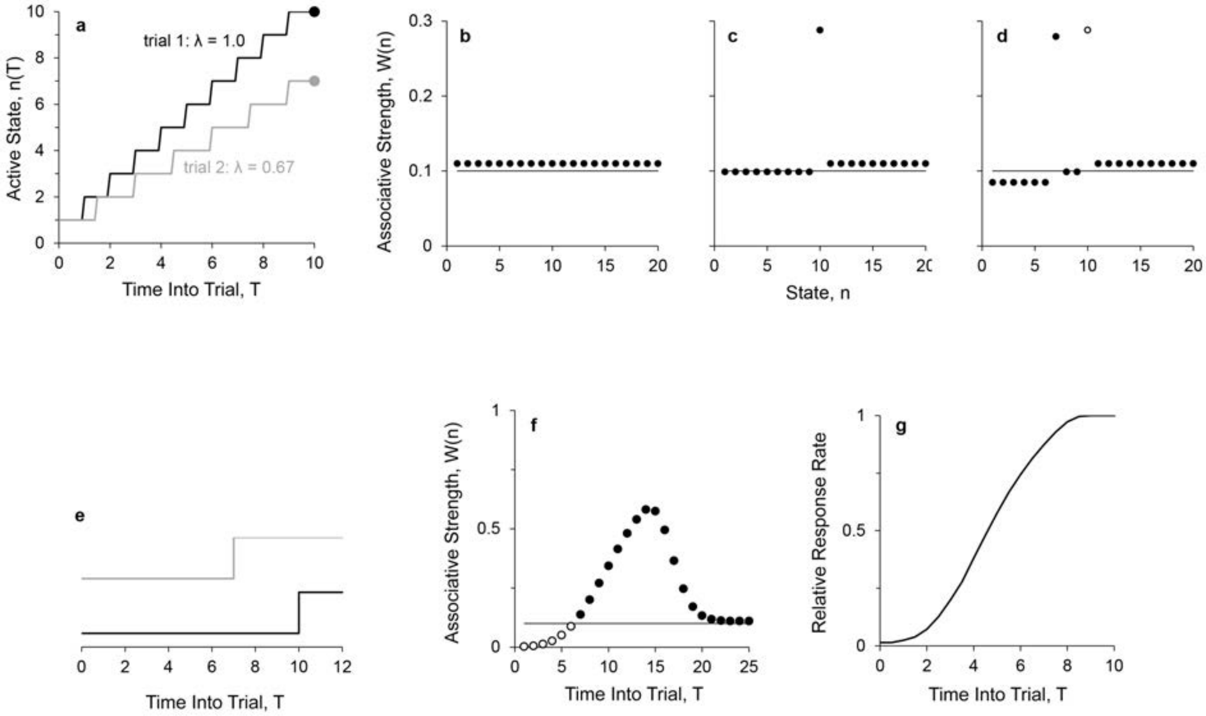

FIGURE 23.11. The dynamics of LeT in a FI 10-s schedule. (a) As time into the trial elapses, the behavioral states activate serially, one at a time, at a rate λ states per second. Two trials are shown, one with λ = .67 and the other with λ = 1.0, with λ sampled at the beginning of each trial from a normal distribution. (b) at the outset or training, the initial strength, W0, of all associative links is greater than the response threshold, θ. In this particular case, W0 = .11 and θ = .10. (c) At the end of trial one, with λ = 1.0, the links from states 1 to 9 weaken, the link from state 10 strengthens, and the links from the remaining states do not change. (d) at the end of trial 2, with λ = .67, the links from states 1 to 6 weaken, the link from state 7 strengthens, and the links from the other states do not change; the white circle represents the link strengthened in trial one. (e) because the states beyond the active state generally have strengths above the threshold, the response profile is break-and-run: When λ = 1.0, responding starts at 10 s and when λ = .67 responding starts at 7 s. (f) at steady state, the link profile shows that state 7 is the first state with a link strength above the threshold. The animal will start to respond when state 7 becomes active. (g) given the variability in the speed of the transition parameter, the average relative response rate curve is sigmoidal, reaching 0.5 at 6 s into the trial.

two competing responses. To illustrate how the model works, consider a bisection task with S_S = 2 s and S_L = 8 s, and red and green keys as choice alternatives. The animal is rewarded for choosing red after the 2 s samples, and green after the 8 s samples. Assume that on a 2 s trial, state n = 2 is active at the end of the sample. The new decision rule states that the subject chooses red according to the relative strength of the links from state 2 to red and green. If we represent the links from state 2 to red and green as WR(2) and WG(2), respectively, then the probability of choosing red equals WR(2) / [WR(2) + WG(2)]. If the subject does choose red and receives food, the link between state 2 and red increases by the amount +β[1 - WR(2)] and the link between state 2 and green decreases by the amount -βWG(2); if instead the subject responds green (and does not receive a reward), the link between state 2 and green decreases by -αWG(2) and the link between state 2 and red increases by the amount +α[1 - WR(2)]. The same learning rule applies on the 8 s trials. According to LeT, training promotes choosing red and avoiding green after 2 s samples, and choosing green and avoiding red after 8 s samples.

Because the first states in the series are more likely to be active at the end of S_S, whereas subsequent states are more likely to be active at the end of S_L, reinforcement and extinction bias the first states toward red and the subsequent states toward green. During test trials, as the sample duration increases and successive states become active, the probability of choosing green over red increases. The net effect is the sigmoid psychometric function typically observed in the bisection task, as those shown in Figure 23.6a, with the point of subjective equality near the geometric mean of the trained stimuli. Figure 23.12 illustrates the dynamics of a 2 s sample and an 8 s sample trial according to LeT.

Interestingly, LeT predicts that the subjects should be indifferent between red and green following intervals considerably shorter than 2 s and considerably longer than 8 s. Because states active at durations considerably shorter than 2 s or considerably longer than 8 s are rarely active during training, their initial link strength (W0) to red and green is preserved. If the generalization tests include not only durations in the 2 s to 8 s range, but also durations outside this range, the predicted generalization gradient should be politonic: preference for green should decrease from indifference to 0 as t ranges from 0 s to 2 s, increase from 0 to 1 as t ranges from 2 s to 8 s, and finally decrease to indifference for t > 8 s. Some studies found politonic gradients consistent with LeT (e.g., Carvalho, Machado, & Tonneau, 2016; Russell & Kirkpatrick, 2007; Siegel, 1986; Vieira de Castro, Machado, & Tomanari, 2013), but some of these same studies and other studies have also found gradients inconsistent with LeT, at least for the longest test durations (Carvalho, Machado, & Tonneau, 2016; Siegel, 1986; Vieira de Castro & Machado, 2012).

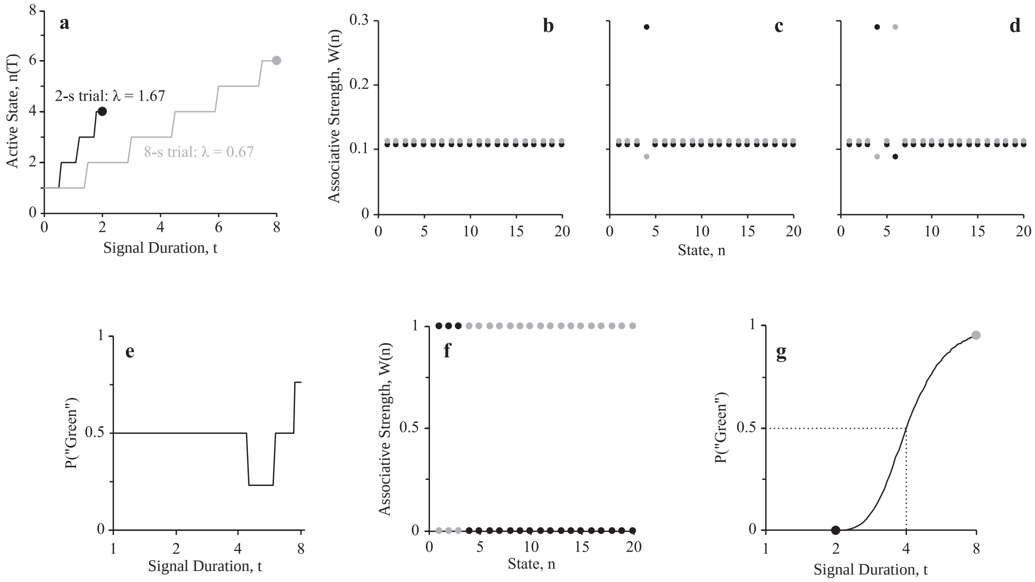

FIGURE 23.12. The dynamics of LeT in a bisection task with a short sample of 2 s and a long sample of 8 s mapped onto red and green, respectively. (a) As time elapses, the behavioral states activate serially, one at a time, at a rate λ states per second. Two trials are shown, the first a 2 s trial with $\lambda = 1.67$ and the second an 8 s trial with $\lambda = .67$, with λ sampled at the beginning of each trial from a normal distribution. (b) initially, all associative strengths, W0, connecting each state to the two possible responses are equal to .11(we offset the links with green slightly to the right to prevent their overlap with the links with red). (c) At the end of trial one, state 4 was active and its link governs choice. Because the animal responded correctly and was rewarded, the link from state 4 to red strengthens and the link from state 4 to green weakens. (d) the learning process repeats at the end of trial two, this time with state 6: its link with green strengthens and its link with red weakens. (e) considering the strength profiles at the end of trial two, the probability of choosing green varies as a function of the sample duration (note that here the *x*-axis is time, not states). (f) at the steady state, the profile of link strengths is well differentiated, inducing (g) the usual smooth and ogival psychometric function, with a Point of Subjective Equality close to the geometric mean of the trained durations.

To summarize, LeT takes three full-fledged principles of learning—stimulus generalization, reinforcement, and extinction—as its foundation stone and is able to account for some of the most relevant findings in the interval timing domain. Through a series of sates, associative links, and operant responses the animal learns an important regularity in its environment, the correlation between time and a biologically potent event such as food.

Contrasting Models of Interval Timing

The comparison of models is an utterly important scientific endeavor. Before long, as models proliferate, its relevance will only increase. Several models are able to accommodate the most robust findings in the field of interval timing (e.g., the scalar property, FI, peak performance), which leaves us with the arduous task of disentangling the models, in terms of their structure and dynamics and their successes and frailties. Statistics may help, but decisions on the basis of small differences in, for example, variance accounted for, seem unsuitable. Still, some of these aspirations can be accomplished by conceptual analyses; others require critical experiments. Here, we aim at contrasting SET and LeT.

Albeit SET and LeT are clearly disparate models in terms of background, dynamics, and even language, they do bear some similarities. They both include a mechanism to keep track of time: the clock (i.e., the pacemaker and accumulator) in SET and the serial organization of states in LeT. On each trial, the pacemaker emits pulses at rate λ (SET) or the states are activated at rate λ (LeT). At each particular moment in the trial, the number of pulses in the accumulator (SET) or the active state (LeT) represents elapsed time. The learning history is also present in both models; as a distribution of (subjective) reinforced times in SET and as differently weighed vectors of associative links in LeT.

Despite these similarities, the models differ in numerous ways mainly because they differ in regard to the learning mechanisms and to what is actually learned in timing tasks. Two of the differences should be conspicuous straightaway: First, whereas SET posits dedicated structures or modules to deal with temporal tasks, LeT relies on general principles of learning (reinforcement, extinction, and generalization) to engender temporally regulated behavior; second, SET captures the steady-state temporal regulation of behavior paying little attention to how it emerges, whereas LeT is a learning model with a strong emphasis on the acquisition of temporal control. Following Machado et al. (2009), we focus our discussion in the structure of memory, the effect of time in retrieval, the contents of memory, and the effect of context on temporally regulated behavior.

The structure of memory differs greatly between the models (cf. Figures 23.7 and 23.10). In SET, long-term memory is concentrated in stores with no particular internal organization. It can literally be conceived as an urn containing balls with the number of pulses inscribed, each ball with the same probability of being selected at retrieval. LeT, on the other hand, conceives of memory as distributed in the links connecting the states to the response. Although, LeT does not strictly speak of memory sampling, the strength of each link is effectively “sampled” only when its coupled state is active. Hence, in LeT, one can conceive of memory as serially structured by state activations.

The just mentioned differences in the structure of memory introduce differences in retrieval, too. In SET, retrieval is time-independent. At any given moment (i.e., regardless of the current number in the accumulator) a sample from long-term memory can be retrieved. The same is not true of LeT: memories, in this case the strength to the associative links, can be accessed only when the coupled sate is active. This makes retrieval time-dependent because the active state represents elapsed time.

Another difference motivated by the models’ dynamics concerns the contents of memory. Consider for instance a FI T-s reinforcement schedule. According to SET, when the animal emits the first response after T and is reinforced the number of pulses representing elapsed time is transferred from the accumulator to the long-term memory store. If, however, no reinforcer is given, nothing is added to memory. The same is true for all responses occurring before T. In other words, memory represents only local relative rates of reinforcement because extinction is left out of the model. Conversely, because LeT considers reinforcement and extinction, the associative links represent the moments of reinforcement and the local absolute rates of reinforcement. The former by the link that is strengthened and the latter by how strong each link is relative to the others. Borrowing an analogy from Machado et al. (2009), the distinction is similar to the one between relative and absolute frequency histograms. In LeT, the strength of the associative links are like an absolute frequency histogram because one can determine (a) whether reinforcement is more likely to occur at one moment than another, say t_1 and t_2, but also (b) how frequent reinforcement is at t_1 and t_2. On the other hand, memory in SET resembles a relative frequency histogram because the animal can infer (a) but not (b) from its contents.

Finally, to fully appreciate the effect of context in memory, we will rely on a task for which SET and LeT make contrasting predictions—the double bisection (Machado & Keen, 1999). The task combines two simple bisections sharing one sample duration. Suppose that in one bisection, the animal learns to choose red after a 1 s sample and to choose green after a 4 s sample. Suppose further that in the other bisection the animal is reinforced for choosing blue after a 4 s sample and for choosing yellow after a 16 s sample. Crucially, the correct choice for the common 4 s sample differs in the two bisections: green in the first and blue in the second. Once the animal masters both simple bisections, probe trials with samples ranging from 1 to 16 s and with green and blue comparisons are introduced. Both colors were associated with the 4-s sample, but their contexts differed. Green was embedded with the 1-s sample and red response, whereas the context for blue was the 16-s sample associated with yellow.

Assuming that animals do not have an *a priori* bias for a color, SET predicts indifference between green and blue regardless of sample duration. The rationale is as follows: During training the animal forms four long-term memories, one per sample duration, indexed by the corresponding correct color (say, M_{red}, M_{green}, M_{blue}, and M_{yellow}). Because the content of each memory store depends only on the reinforced interval, the contents of M_{green} and M_{blue} will be identical (i.e., the distribution of pulses will have the same mean and standard deviation). Therefore, on a probe trial, when the *t*-s sample elapses, with $1 \leq t \leq 16$, the animal will compare the number of pulses in the accumulator with two samples retrieved from memories with identical distributions. The net result is indifference between green and blue independently of the sample duration. This prediction stems directly from the fact that, according to SET, the contents of a particular memory store depend only on the reinforced duration indexed by a particular response with no interference from the context. In other words, in SET, memory is context independent.

For LeT, however, the contexts in which green and blue are reinforced and extinguished are paramount. Put differently, memory is context dependent. At the outset of training, all states are linked equally to blue and green. As the animals learn the two bisections, the choice of green is extinguished when the early states are active because those are most probably 1 s sample trials, and the choice of blue is extinguished when the late states are active because those are most probably 16 s sample trials. Because of these trade-offs, by the end of training blue is more strongly linked to early states than green, and vice-versa for late states. This pattern of correlations predicts that preference for green over blue should increase with sample duration—a *context effect*.

Several studies have yielded data consistent with LeT but not SET: Preference for green increases monotonically with sample duration (e.g., Arantes & Machado, 2008; Machado & Keen, 1999; Machado & Oliveira, 2009; Machado & Pata, 2005; Oliveira & Machado, 2008, 2009). Figure 23.13 contrasts the models' predictions with the context effect reported by Machado and Keen (1999).

On the whole, SET and LeT have some affinities but the differences are unassailable particularly concerning the properties of memory and what is actually learned in timing tasks. On the empirical side, both can account for the most fundamental findings in the interval timing realm; SET's failure in the double bisection task is diagnostic but probably not fatal. We prefer to emphasize more critical issues on the theoretical front. Despite SET's intuitive appeal and influence in the animal and human literature, LeT has its foundations on the solid ground

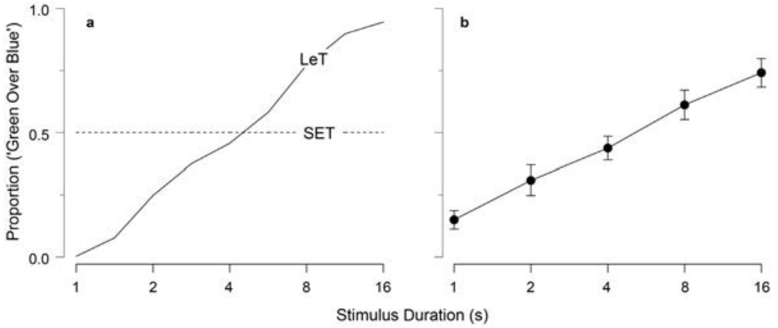

FIGURE 23.13. Proportion of choices of green over blue as a function of stimulus duration in a double bisection task. (a) SET and LeT predictions. (b) Average preference for green (n = 8 pigeons). Note the logarithmic scale on the *x*-axis. From "Learning-to-Time (LeT) or Scalar Expectancy Theory (SET)? A Critical Test of Two Models of Timing," by A. Machado, and R. Keen, 1999, *Psychological Science, 10*, p. 289. Copyright 1999 by Sage. Adapted with permission.

of well-established and general learning principles confirmed across species and research domains. As stated elsewhere (Carvalho, Machado, & Vasconcelos, 2016), we advocate that LeT should be taken as a prudent *null hypothesis*. In our view, the proposal of more sophisticated timing abilities requires a clear treatment of acquisition processes, an equal degree of mathematical explicitness, and a convincingly better account of experimental data.

CONCLUSION

The ability of animals to regulate their behavior spans several orders of magnitude, from seconds to years. Circannual rhythms allow animals to anticipate upcoming seasonal changes increasing their probability of survival and reproduction. Circadian rhythms bestow animals the ability to adjust to the daily light–dark cycle allowing them to prepare for recurring events such as when and where food is available and when and where the risk of predation is high. Interval timing, on the other hand, deals with the animal's ability to temporally regulate its behavior in the range well below 24 hours as a function of biologically relevant events.

Temporal regularities in the range of seconds to minutes may, at first glance, appear artificial but as we have seen they pervade many superficially distinct spheres of animal behavior, from foraging to communication. The bulk of research in interval timing has fitly resorted to the controlled conditions of the laboratory to expose its pivotal properties and mechanisms. Within certain boundary conditions, the psychophysics of animal timing is currently well characterized; many experimental procedures have been devised to study distinct facets of this ability such as concurrent and retrospective time perception. In virtually all of them, the hallmark of interval timing surfaced—the scalar property.

The advancements on the empirical side went hand in hand with theoretical developments through the development of a variety of explanatory models. Here, we introduced and compared two of such models: SET and LeT. Both models account well for most data but differ in their assumptions, structure and dynamics. Because LeT is based on basic principles of learning, we contend that it should be taken as an informed first hypothesis before advancing more elaborate processes.

Meanwhile, many questions remain unanswered. For instance, what is the shape of the psychometric function outside the trained range in a bisection task? Also, do inhibitory processes play a role in temporal control? Recall, for example that in a FI, as training proceeds, animals stop responding in the first section of the interval. Is this simply caused by the lack of excitation or by inhibition as well? The answers to these and many other questions may help to untangle models but, most important, they will spawn new questions and perhaps new procedures, keeping the momentum of the captivating field of interval timing.

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CHAPTER 24

INTERTEMPORAL CHOICE AND DELAYED GRATIFICATION

Jeffrey R. Stevens

A parasitoid wasp has deposited half of her eggs in a host. She now faces the choice between depositing her remaining eggs in the same host or searching for another. Continuing to deposit in the current host provides the immediate payoff of completing her reproductive duties, allowing her to move on to other activities such as foraging or searching for another mate. Searching for another host, in contrast, delays the payoffs of reproducing until a suitable host is found.

This wasp faces an *intertemporal choice*—that is, a choice between options that involve payoffs available at different times (Read, 2004; Stevens, 2010). These choices typically involve a smaller option available sooner and a larger option available later. In the wasp example, depositing all eggs in one host provides the smaller, sooner option because, though curtailing search sooner, increased offspring competition and risk of total failure reduces the overall benefit of this option. The larger, later option of continuing to search involves a time delay but yields a higher payoff with reduced competition and probability of total brood failure.

In addition to reproductive decisions, animals make these choices on a daily basis when foraging, searching for a mate, seeking shelter, avoiding predators, and interacting with social partners (Stevens, 2010; see also Volume 1, Chapters 37, 40, and 42, this handbook and Chapter 14, this volume). Many aspects of life history theory provide examples of intertemporal choices. For instance, allocating energy toward reproduction or growth is a classic life history tradeoff that pits the smaller, sooner payoffs of reproducing now versus the larger, later payoffs for growing and delaying reproduction. At this level of analysis, organisms without a central nervous system, such as plants and bacteria, make intertemporal choices (Kacelnik, 2003). Though not well researched outside of the animal kingdom, researchers have explored intertemporal choices in a wide range of animal species, including insects, fish, birds, rodents, dogs, and primates (see Table 24.1). Comparative psychologists have investigated why individuals should choose either the smaller, sooner or larger, later option via modeling approaches and how different psychological mechanisms regulate intertemporal choice (see Chapter 23, this volume).

APPROACHES AND THEORY

The study of intertemporal choice originated fairly independently in economics, psychology, and behavioral ecology, each starting from a particular perspective with different goals and methods (see Chapters 14 and 16, this volume). In each of these fields, a different normative theory predicts what individuals should choose. Critically, all theories have situations in which choosing the smaller, sooner option is the optimal choice. So, opting for immediate payoffs is not necessarily impulsive. The fields have developed different modeling approaches to investigate whether choices are reasonable or impulsive.

Economic Approaches

The notion of intertemporal choice originated with economists modeling how people choose between

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TABLE 24.1

First References for Various Species Tested in Different Intertemporal Choice Tasks

Species	**Delay choice task**	**Exchange task**	**Delayed gratification task**
Honey bee (*Apis mellifera*)	Cheng, Peña, Porter, and Irwin, 2002		
Guppy (*Poecilia reticulata*)	Mühlhoff, Stevens, and Reader, 2011		
Pigeon (*Columba livia*)	McDiarmid and Rilling, 1965		Grosch and Neuringer, 1981
Chicken (*Gallus gallus domesticus*)	Abeyesinghe, Nicol, Hartnell, and Wathes, 2005		
European starling (*Sturnus vulgaris*)	Bateson and Kacelnik, 1995		
Blue jay (*Cyanocitta cristata*)	Stephens and Anderson, 2001		
Pinyon jay (*Gymnorhinus cyanocephalus*)	Stevens, Kennedy, Morales, and Burks, 2016		
Western scrub jay (*Aphelocoma californica*)	Thom and Clayton, 2014		
Carrion crow (*Corvus corone*)		Dufour, Wascher, Braun, Miller, and Bugnyar, 2012; Wascher, Dufour, and Bugnyar, 2012	Hillemann, Bugnyar, Kotrschal, and Wascher, 2014
Common raven (*Corvus corax*)		Dufour et al., 2012	Hillemann et al., 2014
Goffin's cockatoo (*Cacatua goffini*)		Auersperg, Laumer, and Bugnyar, 2013	
African grey parrot (*Psittacus erithacus*)			Vick, Bovet, and Anderson, 2010
Mouse (*Mus musculus*)	Mitchell, 2014		
Rat (*Rattus norvegicus*)	Van Haaren, Van Hest, and Van De Poll, 1988		Reynolds, de Wit, and Richards, 2002
Domestic dog (*Canis familiaris*)	Wright, Mills, and Pollux, 2012	Leonardi, Vick, and Dufour, 2012	
Black-and-white ruffed lemur (*Varecia variegata*)	Stevens and Mühlhoff, 2012		
Red ruffed lemur (*Varecia rubra*)	Stevens and Mühlhoff, 2012		
Black lemur (*Eulemur macaco*)	Stevens and Mühlhoff, 2012		
Cotton-top tamarin (*Saguinus oedipus*)	Stevens et al., 2005		
Common marmoset (*Callithrix jacchus*)	Stevens et al., 2005		
Squirrel monkey (*Saimiri sciureus*)			Anderson, Kuroshima, and Fujita, 2010
Brown capuchin (*Sapajus apella*)	Amici et al., 2008	Ramseyer et al., 2006	Anderson et al., 2010
Black-handed spider monkey (*Ateles geoffroyi*)	Amici et al., 2008		
Rhesus macaque (*Macaca mulatta*)	Szalda-Petree, Craft, Martin, and Deditius-Island, 2004		Evans and Beran, 2007b
Long-tailed macaque (*Macaca fascicularis*)	Tobin, Logue, Chelonis, Ackerman, and May, 1996	Pelé et al., 2010	Pelé et al., 2010
Tonkean macaque (*Macaca tonkeana*)		Pelé et al., 2011	Pelé et al., 2011
Lowland gorilla (*Gorilla gorilla*)	Amici et al., 2008		
Orangutan (*Pongo pygmaeus*)	Amici et al., 2008		Beran, 2002
Bonobo (*Pan paniscus*)	Rosati et al., 2007		Stevens et al., 2011
Chimpanzee (*Pan troglodytes*)	Rosati et al., 2007	Dufour, Pelé, Sterck, and Thierry, 2007	Beran, Savage-Rumbaugh, Pate, and Rumbaugh, 1999
Human (*Homo sapiens*)	Rodriguez and Logue, 1988	Steelandt, Thierry, Broihanne, and Dufour, 2012	Mischel and Ebbesen, 1970
Total number of species	25	9	14

different streams of future payoffs (e.g., annual salaries). Samuelson (1937) developed the discounted utility model of intertemporal choice. The temporal discounting approach assumes that individuals generate a present value for an option discounted on the basis of the time delay to receiving it: \$100 available in a year is not as valuable as \$100 available now. The specific form of discounting developed by Samuelson is called *exponential discounting*, which calculates the value of a future benefit as $V = Ae^{-\delta t}$, where V represents the present value, A represents the amount of the benefit, δ represents a discount factor related to the rate of discounting, and t represents the time delay to receiving the benefit. A key prediction of exponential discounting is that the rate of discounting (the proportion of value lost over a given time) remains constant across time (Figure 24.1). Economists typically test this model by offering human participants real choices between smaller, sooner monetary rewards and larger, later monetary rewards, such as \$100 today versus \$105 in one month. The empirical data, however, do not support exponential discounting. Instead, they show a decreasing rate of discounting with time delay: Value drops sharply at short delays, but the rate of discounting slows with time (Thaler, 1981).

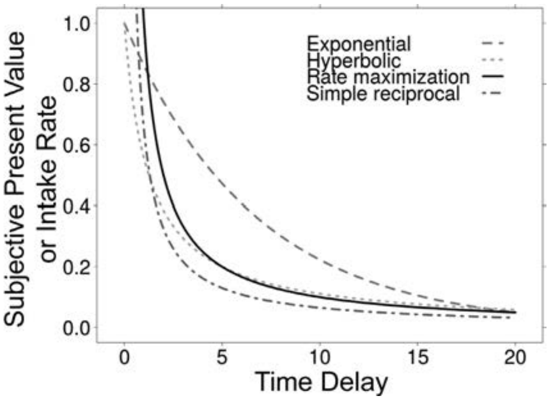


FIGURE 24.1. Intertemporal choice model predictions. Different models of intertemporal choice illustrate how the subjective present value of a delay reward or the reward intake rate decreases with time delay. Exponential discounting predicts a constant rate of discounting, whereas hyperbolic, simple reciprocal, and rate maximization predicts a decreasing rate of discounting. Rate maximization is a special case of simple reciprocal.

Psychological Approaches

Psychologists interested in the effect of delays to reinforcement on choice behavior developed an independent series of models of intertemporal choice on the basis of the matching law (Herrnstein, 1961), in which individuals should prefer the option with the greatest reinforcement rate, or ratio of reward amount to delay to reinforcement A/t (Chung & Herrnstein, 1967). McDiarmid and Rilling (1965) modified this model by including a free parameter to adjust for bias observed in experimental data: $V = kA/t$, where k represents the free parameter. This *simple reciprocal model* of choice has the inconvenient mathematical property that the value goes to infinity as the time delay approaches zero (Figure 24.1). Mazur (1987) proposed a modification of this model $V = A/(1 + kt)$ that assigns the full amount value (rather than infinite value) when the delay is zero (Figure 24.1). Though all of these models generate hyperbolic value functions (meaning the proportional decrease in value is steep at short delays and drops as delay increases), Mazur's model has become the standard *hyperbolic discounting model* in the human and animal literatures (Table 24.2).

TABLE 24.2

Models of Intertemporal Choice

Functional form	Model	Reference
$V = Ae^{-\delta t}$	Exponential discounting	Samuelson, 1937
$V = A/t$	Matching	Chung and Herrnstein, 1967
$V = kA/t$	Simple reciprocal	McDiarmid and Rilling, 1965
$V = A/(1+kt)$	Hyperbolic discounting	Mazur, 1987
$R = A/(T + t + h)$	Long-term rate maximization	Stephens and Krebs, 1986
$R = A/t$ or $R = A/(t + h)$	Short-term rate maximization	Bateson and Kacelnik, 1996; Stephens and Anderson, 2001

Note. V = value of option, R = intake rate, A = reward amount, t = time delay between choice and onset of reward availability, T = time delay between consumption of reward and choice (intertrial interval), h = time between onset of reward availability and final consumption (handling time), δ and k = free parameters associated with discounting rates and amount and time sensitivity.

TABLE 24.3

Intertemporal Choice and Delayed Gratification Tasks

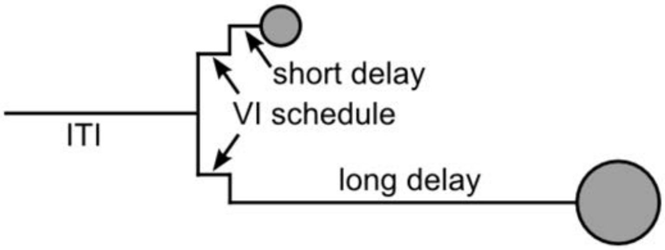
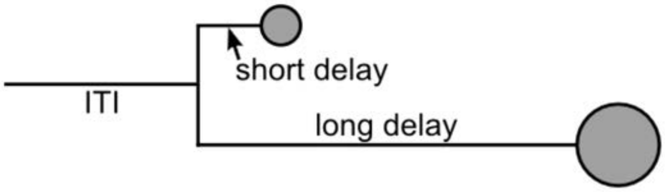
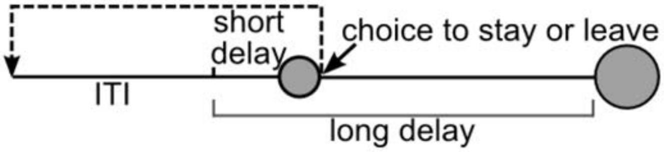
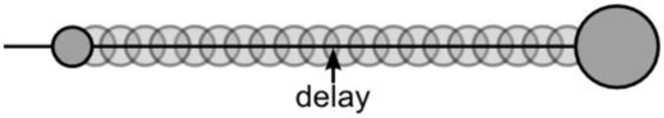
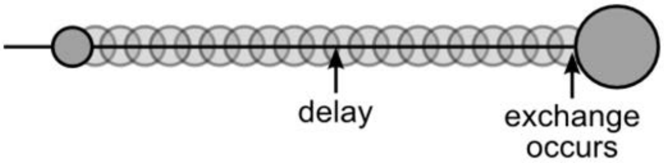
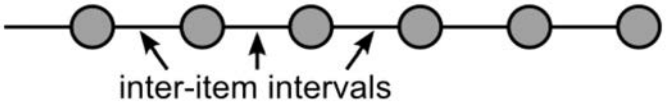
Task	Description	Representative reference
Concurrent chain	In an operant task, subject chooses between a variable interval followed by a smaller, sooner reward and a variable interval followed by a larger, later reward.  	Herrnstein, 1964
Delay choice	Subjects choose between a smaller reward available sooner and larger reward available later. This can be an operant task in which symbols represent the two options or a physical task in which the subjects can see the actual rewards when choosing between them.  	McDiarmid and Rilling, 1965
Patch use	In an operant task, subject initiates trial and waits for short delay before smaller reward is delivered. Then it chooses between continuing on to receive more reward (with total time equaling long delay and total reward equally larger reward) or starting a new trial.  	Stephens and Anderson, 2001
Delay maintenance	In an operant or physical task, subjects can select an option at any time that immediately delivers a smaller reward or wait until a delay expires to receive a larger reward.  	Grosch and Neuringer, 1981
Exchange	Subject receives smaller or lower-quality reward and must wait time delay and exchange it with experimenter to receive larger or higher-quality reward.  	Ramseyer, Pelé, Dufour, Chauvin, and Thierry, 2006

TABLE 24.3 (*Continued*)

Accumulation	 Experimenter or machine delivers rewards at fixed rate (e.g., 1 reward per second). Once subject reaches for reward or puts reward in its mouth, rewards stop accumulating.	Beran et al., 1999

In animals, researchers test these models with a number of different intertemporal choice tasks (Table 24.3). To precisely control aspects of the task needed to estimate model parameters, behavioral psychologists typically use a concurrent-chain procedure or a delay choice task in an operant box. The *concurrent-chain procedure* offers animals (usually pigeons, *Columba livia*) two phases of schedules of reinforcement (see Chapter 15, this volume). In the initial choice phase, subjects choose between two keys that typically lead to a variable interval schedule (a time delay that varies in length around a mean value). After responding to the key again following the expiration of the variable interval, the subject begins the second phase in which it must complete a second schedule of reinforcement. For studies of intertemporal choice, the second phase is often a fixed interval schedule (a fixed time delay) followed by reinforcement (e.g., Grace, Sargisson, & White, 2012). The *delay choice task* (sometimes called self-control or intertemporal choice task) offers animals repeated choices between two simultaneously presented options, one smaller, sooner and one larger, later (McDiarmid & Rilling, 1965). This can involve either arbitrary signals of the options (e.g., colored lights) or visually presenting the actual quantity of food rewards for each option. Once they choose the option, they wait the required time delay to receive the reward amount. These techniques often involve many trials to collect the data needed to create discounting functions (Figure 24.1).

The repeated nature of the choices for animals differs from the typical one-off choices used in human data. Further, the human experiments usually use time delays of days, weeks, months, or years, whereas animal experiments use seconds or minutes. Despite these methodological differences, the hyperbolic discounting model fits human and animal data well and better than the exponential discounting model (Green & Myerson, 2004). Hyperbolic discounting outperforms exponential discounting because it captures the decreasing rate of discounting with time delay, which contradicts the exponential model's requirement of constant discounting. Further, animals show preference reversals not predicted by exponential discounting. For instance, Green et al. (1981) offered pigeons a choice between a smaller, sooner reward and a larger, later reward in which the two reward amounts were held constant and the difference between time delays was always 4 s. As the delay to the smaller reward increased, the pigeons reversed their preferences from the smaller, sooner option to the larger, later option, thereby violating the predictions of exponential discounting. Though still the standard model of intertemporal choice in the psychology literature, the hyperbolic discounting model has come under fire in the human and animal literatures for two reasons. First, hyperbolic discounting fails to account for some aspects of behavioral data. Namely, (a) choice data show effects of reward magnitude, sign (gain or loss), and temporal sequences not predicted by hyperbolic discounting (Read, 2004), (b) preference reversals in humans do not fit predictions of hyperbolic discounting (Luhmann, 2013), and (c) hyperbolic discounting models fit to animal data to not generalize to foraging tasks (Blanchard & Hayden, 2015). Second, hyperbolic discounting fails to provide a clear process model of the mechanisms of intertemporal choice (Rubinstein, 2003; Stevens, 2016).

Behavioral Ecological Approaches

Behavioral ecologists have also investigated intertemporal choice as a key component of foraging behavior (see Chapter 14, this volume). Foraging requires repeatedly acquiring food as energy is depleted to maintain homeostasis, enhance growth, and invest in reproduction. Foraging choices are embedded in a stream of decisions that influence an organism's energy intake rate. Behavioral ecologists, therefore, frame these choices in terms of maximizing intake rates (Stephens & Krebs, 1986). Models of intake rate share the hyperbolic property of the psychologist's reinforcement models (Figure 24.1). However, behavioral ecologists started with the assumption that all time components should be included in the models because they influence the long-term intake rate, the critical currency for optimal foraging. Thus, in addition to the time delay between choice and receiving rewards, the delay between consuming food and receiving another choice (travel time, intertrial interval, or post-trial delay) and the time between receiving and completely consuming the reward (handling time) should be included, generating the *long-term rate maximization model*: $R = A/(t + T + h)$, where T represents travel time and h represents handling time. Across a range of natural and artificial foraging tasks, the long-term rate maximization model fits actual choices. In the delay choice task, however, subjects prefer the smaller, sooner option more often than expected by the long-term rate maximization model (McDiarmid & Rilling, 1965). Further, pigeons and blue jays (*Cyanocitta cristata*) neglect changes in the travel time for delay choice tasks (Stephens & Anderson, 2001), which contradicts long-term rate predictions. In rhesus macaques (*Macaca mulatta*), however, enhancing the salience of the travel time can bias choices in ways consistent with long-term rate maximization (Pearson, Hayden, & Platt, 2010).

Bateson and Kacelnik (1996) demonstrated that, though European starling (*Sturnus vulgaris*) choices in a delay choice task did not match long-term rate-maximizing predictions, they did match a short-term rate maximization models that omit the travel time. The birds maximized only on the basis of delay time $R = A/t$ or delay and handling time $R = A/(t + h)$. Cotton-top tamarins (*Saguinus oedipus*) also matched the model that included handling time (Stevens, Hallinan, & Hauser, 2005).

Stephens and Anderson (2001) suggested that the short-term rate model works well because it is equivalent to a long-term rate model in a more naturalistic foraging task. In the *patch use task*, rather than facing a simultaneous choice between two options, individuals receive the small food amount after the short time delay (Table 24.3). Afterward, individuals must choose to continue to stay in the patch for longer to receive more food or leave the patch to initiate the travel time and then another instance of the smaller, sooner option. Stephens and Anderson argued that this stay-or-go choice more closely resembles a natural foraging decision that animals typically face. Because the short-term rate results in the same choices as the long-term rate, and the short-term rate requires tracking less information (travel time), natural selection might favor this simpler rule for foraging decisions (Stephens, 2002). When applied to an artificial foraging task with simultaneously presented options, the rule fails to maximize intake.

Shapiro, Siller, and Kacelnik (2008) also argued that animals rarely face simultaneously available options in their natural foraging environments. They proposed a *sequential choice model* in which the choices between simultaneously presented options result from sampling from the distributions of latencies to choose the individual options. The logic underlying this model is that (a) animals experience options in their environment sequentially and must decide to accept or reject them and (b) the latency to accept an item indicates strength of preference, with highly preferred items having shorter latencies. When two options are presented simultaneously, the animal effectively samples from each option's distribution of latencies and chooses the option with the shortest latency. This model, therefore, provides a window into the process of choice that rate maximization models do not offer. Shapiro et al. found that the sequential choice model outperformed exponential discounting, hyperbolic discounting, and several rate maximization models, with the exception of a short-term rate model that includes choice delay and choice latency, which performed equally well.

Behavioral ecologists also explore potential adaptive accounts of discounting. Devaluing the future may be beneficial when the future is uncertain (Stephens, 2002). The longer one must wait for a reward, the more likely something will prevent the acquisition of the reward. The parasitoid wasp *Leptopilina heterotoma*, for example, dumps more eggs in a single host as the barometric pressure drops, presumably signaling the possibility of a storm and uncertainty about the wasp's future opportunities to find an additional host (Roitberg, Sircom, Roitberg, van Alphen, & Mangel, 1993). Henly et al. (2007) introduced uncertainty into a delay choice task with blue jays by varying the rate at which the reward was interrupted and not delivered. Though modeling efforts predicted that the interruptions influence intake rates, empirical work suggested that they jays did not attend to the interruptions in the predicted manner. In a different task, however, bonobos (*Pan paniscus*) did reduce waiting times when the reward became more uncertain (Stevens, Rosati, Heilbronner, & Schmücking, 2011). Therefore, under some circumstances, the uncertainty associated with the future can shape intertemporal choices.

Delayed Gratification

Much of the intertemporal choice work in economics and behavioral ecology has focused on binary choice, such as the delay choice task. Some psychologists, however, have explored other ways to study intertemporal choice. Notably, Mischel and colleagues (Mischel & Ebbesen, 1970; Mischel, Ebbesen, & Zeiss, 1972) investigated the notion of *delayed gratification*—that is, choosing to defer immediate gratification for higher long-term gain. Though clearly a subset of intertemporal choices, researchers assess delayed gratification using different measures than the delay choice task (Table 24.3). Mischel and colleagues measured delayed gratification in human children by placing a small reward in front of them (often a cookie or marshmallow) and telling the children that they could have the small reward in front of them or wait until the experimenter returned to receive a larger reward (e.g., two marshmallows). The experimenters then measured how long the children waited.

A key difference between these methods and the delay choice task is that delayed gratification requires the ability to make a choice for a delayed option and maintain that choice in the presence of a constant temptation for immediate gratification (Beran, 2002; Mischel & Ebbesen, 1970). In an operant version of a *delay maintenance task*, pigeons could peck a key and receive a low-quality reward or inhibit pecking during a delay to receive a high-quality reward (Grosch & Neuringer, 1981). At any time during the delay, the pigeon could peck the key for the low-quality reward. In a related delayed gratification paradigm called the *exchange task*, subjects receive a small or low-quality reward and must hold this reward during the delay and exchange it for a large or high-quality reward (Ramseyer, Pelé, Dufour, Chauvin, & Thierry, 2006). Therefore, subjects must avoid consuming the food in a similar way as the children do, but potentially with the food actually in their hands or beaks. Finally, in an *accumulation task*, experimenters provide a stream of rewards at a constant rate, say, one food item every 5 s, and, once the subject reaches for or begins consuming the rewards, the experimenter stops delivering them (Beran, 2002). Though the delay choice task has been tested on more species, recently researchers have begun testing a number of species (particularly primates) in the delayed gratification tasks (see Table 24.1 and Figures 24.2, 24.3, and 24.4).

Understanding Measures of Intertemporal Choice

Having a variety of intertemporal choice measures raises questions about the reliability of choices within and between tasks. Do individuals have consistent preferences? Do preferences carry over across tasks? Humans show fairly high levels of test–retest reliability for intertemporal choices within the same task, with correlation coefficients around 0.70 after a year (Kirby, 2009). Rats (*Rattus norvegicus*) showed comparable levels of test–retest reliability in a delay choice task over the course of days or weeks (Peterson, Hill, & Kirkpatrick, 2015), and dogs (*Canis familiaris*) showed high correlations within individuals (correlation coefficient = 0.80) in a delay choice tasks after 6 years (Riemer, Mills, & Wright, 2014). Intertemporal choices appear to be quite stable within individuals across time when using the same task.

Some tasks have different procedures to evaluate intertemporal choices. In the delay choice task, for example, multiple procedures can measure indifference points. Peterson et al. (2015) compared how rats performed in three different indifference point elicitation procedures in which the small amount,

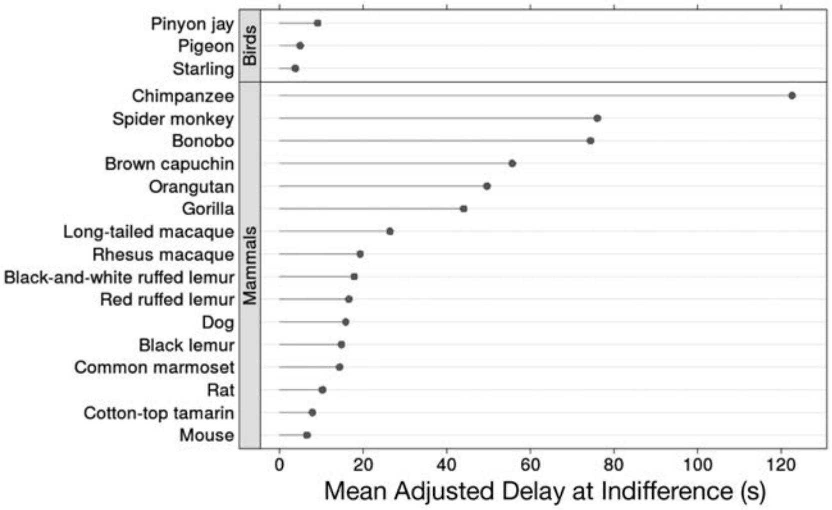


FIGURE 24.2. Delay choice titration task data. In the titration task, the experimenter adjusts the amount or delay to find a point at which the subject is indifferent between a smaller amount available immediately and a larger amount available later. Though not all data here use the same methods, here they are converted into comparable data that provide the mean delay at which subjects are indifferent between one food item available immediately and three food items available after a delay. Data from Addessi, Paglieri, and Focaroli, 2011; Amici et al., 2008; Bateson, Brilot, Gillespie, Monaghan, and Nettle, 2015; Green, Myerson, Shah, Estle, and Holt, 2007; Louie and Glimcher, 2010; Mitchell, 2014; Pearson et al., 2010; Perry, Larson, German, Madden, and Carroll, 2004; Rosati et al., 2007; Stevens et al., 2005, 2016; Stevens and Mühlhoff, 2012; Tobin et al., 1996; Wright et al., 2012.

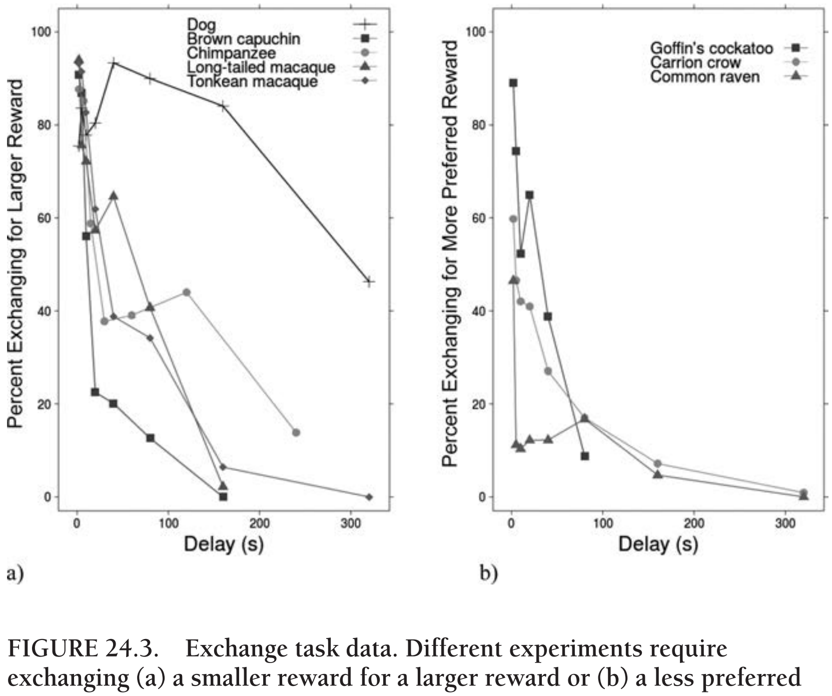


FIGURE 24.3. Exchange task data. Different experiments require exchanging (a) a smaller reward for a larger reward or (b) a less preferred reward for a more preferred reward. For the quantitative exchange task (a), subjects exchanged for a larger reward eight times the size of the smaller reward. Exchanges tend to decrease with the delay to exchange. Data from Auersperg et al., 2013; Dufour et al., 2007; Leonardi et al., 2012; Pelé et al., 2010, 2011; Wascher et al., 2012.

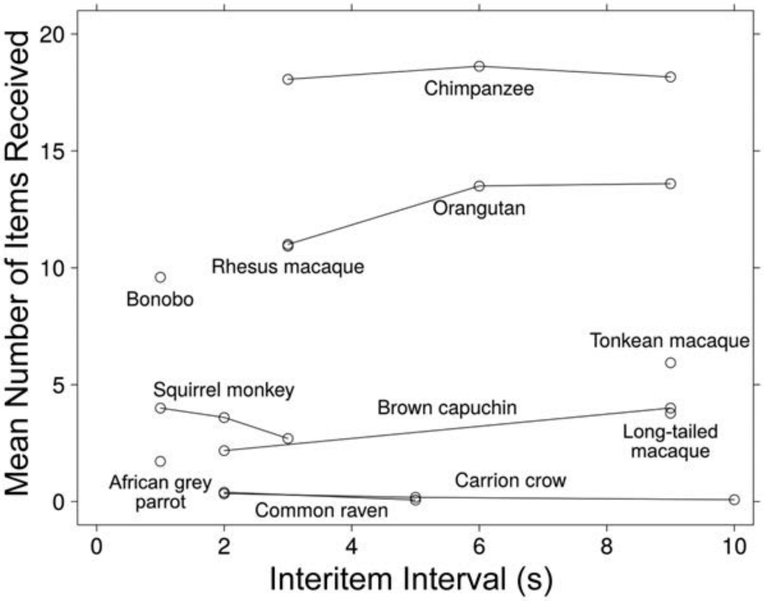


FIGURE 24.4. Accumulation task data. In the accumulation task, rewards accumulate as a machine or experimenter releases food rewards at a fixed interitem interval. Species vary in the number of items that they receive. Data from Addessi et al., 2013; Anderson et al., 2010; Beran, 2002; Evans and Beran, 2007b; Hillemann et al., 2014; Pelé et al., 2010, 2011; Stevens et al., 2011; Vick et al., 2010.

short delay, and large amount were constant and the long delay either varied systematically or adaptively. Systematic procedures consistently increased the delay by a fixed unit either after a fixed block of trials or after a fixed number of sessions, regardless of choice. Adaptive procedures adjusted the delay on the basis of the subject's recent choices, increasing the delay when the subject preferred the later option and decreasing the interval when it preferred the sooner option. Though the two systematic procedures (block- and session-based increases) showed high correlations ($r = 0.61$–0.90), comparisons across systematic and adaptive procedures showed lower correlations ($r = 0.08$–0.51). This suggests that even within a general type of task, different procedures can result in different patterns of choice, as has also been demonstrated in humans (Hardisty, Thompson, Krantz, & Weber, 2013).

Though researchers use delay choice, exchange, and accumulation tasks to measure intertemporal choice, it is not clear that the different tasks measure the same construct. For example, Addessi et al. (2013) found mixed results when offering the same capuchin monkeys a delay choice and an accumulation task: one population of monkeys showed a positive relationship across the two tasks, whereas another did not. This matches findings in human children in which neither boys nor girls showed significant correlations between delay choice and delay maintenance (Toner, Holstein, & Hetherington, 1977). The fact that these tasks differ in the presence or absence of a delay maintenance component may explain this difference. The more closely related exchange and accumulation tasks have been tested in the same individuals, but the within individual correlations were not reported (Pelé, Dufour, Micheletta, & Thierry, 2010; Pelé, Micheletta, Uhlrich, Thierry, & Dufour, 2011). Therefore, we do not have clear evidence that the different tasks measure the same components of intertemporal choice.

PSYCHOLOGICAL MECHANISMS

With the exception of the sequential choice model (Shapiro et al., 2008), most theoretical approaches to animal intertemporal choice neglect psychological mechanisms that are used to make these choices. Nevertheless, empirical research has begun to uncover the cognitive, motivational, and emotional processes involved in intertemporal choice.

Reward Amount and Time Delay Discrimination

Intertemporal choices involve assessing reward amounts and time delays (see Chapters 23 and 25, this volume). Though these core abilities are well studied in isolation from intertemporal choices (reviewed in Brannon, 2005; Meck, 2003), surprisingly little is known about how they relate to these choices. Multiple studies have shown that, when time delays are held constant, choices for the larger, later option increase with the magnitude of the large amount, demonstrating sensitivity to reward magnitude (Freeman, Green, Myerson, & Woolverton, 2009; Marshall, Smith, & Kirkpatrick, 2014). Individual differences in sensitivity to magnitude, however, do not correlate with choice in delay choice tasks (Marshall et al., 2014). Humans show an additional effect of reward amount on intertemporal choice (the magnitude effect), in which the discounting rate declines as the magnitude of the rewards increases (Thaler, 1981). Rats show this magnitude effect in concurrent chain tasks (Grace et al., 2012; Orduña, Valencia-Torres, Cruz, & Bouzas, 2013; Yuki & Okanoya, 2014); however, it has not yet been demonstrated in delay choice tasks (Freeman et al., 2009; Green, Myerson, Holt, Slevin, & Estle, 2004).

Time perception is clearly relevant to intertemporal choices as well (see Chapter 23, this volume). Recent work has found that individual differences in the variance in precision for time perception correlate with intertemporal choices, with rats showing poor precision in time estimates choosing smaller, sooner options more than those with more precise time estimates (Marshall et al., 2014; McClure, Podos, & Richardson, 2014). Behavioral interventions that improve the precision of time estimation also increases choices for larger, later options in delay choice tasks, further supporting the notion that timing estimates play a critical role in intertemporal choice (Smith, Marshall, & Kirkpatrick, 2015).

Inhibitory Control

Animals have a rather difficult time inhibiting strong prepotent responses to selecting higher magnitude rewards over lower magnitude rewards (see Chapter 27, this volume). This difficulty in inhibitory control is evidenced by the reverse contingency task in which subjects can see a high and low magnitude reward and must point at the low magnitude reward to receive the high magnitude reward and vice versa (Boysen & Berntson, 1995). Subjects across a wide range of species have a difficult time inhibiting their prepotent responses to choose the high magnitude reward (Shifferman, 2009). Some researchers suggest that this inhibitory control problem is more difficult for amounts than delays and may result in more choice for a larger, later option in delay choice tasks in which the rewards are visible during choice (Addessi et al., 2014; Genty, Karpel, & Silberberg, 2012).

Commitment

One key cognitive strategy that can help overcome the strong temptation to select immediate payoffs over larger but delayed payoffs is the use of commitment devices that rely on the external environment to solve this problem (see Chapter 15, this volume). An example of using commitment in a human intertemporal choice is placing an alarm clock well out of reach, so that when the alarm goes off, you have committed yourself to get up to turn it off. Rachlin and Green (1972) tested commitment in an operant delay choice task in which pigeons had a commitment option to remove the smaller, sooner option from the choice set. Pigeons faced a choice between two keys: One key resulted in a fixed interval before presenting the simultaneous choice between the smaller, sooner option and larger, later option, whereas the other key resulted in the same fixed interval, but only the larger, later option was presented afterward. Rachlin and Green then varied the fixed interval to influence the overall reinforcement rate, which determines whether the smaller, sooner option or larger, later option yields the higher reinforcement rate. Pigeons, in fact, used the commitment option more when the larger, later option offered the higher rate, suggesting that they could use this commitment device to prevent succumbing to the temptation for the smaller, sooner option when it yielded lower payoffs.

Attention and Distraction

A related cognitive strategy used to avoid the temptation of immediate gratification is directing attention away from the smaller, sooner option. Mischel and Ebbesen (1970) measured whether attention to the rewards influenced delayed gratification in children by leaving the smaller reward, larger reward, both rewards, or neither reward in sight during the delay. They found that having any rewards in view prevented the children from waiting for the delayed reward. Grosch and Neuringer (1981) conducted a similar study in pigeons by varying whether small and large rewards were visible during the waiting period of an operant delayed gratification task. Matching the findings with children, the pigeons waited longer when the food was not visible. In contrast, Genty et al. (2012) found that long-tailed macaques (*Macaca fascicularis*) chose the larger, later option more in a delay choice task when both food rewards were visible compared to hidden. Though the pigeon and children's data imply that attention to any rewards triggers choice for the smaller, sooner option, Genty et al. argued that the visibility of rewards focuses attention exclusively on the large reward, triggering the prepotent response for larger over smaller.

In addition to manipulating the visibility of food rewards, Mischel et al. (1972) manipulated the overall salience of the rewards by comparing a condition in which experimenters instructed children to think about the rewards during the delay to a condition with no instructions to think about rewards. Children waited less for rewards when instructed to think about them. Grosch and Neuringer (1981) mimicked this scenario in pigeons by comparing a condition with an illuminated food bin during the delay to a condition with a darkened food bin. The pigeons waited less with an illuminated food bin, matching the finding in children that enhancing attention to the reward reduces delayed gratification.

Though visibility can draw attention to the reward, individuals may be able to use distraction to break this attention. Mischel et al. (1972) not only enhanced children's attention to the reward but also provided potential distractions by offering toys for children to play with during the delay. Children who had toys to play with waited longer than children without toys. Similarly, Grosch and Neuringer (1981) found that pigeons waited longer when given an additional key to peck in the rear of the operant box compared to when the key was not present. Evans and Beran (2007a) took the study of distraction a step further by assessing whether chimpanzees (*Pan troglodytes*) could self-distract in an accumulation task. Like the Mischel et al. study, the chimpanzees experienced the accumulation task with and without toys provided in the room. In a third condition, toys were provided in the room, but the subject could not access the rewards from the accumulation task. Three out of four chimpanzees received more rewards (a proxy for length of time waited) when toys were present than when absent, suggesting that toys distracted the chimpanzees. Moreover, three out of four chimpanzees also manipulated the toys more when the accumulation of rewards was accessible compared to when not accessible, indicating that the subjects may have actively self-distracted to earn more rewards. Thus, distraction is not only passive but can be an active strategy specifically aimed at delaying gratification.

Working Memory

Some psychological approaches to intertemporal choice attribute impulsivity and self-control to executive function, or the "control mechanisms that modulate the operation of various cognitive subprocesses" (Miyake et al., 2000, p. 50; see Chapter 27, this volume). Working memory is often touted as a key exemplar of executive function that has demonstrated connections to intertemporal choice in humans (see Chapter 10, this volume). Namely, individual differences in working memory correlate with differences in intertemporal choice (Shamosh et al., 2008), and explicit training in working memory performance reduces impulsive choice (Bickel, Yi, Landes, Hill, & Baxter, 2011). Experiments with rats replicate the correlational work, with subjects who chose larger, later options in a delay choice intertemporal choice task also performing well on an operant delayed matching-to-sample working memory task (Renda, Stein, & Madden, 2014). A study using a radial arm maze task to test working memory in rats, however, did not show a relationship between intertemporal choice and working memory (Dellu-Hagedorn & Dellu, 2006). Further, intertemporal choice in rats did not respond to trained improvement in working memory performance (Renda, Stein, & Madden, 2015). The role of working memory in animal intertemporal choice, therefore, remains unresolved.

Prospective Cognition

Intertemporal choices involve dealing with future rewards. But do these choices require animals have prospective cognition in which they represent the future and plan on the basis of this representation (Stevens, 2011; Thom & Clayton, 2014; see also Chapter 11, this volume)? Prospective cognition has been explored across a range of species in a variety of contexts (Raby & Clayton, 2009). For instance, Western scrub jays (*Aphelocoma californica*) have demonstrated elements of prospective cognition in a number of caching tasks (Clayton & Dickinson, 1998; Raby, Alexis, Dickinson, & Clayton, 2007). These studies use rather short time delays to recovery (on the order of hours or days), so we do not know whether prospective cognition is tapped for the longer-term caching decisions that these corvids face in the wild. Nevertheless, given that caching decisions offer a natural example of intertemporal choices (Stevens, 2010; Thom & Clayton, 2014), the work on prospective cognition in caching situations connects this cognitive mechanism to animal intertemporal choice.

Another potential example of prospective cognition relevant to these choices is route planning. Brown capuchin monkeys (*Sapajus apella*) and chacma baboons (*Papio ursinus*) travel from a sleeping site directly to more preferred food locations, bypassing less preferred food on the way (Janson, 2007; Noser & Byrne, 2007). The direct nature of the travel in the absence of visual access to the goal implies that the primates prospectively planned their routes. The fact that they bypassed nearby food indicates that they opted for a larger, later (more distant) reward over a smaller, sooner (less distant reward), a key characteristic of intertemporal choice. Therefore, we have hints that animals may use elements of prospective cognition to make intertemporal choices. More research is needed, however, to investigate how and whether animals use representations about the future in intertemporal choices (Stevens, 2011; Thom & Clayton, 2014).

Motivational Mechanisms and Emotional Responses

In addition to cognitive mechanisms, intertemporal choices involve motivational and emotional mechanisms. Hunger levels are a key motivational factor influencing choice. But should hungry individuals place greater emphasis on getting food sooner or on getting more food? The empirical data reflect this ambiguity. In some studies, for example, pigeons' deprivation level did not influence choice in the delayed choice task (Logue, Chavarro, Rachlin, & Reeder, 1988; Logue & Peña-Correal, 1985). In other studies, increasing deprivation in pigeons increased choice for the smaller, sooner option (Eisenberger, Masterson, & Lowman, 1982; Snyderman, 1983), and honeybees (*Apis mellifera*) showed similar effects (Mayack & Naug, 2015). In contrast, rats demonstrate the opposite finding for liquid rewards (Bradshaw & Szabadi, 1992; Christensen-Szalanski, Goldberg, Anderson, & Mitchell, 1980). Thus, hunger plays a central motivational role for intertemporal choice, but we have yet to unravel the complexity of its motivational effects.

Waiting for the delayed rewards can prove difficult for animals. Rosati and Hare (2013) measured behaviors associated with stress and affect (negative vocalizations, scratching, and banging) in chimpanzees and bonobos during the delay of a delayed choice task. Chimpanzees and bonobos exhibited all three of these measures more following choice for the larger, later option than following choice for the smaller, sooner option. Yet, individual measures of negative affect did not correlate with individual measures of choice. The species did differ, however, in negative affect, with chimpanzees showing more negative vocalizations than bonobos. This maps on a species difference in choice where chimpanzees waited longer than bonobos. So, though chimpanzees show more negative reactions to waiting, they wait longer than bonobos. More work is need to disentangle how motivational influences and emotional responses interact with intertemporal choice.

CONCLUSION

Research on animal intertemporal choice has come a long way in the last 50 years, since McDiarmid and Rilling's (1965) work on the effect of reinforcement rate on pigeon choices. Theorists have developed a rich set of models that capture the behavioral dynamics of these choices (see Table 24.2). Importantly, this theory is moving beyond "as-if" models that purely predict behavior (Berg & Gigerenzer, 2010) to develop models of the cognitive process (e.g., Shapiro et al., 2008; Stevens, 2016). The empirical work on intertemporal choice has greatly expanded recently to test a variety of species across a range of taxa, including invertebrates and fish, as well as birds and mammals (Table 24.1). Moreover, comparative psychologists are developing and testing multiple methods to examine different components of intertemporal choice (Table 24.3). Research on humans clearly demonstrates different subcomponents of impulsivity, where performance correlates across some tasks but not others. Animal intertemporal choice shows a similar mix of relationships across tasks. Delay choice and delay maintenance tasks do not seem to result in similar behavior patterns (Addessi et al., 2013). More work is needed in this area, however, especially comparing performance on the more similar exchange task and accumulation task.

From basic timing, quantification, inhibitory control, and attention processes to more cognitively demanding effects of distraction and prospective cognition, research on psychological mechanisms associated with intertemporal choice has increased rapidly in recent years. Further, new developments in motivational and emotional processes shed light on novel mechanisms of animal intertemporal choice. A mature research program to fully understand intertemporal choice, however, requires integration across a number of levels of analysis. Research in the genetic (Mitchell, 2011), neural (Kalenscher et al., 2005), and hormonal (Bayless, Darling, & Daniel, 2013) underpinnings of choice begin to complete our understanding of the proximate mechanisms of intertemporal choice. Yet, these proximate mechanisms need to be connected to and informed by the ultimate, adaptive explanations for intertemporal choice (Fawcett, McNamara, & Houston, 2012; Stevens & Stephens, 2009). Current work indicates that feeding ecology (Rosati, Stevens, Hare, & Hauser, 2007; Stevens et al., 2005), social system (Amici, Aureli, & Call, 2008), and allometric scaling (Stevens, 2014) predict intertemporal choice. But researchers have not properly integrated evolutionary factors with the mechanistic approach to these choices. A complete understanding of how and why humans and other species make intertemporal choices requires further integration of proximate and ultimate approaches, leveraging models and methods from a range of disciplines.

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CHAPTER 25

QUANTITATIVE COGNITION

Michael J. Beran

Quantitative cognition is the process of using magnitudes, amounts, and numbers. Studying quantitative cognition in animals is one of the most widespread and longest running areas of research in comparative psychology. The research paradigms that have been developed and the data that have emerged from tests with an impressively broad range of animals have informed our understanding of the evolutionary foundations of various perceptual, representational, and decisional mechanisms in animal (and human) minds that rely on quantitative information. This chapter provides an outline of the history, methods, and main results of this area of research.

From the outset, a critical distinction must be made between quantitative cognition and *numerical cognition*. Often, the terms are used interchangeably, which is unfortunate because they refer to broader and more specific capacities (or suites of capacities), respectively. In animal research, the tasks and questions that are asked are such that we can include all cases of numerical cognition within the broader area of quantitative cognition. But the reverse is not true—many quantitative abilities that animals show are not numerical abilities, and this will be highlighted in this chapter. The search for numerical abilities requires unique controls in terms of the stimuli used, and typically requires more training of subjects than some quantitative (but not numerical) tasks. However, this point of clarification does not mean that numerical capacities are only weakly evident in animals, or are only used as a last resort (e.g., Davis & Memmott, 1982; Davis & Perusse, 1988). Rather, it indicates that tests of numerical competence sometimes are harder to design because of the need to instruct animals about the specific task demands. As such, it should not be surprising that animals sometimes require more training to perform these tasks. At the same time, it is fair and appropriate to acknowledge that there are good evolutionary reasons for quantitative abilities (such as choosing more food over less food) to be more widespread and more readily accessible to animals than numerical abilities (such as choosing exactly three food items). Of course, this is also true in human development, and even in the behavior of adult humans in a number of situations. The main point at the outset is that one focus of this article is to highlight the range of quantitative abilities that animals show even if those are not all instances of formal numerical cognition. Another focus is to highlight those cases in which we can infer true numerical abilities given the performance of animals in some kinds of tests.

HISTORICAL APPROACHES TO QUANTITATIVE AND NUMERICAL COGNITION IN ANIMALS

Historically, one of the strongest efforts in comparative psychology, and one of its earliest focus

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areas was on numerical cognition, and more specifically the effort to document counting and more advanced mathematical skills in animals (see Volume 1, Chapter 2, this handbook). This had the unfortunate early effect of giving the area a "black eye" because of the Clever Hans episode, and the resulting backlash against allowing for the possibility that animals could use numerical information (Pfungst, 1911; also see Beran, 2012a; Davis, 1993; Candland, 1995). However, research continued sporadically through the next half of the 20th century. For example, Kuroda (1931) assessed whether a macaque (*Macaca cynomolgus*) could discriminate between one and two sounds, and two and three sounds. Although performance was mixed, the results seemed to indicate that monkeys could be good subjects for numerical discriminations (something we now know is certainly true). Hicks (1956) trained rhesus monkeys (*Macaca mulatta*) in a visual discrimination task in which they had to choose a card with three figures on it from other distracter cards with one to six figures on them. What was interesting in this approach was one of the first real attempts to isolate number as the dimension controlling responding, rather than other features such as area. Hicks anticipated the need to use many different stimulus types, and many different configurations so that the monkeys could not memorize specific stimuli or use non-numerical cues such as total area of the stimuli. With these controls in place, the monkeys still showed some capacity for searching out and finding the cards that demonstrated the concept of "threeness."

Other early reports of animal tests were concerned with number concepts and counting abilities. For example, Ferster (1964) reported that two chimpanzees (*Pan troglodytes*) learned to generate one of two binary "numbers" in a mechanical apparatus to match a presented form with a quantity of shapes on it. However, it took the chimpanzees hundreds of thousands of trials to reach this level. A wide variety of birds including budgerigars (*Melopsittacus undulates*) and ravens (*Corvus cora*) were given tests to see how well they could discriminate simultaneously presented items using a matching-to-sample protocol (e.g., Koehler, 1951; see Figure 25.1). In these tests, a sample was shown with some number of items in it, and the birds had to locate a lid that had the same number of items on it if they wanted to receive food reward. In other tests, birds were trained to eat only a specific number of grains from a pile or risk punishment for not matching that allowable number. Birds were successful in both tasks, suggesting they could match numerosity and also generate sequential responses that were perhaps numerical in form.

FIGURE 25.1. **Examples of animals at work on quantitative cognition tasks. The image at top left is of a bird matching numbers of items across cards (Koehler, 1951). The image at top right is of the parrot Alex surveying an array of items that he could be queried about (e.g., "how many blue blocks"). Those arrays could vary in the size, type, color, and configuration of items from trial to trial, requiring Alex to focus on the number of items as the relevant cue for number questions. Photo courtesy of Arlene Levin and The Alex Foundation. Reprinted with permission.The bottom image is of the chimpanzee Lana performing her constructive enumeration task (Beran & Rumbaugh, 2001), in which she had to use a joystick with her hand to collect dots, one at a time, on the screen to match the value of the Arabic number at the right (in this trial, 7). Photo courtesy of Beran and Rumbaugh.**

Through this period, comparative numerical cognition research began to show better refinements in methodology, particularly with more careful controls for inadvertent cuing of animals. Researchers found themselves pursuing a wide variety of questions that pertained to whether animals could count, what kinds of things they might count, and whether they had a true number sense. These efforts informed us about two things. First, they illustrated what environmental features and stimulus dimensions matter to animals as they have adapted to the ecological niches that they presently occupy. Second, these efforts have been influential in understanding the evolution of numerical cognition and mathematical competence in our own species, as well as in guiding efforts to document and understand the developmental emergence of early quantity manipulation and numerical cognition in humans. The approach to studying numerical cognition in animals has had a large impact on understanding how a true number sense emerges in children and flourishes in human adults through their use of more advanced mathematics (see Brannon & Roitman, 2003; Cantlon, Platt, & Brannon, 2009; Gallistel & Gelman, 2000; Jordan & Brannon, 2006a; Park & Brannon, 2013).

COUNTING ANIMALS

Two things happened starting in the 1970s that put a strong focus on the question of whether animals were capable of counting. The first was the growing recognition that at least some nonhuman species might be capable of symbolic representation, best represented by efforts to teach symbol systems and assess communication abilities in chimpanzees (e.g., Gardner & Gardner, 1969; Premack & Premack, 1983; Rumbaugh, 1977; Savage-Rumbaugh, 1986) and other animals such as dolphins (*Tursiops truncatus*; e.g., Herman, Richards, & Wolz, 1984; see also Volume 1, Chapter 32, this handbook). The second was the growing developmental literature on the early acquisition of counting abilities in children (see Volume 1, Chapter 20, this handbook and Chapter 26, this volume). A highly influential part of this literature focused on documenting and understanding the emergence of young children's competence with certain counting principles (see Gelman & Gallistel, 1978). These principles were offered as a means of understanding how the child comes to understand number, but these principles could easily be applied to tests designed for nonhuman animals, to see if they also might have an understanding of number. Being a proficient counter involves five principles:

- *Stable order principle*—The numerals or other tags that are used to enumerate and represent items within a counted array must be applied in the same order across counting events. In doing this, the counter learns that the labels consistently represent the same number of items.
- *One-to-one correspondence principle*—The numerals or other tags that are used must be applied to each item once, and only once, within a counting event. Otherwise, the resulting tally for the full set will be inaccurate.
- *Ordinality principle*—The numerals or other tags that are applied during counting each represent a given item's sequential place within the array (e.g., first, third, fifth). This principle is important for making relational judgments between different sets that are counted (e.g., relations of more or less).
- *Cardinality principle*—The final numeral or other tag that is applied when someone counts a set of items not only stands for the ordinal position of that item, but also represents the sum total of the set. Knowledge of this principle allows someone to answer the question of how many items, by giving the last numeral that was generated.
- *Abstraction principle*—This principle states that the counting routine can be applied to any array of things—so marshmallows, pencils, beeps of a car horn, or months in a year can be counted using all of the other principles in the same way.

Comparative psychologists took up the challenge of assessing the extent to which nonhuman animals showed evidence of these principles in various kinds of tasks. Although these tasks were designed to be similar to the studies used with children, they also had their own creative and necessary features that were required to get animals to engage in the often long-term and intensive training routines that were used. In some ways, these projects were rousing successes, and in other ways they were failures, but this depended on the framework from which one evaluated the projects. If the goal was to show counting equivalent to that of the 4- or 5-year-old child, the projects all fell short. But, if the goal was to show the extent to which these counting principles might emerge in creatures that could not be verbally instructed, and who were never immersed in a number-rich culture like that of the young child, these projects were quite successful, and many of them remain the hallmarks against which current studies trying to show counting behavior are measured.

Perhaps the most frequently assessed principle in these projects was the cardinality principle, in terms of researchers trying to show that animals could learn symbols of specific numerical concepts, and then apply those symbols across contexts that required enumeration, or that required comparisons of sets of things in terms of their numerousness. Much of this evidence was promising, and hard-earned given the extensive efforts of the research teams that worked with these animals. Some tests required animals to search for or respond to cardinal number values. For example, Davis (1984) trained a raccoon (*Procyon lotor*) to always choose from among multiple alternatives a cube that contained only three items, and those varied in size, color, and other factors so that the raccoon had to use the "threeness" of the set as the only cue that it was the correct choice. Davis (1996) trained ferrets (*Mustela putorius furo*) to eat only three pieces of food from a larger array, controlling the volumetric and spatial aspects of the arrays so that the ferrets could use only the number of items eaten to guide responding.

Three of the longest running and most impressive efforts to demonstrate cardinality in nonhuman animals came from the laboratories of Sarah Boysen, Tetsuro Matsuzawa, and Irene Pepperberg. Boysen and Matsuzawa approached the question of cardinality and counting in chimpanzees mainly by focusing on the capacity of their animals to label sets of objects. Boysen's star chimpanzee was a female named Sheba who learned to use Arabic numerals to label all manner of arrays of items. Sheba's abilities extended even beyond labeling one set of items with the correct numeral label to include labeling summed sets of items found distributed across different places. Sheba could move to two or more locations, view a small collection of items in each location, and then give the numeral label for the total number of things she saw, even though she never saw them all in the same place (Boysen & Berntson, 1989). Sheba also provided some of the clearest behavioral evidence of true tagging of items (suggestive of the one-to-one correspondence principle), with her touches of stimuli during her counting tests (Boysen, Berntson, Shreyer, & Hannan, 1995). And, her knowledge of numeral meanings helped her overcome tasks in which impulsive, prepotent reaches toward more real food over less real food could be offset by using the symbolic nature of those numerals (e.g., Boysen & Berntson, 1995).

Matsuzawa (1985) focused his initial training efforts on labeling of stimuli. His star subject, a female named Ai, could look at arrays of things that differed in the type, color, and number of each subset, and then answer questions about any of those dimensions of the set of items. She became quite adept at correctly labeling numbers of things, as did other chimpanzees in that laboratory, and they transferred numeral knowledge to other tests of cardinality and ordinality (e.g., Biro & Matsuzawa, 2001; Tomonaga & Matsuzawa, 2002). In later years, a major focus has been on ordinality abilities (see Chapter 18, this volume), and specifically the excellent memory performance of these chimpanzees in sequencing Arabic numerals (e.g., Biro & Matsuzawa, 1999; Inoue & Matsuzawa, 2007; Kawai & Matsuzawa, 2000).

Pepperberg's (1987, 1994, 2006, 2013) work with the African Grey parrot (*Psittacus erithacus*) named Alex took a very different approach. Through a competitive modeling training paradigm (Pepperberg, 1999; Pepperberg, Sandefer, Noel, & Ellsworth, 2000), Alex came to learn the verbal numerals, and he could apply those labels much like Ai had—to multi-dimensional sets of things for which number was only one dimension (see Volume 1, Chapter 32, this handbook). Alex could be asked, for example, to look at an array of three green blocks intermixed with four blue corks, often with these classes of items all varying in size, and then answer the question of how many blocks or even see the same items in different colors and label the number of items of only one color (Figure 25.1). The variety of items used in different sizes and colors ensured that Alex had to rely on number as the critical dimension in his responses rather than other features. Pepperberg extended this research to include, among other things, demonstrations of the zero concept (Pepperberg, 2006; Pepperberg & Gordon, 2005), how ordinality and cardinality related to each other in Alex's behavior (e.g., Pepperberg & Carey, 2012), and Alex's ability to comprehend questions in which the number was part of the question rather than always the answer to a question (e.g., Pepperberg, 2012).

Other animals were given a task more like that of Koehler's (1951) test with birds where they had to make specific numbers of sequential responses to a computer task (see Volume 1, Chapter 6, this handbook). The chimpanzee Lana learned to collect boxes on the screen that matched a presented Arabic numeral, and she was proficient for small numbers of items (Rumbaugh, Hopkins, Washburn, & Savage-Rumbaugh, 1989). In subsequent studies, Lana and other chimpanzees learned to collect dots on a computer screen, one-at-a-time, to match a presented Arabic numeral (see Figure 25.1). They did this for as many as seven dots to match the Arabic numerals 1 to 7 (Beran & Rumbaugh, 2001; Beran, Rumbaugh, & Savage-Rumbaugh, 1998). Another research team showed that pigeons could use numerals bidirectionally by either constructing sets of items to match a given numeral or labeling sets of presented items with the correct numerals (e.g., Xia, Emmerton, Siemann, & Delius, 2001; Xia, Siemann, & Delius, 2000).

Other projects showed that animals could use symbols for quantities, which led to new approaches to studying things such as ordinal knowledge. For example, rhesus monkeys learned the ordinal relations of Arabic numerals, selecting the larger member of any given pair of numbers from 1 to 9, and even selecting from arrays of up to five numerals in the correct descending sequence (Washburn & Rumbaugh, 1991). Pigeons (Olthof & Roberts, 2000) and squirrel monkeys (*Saimiri sciurius*; Olthof, Iden, & Roberts, 1997) also learned to use numerals in a similar fashion to the rhesus monkeys and even appeared to sum those numerals. In many of these tests, some of the same effects of ordinal knowledge in humans also were found in animals, such as transitivity (e.g., Boysen, Berntson, Shreyer, & Quigley, 1993; see also Chapter 18, this volume), symbolic distance effects (e.g., Washburn & Rumbaugh, 1991; see also Chapter 18, this volume), and magnitude and ratio effects (see Chapters 16 and 23, this volume), as will be discussed in more detail later in this chapter.

Another productive approach for showing aspects of ordinal knowledge and perhaps also cardinal knowledge was through training animals to enumerate a specific number of runs they made, for example, in a maze, allowing for control over nonnumerical cues such as time, distance, and other factors. Davis and Bradford (1986, 1987) trained rats to run to a specific tunnel in an enclosure, designated only by its ordinal position among the tunnels the rats came across in the enclosure, and not by any absolute location. Capaldi and Miller (1988) trained rats to anticipate unrewarded runs to the end of maze that came at some ordinal point in the series. For example, they might have learned that three runs that were rewarded meant the next run would not be rewarded. Capaldi and Miller included important controls to ensure the rats could only use the number of runs or the ordinal position of a particular run number to discriminate when nonreward was likely (see also Burns, Goettl, & Burt, 1995).

Other behaviors that included evidence of some of the counting principles also came from traditional laboratory species such as pigeons (*Columba livia*; e.g., Roberts & Mitchell, 1994) but also from less well-studied species including insects such as bees (*Apis mellifera*; e.g., Chittka & Geiger, 1995; Dacke & Srinivasan, 2008) and ants (genus *Formica*; Reznikova & Ryabko, 2011). Despite all of these approaches, and the wealth of data suggestive of proto-counting abilities in many species, to date there have been no truly convincing reports of counting abilities in an animal that match the abilities of a 4- to 5-year-old human child. However, this comparative evidence re-established that, with more proper controls and intensive training, some species showed forms of quantitative cognition that approached the counting performances of humans, even if those performances were not equivalent. Specifically, there is evidence of ordinality, cardinality, and abstraction, although there is more limited evidence that animals use one-to-one correspondence or establish a stable order for their enumerative sequences, which may help explain the "fuzzy" nature of counting in animals compared to the degree of competence shown by most school-age children. Thus, although nonhuman animals do not meet the full definition of being able to count, some aspects of their cognition possess what we can clearly identify as elements of counting. And, the results of testing animal counting, including in symbolic modes, matches the results found in studies of animal language which often concluded that although no animals possess the full language capacities of humans many species possess elements of language (see Volume 1, Chapters 14 and 32, this handbook).

RELATIVE QUANTITY JUDGMENTS

Perhaps the most widely studied capacity is that for making relative quantity judgments (RQJs). These are choices made after comparison of two or more items or sets of items on the basis of their magnitude (e.g., size, amount). These judgments are not purely numerical because factors other than the number of items in the choice sets covary with number, allowing the animal potentially to use those other dimensions. For example, choosing the larger of two sets of grapes does not have to result from counting the number of grapes or even using number concepts like "three" and "five" but could result from summing the amount of grapes in each set. This does not mean these judgments are not made on the basis of number—they may still be, but when other stimulus dimensions covary with number it is important to remain agnostic as to whether these are truly numerical judgments, at least until more controlled stimuli are used. When such controls are put into place, and only number can serve as the dimension to indicate the correct choice, then a relative numerousness judgment (RNJ) is required.

One of the most impressive and convincing aspects of the literature on animal quantification skills is the breadth of things that have been given to animals to quantify, usually in a RQJ task but sometimes as an RNJ task. Researchers in this area have shown great creativity in finding stimuli that animals must discriminate, enumerate, or otherwise quantify, and these things typically fall into two broad categories—natural stimuli and arbitrary, nonnatural stimuli. They also can be presented in various modalities—visual stimuli, auditory stimuli, and even olfactory or tactile stimuli. In this section, I will outline the breadth of this literature, although of course there must be some selectivity given the limits of space. The key point is that, for all of the types of things outlined following, the evidence is clear that animals quantify those things, and in some cases remember or manipulate quantities.

Quantifying Visually Presented Discrete Food Items

Food items make excellent stimuli for quantity judgment tasks because obtaining food is a common drive across all species. One type of quantity judgment that makes use of food items is a size judgment. Here, animals are presented with two or more food items of the same type but different size. For example, Menzel (1960) presented chimpanzees with pieces of banana and allowed them to select the pieces in any order. The chimpanzees selected larger pieces first, and their precision for such judgments corresponded closely to human visual judgments of size. Subsequent work with chimpanzees using these size judgments demonstrated other similarities with human perception and also showed how sensitive chimpanzees could be to small differences in the items (e.g., Menzel, 1961; Menzel & Davenport, 1962; for a more recent comparative test of size comparison of nonfood items, see Schmitt, Kröger, Zinner, Call, & Fischer, 2013).

The abilities of different species to make these size judgments also allows researchers to ask other kinds of questions that relate to quantification but with a focus on how contexts in which items are presented can impact judgments. One well-studied phenomenon in human cognition, and particularly the development of young children, is conservation of quantity (e.g., Piaget, 1965; see also Chapter 26, this volume). Conservation tasks present children with a transformation of one quantity in a way that makes it look different without changing its quantity. For example, liquids in tall, skinny containers can be poured in short, wide containers, and the typical perceptual experience that many children (and adults) have is that suddenly it looks like there is less of that liquid compared to before the transformation. But, individuals who understand that the quantity is still conserved know that there is no actual change. This is an important developmental milestone for children, but also a capacity that we know exists in some other species. For example, Suda and Call (2004, 2005) presented chimpanzees, bonobos (*Pan paniscus*), and orangutans (*Pongo pygmaeus*) with conservation tasks of continuous (liquid) and discrete (solid food item) quantities and found that the apes were successful in both cases (see also Woodruff, Premack, & Kennel, 1978). Call and Rochat (1996) directly compared humans with orangutans on solid and liquid conservation tasks, with orangutans showing conservation. Using discrete quantities, Muncer (1983) tested a chimpanzee using a task in which two rows of candies were presented, and those rows underwent a transformation in which they were compressed or extended. The chimpanzee succeeded in still obtaining that larger number of items. Some monkey species including rhesus monkeys and capuchin monkeys (*Cebus apella*) also show conservation of discrete quantities in computerized RQJ tasks (e.g., Beran, 2006, 2008a).

This is not to say that the context used for presenting quantities never affects quantity perception in animals (see Chapters 1 and 8, this volume). It does, and perhaps this is best documented for humans. Much of the evidence comes from the human consumption literature, in which people make judgments of real food amounts, and show certain biases in terms of how the food is viewed given the context in which it is presented (see Chapters 15 and 16, this volume). As noted, liquids are overestimated regarding their volume when in taller, narrow containers versus shorter ones that are wider. People also overestimate how much food is on a small plate relative to the same amount of food on a large plate, and this leads to overserving oneself when given a large plate instead of a small one. People also tend to prefer food quantities that overflow the containers in which they are placed (such as ice cream that overflows its cup) relative to the same amount of that food that is instead nestled down into a container, giving the sense that the container is less full (e.g., Hsee, 1998; Van Ittersum & Wansink, 2012; Wansink, 2004). We now know that chimpanzees show some of these same biases. For example, when two plates (a large one and a small one) were presented with the same-sized food item on each, chimpanzees preferred the smaller plate, suggesting that the food item on that plate looked larger than the one on the large plate. Sometimes, chimpanzees even preferred less food presented on a small plate relative to more food presented on a large plate, even though they rarely made that mistake when those differing food sizes were both presented on small plates or both presented on large plates (Parrish & Beran, 2014b). Chimpanzees also preferred containers that overflowed with food items rather than being bigger with those items nestled more inside. Again, this preference sometimes comes at the cost of obtaining less food rather than more food, and even though the chimpanzees did not make such errors when both containers were the same (Parrish & Beran, 2014a; see Figure 25.2). So, for some animals, like for humans, quantification depends on the context in which stimuli are presented.

Another quantification task with foods consists of discrete items that must be summed or enumerated to generate a perception (or representation) of the full quantity of that set. Dooley and Gill (1977) trained a chimpanzee named Lana to choose between two sets of cereal pieces, and she often chose the larger quantity of each pair when up to 10 pieces of food were presented in each quantity. However, her performance declined when both quantities were nearer the upper limit of that range and they were close in number. Rumbaugh, Savage-Rumbaugh, and Hegel (1987) gave chimpanzees trials where two separate food quantities had to be summed (or combined) to determine which pair of quantities was the larger total amount. In this case, the chimpanzees saw individual food items in two pairs of two food wells, and they were allowed to choose one of the pairs. The chimpanzees proved adept at selecting the larger overall food quantity, even when that set of wells might not hold the overall largest individual set (e.g., choosing the pairs with three and four items over a pair with one and five items). Since then, this kind of simultaneous choice task, where both sets of food items to choose between can be seen at the same time, has been given to a wide range of species (see Table 25.1 for some examples). Although the sensitivity to smaller differences between set sizes varies across these

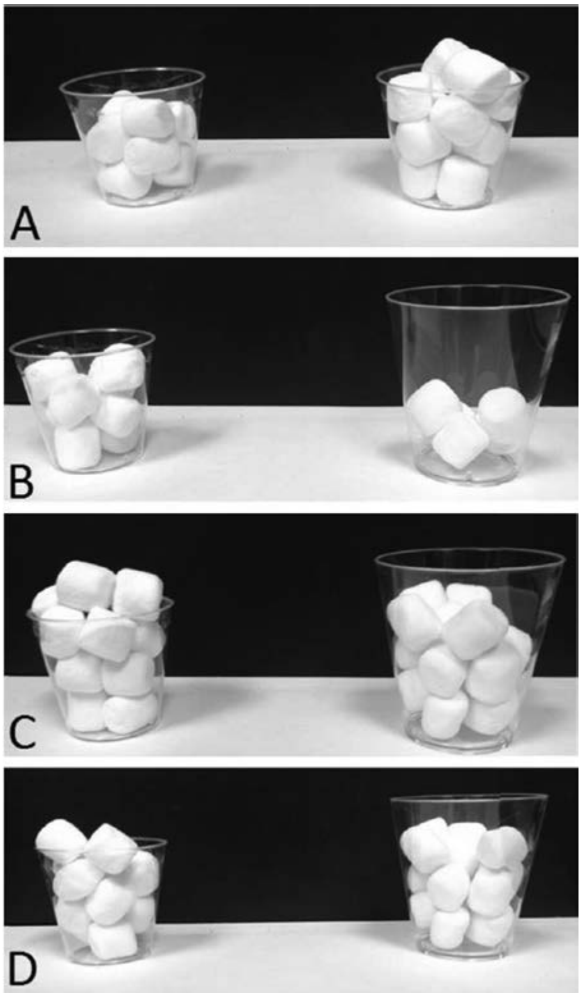

FIGURE 25.2. Example test stimuli from Parrish and Beran (2014a), presented to chimpanzees. Panel A shows an example trial where both containers are the same size and only the number of marshmallows varied. Panel B shows an example trial where the smaller container also held more items. These two trials types were very easy for the chimpanzees to choose the largest amount of food. In Panel C, the number of marshmallows in the two containers was the same, but the chimpanzees showed a bias to select the smaller container, presumably because it looked more full. In Panel D, there are fewer marshmallows in the small container, but even here chimpanzees sometimes showed a bias for this container over the other one that had more items in it. From "Chimpanzees Sometimes See Fuller as Better: Judgments of Food Quantities Based on Container Size and Fullness," by A. E. Parrish & M. J. Beran, 2014, *Behavioural Processes, 103,* p. 189. Copyright 2013 by Elsevier. Reprinted with permission.

species, in general these species seek out and choose the larger food amount.

A more challenging task involves the sequential presentation of these food items, typically into opaque containers. This sequential presentation sometimes involves revealing full sets one after another rather than at the same time, so that the animals must remember what the total quantity is in each set (e.g., Call, 2000). But, more frequently, the sequential tasks involve the presentation of each set as a one-by-one transfer of items into the opaque containers, and then the animal makes its choice from among the containers. Full sets are never seen at once, and the animal must track and tally each item as it updates its representation of the set number (or amount), and then compare those representations as the basis for making its choice, because it cannot directly see the total quantities in the sets. This test eliminates many of the concerns that animals could be using a mechanism that provides a parallel (or immediate) apprehension of quantity without need of enumeration (Mandler & Shebo, 1982), a mechanism that does appear to exist in some nonhuman species (e.g,, Agrillo, Miletto Petrazzini, & Bisazza, 2014; Murofushi, 1997; Tomonaga & Matsuzawa, 2002). When items are presented in sequence, there cannot be any immediate apprehension of the set's quantity but an enumerative process must occur.

One effort with this method tested chimpanzees (Beran, 2001). On each trial the chimpanzees observed an experimenter dropping food items, one-at-at-time, into one of two opaque containers. The chimpanzees were quite proficient in selecting the larger set. Subsequent to this, additional operations were presented—sets were added to each container at different times (e.g., 2 + 3 vs. 3 + 1). Again, the chimpanzees were good at choosing the larger set. This was true even when three sets were added to each container (e.g., 2 + 2 + 3 vs. 3 + 4 + 1). These results indicated that chimpanzees mentally represented the summed quantities in each set and compared these nonvisible, sequentially presented sets of items (see also Beran, 2004).

Subsequent studies with chimpanzees showed that they could make these relative quantity judgments even when each set was not presented individually, but instead were presented through continuous alternation between the containers, and even when the total trial duration was 20 min, requiring the chimpanzees to engage long-term

TABLE 25.1

Examples of the Diverse Species Given Relative Quantity Judgement Tasks With Food Items

Species	Representative citations
Chimpanzees (*Pan troglodytes)*	Boysen et al. (1995); Rumbaugh et al. (1987)
Orangutans (*Pongo pygmaeus*)	Anderson et al. (2007); Call (2000)
Gorillas (*Gorilla gorilla*)	Anderson et al. (2005)
Bonobos (*Pan paniscus*)	Hanus & Call (2007)
Capuchin monkeys (*Cebus apella*)	Addessi et al. (2008); Beran et al. (2008)
Olive baboons (*Papio anubis*)	Barnard et al. (2013)
Sea lions (*Otaria flavescens*)	Abramson et al. (2011)
Beluga whale (*Delphinapterus leucas*)	Abramson et al. (2013)
Dolphins (*Tursiops truncatus)*	Abramson et al. (2013)
Horses (*Equus caballus*)	Uller & Lewis (2009)
Dogs (*Canus lupus*)	Ward & Smuts (2006); West & Young (2002)
Coyotes (*Canis latrans*)	Baker et al. (2011, 2012)
North Island robins (*Petroica longipes*)	Garland et al. (2012)
Crows (*Corvus macrorhynchos*)	Bogale et al. (2014)
Frogs (*Bombina orientalis*)	Stancher et al. (2015)
Salamanders (*Plethodon cinereus*)	Uller et al. (2003)

memory for quantity rather than working memory or short-term memory only (Beran & Beran, 2004). Another study showed that all four great ape species also passed this sequential presentation test as well as other presentation formats (Hanus & Call, 2007), as did baboons (*Papio anubis*; Barnard et al., 2013), capuchin monkeys (Beran et al., 2008; Evans, Beran, Harris, & Rice, 2009), lemurs (*Eulemur mongoz*; Lewis, Jaffe, & Brannon, 2005), a beluga whale and dolphins (Abramson et al., 2013), elephants (*Loxodonta africana*; Perdue, Talbot, Stone, & Beran, 2012), fish (*Gambusia holbrooki*; Dadda, Piffer, Agrillo, & Bisazza, 2009), and North Island robins (*Petroica longipes*; Garland et al., 2012; Hunt, Low, & Burns, 2008). Other sequential presentation formats have been used, such as showing each item separately in unique locations within larger spatial arrays and allowing animals such as chimpanzees or robins to choose one spatial area within the testing location (Beran, McIntyre, Garland, & Evans, 2013; Garland, Beran, McIntyre, & Low, 2014).

Quantifying Sets of Visually Presented Continuous Food Items

Other studies have made use of continuous quantity rather than discrete quantity in the RQJ format. For example, Aïn, Giret, Grand, Kreutzer, and Bovet (2009) showed that African Grey parrots were good at choosing the larger amount of parrot formula, and Beran (2010) reported that chimpanzees accurately selected the larger of two amounts of liquids that were each poured into opaque containers. vanMarle, Aw, McCrink, and Santos (2006) also showed that capuchin monkeys could discriminate among differences in poured amounts of banana puree. These examples highlight that continuous and discrete quantities appear to be equally well managed in the quantitative cognition of animals.

Quantifying Food Stimuli Presented in Auditory Form

The idea that animals might make relative or absolute judgments of quantities presented in nonvisual formats has support from a variety of species tested in laboratories. For example, Beran (2012b) presented chimpanzees with food items that were dropped into opaque containers behind a screen, so that the chimpanzees only heard the items land in the containers rather than seeing them (in essence, an occluded version of the sequential presentation paradigm previously outlined). The chimpanzees' performances in this case matched what their proficiency was in tests where they saw the items (e.g., Beran, 2004). And, they even chose the larger quantity when a sequentially presented auditory set was compared with a fully visible set, suggesting that they formed a representation of the set they heard that could be compared to a set they could see.

Quantifying Individuals

An interesting and ecologically relevant approach to studying animal quantification asks how well animals quantify other individuals. Take, for example, a fish that finds itself separated from its shoal. This can be a dangerous situation to find oneself in, because there is safety in numbers. If two shoals are present, there is good reason to expect the fish might attempt to place itself into the larger shoal for the greater safety. Such tests have been given to fish, with compelling results that show fish can make these judgments (e.g., Agrillo, Dadda, Serena, & Bisazza, 2008; Gómez-Laplaza & Gerlai, 2011a, 2011b; Piffer, Agrillo, & Hyde, 2012). What remained to be seen was exactly what the fish quantify—is it the number of conspecifics in the shoals, or the amount of conspecifics in the shoal? Do bigger individual fish in one group bias choices of that shoal versus a numerically larger shoal but with smaller individuals? This is an important question, and a good test case for assessing whether choice is controlled by numerical properties of the shoals or other more continuous, quantitative properties that do not require understanding and using number. As one might expect, fish can use number when it is the necessary dimension to attend to, as with tasks that use arbitrary stimuli (e.g., Agrillo, Piffer, & Bisazza, 2011) but they sometimes also rely on dimensions that covary with number and that work to allow them back into a larger shoal (e.g., Dadda et al., 2009; Gómez-Laplaza & Gerlai, 2013). Discriminating between quantities of conspecifics is not limited to fish, as rats use the relative quantities of other rats as a discriminative cue (Davis & Hiestand, 1992).

Some species seem to use the number of calls of individuals in another group to estimate group strength, and then to modify approach or avoidance behavior. When chimpanzees in the wild were presented with playback recordings of the calls of a male from outside their group, their decision to approach or avoid that individual was dictated by the number of individuals within their own group (Wilson, Hauser, & Wrangham, 2001). Playback experiments also were used with lions (*Panthera leo*), where the number of roaring lions in the intruder group varied. Roars from more intruders led the focal subject lions to avoid rather than approach the direction of the roars versus when only a single intruder roared, and approaches then increased. The lions, like chimpanzees, also appeared to approach the playback of more roaring with greater caution, and the lions adjusted their approach according to the size and composition of their own group as well (McComb, Packer, & Pusey, 1994). Black howler monkeys (*Alouatta pigra*) also showed approach responses that were weakest when the subjects faced unfavorable odds given the number of animals that were represented by playback calls whereas approach was more likely with favorable odds (Kitchen, 2004). Wild spotted hyenas (*Crocuta crocuta*) appeared to assess intruder strength in a similar manner, at least for small number of potential intruder calls, as they responded with increasing levels of vigilance to calls produced by one, two and three unknown intruders. They also showed the pattern of greater approach when their own group shared a numerical advantage in relation to the calling intruders (Benson-Amram, Heinen, Dryer, & Holekamp, 2011). And, wild dogs show this pattern in conflict situations, by showing greater likelihood of approaching opponents aggressively with a larger relative advantage in the number of pack members to rivals (Bonanni, Natoli, Cafazzo, & Valsecchi, 2011). These are impressive instances in which quantitative cognition serves important and potentially life-preserving interactions between animals. Although it cannot be confirmed that these species are making RNJs when they assess their group strength versus intruder group strength, even the RQJs that likely are used highlight the salience of quantity estimation and calculation in daily lives of wild animals. And, each of these cases highlights the capacity of animals to perceive and use quantitative information presented in nonvisual formats, and important aspect of showing that quantitative cognition is modality independent.

Quantifying Olfactory and Tactile Stimuli

One intriguing species for assessing quantitative cognition in an understudied sensory modality is the meadow vole (*Microtus pennsylvanicus*). These animals spend a lot of time scent marking territory and responding to the scent marks of conspecifics, leading to the question of exactly what they might attend to when doing these behaviors. Although there are a number of factors, quantity is one of the most relevant. For example, male voles will overmark the scents of other males, leading to potential locations where more or less marks from different males might be present. In these cases, voles do distinguish between males who leave more marks and those who leave less, indicating that they are making a RQJ for scent marks (e.g., Ferkin, Pierce, & Sealand, 2009; Ferkin, Pierce, Sealand, & Delbarco-Trillo, 2005). And, this capacity for judging relative quantities impacts the memory of female voles that show a preference at a later time for those males who produce more scent marks versus less scent marks (Ferkin & Hobbs, 2014).

Researchers working with rats also have generated a number of creative designs for looking at quantity judgment and discrimination in nonvisual modalities. For example, Davis and Albert (1986) trained rats to respond when they heard three bursts of noise but not two or four bursts. Davis, MacKenzie, and Morrison (1989) trained rats to respond to differing numbers of touches to parts of their bodies, although this was not an easy discrimination for the rats.

RELATIVE NUMEROUSNESS JUDGMENTS

The RNJ task is basically identical to the RQJ tasks that were previously discussed, but with the exception that careful attention is given to controlling any nonnumerical cues that could be used to discern the correct response, without need of focusing on number cues. This can be a very difficult set of controls, especially when working with visual stimuli. Controlling total area allows density to become confounded with number. Controlling size allows density to become confounded with number. Controlling total amount allows average size to become confounded, and so on. This is unavoidable, and so the best approaches are those that make use of highly varied stimuli, or that control within each trial some of the features but across all trials eventually all of these features. The resulting performances of the animals then can be used to determine whether responding was under the control of number or was not.

Thomas, Fowlkes, and Vickery (1980) gave squirrel monkeys a task in which they had to choose a card displaying fewer items among pairs of cards representing quantities between two and nine, where the items varied in a number of features. Thomas and Chase (1980) also assessed whether these monkeys could flexibly choose on the basis of smallest, intermediate or largest when given three choices, and the monkeys were successful. Terrell and Thomas (1990) trained squirrel monkeys to make these judgments with variable polygons that all had different numbers of sides and angles, ensuring that the monkeys could not memorize specific stimuli or use nonnumerical features across trials. Again, the monkeys were successful.

Pigeons have been tested frequently for their capacities for judging relative numbers of items, and researchers who work with pigeons have provided some of the strongest methods to control for nonnumerical cues and ensure that judgments are made on the basis of number. For example, Emmerton (1998) reported that pigeons could chose the visual array containing fewer numbers of items, although pigeons also were affected by the density of the arranged items in each array. Santi and Hope (2001) also found that although pigeons could use numerical information when discriminating between numbers of light flashes, they also tended to confound number and duration of flashes in some cases (see also Fetterman, 1993; Roberts, Coughlin, & Roberts, 2000; Roberts, Roberts, & Kit, 2002).

In some tests, the relative discrimination is made for intermixed stimuli. These RNJs require animals to attend to subsets within sets, and then compare those to each other. Alsop and Honig (1991) showed pigeons sequences of flashing red and blue lights, and the pigeons had to indicate which of the two colors was more numerous. They could do so, although performance was affected by the relative difference in the two colors and the more recent flashes tended to be overemphasized in the final response of the birds. Monkeys also can track and enumerate moving items of one type within a larger set, indicating which subset is more numerous (Beran, 2008b; Beran, Decker, Schwartz, & Schultz, 2011) as can gorillas (Vonk et al., 2014) and black bears (*Ursus americanus*; Vonk & Beran, 2012).

The most systematic effort to establish control by number in relative judgment tasks comes from Brannon and her colleagues. They have developed computer software that controls for each of the non-numerical stimulus dimensions in different trials, so that when an animal performs at high levels in this task, it must be on the basis of using number exclusively or predominantly. In this task, animals are presented with sets of things, where each set consists of all manner of items in varying colors, sizes, and distances from each other. It is relative discrimination, and so reward is given for choosing arrays on the basis of smaller or larger numbers of items. Rhesus monkeys originally passed this test, showing that they used number as the relevant cue to which they responded (Brannon & Terrace, 1998, 2000). Brannon and her colleagues then asked new questions about numerical judgments in this species. They found that monkeys performed just as well with heterogeneous stimuli (mixed colors, sizes and shapes) as homogeneous stimuli even when they were trained with all homogeneous stimuli (Cantlon & Brannon, 2005). They found that reference points (the first trained value in a sequence) impacted the performance of monkeys in making relative judgments (e.g., Brannon, Cantlon, & Terrace, 2006). They found that decision time in choosing the numerically larger or numerically smaller of two sets of items was influenced by the congruity between the cue that indicated the choice rule on a trial (e.g., "choose smaller" or "choose larger") and the magnitude of the choice stimuli (i.e., whether the arrays were of generally small or generally large numbers of dots; Cantlon & Brannon, 2005; Jones, Cantlon, Merritt, & Brannon, 2010). And, they documented a number of similarities between monkeys and humans in terms of the mechanisms that underlie such judgments (e.g., Cantlon & Brannon, 2006b, 2007), a point which will be discussed in more detail later in this chapter. This task was widely adopted, and produced similar data indicating that relative number judgments could be made by a baboon and squirrel monkey (Smith, Piel, & Candland, 2003), capuchin monkeys (Judge, Evans, & Vyas, 2005), lemurs (Merritt, MacLean, Crawford, & Brannon, 2011), and pigeons (Scarf, Hayne, & Colombo, 2011).

There is good reason to expect that evidence for competence in making RQJs would be more prevalent in animals than evidence for RNJs. In many natural situations, number *should be* less relevant than other stimulus dimensions such as amount. A monkey approaching two trees with fruits in them should not select the tree with the larger number of fruits if those are also smaller in size compared to the neighboring tree. To do that is to get less overall food, which is maladaptive. A fish searching for safety in a shoal should not move to the shoal of many small fish when it can hide in a larger mass of fish that might be smaller in terms of the number of fish in it. However, there are also many creative approaches to such judgments tasks that have shown that animals can and will use the number of items in sets to make judgments, ignoring other stimulus dimensions when they have to do that.

NUMBER MATCHING TASKS

A productive approach is the use of a matching-to-sample procedure whereby the sample and correct match choices are determined by the number of items within them, rather than by any other features they might share, such as size or color. These tasks require that an animal view the sample, determine its numerosity, and then seek an equal numerosity in another format. Such tests are not easy for animals to acquire, but when they do, they show good matching performance, suggestive of the use of number as the key feature in the sample and match choices to which the animal responds. This type of matching task has been given to species ranging from orangutans (Vonk, 2014) and monkeys (Jordan & Brannon, 2006b) to crows (Smirnova, Lazareva, & Zorina, 2000) and honey bees (Gross et al., 2009). In some cases, such matching even occurred across modalities as when monkeys matched the number of voices they heard with an equal number of faces

(Jordan, Brannon, Logothetis, & Ghazanfar, 2005) or they matched the number of sounds they heard with the number of arbitrary items they saw on a computer screen (Jordan, Maclean, & Brannon, 2008).

MECHANISMS FOR QUANTITATIVE COGNITION IN ANIMALS

Given all of the successes of animals in making relative and absolute judgments of quantities and even numbers of things, a dominant question in this area pertains to what mechanism or mechanisms underlie these performances. At present, two candidate mechanisms have been proposed, and are evaluated in many of the comparative studies. The first is often called the approximate number system (ANS) or analog magnitude system. This system represents number with increasing variability as a function of true set size. It is related to temporal, spatial, and other magnitude processes that animals use in making choices (e.g., Gibbon, 1977; Mechner, 1958; Meck & Church, 1983; see also Chapters 16 and 23, this volume). In this system, quantity representations, including numerical representations, are inexact, with greater fuzziness in the representation of quantity as a function of true set size (see Chapter 1, this volume). This produces two behavioral effects in tasks such as RQJs and RNJs. The first is that performance improves in judging between sets as the difference between those sets increases (e.g., comparing five items to eight items is easier than comparing five items to six items). And, when the difference between sets is held constant, performance is better when comparing small sets rather than large sets (e.g., comparing four items to six items is easier than comparing seven items to nine items). These two effects are called the *distance effect* (see Chapter 18, this volume) and the *size effect* (or magnitude effect; for reviews and greater discussion of how the ANS may work, see Beran, Parrish, & Evans, 2015; Brannon & Roitman, 2003; Cantlon et al. 2009; Dehaene, 1997; Gallistel & Gelman, 2000; see also Figure 25.3).

A second system for numerical representation has been proposed to also account for how animals (and, in some cases, humans) represent number. The object file model is not an alternate to the ANS but a proposed second system that humans, and perhaps some animals, have that allows for discriminations to be made with high degrees of accuracy for small numerosities but not for large numerosities (see Volume 1, Chapter 20, this handbook and Chapter 26, this volume). In this system (sometimes called a parallel individuation system), there are attentional and memory limits for the individuation of items. Only a small number of things can be enumerated or summed with high precision, with three or perhaps four "files" available in short-term or working memory to faithfully represent those items. Thus, items that are enumerated are encoded in terms of separate object files (i.e., stored in those files) which operate as representations of items within the array and can hold information about item identity and features. The system also can access the number of filled files to generate quantity/numerical information (Feigenson, Carey, & Hauser, 2002; Uller, Carey, Huntley-Fennner, & Klatt, 1999). One key behavioral feature of this system is very high accuracy for relational judgments of two small sets (e.g., discriminating one item and three items is no easier than discriminating two items and three items). This feature has been found in some studies with children (e.g., Feigenson & Carey, 2005; Xu, 2003), but not in others, where the ANS appears to be the only system at work (e.g., Cantlon, Safford, & Brannon, 2010; Cordes & Brannon, 2009).

A third process, perhaps related to the object file model, has been proposed to account for evidence that humans are particularly fast and accurate at reporting small numbers of items (usually four or less) compared to larger numbers of item (greater than four) which instead produce a gradually increasing response time slope and a gradually decreasing performance slope. The process underlying this performance pattern typically is referred to as *subitization*. It has attracted a lot of research in human perception and cognition, with some research teams reporting "super-precision" and speed for small numbers of items (e.g., Choo & Franconeri, 2014; Dehaene & Cohen, 1994; Kaufman, Lord, Reese, & Volkmann, 1949; Mandler & Shebo, 1982; Trick & Pylyshyn, 1994) but others finding less evidence that small numbers are

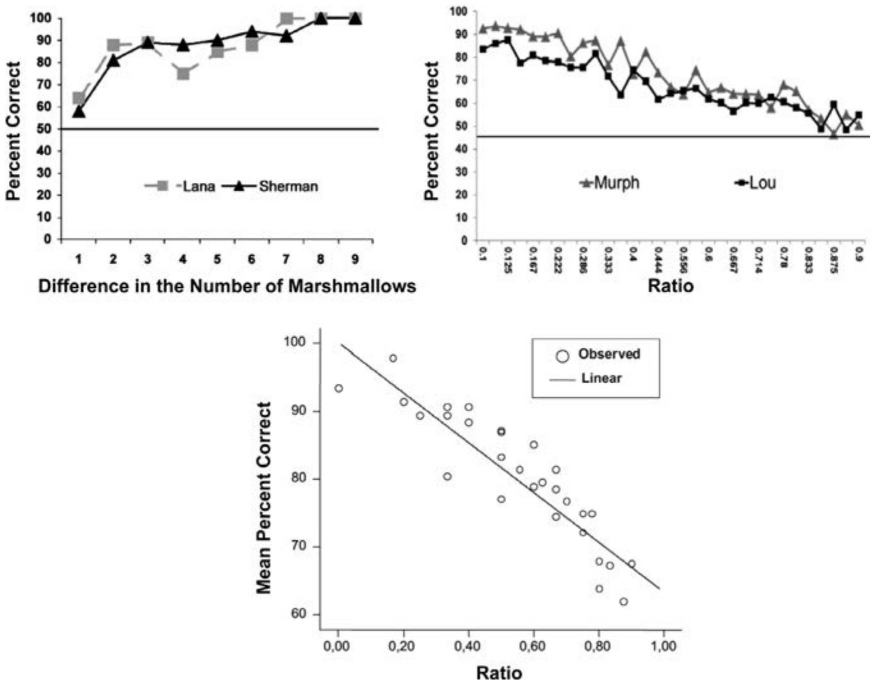

FIGURE 25.3. Distance and ratio effects across species. The top left panel shows a distance effect for chimpanzee judgments of two sets of food items. As the difference in the two amounts increases, the chimpanzees' performance improves. Reprinted from "Chimpanzees (*Pan troglodytes*) Respond to Nonvisible Sets After One-By-One Addition and Removal of Items," by M. J. Beran, 2004, *Journal of Comparative Psychology, 118,* p. 28. Copyright 2004 by the American Psychological Association. The top right panel shows the performance of two rhesus monkeys in choosing between two sequentially presented sets of items. Ratio is calculated by dividing the numerically smaller set by the numerically larger one. As this ratio increases, performance decreases. Reprinted from "Rhesus Monkeys (*Macaca mulatta*) Enumerate Large and Small Sequentially Presented Sets of Items Using Analog Numerical Representations," by M. J. Beran, 2007, *Journal of Experimental Psychology: Animal Behavior Processes, 33,* p. 46. Copyright 2007 by the American Psychological Association. The bottom panel also shows the ratio effect for another sample of apes making relative quantity judgments of food items. Reprinted from "Discrete Quantity Judgments in the Great Apes (*Pan paniscus, Pan troglodytes, Gorilla gorilla, Pongo pygmaeus*): The Effect of Presenting Whole Sets Versus Item-by-Item," by D. Hanus & J. Call, 2007, *Journal of Comparative Psychology, 121,* p. 245. Copyright 2007 by the American Psychological Association.

treated differently in terms of behavioral responding (e.g., Balakrishnan & Ashby, 1991, 1992) or neural activation (e.g., Piazza, Mechelli, Butterworth, & Price, 2002). Subitization has not been as extensively studied in nonhuman animals, especially in recent years where the object file model and ANS typically have been evaluated, but there are reports suggesting that some species such as fish (Agrillo et al., 2014) or chimpanzees (Murofushi, 1997; Tomonaga & Matsuzawa, 2002) may also exhibit a form of subitization in certain quantitative tasks.

There is no doubt of the existence and role of the ANS in the quantitative cognition of nonhuman species. Most studies that have looked for a ratio effect in performance have found one, and this is particularly true for mammal species, and especially true for nonhuman primates. And, in a few cases, the ANS has even been shown in humans when they are given tasks like those used with animals, provided humans are prevented from counting through speeded responding or the use of techniques such as articulatory suppression to prevent subvocal counting (e.g., Beran, Taglialatela, Flemming, James, & Washburn, 2006; Boisvert, Abroms, & Roberts, 2003; Cordes, Gelman, Gallistel, & Whalen, 2001; Whalen, Gallistel, & Gelman, 1999).

Only one study has shown no ratio effect but evidence for the object file model in a nonhuman primate—with rhesus macaques (Hauser, Carey, & Hauser, 2000). That study made use of the sequential presentation method of items into containers. The monkeys struggled with trials in which a small set was compared to a large one (e.g., three items vs. eight items) whereas comparisons of two small sets were easier. However, Beran (2007) found strong ratio effects when rhesus monkeys watched differing numbers of items "fall" into containers on a computer screen. Other tests using the sequential presentation method with primates also found evidence only of ratio effects, but not of set size effects that would reflect the object file model (e.g., Barnard et al., 2013; Beran, 2004; Cantlon & Brannon, 2006a, 2006b; Hanus & Call, 2007; Merritt et al., 2011), and this also is true for a large number of nonprimate species ranging from sea lions (e.g., Abramson et al., 2011) and dolphins (Jaakkola Fellner, Erb, Rodriguez, & Guarino, 2005) to parrots (e.g., Aïn et al., 2009) and pigeons (e.g., Roberts, 2010). Some evidence suggests that some fish species may show specialized skills with small numbers of items (e.g., Agrillo et al., 2014; Gómez-Laplaza & Gerlai, 2011b; Piffer et al., 2012; but see Stancher et al., 2015), and occasional reports indicate that other species show patterns that may reflect the workings of an object file system including robins (Garland et al., 2012) and Asian elephants (*Elephas maximus*; Irie-Sugimoto, Kobayashi, Sato, & Hasegawa, 2009, but see Perdue et al., 2012, for a report indicating no evidence for an object file system in African elephants). Thus, although a strong consensus has emerged that nearly all nonhuman animals show evidence of the ANS and use analog magnitude estimation there is not yet a clear answer as to whether a second system like the object file model exists or not.

NEUROBIOLOGY OF QUANTITATIVE COGNITION IN ANIMALS

The importance of understanding the emergence of numerical competence in humans and learning about how and why math deficiencies occur in our species has generated a lot of interest in studying brain-behavior links in numerical cognition (see Chapter 18, this volume). Two areas of the human brain, the parietal lobe, and particularly the intraparietal sulcus (IPS), and the prefrontal cortex (PFC), seem intricately linked to numerical cognition in humans (Cantlon, Brannon, Carter, & Pelphrey, 2006; Dehaene & Cohen, 1997; Dehaene, Molko, Cohen, & Wilson, 2004; Dehaene, Piazza, Pinel, & Cohen, 2003; Kadosh & Walsh, 2009; Piazza, Pinel, Le Bihan, & Dehaene, 2007; for overviews, see Butterworth, 1999; Dehaene, 1997; Nieder & Dehaene, 2009). Comparative approaches to numerical cognition increasingly have asked what areas of animal brains are critical during the tasks those animals perform, and whether there are similarities in relevant brain areas for tasks given to human and nonhuman animals.

The data from nonhuman primate studies show that, in many cases, especially for magnitude estimation, nonhuman animal brains work much like human brains when they deal with quantity and numerical information (Nieder, 2005). For example, there appear to be distinct neural populations and activations within the IPS for different quantity presentation types (e.g., sequential enumeration versus simultaneous enumeration) in monkeys and perhaps also for abstract representations that occur later in processing (Nieder, Diester, & Tudusciuc, 2006). Single neurons in the ventral intraparietal region and PFC in monkey brains appear to be tuned to specific numerical values (Nieder, Freedman, & Miller, 2002; Nieder & Miller, 2003, 2004) such that specific neurons fire maximally to one value with drop-offs in firing rates with greater numerical distances from that preferred value (see Figure 25.4). Another area of the monkey brain, the lateral intraparietal region, also seems critical for representing accumulated magnitudes, and perhaps is relevant to learning cardinal values (Roitman, Brannon, & Platt, 2007; also see Nieder & Merten, 2007).

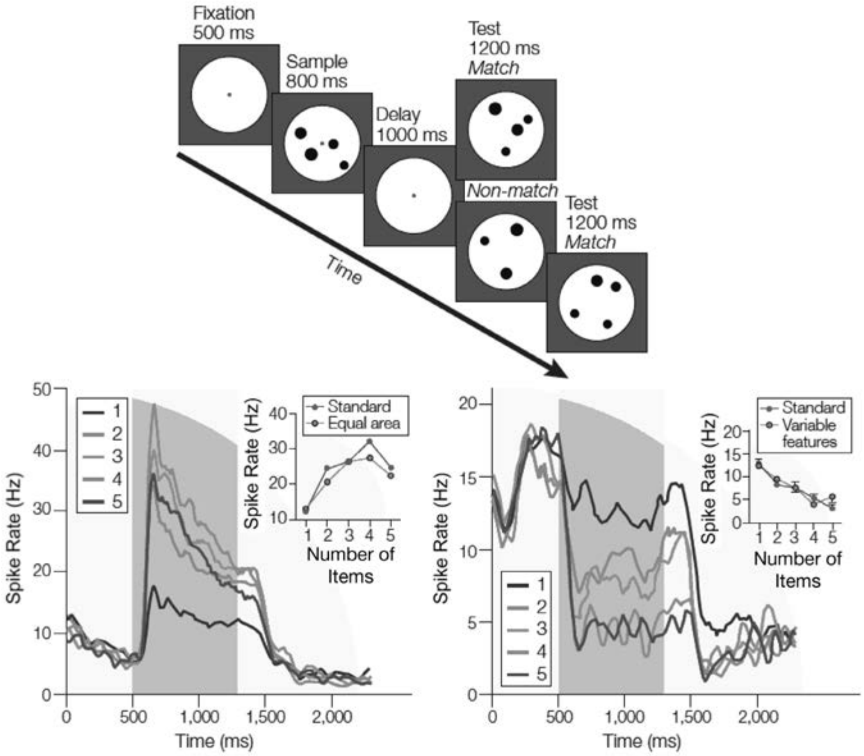

FIGURE 25.4. The top panel shows a delayed numerosity matching task presented to monkeys. Monkeys had to view the sample numerosity and then discern test displays that showed the same numerosity (but with a different visual pattern) from those that differed in numerosity from the sample. The bottom panels show responses of single neurons that were recorded from the prefrontal cortex (bottom left) and the intraparietal sulcus (bottom right). Both neurons show a graded discharge during sample presentation (interval shaded in green, 500 ms–1300 ms) as a function of numerosities 1 to 5. The insets in the upper right corners of the panels show the tuning of both neurons and their responses to different control stimuli. This reflects that the preferred numerosity was 4 for the prefrontal cortex neuron (left) and 1 for the intraparietal sulcus neuron (right). From "Counting on Neurons: The Neurobiology of Numerical Competence," by A. Nieder, 2005, *Nature Reviews Neuroscience, 121,* p. 181. Copyright 2005 by Nature Publishing Group. Adapted with permission.

Human mathematical abilities, of course, are highly dependent on symbolic representations of number. In some cases, there is clear similarity in brain activity across humans and monkeys (Diester & Nieder, 2007). For example, when monkeys were trained to associate Arabic numerals with specific, cardinal values, PFC neurons were selectively responsive to given numerical values. This was true whether those values were presented in the symbolic format as numerals or as analog quantities with that value. This suggests the association of symbols with magnitudes, a critical process in taking approximate numerical information and generating number concepts from that information. This would be a starting point to a truly symbolic notation system, which itself is the starting point for all other mathematical advances.

CONCLUSION

As outlined in this chapter, the psychology of nonhuman animals is closely attuned to, and dependent on, quantitative information. Quantitative cognition is applied across contexts, modalities, and by many species. In many instances, number concepts can be used by animals in their comparisons, judgments, and representations. Although capacities such as fully developed counting routines and more advanced mathematical abilities have yet to be shown in other species, and may never be, the basic quantitative capacities that underlie human mathematics are present in other species. Certainly, many species share with humans a foundational system for the approximate representation of quantitative information, and they may share with humans more specialized systems for representing small numbers of items, although at present this is not clearly demonstrated. Ongoing efforts to understand the neurobiology of comparative quantitative cognition as well as continued efforts to document the behavioral capacities of nonhuman species in quantity tasks and with numerical stimuli have great potential to shed led on how human numerical cognition and mathematic reasoning emerged through evolution.

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CHAPTER 26

COMPARATIVE METAPHYSICS: THINKING ABOUT OBJECTS IN SPACE AND TIME

Trix Cacchione and Hannes Rakoczy

What is the most basic structure of the world as we think of it? What are the most fundamental perceptual and conceptual categories through which we see our surroundings? Which categories does a thinker need to have if he/she is to be credited with any form of thought about an objective world? And how are such categories shaped by the way our languages carve up the world? Such questions have a long history in philosophical inquiry under the rubric *descriptive metaphysics*, with roots going back at least to Kant (1781/1997). Questions of descriptive metaphysics have become a topic of empirical cognitive science in the last decades, investigating which categories and concepts people use (see Chapter 5, this volume), how these categories and concepts shape world views, how such world views may differ cross-culturally, and how world views develop over time in ontogeny (see Volume 1, Chapter 20, this handbook). In fact, it was Piaget (1952) who established descriptive metaphysics as a topic of cognitive science by exploring the developmental foundations of our basic world view. More recently, and inspired by Piaget's Kantian program and his followers in developmental psychology, questions of fundamental perceptual and conceptual structures have become a systematic focus of inquiry in comparative psychology: How similar are different types of creatures with regard to such world views, and how might these increasingly complex world views have evolved? These questions constitute the field of what could be called *comparative metaphysics* (see Mendes, Rakoczy, & Call, 2008; Rakoczy, 2014). The present chapter will give an overview of this field focusing on what, arguably, is the most fundamental conceptual structure of our way of seeing the world: The capacity to segment the world into discrete objects that are independent from us, persist over time, and can be reidentified.

The most basic form of any objective thought—thought about a world out there that exists and persists independently from us and our perception of it—is representing the world as made up of enduring individual objects. But what does it mean to represent objects as enduring and perception-independent entities? And how can such cognitive capacities be measured empirically, particularly in the absence of language?

These questions have been approached from different perspectives in developmental and cognitive psychology, with diverging theoretical and methodological consequences. Piaget, setting the scene for the cognitive science of object concepts, assumed that the child starts off caught in booming and buzzing perceptual confusion, with no notion of objectivity whatsoever, and that a proper concept of "object" develops only slowly (Piaget, 1952). Methodologically, Piaget's research was built on the premise that a proper object concept reveals itself most clearly in the capacity to keep track of, reason about, and rationally act vis-à-vis (i.e., search for objects currently not perceived). Empirically, Piaget's findings suggest that such complex reasoning and searching competence—and thus a concept of object—develop during the first 2 years of life. And they develop in tandem with other cognitive competencies (e.g., language) that were considered

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by Piaget to be diverse expressions of an underlying domain-general reasoning capacity.

More recent core knowledge and related accounts were strongly inspired by Piaget's questions, but departed substantially from his theoretical and methodological premises. In contrast to Piaget, such accounts assume that basic forms of object cognition might be a more fundamental property of our perceptual and cognitive makeup (Carey, 2009; Spelke, 1990). In particular, the most fundamental form of object perception and cognition might be the capacity to segment the world into bodies: discrete, solid, and cohesive bundles of matter that move continuously through space and time which we can keep track. In light of the seminal work in this area by the cognitive scientist Elizabeth Spelke, such a rudimentary notion of objects as solid, cohesive bodies moving continuously in space and time has been described as notion of *Spelke objects* (Carey, 2009). According to the core knowledge and related accounts, keeping track of Spelke objects as the foundational kind of object cognition may well be a domain-specific, even a modular, capacity. Such a capacity can thus be present in infants and other animals, without directly translating into systematic rational action (e.g., searching behavior) and without necessarily being integrated with other cognitive domains or with higher cognitive functions (e.g., logical reasoning; see Chapter 29, this volume). Methodologically, such accounts have therefore approached infant object cognition in very different ways, controlling more carefully for extraneous task demands. They have thus relied less on searching and other forms of action (which might mask cognitive capacities because of motoric, executive, and other task demands), and on tasks that require children to reason in complex ways about unseen objects. Rather, they have relied on habituation and other looking time measures, and on simplified action measures. As a consequence, the empirical conclusions drawn from this work have been very different from Piaget's, suggesting that a basic (Spelke) object concept is present very early in ontogeny (perhaps even at birth), long before it translates into systematic action and logical inference.

Turning to comparative metaphysics, it should be noted that different strands in the comparative psychology of object cognition have been informed by either of these two different traditions. This has often resulted in diverging theoretical and methodological approaches, with findings that at first sight appear incompatible with each other. Another complication for a comprehensive study in comparative metaphysics is the fact that most of the existing experiments have largely used one or the other method with one or the other species. Unfortunately, this makes comparisons across studies and the extraction of a bigger picture difficult.

In the following, we will try to review and integrate the main results from such different lines of research on animals' object cognition. We will focus, in turn, on representations of continuity (i.e., representing objects as continuously existing in space and time), cohesion (i.e., representing objects as having a cohesive inner structure), solidity (i.e., representing objects as solid extended bodies), and identity (i.e., individuating and reidentifying objects). Because most of the animal work strongly builds on cognitive and developmental studies with humans (conceptually and methodologically), in most of the sections we will start in a somewhat anthropocentric fashion, from the relevant work with human infants.

CONTINUITY: THINKING OF OBJECTS AS CONTINUOUSLY EXISTING IN SPACE AND TIME

In his foundational work, Piaget assumed that the most basic form of object cognition, *object permanence* (i.e., the capacity to grasp objects as mind-independent enduring objects that move continuously in space and time), develops in stage-like fashion over the course of infancy. According to Piaget, cognitive development in infancy proceeded in six stages. In the first three of these, covering the first 8 months of life, the child lacks any insight into the permanence of objects once they are out of sight. Basic object permanence appears in stages 4 and 5 from around 8 months of age, when the child begins to keep track of and search for occluded objects. In stage 4 tasks, children search for objects that are hidden or otherwise occluded. Yet they commit a strange mistake, the so-called A-not-B error: After repeatedly seeing an object being hidden at location A and successfully retrieving it there, infants continue to search for it at location A, even when seeing the object being hidden—right before their eyes—at location B. In stage 5 tasks, children overcome this mistake and track objects over such repeated *visible displacements*. However, according to Piaget, object permanence is still incomplete at this stage, because the infant cannot yet reason in systematic ways about the object's fate once it is out of view, failing to understand *invisible displacements*. In typical invisible displacement tasks, the infant sees an object being hidden in a hand. This hand then visits, for instance, locations A and B, reappears empty and finally visits location C. Mature reasoning leads to the conclusion that the object must be in location A or location B and therefore, if one starts to search at location A and finds it empty, it must be at location B. Children master such tasks by systematically and sequentially searching location A and location B, when they are in Piaget's stage 6, from around 18 months of age. In Piaget's view, stage 6 marks the emergence of truly representational thought (termed *semiotic function*), which reveals itself in proper object permanence as well as in other representational capacities, such as language or future planning.

Empirically, Piaget's findings have turned out to be surprisingly robust and reliable even under controlled experimental conditions, although they were gathered from natural observations on very small samples of children. Conceptually, however, they have been disputed in many respects (see Lourenço & Machado, 1996, for a review). First, many accounts would consider stage 4 capacities—a basic awareness of the continuity of bodies—as the first true and proper form of object permanence, whereas later competence in understanding invisible displacements would be merely secondary developments resulting from the integration of basic object cognition with more domain-general reasoning capacities. Second, it has been widely argued that Piaget's active action measures underestimate early cognitive competence because of motoric and executive performance factors, and that looking time and other less taxing measures are thus preferable for tapping precocious competence.

These different forms and levels of object permanence have been investigated with different methods borrowed from developmental inquiry. We will start with a section summarizing research on *basic skills,* where we present data on the earliest manifestations of object representations at the interface of perception and cognition (Piaget's stages 1–3), and findings from search tasks with moderate task demands (i.e., search for visibly displaced objects; Piaget's stages 4–5). We will then present research on *advanced skills*, summarizing data on invisible displacement tasks which reveal more sophisticated reasoning abilities (Piaget's stage 6).

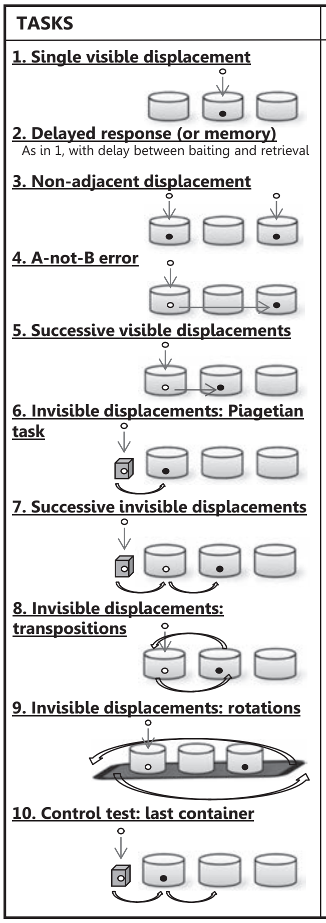
Basic Skills

Perception-based measures. Recent accounts of core cognition suggest that the nervous system is innately disposed for the conceptual decomposition of visual events (e.g., Carey, 2009). According to this view, the innate stock of primitives is not limited to perceptual representations, but also involves innate conceptual representations, sharing some structural similarity with perceptual representations. A core concept of continuity holds that physical bodies follow exactly one connected trajectory in space–time. A mind endowed with the notion of object continuity would therefore experience ambivalence when confronted with objects jumping in and out of existence (continuity violation) or moving through each other (solidity violation). There is ample evidence that infants from about 2.5 months appreciate object continuity, long before they are able to reach for objects (e.g., Baillargeon & DeVos, 1991; Spelke, Breinlinger, Macomber, & Jacobson, 1992). For example, infants significantly react to the sight of an object passing behind a screen and not reappearing in a large window (Baillargeon & DeVos, 1991).

Also in nonhuman animals there is ample evidence for rich representations of solid, three-dimensional and continuously existing objects (e.g., Fujita, 2001). Because most of these studies focus on object cohesion and solidity rather than on continuity per se, they will be discussed in the following sections.

Action-based measures. To locate visibly displaced objects, subjects must not only appreciate their permanence, but also deal with executive demands such as visually tracking the object to its final location, keeping up its memory trace, planning behavior and inhibiting prepotent false choices. Success in visible displacement tasks therefore not only indicates whether an organism has a basic object representation, but also how successfully this representation can be implemented into search. In human infants, nearly every aspect of how executive demands and context factors affect performance in visible displacement tasks has been investigated, including the distinctiveness, distance, number, and transparency of the covers, the delay between hiding and search, whether the tasks involved manual search or just looking time, and the presence of landmarks in the environment (see, e.g., Thelen, Schöner, Scheier, & Smith, 2001, for a review).

Searching for visibly displaced objects has also been investigated in many animal species. The basic finding has been that several species of primates, other mammals, and birds can reliably locate and search for visibly displaced objects (see Figure 26.1). However, whether these findings really indicate basic object knowledge in animals is still intensely debated. Criticism centers on methodological issues,



SPECIES	STUDIES (AND REPORTED PERFORMANCE ACROSS TASKS)
Apes: *Gorilla gorilla, Pan troglodytes, P. paniscus, Pongo abelii;* *Hylobates lar, H. leucogenys, Nomascus gabriellae, Symphalangus syndactylus*	Albiach-Serrano, Call, Barth, 2010, AJP 72:349 (**9**); Anderson, 2012, BE 149:441 (**1,8**); Barth, Call, 2006, JEP 32:239 (**2,3,4,6,7,8,9**); Beran, Minahan, 2000, IJCP 13:1 (**1,8,9**); Beran, Beran, Menzel, 2005, JCP 119:14 (**1,3,**9); Beran, Beran, Menzel, 2005, PR 46:255 (**9**); Call, 2001, JCP 115:159 (**1,3,5,6,7**); Call, 2003, PR 44:347 (**8,9**); Collier-Baker, Davis, Nielsen, Suddendorf, 2006, AC 9:55 (**6,10,11**); Collier-Baker, Suddendorf, 2006, JCP 120:89 (**7**); de Blois, Novak, Bond, 1998, JCP 112:137 (**1,4,5,6**,7,**10**); Fedor, Skollar, Szerencsy, Ujhelyi, 2008, JCP 122:403 (**1,4,6**,7,**10**); Hoffman, Beran, 2006, JCP 120:389 (**9**); Hribar, Call, 2011, AC 14:623 (**2**); Mallavarapu, Stoinski, Perdue, Maple, 2014, PR 55:549 (**7**); Mathieu, Bouchard, Granger, Herscovitch, 1976, AB 24:585 (**1,5,7**); Natale, Antinucci, Spinozzi, Poti, 1986, JCP 100:335 (**6,10**); Okamoto-Barth, Call, 2008, DP 44:1396 (**9**); Redshaw, 1978, JHE 7:133 (**1,4,5,6,7**); Rooijakkers, Kaminski, Call, 2009, AC 12:789 (**8**); Wood, Moriartry, Gardner, Gardner, 1980, ALB 8:3 (**1,4,5,6,7**)
Old world monkeys: *Macaca fascicularis, M. fuscata, M. mulatta, Mandrillus sphinx*	Amici, Call, Aureli, 2008, CB 18:1415 (3,**4**); Amici, Aureli, Call, 2010, AJPA 143:188 (**8**); de Blois, Novak, 1994, JCP 108:318 (**1,4,5,**6,7,**10**); Gabel et al, 2009, OBJ 2:137 (**1,5**,8); Hughes, Santos, 2012, JCP 126:421 (**9**); Natale, Antinucci, Spinozzi, Poti, 1986, JCP 100:335 (**6**,10); Schino, Spinozzi, Berlinguer, 1990, PR 31:537 (**6,7**,10); Wise, Wise, Zimmermann, 1974, DP 10:429 (**1,4,5,6,9**)
New world monkeys: *Ateles geoffroyi, Callithrix jacchus, Cebus capucinus, Lagothrica flavicauda, Saguinus oedipus, Saimiri sciureus, Sapajus apella*	Amici, Aureli, Call, 2010, AJPA 143:188 (**8**); Amici, Call, Aureli, 2008, CB 18:1415 (**3,4**); de Blois, Novak, Bond, 1998, JCP 112:137 (**1,4,5**,6,7,10); Kis, Gacsi, Range, Viranyi, 2012, AC 15:97 (4); Mathieu, Bouchard, Granger, Herscovitch, 1976, AB 24:585 (**1,5,7**); Mendes, Huber, 2004, JCP 118:103 (**1,4,5,6,7,10**); Neiworth et al, 2003, AC 6:27 (**1,4,5,6,7,10**); Schino, Spinozzi, Berlinguer, 1990, PR 31:537 (**6,7,10**); Vaughter, Smotherman, Ordy, 1972, DP 7:34 (**1**)
Lemurs: *Eulemur fulvus, E. mongoz, Hapalemur griseus, Lemur catta, Varecia variegata*	Deppe, Wright, Szelistowski, 2009, AC 12:381 (**1,4,**2,**5**,6,7,**10**); Mallavarapu, Perdue, Stoinski, Maple, 2013, AJP 75:376 (**1,5,6,7**,10)
Dogs and wolves: *Canis lupus familiaris, C. lupus*	Ashton, De Lillo, 2011, JCP 125:194 (**1**,4); Collier-Baker, Davis, Suddendorf, 2004, JCP 118:421 (**1,6,**10,**11**); Doré, Fiset, Goulet, Dumas, Gagnon, 1996, ALB 24:142 (8); Fiset, Beaulieu, Landry, 2003, AC 6:1 (**2**); Fiset, Beaulieu, Le Blanc, Dubé, 2007, JEP 33:497 (**1,6**); Fiset, Gagnon, Beaulieu, 2000, JCP 114:315 (8); Fiset, Le Blanc, 2007, AC 19:211 (**1,6**,10); Fiset, Plourde, 2013, JCP 127:115 (**1,4,5**,8); Gagnon, Doré, 1992, JCP 106:58 (**1,4,5,6,7,10,11**); Gagnon, Doré, 1993, ALB 21:246 (**1,2,5,6,7**); Gagnon, Doré, 1994, JCP 108:220 (**1,4,5,6,7**); Kis et al, 2012, AC 15:737 (**4**); Miller, Gipson, Vaughan, Rayburn-Reeves, Zentall, 2009, PBR 16:150 (**9**); Rooijakkers, Kaminski, Call, 2009, AC 12:789 (8); Triana, Pasnak, 1981, ALB 9:135 (**1,5,6,**7)
Cats: *Felis catus*	Doré, Fiset, Goulet, Dumas, Gagnon, 1996, ALB 24:142 (8); Doré, 1986, JCP 100:340 (**1,4,5**,6,7); Dumas, Doré, 1989, JCP 103:191 (**1,4,5**,6,7); Dumas, 1992, JCP 106:404 (**6**); Goulet, Doré, Rousseau, 1994, JEP 20:347 (**1,5**,6,7); Triana, Pasnak, 1981, ALB 9:135 (**1,5**,6,7); Fiset, Doré, 2006, AC 9:62 (**2**)
Dolphins: *Tursiops truncatus*	Jaakkola, Guarino, Rodriguez, Erb, Trone, 2010, AC 13:103 (**1,5**,6,8,**10**,11)
Corvids: *Aphelocoma californica, Corvus corone, C. corax, C. monedula, Garrulus glandarius, Pica pica*	Bugnyar, Stoewe, Heinrich, 2007, AB 74:757 (**1,4,5,6,7**); Hoffman, Ruettler, Nieder, 2011, AB 82:359 (**1,4,5,6,7,8,9**); Pollok, Prior, Guntiirkiin, 2000, JCP 114:148 (**1,4,5,6,7,10**); Salwiczek, Emery, Schlinger, Clayton, 2009, JCP 123:295 (**1**); Ujfalussy, Miklosi, Bugnyar, 2013, AC 16:405 (**1,4,5,6,7,10**); Zucca, Milos, Vallortigara, 2007, AC 10:243 (**1,4,5,6,7**)
Parrots: *Ara maracana, Cacatua goffini, Cyanoramphus auriceps, Psittacus erithacus,, Melopsittacus undulatus, Nymphicus hollandicus*	Auersperg, Szabo, von Bayern, Bugnyar, 2014, JCP 128:88 (**1,5,6,7,8,9**); Funk, Matteson, 2004, LB 32:427 (**1,4,5,6,7**); Funk, 1996, ALB 24:375 (**1,4,5,6,7**); Pepperberg, Kozak, 1986, ALB 14:322 (**1,4,5,6,7**); Pepperberg, Funk, 1990, ALB 18:97 (**1,4,5,6,7**); Pepperberg, Willner, Gravitz, 1997, JCP 111:63 (**1,4,5,6,7**)
Other birds: *Columba livia, Gallus gallus, Gracula religiosa, Streptopelia risoria*	Dumas, Wilkie, 1995, JCP 109:142 (**1**,4); Regolin, Vallortigara, Zanforlin, 1995, AB 49:195 (**1**); Plowright, Reid, Kilian, 1988, JCP 112:13 (**1**,6)

FIGURE 26.1. Illustrations of the tasks most commonly used to test for continuity and object permanence. White dots indicate initial (and intermediate) positions of rewards and black dots indicate the final position. Small gray arrows indicate that only food is moved, thick white arrows indicate that the containers/substrate are moved. Successive displacements (tasks 5 and 7) also control for selections of first cups visited by the experimenter. Task 10 controls for selections of last cups visited by experimenter. For each group of species, the most important studies investigating object permanence are reported (numbers in parentheses = task used; in bold if successful). Procedures across tasks were highly different (e.g., in terms of type, number, and saliency of cups; training; handling; number of trials; implementation of controls) and results are not directly comparable. AB: Animal Behavior; AC: Animal Cognition; AJP: American Journal of Primatology; AJPA: American Journal of Physical Anthropology; ALB: Animal Learning & Behavior; BE: Behavior; CB: Current Biology; DP: Developmental Psychology; IJP: International Journal of Comparative Psychology; JCP: Journal of Comparative Psychology; JEP: Journal of Experimental Psychology; JHE: Journal of Human Evolution; LB: Learning & Behavior; OPB: Open Biology Journal; PBR: Psychonomic Bulletin & Review; PR: Primates; PRSB: Proceedings of the Royal Society B.

and especially on the often large number of trials administered, on the use of fixed protocols allowing for associative learning, and on the lack of controls (e.g., sensory cues, associative cues, social cueing).

In many studies, variations of the original Piagetian tasks have been used (e.g., the scales developed by de Blois & Novak, 1994, and Uzgiris & Hunt, 1975). Especially Uzgiris and Hunt's (1975) battery has often been criticized, because it involves systematic tests on progressively complex tasks over large numbers of sessions, thus providing ample possibilities to learn associative strategies (e.g., selecting the location first/last touched, or the nearest location; see Jaakkola, 2014). Studies including a limited number of trials (e.g., 20–30) were suggested to provide a certain quality benchmark by evidencing spontaneous capacities (see, e.g., Jaakkola, 2014). Up to now, however, few studies meet this quality standard. Moreover, even if few trials were administered, subjects often needed extensive training to understand the testing procedure. Furthermore, among the studies including few trials, very few have also implemented controls to rule out the use of low-level alternative strategies (e.g., selecting the first/last location touched).

We summarize the current state of research on nonhuman animals' search for visibly displaced objects in the follwing section, focusing on four aspects that were also found to significantly affect human infants' search performance: (a) the time delay between hiding and searching, (b) the number and relative position of hiding places, (c) the number of consecutive searches at the same location, and (d) sequential displacements to multiple locations.

Time delay between hiding and searching. Numerous species have been tested with a delayed response task, which increases executive demands in terms of working memory (see Figure 26.1). In this task, a food item is usually hidden below one of 2–4 cups, and the participant has to wait for a specific time interval before starting the search. To successfully locate the object, the animal must not only maintain an active mental representation of the hiding location and later recall it, but also manage to reset the encoded information after each trial and build up a representation for the new position (see Zosh & Feigenson, 2009, on the interaction between memory capacity and the resolution of object representations). Barth and Call (2006) presented great apes and 2.5-year-old human children with 30 s delays between hiding and retrieval. All apes and children reliably located the reward after the delay, but made more errors than in conditions without delay. Similar results were found in other primates (e.g., chimpanzees [*Pan troglodytes*], bonobos [*P. paniscus*], orangutans [*Pongo abelii*]; Hribar & Call, 2011; capuchin monkeys [*Sapajus apella*], spider monkeys [*Ateles geoffroyi*], long-tailed macaques [*Macaca fascicularis*]; Amici, Aureli, & Call , 2010; red-fronted lemurs [*Eulemur fulvus rufus*], mongoose lemurs [*E. Mongoz*], ring-tailed lemurs [*Lemur catta*], gentle bamboo lemurs [*Hapalemur griseus*]; Deppe, Wright, & Szelistowski, 2009), although differences in the number of locations and length of delay make it hard to compare performances across taxa. Also dogs (*Canis familiaris*) and cats (*Felis catus*) successfully find rewards after delays, and their performance declines with increasing time intervals (Fiset, Beaulieu, & Landry, 2003; Fiset & Doré, 2006). In both species, errors did not depend on failure to successively encode and reset new locations (as subjects did not tend to select the previously rewarded box), but rather on the deteriorating effect of delays on memory (as errors occurred as a function of proximity to the actual hiding location).

Number and relative position of hiding places. The number of potential hiding places is certainly a factor affecting search, and must be kept in mind when comparing studies carried out across different species. To our knowledge, however, no comparative study directly examined its influence in an object permanence context. Some studies have instead investigated the impact of the relative position of the hiding location on the performance of different species, by, for example, baiting either two adjacent or nonadjacent locations (see Figure 26.1). Chimpanzees, orangutans, and human infants, for example, perform reliably better when three cups are horizontally aligned and the two baited locations are adjacent rather than nonadjacent, in nonadjacent trials they tend to successfully select the first cup and then choose the middle empty cup (Call, 2001), like dogs (Müller, Riemer, Range, & Huber, 2014a) and Goffin cockatoos (*Cacatua goffini*; Auersperg, Szabo, von Bayern, & Bugnyar, 2014).

The relative position of the locations is a factor that substantially affects choices in single visible displacement tasks, when multiple locations are baited (*inhibition task*), but also in multiple visible and invisible displacements. There are two contrasting explanations as to why nonadjacent trials are more difficult than adjacent ones. First, there might be a memory deficit when more locations are baited (e.g., Beran, Beran, & Menzel, 2005). Adjacent trials might thus be easier, because participants fail to remember the second exact location, search in proximity of previously visited locations, and, more likely, find the reward in the adjacent trials (at least in three location arrays). Second, nonadjacent trials might be especially demanding by requiring inhibition of a prepotent response (Amici, Aureli, & Call, 2008; Barth & Call, 2006). In particular, errors in nonadjacent trials occur because of a typical left-biased search pattern found in some apes, who tend to just continue their search in a row from left to right without skipping containers (Call, 2001). Beran and colleagues (2005) provided support for the first hypothesis showing that in arrays with five or seven aligned containers search success for the second reward varies as a function of the distance between the baited locations. Moreover, performance steadily recovered proportionally to the distance between the baited cups (see also Hribar & Call, 2011), increasing if more empty cups were between the baited ones. These results supported the hypothesis that apes search in proximity of the exact position, as the inhibition hypothesis would have instead predicted that error distribution is independent of the distance between the baited containers. However, the observed search pattern does not completely rule out some impact of inhibition: If memory failure alone were responsible for erroneous searches, these would have been equally distributed to the left and right of the baited locations, and not more often to the right, as instead shown by Barth & Call (2006; but see Hribar & Call, 2011).

Number of consecutive successful searches at the same location. Around 12 months of age (Piagetian stage 4), human infants show a characteristic transitional error, the A-not-B error. Although they can successfully retrieve a hidden toy, when the toy is repeatedly hidden (and found) at the same location A, the child will continue to search at location A, even if the toy is visibly transferred to a second location B. In the past decades, this phenomenon has been replicated in laboratories all over the world, and many different explanations have been offered as to the causes of this error (see, e.g., review by Marcovitch & Zelazo, 1999).

In the infant literature there is a general consensus that the A-not-B error is not a conceptual problem. Instead, it might be related to immature executive functions (Munakata, McClelland, Johnson, & Siegler, 1997). In particular, after reaching several times to location A, infants are unable to inhibit the prepotent motor response to reach again for location A, even if they know that the object is at location B (e.g., Diamond, 1990). Indeed, the likelihood of the error increases with the number of trials at location A (e.g., Marcovitch, Zelazo, & Schmuckler, 2002), as well as with the delay between hiding at location B and searching (because the memory of location B as a hiding place and the ability to inhibit reaching to location A decline over time). Successful performance after 12 months would thus emerge as a consequence of advances in inhibitory control, but the A-not-B error may reappear when the cognitive demands of the task increase, even in human adults (see Thelen et al., 2001). The investigation of A-not-B errors is therefore not only relevant from a developmental perspective, but is also crucial to assess differential susceptibility to perseveration across taxa.

Like humans, most adult primates do not continue searching in previously rewarded locations (see Figure 26.1). They overcome the A-not-B error at different stages during development (e.g., rhesus macaques [*Macaca mulatta*] at about 4 months and apes at 8 months; Gómez, 2005), evidencing a similar ability to build up new representations of objects' position and inhibiting the competing motor response to reach for previously rewarded locations. The same is true for lemurs, who can overcome the A-not-B error, but show perseveration errors in more complex tasks (Deppe et al., 2009; Mallavarapu, Perdue, Stoinski, & Maple, 2013). Recent studies clearly evidence that inhibitory control varies among primate species (Amici et al., 2008), and it is connected to their varying susceptibility to perseveration. Finally, birds usually show a transitional phase with A-not-B errors before reaching varying degrees of inhibitory control as adults (e.g., ravens [*Corvus* *corax*]; Bugnyar, Stöwe, & Heinrich, 2007; carrion crows [*C. corone*]; Hoffmann, Rüttler, & Nieder, 2011; jackdaws [*C. monedula*]; Ujfalussy, Miklósi, & Bugnyar, 2013; grey parrots [*Psittacus erithacus*]; Pepperberg, Willner, & Gravitz, 1997; grey parrots, Illiger mini macaws [*Ara maracana*], parakeets [*Melopsittacus undulatus*], cockatiels [*Nymphicus hollandicus*]; Pepperberg & Funk, 1990; but see Pollok, Prior, & Güntürkün, 2000, in magpies [*Pica pica*] and Zucca et al., 2007, in Eurasian jays [*Garrulus glandarius*] for lack of A-not-B errors).

In contrast to that, the A-not-B error appears to be absent in the development of dogs (see Gagnon & Doré, 1994) and cats (Dumas & Doré, 1989). More recent studies with dogs and wolves (*Canis lupus*) found no A-not-B errors in canid species (Fiset & Plourde, 2013), or very few (Müller et al., 2014a). However, dogs obviously show perseverative searches in other situations, selecting the previously rewarded location in invisible displacements (Fiset & Plourde, 2013), failing to switch to a new location when tested in a spatial version of the mediational learning paradigm (Ashton & De Lillo, 2011), or after the experimenter gave ostensive-communicative cues during the hiding (Topál, Gergely, Erdohegyi, Csibra, & Miklósi, 2009; but see Sümegi, Kis, Miklósi, & Topál, 2014; see also Volume 1, Chapter 33, this handbook). The lack of such errors in the traditional task might thus be connected to procedural aspects of the task rather than lack of preservative action in dogs.

Sequential displacements within one trial. In multiple visible displacements an object is first placed into a container and then swapped to another container within the same trial. Multiple displacements are more challenging than single displacements in terms of visual tracking, remembering, and inhibiting successive locations, and probably require more mature representations (for results with children, see Piaget, 1954). Also primates perform worse in conditions involving one swap (great apes; Call, 2001) or two (marmosets [*Callithrix jacchus*]; Mendes & Huber, 2004), although most primates were successful with single and double swaps (great apes; Call, 2001; tamarins [*Saguinus oedipus*]; Neiworth et al., 2003; lemurs; Deppe et al., 2009). Data on birds are more difficult to interpret, as birds were usually tested with the Uzgiris–Hunt task, double swap conditions always followed conditions without swaps and the effect of experience was confounded with the effect of task difficulty. In general, sequential displacements were rather challenging for some birds (e.g., magpies; Pollok et al., 2000). Double swap transpositions were demanding for carrion crows, which experienced problems to keep the attentional span during displacements and made many errors (Hoffmann et al., 2011). Dogs and cats could generally solve swap conditions, but earlier studies either confounded number of swaps with test order or involved very high numbers of trials (e.g., Gagnon & Doré, 1994; Goulet, Doré, & Rousseau, 1994). More recently, Fiset and Plourde (2013) found that dogs and wolves succeed with single visible swaps, even though rewards were moved inside a bowl that passed behind two screens (which complicates the task and hardly qualifies it as a fully visible displacement, given that the use of even transparent containers can affect performance in cats and dogs; Goulet et al., 1994; Müller, Riemer, Range, & Huber, 2014b). The only study with dolphins (*Tursiops truncatus*) revealed that they fail to find the reward after a single swap (Jaakkola, Guarino, Rodriguez, Erb, & Trone, 2010).

Advanced Skills

The capacity to deal with invisible displacements may be viewed as a second quantum leap in cognitive development. In invisible displacement tasks, objects are hidden at some locations and then invisibly moved to a different location. Mastering such tasks goes way beyond a basic awareness of continuously existing objects. It involves the mental reconstruction of an unseen trajectory and therefore advanced spatial reasoning skills. Moreover, it involves the adoption of multiple hypothetical models of a situation and requires rudimentary logical reasoning (i.e., understanding disjunction—"It must be in A or B"—and reasoning from negated disjuncts—"It is not in B, therefore it must be in A"; see Chapter 29, this volume). Localizing invisibly displaced objects therefore requires a rich object concept and advanced reasoning skills, as well as advanced inhibitory and memory capacities. Children develop the capacity to deal with invisible displacements around 18–24 months. At the same time, they acquire various other cognitive capacities such as self-concept, language and instrumental problem-solving—all of which have been considered to be expressions of the newly emerging underlying capacity to coordinate multiple representations of reality (Perner, 1991). Conceptually, evidencing the prevalence of such advanced reasoning capacities across species has thus important implications in modelling the evolution of higher cognition (Suddendorf & Whiten, 2001; see also Volume 1, Chapter 20, this handbook). Empirically, however, unambiguous interpretation of available data is often difficult, because invisible displacement tasks involve a conglomerate of executive demands (inhibition, memory; see Chapter 27, this volume), reasoning demands (coordinate representation, logical inference, spatial reasoning; see Chapter 21, this volume) and context factors (number and spatial relation of locations, use of displacement devices, number of trials, aspects of presentation).

In general, there is wide-reaching consensus that humans, great apes, and parrots understand invisible displacements (e.g., Barth & Call, 2006; Collier-Baker, Davis, Nielsen, & Suddendorf, 2006; Pepperberg et al., 1997), whereas findings on other species are more controversial (but see Jaakkola, 2014). Following, we summarize recent research using three types of invisible displacement tasks (see Figure 26.1), in which the object always moves hidden inside a repository, either (a) with a hiding device (*standard Piagetian task*), (b) with the baited container (*transposition task*), or (c) with the full array (*rotation task*). In the standard Piagetian task, the object is hidden in a device (e.g., cup or hand), moved to one of a set of containers and secretly left under it. The device is then removed from the container and shown to be empty. The device may visit only one container or multiple containers (single, double swaps). In the transposition task, the object is visibly placed into the container and the container moved to another location, either one or multiple times (swaps). In the rotation task, the full array is moved by rotating the platform with the containers (e.g., 90°, 180°, or 360°). The difficulties of these tasks are (a) to understand that the object continues to exist, (b) to infer that it moves with the containing repository, (c) to infer that it must have been deposited along the invisible trajectory after the empty repository is shown, (d) to continuously update locations during its journey, and (e) to inhibit prepotent responses. The three tasks vary in demands on cognitive processing: The standard task involves complex nested movements/transfers and is logically challenging, whereas transpositions and rotations are more demanding in terms of tracking and spatial reasoning. Great apes pass all three tasks (see Figure 26.1). Although for human children the standard task is easier than the transposition task (Barth & Call, 2006), great apes perform equally well in both tasks, although chimpanzees and bonobos outperform gorillas and orangutans (Barth & Call, 2006). For 30-month-old children and apes, however, 180° rotations are most challenging (Barth & Call, 2006). Further studies revealed that apes' performance increases if persisting landmarks (e.g., differently colored cups) are added, but only if rotations are observed, suggesting that apes' judgment is based on tracking the opaque repository rather than on posthoc logical inferences (Okamoto-Barth & Call, 2008). Also gibbons (*Symphalangus syndactylus, Hylobates lar, Nomascus gabriellae*, and *Nomascus leucogenys*) succeed with the standard task and transpositions (Fedor, Skollár, Szerencsy, & Ujhelyi, 2008), but data on monkeys and prosimians do not allow any conclusion. Although some studies suggest that monkeys do not understand invisible displacements (de Blois & Novak, 1994; de Blois, Novak, & Bond, 1998), other studies reported success (Amici et al., 2010; Neiworth et al., 2003; Mendes & Huber, 2004). However, most of these studies failed to include proper controls (but see Neiworth et al., 2003), included too many trials, graded series of increasingly difficult tasks, or failed to interpret results from a more integral perspective. Therefore, no conclusion can be drawn on monkeys and prosimians' ability to master invisible displacements. To date, only one study investigated monkeys' performance on transpositions, comparing macaques, spider monkeys, and capuchin monkeys (Amici et al., 2010). Although macaques' performance equalled that of apes (mastering single and double transpositions), spider monkeys and capuchin monkeys were only successful with single transpositions. Data are scarce on monkeys' understanding of rotation. Using an expectancy-violation rotational displacement task, Hughes and Santos

(2012) found that adult but not infant or juvenile rhesus macaques expected the object at the correct location after a 180° rotation. Finally, a recent study on spatial reasoning suggests that rotations are harder for monkeys than transpositions (Nekovarova, Nedvidek, Klement, Rokyta, & Bures, 2013).

Whereas earlier studies reported success in standard tasks for cats and dogs (Triana & Pasnak, 1981; Gagnon & Doré, 1992, 1993), later studies suggested success with visible displacements only (Collier-Baker, Davis, & Suddendorf, 2004; Dumas & Doré, 1989; Goulet et al., 1994). In invisible displacement tasks, dogs were typically found to search the final location of the displacement device (Collier-Baker et al., 2004), suggesting that they used an associative strategy to select the location. A recent study, however, suggests that the use of a displacement device probably complicates the task for dogs, because it introduces a salient and potentially misleading cue. Müller and colleagues (2014b) found that also in a visible displacement task, the use of a displacement device reliably impaired dogs' performance, either because of the strong associative cues overriding location information or because of the dogs' failure to individuate the reward as separate from device (see Goulet et al., 1994, for a similar effect in cats). Even though this does not show that dogs would master invisible displacements if distracting cues were removed, it certainly highlights the importance of carefully considering whether task demands might mask conceptual abilities. To our knowledge, only one study tested cat's ability to deal with transpositions (Doré, Fiset, Goulet, Dumas, & Gagnon, 1996), whereas dogs were tested with transpositions and rotations (Doré et al., 1996; Fiset & Plourde, 2013; Miller, Gipson, Vaughan, Rayburn-Reeves, & Zentall, 2009; Miller, Rayburn-Reeves, & Zentall, 2009; Rooijakkers, Kaminski, & Call, 2009). Cats and dogs were successful only in simple lateral transpositions, but failed if containers were transposed along more complex (e.g., crossing) paths (Doré et al., 1996; Fiset & Plourde, 2013). A direct comparison of dogs with apes confirmed that dogs are clearly outperformed by apes (Rooijakkers et al., 2009). Finally, dogs managed to locate rewards after 90° but not 180° rotations (Miller, Gipson, et al., 2009; Miller, Rayburn-Reeves, & Zentall, 2009).

To our knowledge, the only other mammals that have been tested are dolphins, who failed the standard task (Jaakkola et al., 2010), and wild and domestic pigs (*Sus scrofa scrofa, S. s. domestica*), who failed transpositions (Albiach-Serrano, Bräuer, Cacchione, Zickert, & Amici, 2012).

Finally, five species of the corvid family and five of the psittacid family were reported to pass invisible displacements (see Figure 26.1). However, most of them used the Uzgiri–-Hunt scale, and only four studies implemented associative controls (Auersperg et al., 2014; Funk, 1996; Pepperberg et al., 1997; Zucca et al., 2007). Corvids and parrots were also tested with transpositions (corvids; Hoffmann et al., 2011; Ujfalussy et al., 2013; Zucca et al., 2007; parrots; Auersperg et al., 2014; Pepperberg et al., 1997), and all of them succeeded, with the exception of crows (Hoffmann et al., 2011). Finally, 90°, 180°, and 360° rotations were implemented for crows and cockatoos. Whereas crows managed only 90° rotations (Hoffmann et al., 2011), cockatoos passed all of them, and also 270° (Auersperg et al., 2014). However, because the rewards were moved by magnets and many birds are able to perceive magnetism (see Chapter 22, this volume) this was suggested as an alternative source of success (Jaakkola, 2014).

Conclusion

The general picture that emerges from decades of comparative research on object permanence is the following: Many mammals and birds successfully solve visible displacement tasks; yet so far we have positive evidence for an understanding of invisible displacement only in great apes and some birds. However, the validity and proper interpretation of these findings remain controversial in light of fundamental methodological complications. On the one hand, conservative approaches point out the danger of false positives: In the absence of stringent control conditions, associative strategies might be mistaken for conceptual capacities (e.g., Jaakkola, 2014). On the other hand, core knowledge and related accounts have argued that many traditional searching measures radically underestimate conceptual competence because of extraneous (e.g., motoric, executive) performance factors.

Future research should thus use different methodological approaches with multiple species to yield a more comprehensive picture. One particularly exciting open question in this context, for instance, is whether the emergence of complex object-based reasoning (as indicated in invisible displacement tasks) goes along with a structurally comparable cognitive revolution (e.g., coemerging self-concept, hypothetical reasoning, imagination, etc.) also in species other than humans.

COHESION: THINKING OF OBJECTS AS HAVING A COHESIVE INNER STRUCTURE

In the past decades, infant research has revealed that core object concepts provide intuitions about spatiotemporal properties (object continuity) and featural properties (object size, shape, volume, solidity, etc.). Also, comparative research has increasingly focused on animals' knowledge about object properties (i.e., cohesion, spatial extension, and solidity). In the following two sections, we will summarize comparative research investigating knowledge of object cohesion and solidity.

Perception-Based Measures

Even in very young infants, the foundation for the perception of objects is present. It builds on core object principles such as the principle of cohesion, on which infants rely when tracking and identifying objects. The cohesion principle works as a pattern-detector defining objecthood (Pinker, 1997): All portions of matter that move as bounded cohesive units are indexed as objects.

A basic manifestation of the capacity to perceive objects as cohesive wholes is called *perceptual completion* (e.g., mentally bridging the gaps when perceiving the unity of partially occluded objects). From about 2 month of age, human infants integrate motion patterns to perceive center-occluded objects as unitary connected wholes (e.g., Johnson, 2004). Indeed, the perception of object unity appears to be a more basic ability than the perception of object form. In a seminal study, 4-month-old human infants were first habituated to a three-dimensional object whose ends were visible but whose center was occluded, and were then shown two test displays with no occluder present (Kellman, Spelke, & Short, 1986; see Figure 26.2). In one display, the two ends of the object were connected in the place where the occluder had been, although in the other display, the two ends were separated by a gap. Infants looked longer at the second display (while perceiving it as different from the occluded object), suggesting that they perceive center-occluded objects as being connected behind the occluder, when their visible ends share a common lateral translation in space (Kellman et al., 1986). These results show that from a very early age humans perceive objects according to the principles governing the motions of material bodies (e.g., coherence of motion), depending on an inherent conception of what are objects (Kellman et al., 1986).

Just like human infants, chimpanzees and capuchin monkeys engage in perceptual completion and thus in the perception of objects as cohesive entities (Fujita & Giersch, 2005; Sato, Kanazawa, & Fujita, 1997; see also Chapter 8, this volume). When matching the sample with a center-occluded rod, for instance, monkeys largely selected a straight rod over disconnected rods and rods with irregular shapes at their center, even when their visible ends did not share a common motion (Fujita & Giersch, 2005). Similarly, rhesus macaques, like adult humans, overestimate the length of a bar that abuts the edge of a large rectangle, suggesting that they believe it continues behind the rectangle and they represent the rod beyond perception (Fujita, 2001). It should be noted, however, that methodological differences make direct comparisons to human studies difficult: The latter usually monitor spontaneous looking behavior in infants in the absence of any training, whereas nonhuman primates often underwent extensive training before they could be tested with match-to-sample or related tasks.

Action-Based Measures

For Piaget, object permanence was the first step in direction of a more general understanding of physical constancy, including the understanding that also many featural object properties such as mass, volume, size, and shape are constant across different spatial arrangements (e.g., splitting an object or filling liquid in another container does not change the mass of the transformed entity). Also the core cognition approach considers that appreciating cohesion and appreciating continuity are logically linked, albeit in other ways. Once infants have recognized a given portion of matter as an object, they expect this object to continue existing and keep up its boundaries and inner structure while moving (e.g., Spelke, 1990). An open question is whether perceived object cohesion is really crucial for appreciating the permanence of matter per se. An alternative possibility would be that it is rather a prerequisite to appreciate the permanence of a given entity or spatial arrangement of matter. Several studies suggest that at an early age, the first might be true, and that for young infants the notion of permanence pertains to object-like entities only, whereas nonsolid substances (e.g., water, sand) or decomposed (noncohesive) objects are not recognized as continuously existing (e.g., Cheries, Mitroff, Wynn, & Scholl, 2008; Huntley-Fenner, Carey, & Solimando, 2002). In a typical forced choice paradigm, infants were presented with two cups baited with crackers of different size (e.g., Cheries et al., 2008; see Figure 26.2). Although 12-month-old human infants usually chose the bigger cracker, they failed to do so if the cracker was fragmented before being hidden, suggesting that they failed to further represent it. Later studies, however, revealed that infants appreciated that also a fragmented cracker is composed of permanent material, but they failed to update the featural information needed to estimate its size (Cacchione, 2013). That is, while appreciating that the manipulation does not alter crackers' continuity (i.e., crumbs of a fragmented cracker do not stop existing), infants fail to appreciate that their mass remains constant through the transformation.

From an evolutionary perspective, it is indeed hard to understand why the notion of permanence should not pertain to the class of matter per se. In the context of foraging, for example, representing and localizing all kinds of substances and objects should have the same adaptive value. Recently, two studies modelled after the infant forced choice methodology (e.g., Cacchione, 2013) questioned whether great apes would appreciate that fragmented (noncohesive) objects are still composed of permanent matter (Cacchione & Call, 2010; Cacchione, Hrubesch, & Call, 2013). In these studies, great apes were presented with different conditions in which a solid food object (cracker) was visibly fragmented into increasingly noncohesive patterns (i.e., from two halves into uncountable smithereens), and then hidden. Apes could then choose between the bigger (fragmented) cracker and a smaller not fragmented one. As human infants, great apes further represented the permanence of the fragmented crackers, but failed to estimate their size if they were heavily fragmented. As human infants, apes therefore appreciated the permanence of noncohesive objects, but failed to process their featural properties (e.g., the amount of mass), suggesting that they do not have an advanced understanding of physical constancy.

SOLIDITY: THINKING OF OBJECTS AS SOLID EXTENDED BODIES

Understanding object continuity also is logically linked to understanding their solidity: each object follows exactly one trajectory, and two objects can never occupy exactly the same coordinate in space–time (e.g., Spelke et al., 1992). At the very basic level, therefore, grasping object solidity means little more than tacitly expecting that solid objects may not move through each other.

Basic Skills

Perception-based measures. In their now classical drawbridge experiment, Baillargeon, Spelke, and Wasserman (1985) presented 5-month-old human infants with a screen that moved back and forth through a 180-degree arc. Then a solid box was placed on the stage and the screen set in motion. Infants looked longer at an event where the screen continued moving until it reached the stage, as compared to an event where the screen stopped when reaching the box. This suggests that infants realize that solid objects (screen) cannot move through the space occupied by other solid objects (box). Later experiments revealed that from 2 months of age human infants perform in accord with solidity (e.g., looking longer if an invisibly falling object reappears on the lower of two solid surfaces; Spelke et al., 1992).

If tested with perceptual measures, rhesus macaques appear to appreciate object solidity: They tend to look longer at an event where an apple appeared to fall through a solid shelf, as compared to an event where this was not the case (Santos & Hauser, 2002; see Figure 26.2). As with infants, dogs who were tested with a looking time version of the drawbridge paradigm looked reliably longer at impossible events (i.e., a screen rotating 180° through a bone) as compared to possible events (i.e., a screen stopping when reaching the bone; Pattison, Miller, Rayburn-Reeves, & Zentall, 2010).

Action-based measures. Inspired by infant research, various recent comparative studies designed action tasks with low demands. As in traditional tasks, the animals are required to locate hidden objects, but must do so with the help of various sensory cues (e.g., visible, acoustic, tactile). These cues, however, are only informative to the animal, if it appreciates that solid objects relate causally to each other as a function of their properties (mass, weight, extension; see Chapter 29, this volume). Call (2007), for example, modelled an action task after the drawbridge paradigm used by Baillargeon and colleagues (1985). When presented with two small rectangular boards on a platform, one of which was inclined because of the presence of a hidden food reward under it, apes preferentially selected the inclined board (see Figure 26.2). This suggests that apes appreciated the solidity and continuous existence of hidden food, and used the different orientation of the boards as index to infer its current position (Call, 2007). However, apes' performance in the inclined board task also had limits. For instance, when presented with two equally inclined boards and only one was visibly supported by a wooden block, apes failed to logically infer that food was hidden under the unsupported board (Call, 2007). Moreover, apes could infer the location of a food reward in a similar task (the noisy-cup task), which provided acoustic rather than visual cues to solidity (Call, 2004; see Figure 26.2). When presented with two identical cups, apes selected the one that produced a rattling sound when shaken, or the opposite cup when the shaken cup produced no noise, suggesting that apes understand that solid objects cause noise (Call, 2004). Finally, in a similar situation apes were also able to infer the position of a hidden reward using weight information (Schrauf & Call, 2011). In particular, when presented with two opaque cups and only one was baited, apes successfully localized the food by lifting the cups and comparing their weight.

Recent studies report similar findings in long-tailed macaques, who successfully used the boards' inclination to localize food (Schloegl, Waldmann, & Fischer, 2013). However, macaques failed to use the lack of inclination as a cue, showing a rather rudimentary understanding of causal object relations. Further, low demanding action tasks were also implemented with domestic pigs (Albiach-Serrano et al., 2012) and chicks (*Gallus gallus*; Chiandetti & Vallortigara, 2011). Albiach-Serrano and colleagues (2012) compared wild boars and two groups of domestic pigs living in more and less enriched conditions, using the inclined board and the noisy-cup tasks. Enriched pigs successfully located rewards only in the noisy cups, nonenriched pigs only located rewards below inclined boards, and wild boars failed in both tasks, suggesting that experience with specific stimuli during ontogeny influences performance in these tasks. Finally, Chiandetti and Vallortigara (2011) imprinted newborn chicks with a plastic cylinder and accustomed them to rejoin it when it was hidden behind an opaque screen. In the test, chicks were faced with two screens of different slants, height or width, that were either compatible or incompatible with the presence of the cylinder behind them. Chicks consistently chose the screen behind which the cylinder could possibly hide (disregarding flat-to-floor- screens or too small screens). These highly interesting findings suggest that chicks not only represent the physical properties of the imprinting object, but can also match them to the proportion of the hiding screen to infer its location. This is especially remarkable, because human infants before 3.5 months are not able to use height to infer an object's potential presence behind a screen (Luo & Baillargeon, 2005).

Advanced Skills

Although children appear to appreciate object solidity from early on, only much later do they systematically use this knowledge in action tasks (e.g., Hood, Carey, & Prasada, 2000). In a typical action task on children's understanding of object solidity, an object moves along a certain trajectory, first visibly and then under occlusion (e.g., falling behind a screen; rolling along a plane). The invisible trajectory of the object is visibly blocked by some solid barrier (e.g., by a horizontal plane behind the screen on which the object falls; by a vertical wall along the horizontal plane where the object rolls), and the question is whether infants indicate an understanding of the obstacle's solidity and search for the object there (rather than at the location where the object would have ended up without the barrier; see Figure 26.2). Empirically, children have been found to show such systematic searching behavior only from around 2.5 years of age (Hood et al., 2000), although 4- to 6-month-olds show sensitivity to a very similar scenario with looking time measures (e.g., Spelke et al., 1992).

Beside executive demands, the difficulty in such action-based invisible displacement tasks is that they typically involve feedforward logic-causal inferences. Because the object is invisibly displaced, its final location must be logically inferred by mentally reconstructing the causal impact of solidity on its movements (e.g., a barrier stopping it). This might render search tasks much harder than looking tasks, where noticing the anomaly after revealing the object location is sufficient for success.

The perception–action dissociation, as observed in very young children, was also observed in rhesus macaques (e.g., Hauser, 2003; Gómez, 2005). Rhesus macaques, for instance, failed to implement solidity knowledge to localize an invisibly falling apple on top of a shelf, instead of below it (Hauser, 2001). When tested with an expectancy violation version of the same task, however, macaques looked longer when the apple appeared to move through solid barriers (Santos & Hauser, 2002). Moreover, searches were more successful if objects invisibly moved along the horizontal plane (Hauser, 2003). Failure in the vertical version of the task might therefore also depend on monkeys' susceptibility to gravity errors (i.e., on perseverative searching at the lowest point of the falling line; see Gómez, 2005).

Comparable findings were also obtained when the four great ape species were tested in a similar search task (Cacchione, Call, & Zingg, 2009). In particular, apes correctly inferred the position of objects after horizontal but not vertical displacements, although they showed no reliable gravity bias. In the more demanding tube task (where a food item is dropped down a tube connected to one of multiple opaque cups, and subjects must infer that the trajectory of the falling object is constrained by the solid tube; see Figure 26.2), apes failed to understand the object–tube interaction, despite integrating some tube-related causal information (Cacchione & Call, 2010). Finally, Hanus and Call (2008) also tested apes' use of weight cues in an invisible displacement task. A food item was hidden in one of two cups mounted on opposite sides of a balanced beam, and apes observed the balance beam tilting to one side. Apes successfully inferred the presence of the bait in the lower cup (despite having no baseline preference for lower cups). Together these findings show that apes and rhesus macaques appreciate that objects are solid, extended, and causally related to each other, but fail in conditions imposing high demands on logic-causal processing (see Chapters 27 and 29, this volume).

Dogs also mostly failed to implement solidity knowledge to logically infer the location of an invisibly displaced object, and instead resorted to associative strategies (e.g., Osthaus, Slater, & Lea, 2003; Müller et al., 2014a). One recent study, however, reported surprising performance in a modified tube task posing high demands on logic-causal reasoning (Kundey, De Los Reyes, Taglang, Baruch, & German, 2010). In this task, a food item was rolled down a slanted transparent tube into an opaque box, in the middle of which a wall could be inserted. From the first trial, dogs successfully located the food in the far location (in trials where the wall was not inserted) or in the near location (in trials where the wall was inserted and blocked the trajectory of the food). However, dogs in this study might have used perceptual movement cues (e.g., acoustic cues, small movement cues on the doors) to locate the food, as suggested by another study in which dogs failed with a similar set-up involving no object movements (Müller et al., 2014a). At present, however, no clear conclusion may be drawn, as the two studies importantly differed in other ways (e.g., no ostensive cues were used in the latter study to attract dogs' attention to the barrier, and the final position of the object had to be inferred before it actually moved to it). More studies are surely needed to get a clearer picture of dogs' understanding of solidity.

IDENTITY: INDIVIDUATING AND REIDENTIFYING OBJECTS

Impressive as it is, keeping track of the spatio-temporal history of continuously moving, cohesive, and solid bodies constitutes only the most rudimentary form of how humans think of objects. As adult humans, we do not just see portions of matter moving around us through space and time. Rather, we see the world around us as made up of specific objects of certain kinds—trees, dogs, stones, and so on. Rather than just tracking spatio-temporal trajectories of bodies, we more generally engage in object individuation ("How many dogs are there?") and object identification ("Is this the same dog as the one I saw there before?"). Tracking Spelke objects by object files enables some simple form of object individuation on the basis of spatio-temporal information, yet with clear and characteristic signature limits (see Volume 1, Chapter 20, this handbook and Chapter 25, this volume). For example, on spatio-temporal grounds one can solve the following problem: At time 1, one sees object A (e.g., a ball) and object B (e.g., a toy duck) disappear behind a screen, then at time 2 object B reappears and disappears again, followed by the same sequence with object A. Here, because object A and object B move in separate continuous trajectories each as a solid and cohesive body, spatio-temporal tracking results in the subject's expectation that there must be two distinct bodies behind the screen. Confronted with either one object behind the screen (unexpected) or two (expected) in looking time studies, subjects should thus look longer at the former than at the latter. Many studies using looking time or simple search measures (e.g., box task; see Figure 26.2) have documented success in human infants early in the first year of life (for review, see Xu, 2007).

However, there are clear limits to the kinds of problems one can solve with such purely spatio-temporal tracking: If object A and object B are never seen simultaneously, such that object B appears from behind the screen and disappears again, and then the same sequence is shown with object A, on purely spatio-temporal grounds there is no evidence for two distinct objects. In terms of bodies, the situation is ambiguous: At different times one could have seen the same Spelke object repeatedly, or different ones. What is required to keep track of the number of objects and thus to solve such a task is *sortal object individuation*—keeping track of which kinds of objects (duck, ball), and as a consequence, how many distinct ones (at least two).

Developmental work with human infants has shown that the capacity to solve these more complex individuation problems emerges later in ontogeny, only around one year of age (Xu, 2007). Interestingly, such individuation competence is related to language in infants: Individual performance in object individuation studies correlates with receptive language proficiency such that children mastering individuation tasks involving ducks and balls tend to be those who already understand the words *duck* and *ball* (Xu & Carey, 1996). Performance generally is also boosted when the objects are labeled linguistically in the experimental procedure ("Look, a duck/a ball"). Such findings have led to the psychological version of a claim long popular in philosophy (e.g., Quine, 1957)—that sortal object individuation is on the basis of language acquisition and should therefore be a uniquely human capacity.

Comparative research in recent years has explicitly addressed this claim by testing various species with analogous tasks as those developed for human infants. Experiments with rhesus macaques (Phillips & Santos, 2007; Santos, Sulkowski, Spaepen, & Hauser, 2002), apes (Mendes et al., 2008; Mendes, Rakoczy, & Call, 2011) and dogs (Bräuer & Call, 2011) used manual search methods developed in infancy research. Subjects at time 1 see an object of type A enter into a box and then at time 2 either find a qualitatively identical object of type A, or a different object of type B, after which they have the opportunity to continue searching in the box (see Figure 26.2). Searching time here serves as an indicator of numerical expectations as to whether there is still an object in the box, and longer searching in the A/B case compared to the A/A case is seen as an indicator

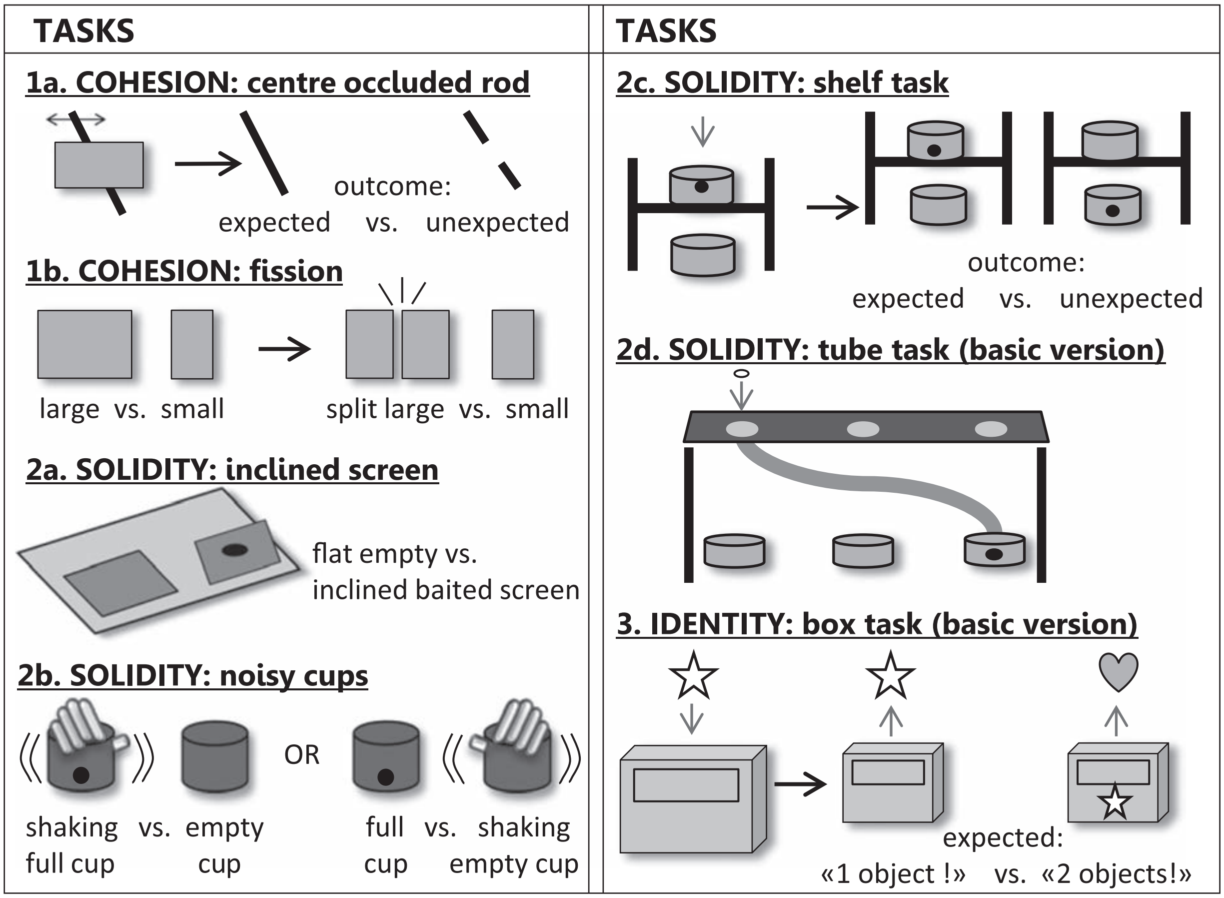


FIGURE 26.2. **Illustrations of the tasks most commonly used to test (1) cohesion, (2) solidity and (3) identity. White figures indicate the initial (and intermediate) position of the objects, whereas black figures indicate their final position. Small gray arrows indicate that the object is visibly displaced, while black thicker arrows indicate that a manipulation occurs before subjects see the outcome.**

of sortal (kind-based) object individuation. Studies with chicks had a slightly different methodological approach (Fontanari, Rugani, Regolin, & Vallortigara, 2011, 2014). An object of type A disappeared behind screen 1, then a qualitatively identical object of type A reappeared and disappeared again behind screen 1 (licensing the inferences that there is at least one object behind screen 1). In the same way, an object of type A first disappeared behind screen 2. Then, however, an object of type B appeared from behind the screen and disappeared again behind the screen (licensing the inference that there are at least two objects behind screen 2). Given that chicks have a known tendency to approach the bigger set of objects in such contexts, the dependent measure was differential approaching behavior toward the two screens.

The findings of these studies yield a largely consistent picture: They show that the same kinds of competencies (in the form of differential searching/approach behavior in A/A conditions compared to A/B conditions) that had been found to develop in human infants from around 1 year and to be correlated with language are well present in nonhuman animals in the absence of language (see Volume 1, Chapter 20, this handbook and Chapter 17, this volume).

A fundamental question, however, for animal and infant studies, is whether the tasks developed to tap sortal object individuation truly require subjects to apply sortal object concepts, or whether there might be ways to solve the tasks with simpler cognitive processes such as discriminating and tracking object features. The underlying problem is that in normal circumstances, object types and object features are necessarily confounded—balls are different in type from ducks and banana slices are different from carrot slices, but they also differ in terms of superficial perceptible features (see Chapter 5, this volume). Perhaps, thus, subjects were not individuating objects in terms of their types, and thus searching for a missing object of a certain type ("there still must be this this banana slice around here"). Rather, they might have relied on simpler feature-based individuation, searching for some missing features ("there must still be some yellowness around here"). The only way to stringently address this concern is to systematically deconfound *deep properties* of an object (that define its kind and thus cannot be changed without altering the nature of the object), and merely superficial features (that can be transformed without changing the object as such). Such contrasts have long been used in verbal studies with older children and adults to probe their intuitions of psychological essentialism (e.g., Keil, 1989). In some classical vignettes, an animal was superficially transformed to look like another one (e.g., a squirrel was shaved and painted like a raccoon), and subjects were asked to judge what kind of animal it would turn out to be. Adults and older children in such studies based their explicit identity judgments exclusively on the original kind of the animal and disregarded superficial property transformations. Recent infant and comparative research therefore has tried to combine such transformation scenarios from experiments on psychological essentialism with established object individuation methods. Although this work has just begun, it has produced first evidence that, in infants and nonhuman primates, early object individuation builds on representations of objects' kinds and not just on tracking superficial properties (Cacchione, Hrubesch, Call, & Rakoczy, 2016; Cacchione, Schaub, & Rakoczy, 2013; Phillips & Santos, 2007).

CONCLUSION

In this chapter, we focused on the roots of object thought in comparative psychology, that is, on the way different species think about objects that exist independently from them and persist over time. The most basic form of such object cognition is object permanence, or the capacity to keep track of the histories of solid and cohesive bodies moving continuously in space and time. This capacity is widespread in the animal kingdom and thus seems to have deep evolutionary roots. Object permanence in its simplest form (searching for objects not currently perceived) has been found in numerous mammal and bird species. Even more complex forms of thinking about objects (e.g., rudimentary logical and hypothetical reasoning and kind-based object individuation) are not confined to humans. In contrast to long-standing assumptions, therefore, more complex forms of reasoning about kinds and objects seem to be evolutionarily older than and independent from language. Similar capacities as those emerging in human ontogeny around age one have recently been documented in nonhuman primates, other mammals (dogs), and some birds (chicks). Some of the most exciting open questions in this field currently are how far the cognitive commonalities go between humans and other species, and whether sortal object individuation may constitute the evolutionary roots of psychological essentialism (Rakoczy & Cacchione, 2014).

Piaget set the stage for investigating the roots of the fundamentals of our worldviews in developmental metaphysics, and by this, indirectly prepared the field for comparative metaphysics. Although many of the kinds of questions he asked were and still are at the center of this kind of inquiry, novel methodological and theoretical approaches have led to findings that deviate fundamentally from his assumptions. In particular, when measured with alternative methods, cognitive competence has been shown to be present much earlier, and to be more domain-specific than assumed by Piaget. However, what is potentially interesting for research on comparative metaphysics, and for comparative psychology more generally, is a partial revival of the central Piagetian emphasis on domain-general cognitive integration in recent developmental theories (e.g., Carey, 2009; Gopnik & Schulz, 2004; Karmiloff-Smith, 1992; Spelke, 2003). Though differing widely in specific theoretical leanings and commitments, these recent accounts stress that crucial steps in cognitive development beyond human infancy consist in the integration of information across initially separated domains.

The main reason such theories are interesting for comparative research is that they might allow us to describe cognitive commonalities and differences between humans and other species. More precisely, recent findings show more and more commonalities in domain-specific capacities, for example, concerning numerical, spatial, or social cognition (e.g., Carey, 2009; see also Volume 1, Chapter 20, this handbook). Key differences between humans and other species might then be found not in any given domain per se, but in the integration across domains. In the particular case of object cognition, that was our focus here: Although capacities for tracking and individuating objects might be largely comparable in humans and other species, what is special about human object cognition might be the way such capacities are integrated widely with other cognitive faculties and domain-general reasoning. For example, when tracking and searching for objects, human children make use of general logical reasoning capacities, e.g., reasoning from negated disjuncts (p or q: not q, therefore p). When they see an object being hidden in one of three locations A, B or C, without knowing in which, they start searching at one location, say C, then move on to location B and finally to location A (Watson et al., 2001). Crucially, with each step the latencies decrease—indicating that the degree of certainty increases, which in turn suggests that subjects reason from negated disjuncts ("It must be in A, B, or C. It is not in C, therefore it must be in A or B. It is not in B, therefore, it must be in A"). In a comparative study with the same methodology, dogs also searched sequentially, but did not show the pattern of decreasing latencies—a finding compatible with the possibility that dogs might have engaged in less complex forms of reasoning (Watson et al., 2001).

Whether such integration of domain-specific object tracking and domain-general reasoning capacities is in fact something peculiar about humans, or if not, how far it extends into the primate lineage or beyond, is one of the most exciting questions for future research in this area.

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CHAPTER 27

PROBLEM SOLVING

Amanda Seed and Carolina Mayer

The piassava nut that grows on palm trees in Brazil contains high-energy food, but getting access to it poses a problem: It requires around 11.5 kN of force to crack, up to 13 times that of a walnut (Visalberghi et al., 2008). Bearded capuchin monkeys (*Sapajus libidinosus*) carefully position these nuts on anvils and use stones weighing up to 77% of their own body weight, lifting them above their heads to smash the nuts open (Liu et al., 2009). The task requires hard, nonbrittle stones, which are quite rare in the environment inhabited by the monkeys, meaning that they most likely have to be transported from elsewhere to suitable anvil sites (Visalberghi et al., 2009; see also Chapter 30, this volume). The monkeys' solution to the palm nut problem raises fascinating questions about their cognitive skills, which parallel those asked by anthropologists about hominid stone tool-making: What do they know about the properties of their tools? How do they acquire this complex behavior? Does tool transport reveal an ability to plan for the future? Luckily for comparative psychologists, capuchin monkeys, unlike ancient hominids, are alive and well and these questions can be addressed through empirical study (for reviews, see Ottoni & Izar, 2008; Visalberghi & Fragaszy, 2013).

But for a hyacinth macaw (*Anodorhynchus hyacinthinus*), cracking palm nuts is not much of a problem. Its heavy-duty beak has enough muscle power to crack open the nuts without the need for tools. A "problem" is therefore in the eye, or rather the whole body, of the beholder. For comparative psychologists, problem solving is at its most interesting when it involves individuals gaining some benefit, such as increased foraging success or efficiency, by overcoming some obstacle for which evolution has not provided them with a species-typical solution. The interest comes from two different perspectives. The first is ultimate: Why does problem solving evolve? The second is proximate: What mechanisms underpin problem solving?

In this chapter, we examine what comparative study can tell us about what makes some species (such as humans) better problem-solvers than others, and why these differences might arise over the course of evolution. We also address methodological and conceptual issues that arise when trying to dissect the cognitive components of problem solving and then make some suggestions for future directions.

WHAT IS PROBLEM SOLVING?

Much of the research in comparative psychology examining the extents and limits of animal cognition can be said to involve problem solving in some sense of the term (see Volume 1, Chapter 6, this handbook). For example, studies of memory, such as those conducted in the field with rufous hummingbirds (*Selasphorus rufus*), involve setting a problem, such as a range of artificial flowers that refresh at different rates (Henderson, Hurly, & Healy, 2006; see also Chapter 23, this volume). Although problems such as these capitalize on the activities that animals complete in their day-to-day lives, for the purposes of this chapter we need to

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define problem solving more narrowly and differentiate it from other terms, such as innovation (see Chapter 28, this volume) or tool use (see Chapter 30, this volume). We consider two important criteria to define a behavior as problem solving: (a) The solution to the problem is not in the species-typical behavioral repertoire. As outlined in the introductory example, cracking a Brazil nut is likely to pose a problem to capuchin monkeys but not to the hyacinth macaw. (b) The solution to the problem is not socially learned. Although learning from others can be an excellent strategy to gain a new behavioral solution, it is likely to involve different psychological skills than those involved in generating the behavior individually. Therefore, a useful definition for problem solving could be as follows: overcoming some obstacle to achieve a goal when the entire solution is neither in the species-typical repertoire nor socially learned.

Problem solving can be distinguished from innovation because of an asymmetry in the relationship between the two terms: Even though problem solving involves behavioral innovation, defined as the invention of a new behavior pattern or the modification of a previously learned one in a novel context (Reader & Laland, 2003), not all innovation involves problem solving. Innovation can involve simply feeding on a new resource, without any obstacle being overcome. Similarly, although tool use is one of the most prominent candidates for problem solving, problem solving is not the sole province of tool users, and not all tool use would be classified as problem solving according to this definition.

This definition is not a sharp one, some species-typical behavior is likely to be involved. The degree of emancipation therefore can be seen as a quantitative rather than a qualitative difference. What is important is that by solving the problem the animal is exhibiting flexibility. Such cases are interesting from an ultimate, evolutionary perspective. Behavioral flexibility can be a source of variability, and especially when accompanied by social learning, it can serve as an engine for adaptive change, through processes such as niche construction and gene-culture evolution (the behavioral drive hypothesis; Bouchard, Goodyer, & Lefebvre, 2007; Wyles, Kunkel, & Wilson, 1983; see also Volume 1, Chapter 15, this handbook and Chapter 20, this volume). Additionally, from a purely proximate, psychological perspective, flexible problem solving is interesting because it provides a window on such fascinating skills as reasoning, planning, and even consciousness. These biological traits have evolved at least once, in humans, but their mechanisms and origins are poorly understood. Yet it would also be interesting to psychologists if problem solving can emerge from simple mechanisms, and this in turn might inform work in artificial intelligence and robotics (see Volume 1, Chapter 28 this handbook).

Following Shettleworth (1998), if we define cognition as the process by which animals acquire, process, store, and act on information, then cognitive adaptations for problem solving could come from any part of that process, including perception, representation, learning, memory, planning, decision making, and controlling behavioral output. From an ultimate perspective, we can ask some questions about the causes and consequences of flexible and innovative behavior without a complete understanding of the cognitive mechanisms behind this adaptive response. For example, what kinds of socioecological conditions favor the evolution of problem solving? Are problem-solving species more successful in certain environments than in others (see Volume 1, Chapter 12, this handbook)? But in line with Tinbergen's (1963) famous call for integration, we argue that this question cannot be answered satisfactorily in isolation from the proximate perspective. Most of the research we review in this chapter has tried to home in on what specific cognitive abilities underpin problem solving, by focusing on species with a high proclivity for problem solving to try to characterize their cognition and comparing species that seem to have a greater or lesser degree of problem-solving skill.

The previous examples all involve foraging, but it should be acknowledged that problems can arise from the challenges and opportunities provided by social living (see Volume 1, Chapter 7, this handbook and Chapter 32, this volume). To the extent that social behavior is outside the normal repertoire, it would fall under the banner of problem solving as defined earlier. For example, one individual might exhibit the flexibility to cooperate with another to catch prey, exploit another as a social tool, or deceive another. However, in this chapter we will focus on physical problem solving by individuals acting alone.

Why Does Problem Solving Evolve?

Hypotheses for the evolution of problem solving or physical intelligence fall into two broad categories:

- *Direct selection* in response to properties of the environment: Some theories emphasize need—problem solving enhances survival chances in challenging or unpredictable environments (e.g., cognitive buffer hypothesis; Sol, 2009). Others emphasize opportunity—technical intelligence might evolve in habitats that offer high pay-offs, such as environments rich in defended or varied resources (e.g., Byrne, 1997).
- *By-product*: Problem solving is an expression of intelligence that evolved in response to selection from another domain (e.g., social or cultural intelligence hypotheses; Humphrey, 1976; Tomasello, Carpenter, Call, Behne, & Moll, 2005).

The raw material for testing these different hypotheses is variation. Comparisons have been made across a wide number of species to explore relationships between innovation and other variables. Such broad comparisons call for fairly “quick and dirty” forms of measurement. Counts of innovation in specialist journals for different species have been correlated with size of the brain relative to the body or brainstem, or the size of the forebrain or particular forebrain areas associated with executive function and learning (neocortex for mammals, nidopallium for birds) relative to the rest of the brain (see Volume 1, Chapters 12 and 24, this handbook). Interestingly, counts of innovation correlate with counts of tool use and relative brain size in primates and birds (Lefebvre, Reader, & Sol, 2004). More important for the question of problem solving, the diversity of technical innovations displayed by bird families was a much better predictor of residual brain size than was the number of food-type innovations (Overington, Morand-Ferron, Boogert, & Lefebvre, 2009). Interestingly, forebrain size and innovation rate are associated with the ability of birds to establish themselves in new environments (Lefebvre et al., 2004). Together, these results lend support to the direct selection account, because they demonstrate that there are heritable benefits to innovation.

But the relative size of the neocortex also correlates with group size in mammals (Dunbar & Shultz, 2007) and with relationship quality in birds (Emery, Seed, von Bayern, & Clayton, 2007). For this reason, analyses ideally should take into account other competing variables and phylogenetic distance, if they are to sort between the direct selection and by-product accounts, or reveal how they might work in combination (MacLean et al., 2012; see also Volume 1, Chapter 10, this handbook). Some researchers have also argued that these kinds of analyses cannot tell us much about the evolution of intelligence, because the measures are too indirect and the assumption that one brain area (e.g., the neocortex) is responsible for complex behavior (e.g., problem solving or social strategizing) may not hold true (Healy & Rowe, 2007).

What Makes a Good Problem-Solver?

General intelligence. Bigger-brained species have higher counts of technical innovation, but what are bigger brains doing? A large-scale meta-analysis of studies of nonhuman primates found a positive relationship between overall brain size and performance on cognitive tests over a wide range of paradigms (Deaner, Isler, Burkart, & van Schaik, 2007). This meta-analysis in turn relied on an earlier meta-analysis by Deaner, van Schaik, and Johnson (2006), which consisted of 30 measures on learning ability and 229 genus-by-genus comparisons and suggested a gradual increase in learning ability over primate evolution. A wide range of experimental paradigms was included, such as *patterned-string problems*, which require subjects to choose the one string (among several) that is connected to a reward; *tool use*, requiring subjects to use a tool to extract an out-of-reach reward; and *discrimination and reversal learning*, wherein subjects need to learn that one of two objects is arbitrarily related to reward and this initial discrimination is subsequently reversed (i.e., the previously unrewarded object is now rewarded).

Deaner and colleagues suggested that this reflected a *general learning ability* in nonhuman primates, similar to the notion of general fluid intelligence (i.e., *g*) in cognitive psychology (Blair, 2006). In humans, the performance on different IQ measures tends to correlate and this covariance is thought to reflect an underlying g factor, an aspect of human intelligence that might be rooted in an evolved cognitive adaptation (Jensen, 1998).

Deaner and colleagues (2006) found that some primate taxa (specifically, apes) consistently outperformed others on a large range of problems, suggesting, indeed, that this taxonomic family was somehow "better at everything." Group performance on these tasks was positively correlated and a single factor accounted for 85% of the variance. Other meta-analyses, including measures on innovation and social learning (Reader & Laland, 2002), and more recently, measures on tactical deception (Reader, Hager, & Laland, 2011), further indicate an increase in task performance with enhanced brain size in nonhuman primates. Additionally, similar to Deaner et al., the measures seemingly covaried: Primate genera that performed well in one task also performed well on other tasks and about 65% of the variance overlapped (Reader et al., 2011; Reader & Laland, 2002).

Can we conclude that species differences in brain size (and problem solving) reflect difference in some kind of general fluid intelligence? It is important to note that in humans, the investigation of g is based on the analysis of individual differences. In contrast, an approach on the basis of the group performance of a species does not take into consideration whether separable processes could have driven individual differences in performance. Group performance of a species on a wide range of tasks could be higher than that of others without necessarily implying the existence of a g factor in this species; rather, better performance could be the cumulative result of several unrelated differences (e.g., in learning, motivation, attention, temperament, or representational skill, to name just a few).

More recent studies have used an individual differences approach to study g in nonhuman primates (Herrmann & Call, 2012; Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007; Herrmann, Hernández-Lloreda, Call, Hare, & Tomasello, 2010). These challenge the notion of a g factor, at least in our closest primate relative, the chimpanzee. In contrast to the meta-analyses described previously, these studies analyzed individual performance scores on several cognitive tests and found that the scores clustered on separable components. For instance, Herrmann and Call (2012) extracted three distinct factors, described as learning (comprising discrimination learning), inference (including causal reasoning and reasoning by exclusion), and physical understanding (including quantity estimations, tool use, spatial understanding, and size discriminations). Similarly, in the study by Herrmann and colleagues (2010), a test battery designed for nonhuman primates (the primate cognition test battery; PCTB) revealed two separable cognitive factors in chimpanzees (*Pan troglodytes*): one spatial component (including measures on spatial memory and tracking the position of a reward after a change in location) and one physical-social factor (including measures of gaze-following for the social domain, and quantity estimation for the physical domain).

However, from the reported analyses it was not clear whether extracted factors could have shared some additional common variance that could reflect an underlying g. A recent study using a modified version of the PCTB found that two different factors could again be extracted, corresponding broadly to social and physical cognition, but there was also an underlying g factor that accounted for 55% of the variance (Hopkins, Russell, & Schaeffer, 2014). Moreover, this factor was found to be heritable by quantitative genetic analysis. The notion of g remains controversial, but nevertheless the individual differences approach reveals that there is more to primate cognition than a general learning ability, and in principle these different factors might be playing dissociable roles over evolution in response to the pressure to solve problems.

The correlations between the relative size of the brain (or brain area) and innovation in birds and primates—together with the finding that, in primates at least, species with bigger brains perform consistently better in cognitive tests—implies that there are cognitive differences between species that are associated with differences in problem-solving ability. However, there is little direct evidence identifying what mechanisms explain the correlations, although recent work harnessing individual differences on test batteries reveals that there are likely to be multiple factors at work. A better understanding of the nature of the cognitive mechanisms underpinning problem solving will be essential for making progress on the question of what exactly these larger brain areas are doing to earn their metabolic keep. Progress on this question will be reviewed in the section on cognitive mechanisms.

Other factors. What other adaptations, besides intelligence, could explain an increased ability to solve problems? A growing number of comparative studies have compared problem-solving performance in a smaller number of species while gathering richer information about what differs between them by taking other measurements concerning individual variation in cognitive, motivational, temperamental, and motoric factors. This allows for comparison between species and between individuals of the same species. In these studies, the problem usually involves accessing food by lifting a lid or opening a puzzle box—a similar kind of technical challenge to the famous example of innovation displayed by great tits learning to lift the lids from milk bottles. Individuals can be ranked in terms of whether they solved the puzzle, and if so how long they took to solve it. From the other measurements taken it is possible to examine whether any other traits predict performance.

A recent survey of the available evidence makes it clear that finding any general principles for what characterizes a good problem-solver is a complicated task (Griffin & Guez, 2014). For example, a tendency to approach novelty is a good candidate for being an important ingredient in the make-up of a problem-solver, and one that has been investigated the most often. But neophobia and neophilia (fear of and attraction to novelty; see Chapter 28, this volume) seem to be two separable features of an animal's temperament: The speed with which animals overcome neophobia to get access to reward does not always correlate with how quickly they approach a novel object in the absence of food (Greenberg & Mettke-Hofmann, 2001). Some studies report a relationship between reaction to novelty and problem-solving capacity, but others find no relationship, with the details of the behavioral assay used important in determining the outcome (few studies measure neophobia and neophilia; though see Biondi, Bó, & Vassallo, 2010). Most of the positive relationships are found between problem-solving outcome and the latency to approach the task itself, which might be problematic as the two data points are not truly independent: An animal that is very fearful of a task is unlikely to solve it. A similar picture emerges for motivation: Degree of persistence on the problem-solving task predicts likelihood of success in meerkats (*Suricata suricatta*) and spotted hyenas (*Crocuta crocuta*; Benson-Amram & Holekamp, 2012; Thornton & Samson, 2012), but Griffin and Guez (2014) reported that there is no clear picture regarding a relationship between problem solving and motivation or persistence when considering studies that used independent assays.

Griffin and Guez (2014) argued that one of the most compelling results to emerge from their survey is a relationship between motor diversity and problem solving. Although there have been relatively few studies exploring this relationship, all have found a positive relationship. Indian mynas (*Acridotheres tristis*) express greater variation in the range of motor actions while attempting to solve problems than do noisy miners (*Manorina melanocephala*), and this variation was a significant predictor of their significantly greater problem-solving abilities (Griffin & Diquelou, 2015). At the intraspecific level, spotted hyenas, Indian mynas, and great apes that express a greater range of motor actions were more likely or faster to solve a problem-solving device (Benson-Amram & Holekamp, 2012; Griffin, Diquelou, & Perea, 2014; Manrique, Völter, & Call, 2013). This is interesting in light of the recent finding that neocortex expansion was correlated with cerebellum expansion in the primate lineage (Barton, 2012). The cerebellum is involved in sensory motor control, motor learning, and processing sequences (Barton, 2012). The correlation at the neural level seems to have a counterpart at the behavioral level, given the finding that high levels of motor diversity are associated with problem-solving skill.

However, it should be noted that the correlations between problem solving and motor diversity come from the same task-solving episode. It remains possible that a third variable is responsible for the relationship between behavioral diversity and success on that particular task, such as previous experience with a similar problem leading to differing expectation of reward. The same caution applies when considering correlations between problem solving and approach latency, or persistence, when the measures are all taken from the same problem. Converging evidence from independent assays and multiple problems would be an important next step in testing whether these relationships extend beyond a specific task. The mechanism underpinning the correlation is also unclear. Does motor diversity directly impact on likelihood to solve the problem, because the right action is more likely to be hit upon? Or might motor diversity be an expression of some other cognitive skill, such as hypothesis testing or imagination?

Finally, a handful of studies have explored the relationship between associative learning and problem solving by comparing individual differences in solving a novel task with performance on simple discrimination learning tasks (e.g., peck a blue rather than a white key). Unlike the meta-analyses or test batteries described previously, this work aims to test a specific hypothesis concerning one cognitive mechanism. Positive relationships have been found in Indian mynas in discrimination learning, though interestingly not in speed to reverse an already-learned rule (e.g., switch from the blue key to the white; Griffin, Guez, Lermite, & Patience, 2013). Performance on discrimination tasks did not predict problem solving in spotted bowerbirds (*Ptilonorhynchus maculatus*), though a single principle component was found to underpin variance on all cognitive tasks given (Isden, Panayi, Dingle, & Madden, 2013). However, although woodpecker finches (*Camarhynchus pallida*) outperformed small-tree finches (*Camarhynchus parvulus*) on an extractive foraging task, they did not differ in speed of discrimination learning nor reversal learning (Tebbich, Sterelny, & Teschke, 2010). Interestingly, in the test battery administered to chimpanzees by Herrmann and Call (2012), the ability to solve tasks involving tools and causality loaded on different factors than those requiring spatial and discrimination learning. There does not seem to be a straightforward relationship between learning and problem solving. Perhaps this is not surprising, as problem solving seems likely to involve a broader set of cognitive skills than operant learning, where there is no need to generate a new behavior or react to a novel context (Griffin et al., 2013). Studies conducting independent assays measuring specific cognitive skills and looking at the relationship with problem solving are rare. This is perhaps because the range of cognitive skills that might be recruited by different animal species solving problems is not well understood (Clayton, 2004). In the next section, we will examine comparative research that has tried to expand our knowledge of animal cognition in a problem-solving context.

Species differences in problem-solving ability or innovativeness are likely to be made up of an assemblage of differences, one or more of which might come into play when focusing on a particular problem in a particular context, and each of which might be modulated by multiple variables (e.g., availability of directly-accessible food, past experience, life-history stage). Currently, the picture that emerges from the survey of work comparing species that differ in how readily they solve a problem is a mixed and at times conflicting one (Griffin & Guez, 2014). Perhaps part of the problem is an incomplete understanding of the range of psychological mechanisms at work when different species engage with problems. The cognitive mechanisms for problem solving are likely to have important consequences for hypotheses concerning what makes some species better problem-solvers than others. For example, if trial-and-error learning is thought to be at the heart of problem solving, then a species whose make-up favors higher and more diverse levels of interaction with a problem should have a higher chance of success (e.g., factors such as low neophobia, high motoric diversity, high persistence, and fast learning speed could lead to greater problem-solving proclivity). However, if other mechanisms are at work then these relationships might not exist or could even reverse. For example, if other animals besides humans can solve a problem without needing a chance action to be rewarded with food availability but instead by considering its similarity to another problem, or by considering how the elements might interact before acting on them, then other factors might be more important, such as behavioral inhibition, attentional focus, or memory. Importantly, this could lead to conflicting predictions about what kinds of personality or temperament variants should be associated with greater problem-solving proclivity.

When trying to extract common principles from comparisons of disparate species solving disparate tasks (from bowerbirds to hyenas), a failure to consider the cognitive mechanisms recruited during problem solving by those species might cause a confusing picture to emerge. In the next section, we review some of the recent work that has aimed to explore the cognitive mechanisms recruited by different animal species when solving problems.

COGNITIVE MECHANISMS FOR PROBLEM SOLVING

In the associative tradition, animal learning is studied in a context that is as far removed from the natural environment as possible, to isolate learning from innate predispositions (see Volume 1, Chapter 2, this handbook). For example, animals in an operant learning chamber might have to learn a relationship between a pattern presented on a screen and pressing one of two buttons, enabling researchers to study how this learning is generalized across different stimuli. However, in the early part of the 20th century, Wolfgang Köhler pointed out that using artificial stimuli and responses with no causal relevance to the outcome limits animals to trial-and-error learning of chance relationships, and any other abilities that they have would remain undetected (Köhler, 1926). In his research, Köhler (1926) posed problems to chimpanzees where the means for reaching a reward was causal and transparent, rather than arbitrary and opaque as it is in an operant conditioning chamber. He posed problems that were within the range of those likely to be encountered in the natural environment, but by doing so in a research center he was able to take detailed and complete observations of the steps taken to solve the problem, as well as manipulate the materials available for doing so (see Volume 1, Chapter 6, this handbook). He described chimpanzees as having "insight" into problems, which allowed them to arrive at solutions without the extended period of trial-and-error learning that typified associative learning described by Thorndike (1898). He also made some observations that hinted at ways in which these insights might be limited compared to human problem solving. For example, he suggested that chimpanzees might be limited to the "optics" of a situation, rather than operating on the kinds of abstract notions of connection and support that characterize problem solving in human adults.

This cognitive revolution was of great theoretical importance in seeking to understand the continuity between human and nonhuman animal minds, making it possible to explore the evolutionary roots of cognitive abilities other than learning and memory, such as reasoning, representation, and planning. These have sometimes been referred to collectively as *nonassociative processes*. Trial-and-error learning is still recognized as an important process, but in some cases it seems insufficient to explain the kinds of behavior seen in problem-solving contexts.

Rather than stripping away information that a species might have evolved mechanisms to process, comparative researchers interested in problem solving have tried to systematically manipulate this information, to find out more about how it is processed by different species. For the most part this research has followed in the tradition of focusing on large-brained species with a reputation for problem-solving behavior, such as large-brained primates and birds. The research is still in an exploratory phase, and the challenge is to characterize these nonassociative processes in more detail and to explore their extents and limits in other species.

Insight

Köhler suggested that chimpanzees were capable of perceiving meaningful relations between objects, which in turn allowed them to solve problems in a way not well explained by chance actions being shaped toward a correct solution by rewarding feedback (i.e., trial-and-error learning; Thorndike, 1898). Thorpe (1956) put forward a more formal operational definition of insight, as the "the sudden production of a new adaptive response not arrived at by trial behavior or the solution of a problem by the sudden adaptive reorganization of experience" (p. 100). Birch (1945) showed empirically that experience was important for insightful solutions to emerge: Playing with sticks facilitated the ability of young chimpanzees to use a stick as a tool to bring in an out-of-reach food item. He suggested that the chimpanzees' ability to perceive a functional relation between the stick, the food, and themselves resulted from the opportunity to learn something about sticks and their possible use from experience. Epstein and colleagues (1984) also stressed that experience was important but with a different interpretational slant. They showed that pigeons (*Columba livia domestica*) could "solve" one of Köhler's famous problems, in which the subject needs to move a box so as to stand on it and retrieve a reward suspended from the ceiling, if they first learned to move boxes to a point on the floor for a reward and, in a separate session, to peck a (banana-shaped) target. Epstein and colleagues showed that each element of the problem needed to be learned, and they argued that the elements were automatically "chained" together to form the novel combination. For Epstein and Birch, past experience with the elements of a problem is important in enabling animals to solve it, but whereas chaining requires that the intermediate steps are reinforced through association with reward, Birch stressed that experience is used to learn functional relationships between objects that could then be generalized to different contexts, goals, and actions (see Shettleworth, 2012, for detailed review).

Recently, there has been a resurgence of experiments on the topic of insight, especially concerning how past experience is translated into problem solving. To date there has not been much work that examines insight in terms of the "aha" experience that is central to the definition of insight in human cognition, the moment of transition from impasse to solution, perhaps because of difficulties inherent in recognizing an impasse or categorizing what is meant by *sudden* (Seed & Boogert, 2013; Shettleworth, 2012). Call (2013) suggested that progress on this could be made by considering different models in the human cognitive literature for how information might be recombined. Future comparative work would do well to draw on these or at least formulate a more specific model for how problem solving might be achieved in the absence of associative learning, to move beyond using *insight* as a place-holder for all processes that seem to involve information restructuring or recombination in the absence of direct reinforcement of behavior. However, there remains considerable debate in the literature as to whether such processes exist in animals.

For example, the vertical string-pulling task given to birds, in which subjects have to pull up a long string, trapping successive loops underfoot, had been suggested to represent a case of insightful problem solving, because learning through trial and error cannot explain the emergence of a complete solution on the first trial (Heinrich, 1995; Thorpe, 1943). However, recent work with New Caledonian crows (*Corvus moneduloides*) has led to an alternative proposal: the perceptual-motor feedback loop hypothesis (Taylor, Knaebe, & Gray, 2012; Taylor et al., 2010). According to this hypothesis, the sight of the food coming closer to the subject provides reinforcement for pulling, which is consequently repeated. Together with the notion that the initial act of pulling-up and stepping might be due to species-typical feeding motor patterns (Seibt & Wickler, 2006; Shettleworth, 2010), which could explain first-trial success.

Support for the perceptual-motor feedback loop hypothesis in New Caledonian crows comes from two findings. First, when crows had to pull up the string through a small hole in a visual occluder, they performed more poorly than they did on the basic problem (Taylor et al., 2010). Second, the majority of birds tested on a horizontally presented looped string task failed to solve it. Like the vertical task, the looped string task requires multiple pulling actions before the reward can be obtained, but in contrast to the vertical task the food does not come closer with the initial pulls, which only serve to pick up the slack in the string (Taylor et al., 2012). Taylor et al. (2012) suggested that crows do not anticipate the consequence of pulling the string but merely continue to pull in the vertical task because of the rewarding nature of seeing the food come closer. It would be interesting to know how crows with more experience with string would perform. Would they improve even if the experience was not reinforced, in the way that the naive chimpanzees' tool use improved after Birch (1945) gave them experience playing with sticks? Or would each step of the process need to be reinforced as was the case for Epstein's pigeons, even if only by seeing food come closer?

There is evidence that visual feedback also plays an important role when apes solve novel problems. Völter and Call (2012) found that apes failed to solve a novel problem (turning a crank to bring food into reach) if the movement of the food was obscured. However, once apes had found the solution in a visible condition, obscuring the movement of the food did not impede success. Visual experience was important, but again it would be interesting to manipulate the reinforcement of the behavior to differentiate between accounts on the basis of chaining or secondary reinforcement from those on the basis of the learning of functional relations.

von Bayern, Heathcote, Rutz, and Kacelnik (2009) explored the role of past experience for another interesting case of problem solving. The task (developed by Bird & Emery, 2009a) involves dropping stones into a vertical tube to collapse an out-of-reach platform in a transparent box and release a reward. Rooks (*Corvus frugilegus*) in the original study were trained to nudge stones into the tube. Following this experience, they spontaneously collected stones from their aviary and dropped them. Lind, Ghirlanda, and Enquist (2009) argued that this experience meant that the final solution was not insightful but shaped, through a process along the lines of chaining as described by Epstein. However, it is harder to explain the ability of the rooks to use twigs to depress the platform when stones were no longer available without any additional training (Bird & Emery, 2009b). von Bayern et al. (2009) manipulated the experience of two groups of New Caledonian crows: half were trained to nudge stones into the platform as in the original study, and the other half were able to peck the platform directly through the tube. Birds in both groups went on to solve the problem by picking up stones and dropping them. The ability to generalize from experience gained using one action to solve the same problem with a very different one is not well explained by a process of shaping, and the authors argued that the birds understood the functional relationship between contacting the platform and releasing the food.

The question of whether or not animals reorganize past experience in the light of a new problem is still very much an open one. Some recent results support the view championed by Birch and Kohler, that animals build a representation about the functional relationships between objects that allow them to solve novel configurations of these elements using a new action (von Bayern et al., 2009). In other experiments (Taylor et al., 2012; Völter & Call, 2012), explanations on the basis of automatic chaining and secondary reinforcement could explain the emergence of the solution, but so could an account on the basis of the use of visual experience of interactions between objects to build some comprehension of their function. What does it mean to suggest that animals such as apes or crows are able to learn about the functional relationships between objects? What is the nature of their representations? Do they represent a causal connection or just an association? How abstract is their knowledge of objects and their properties?

Objects and Causality

Objects in the environment have physical properties that dictate the possible ways in which they can interact with one another (e.g., solid objects cannot pass through one another; see Chapter 26, this volume) to cause outcomes (e.g., heavy objects can tip a balance beam and sink in water). Knowledge of these properties, such as solidity, continuity, weight, and rigidity, is an important feature of flexible problem solving in humans. However, in the absence of verbal report, when an animal solves a problem it is impossible to know if it has inferred anything about object properties, or if its behavior is the result of associative learning on the basis of surface-level perceptual characteristics. How can we tease these different explanations apart? After all, in the absence of instruction, our only route to uncovering causal relationships is through our senses, and with no perceivable information, problem solving would be impossible. Some of the different empirical approaches to addressing this question are outlined following and summarized in Figure 27.1. In the following section, we will review some of the key studies that have adopted these different approaches, with a view to highlighting their merits and drawbacks. Note that a distinct line of comparative research has examined the ability to represent cause-and-effect relationships independently from knowledge of the physical mechanisms or object properties involved (for a review of this literature, see Chapter 29, this volume).

Transfer tasks. One approach to finding out if animals can go beyond the specific perceptual configuration of the problem is to confront the animal with a series of tasks in which the perceptual configuration is different but the underlying causal relationship is still at work (see Figure 27.1, Transfer panel). For example, many species of primate, and birds such as parrots and corvids, are proficient at solving tasks which involve using string, cloth, or a tool to bring a reward into reach (recently, these have been comprehensively reviewed by Jacobs & Osvath, 2015). For example, chimpanzees, capuchin monkeys, and cotton-top tamarins (*Saguinus oedipus*) that learned to pull an intact object rather than a broken one to bring food within reach then transferred their solution across tasks that varied the tools' shape and position (Fujita, Sato, & Kuroshima, 2011; Hauser, Kralik, & Botto-mahan, 1999; Hauser, Pearson, & Seelig, 2002; Povinelli, 2000; Santos, Pearson, Spaepen, Tsao, & Hauser, 2006; Yocom & Boysen, 2010). Interestingly, the primates generalized their solution seemingly more readily than pigeons (Schmidt & Cook, 2006). This indicates that they had attended to the functionally relevant features of the problem. However, this result does not necessarily mean that they had formed a representation or understanding of the causal relationship between those features and the outcome, nor an abstract knowledge of the object properties such as connection or continuity (Fujita, Kuroshima, & Asai, 2003; Povinelli, 2000; Vonk & Povinelli, 2006).

This same interpretive problem has been encountered in a more recent paradigm in which transfer tasks were used: the Aesop's fable task. This task involves dropping objects into tubes partly filled with water, to raise the level of the water and obtain a floating food reward. Having learned to drop stones into a water-filled cylinder (if necessary, subjects can be taught as previously described), subjects are then given choices between different objects (e.g., heavy or light; hollow or filled) and different tubes (e.g., wide vs. narrow, filled with water or sand). This series of tasks has been conducted (so far) with three species of corvid, and for the most part subjects perform above chance on these different challenges. However, from the transfer tasks alone it is difficult to rule out a bias to select certain objects as a result of generalization from the original training object (Jelbert, Taylor, & Gray, 2015). Further approaches have been taken to understanding the birds' cognition, as described in the following sections.

The results of further transfer studies run by Povinelli (2000) were consistent with chimpanzees using perceptually based information, because when the difference between the connected and disconnected options was made less obvious (e.g., a cloth was wrapped around the reward), the chimpanzees no longer discriminated between them. However, there is a difficulty in interpreting this negative result, because as the visual discrimination becomes more difficult, the task becomes more demanding for reasons that are not related to object knowledge, such as attentional focus. It must be emphasized that strategies based on perceptual features and causal or object knowledge are not mutually exclusive (see Chapters 5 and 17, this volume), and indeed human adults also show biases on the basis of perceptual features when solving problems (Silva, Page, & Silva, 2005).

A natural extension of this line of work making the perceptual distinction between the two options more and more subtle is to remove it altogether, so that at the time of choice the animal must remember the causal properties of the two options rather than basing its choice on a perceptual heuristic. For example, Povinelli (2000) showed that chimpanzees failed tasks in which there was perceptual contact but no physical connection between means and end, such as one in which they had to choose between a broken and an intact tool when the ends of the

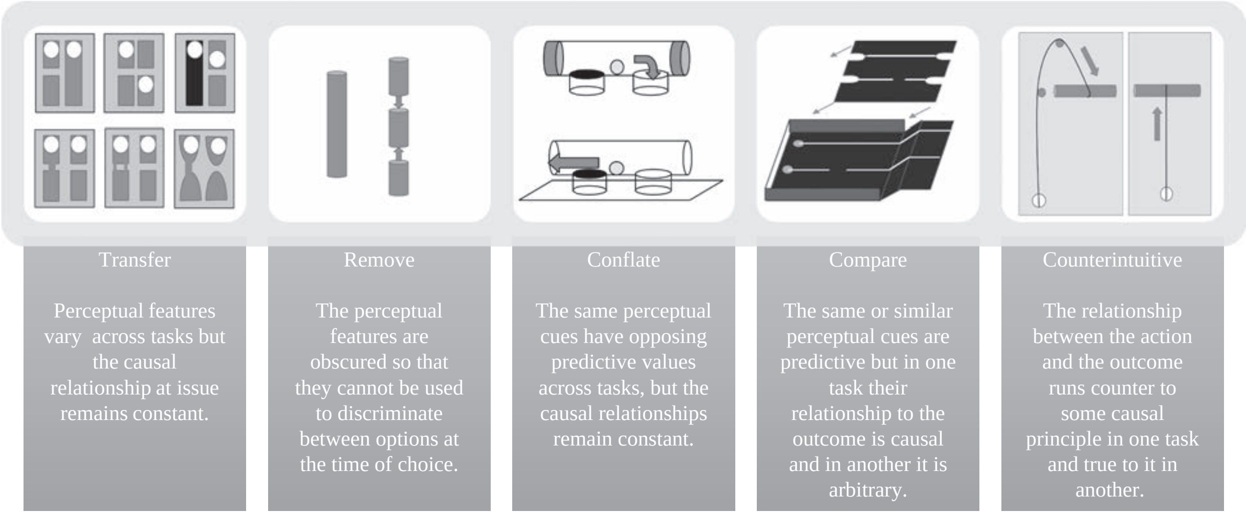

FIGURE 27.1. Different approaches to disentangling problem solving based on the causal role played by surface-level perceptual characteristics of objects. Illustrated examples of the different approaches from Transfer (Hauser, Kralik, & Botto-Mahan, 1999), Remove (Povinelli, 2000), Conflate (Seed, Tebbich, Emery, & Clayton, 2006), Compare (Mayer et al., 2014), and Counterintuitive (Heinrich & Bugnyar, 2005).

broken tool were aligned before they had a chance to choose (see Figure 27.1, Remove panel).

However, as previously pointed out, and as acknowledged by the original authors, making the subjects rely on a memory of a past manipulation to make their discrimination also increases demands on memory and attention. More recently, some chimpanzees passed a version of the aligned-tool test when the procedure was modified to reduce these demands (Seed, Seddon, Greene, & Call, 2012). Importantly these individuals were more likely to also solve tasks in which the two options were covered up (rather than aligned), illustrating that the appearance of perceptual completeness was not the only reason for the failure of other chimpanzees to solve the task: Attending to or remembering what was where remains a viable alternative explanation.

The transfer task approach gives a good indication of what perceptual features were used to make the discrimination. In a comparative framework this can provide an illuminating perspective on species differences in how different problems are solved; for example, in the broken-tool task primates seem to rely on functionally relevant information, whereas pigeons did not transfer their solution across small changes to the perceptual configuration of the task. Another good feature of the approach is that the point of failure can be quite precisely pinpointed, because the subject has already demonstrated competence in the general experimental setting. However, it can still be difficult to isolate what difference between tasks that are passed and failed is responsible for the difference in performance, and what that means for cognition. Further work, such as examining individual differences across further cognitive tasks, might be needed (Seed et al., 2012). Another drawback is that as some perceptual information must always be provided for the problem to be solved, this approach cannot be used to decisively rule out an explanation based on a bias to respond to certain object features.

Conflating cues. Another approach is to conflate the cues, so that the same feature has to be treated differently depending on the causal role it plays, such as steering food away from a block when it serves as a barrier but toward it when it serves as a supporting surface (Seed, Call, Emery, & Clayton, 2009). The two-trap problem (Seed et al., 2009; Seed, Tebbich, Emery, & Clayton, 2006) was developed to try to respond to some of the methodological problems identified for the trap-tube task (Silva et al., 2005). In the crucial transfers, a single object acts as a barrier or supporting surface in different conditions, thus requiring a flexible response (see Figure 27.1, Conflate panel). One rook, one chimpanzee, and the majority of children from the age of 2.5 years and up solved both transfers (Seed & Call, 2014; Seed et al., 2009). However, the trap task seems to be difficult for many species: parrots (keas [*Nestor notabilis*], macaws [*Arachloroptera*], and a cockatoo [*Cacatua sulphurea*]), woodpecker finches, and rooks in another study all found the task challenging, with few (or no) subjects learning to avoid the trap, and those that did so failing to solve the transfer tasks (Liedtke, Werdenich, Gajdon, Huber, & Wanker, 2011; Tebbich, Seed, Emery, & Clayton, 2007; Teschke & Tebbich, 2011). For chimpanzees, the manner of task presentation is extremely important; for example, far fewer subjects pass the task if they have to push the food away from themselves than if they can rake it in, and they perform even better if they do not have to use a tool (Call, 2010). The trap task might not be ideally suited for comparative study of object knowledge given the peripheral task demands involved. However, the principle of conflating cues to see if learning about a physical feature can support responding differently to it in a transfer task is a promising method for disentangling explanations on the basis of perceptual features from those on the basis of the functional role of an object in a given context.

Comparing contexts. Another approach that is concerned with whether cues are treated as causally relevant or merely predictive involves comparing performance in two contexts, one *causal*, in which the cues have mechanical relevance to the outcome, and one *arbitrary*, in which the same cue, although 100% predictive, has no mechanical relevance to the outcome (see Chapter 29, this volume). For example, a recent pair of studies compared causal and arbitrary versions of the broken-tool problem (Albiach-Serrano, Sebastián-Enesco, Seed, Colmenares, & Call, 2015; Mayer et al., 2014). In the causal, or uncovered, version everything was visible: One option (a string or paper strip) was connected to a reward and the other was broken in two clear pieces. In the arbitrary, or covered, version subjects had to use a very similar visual pattern to learn which option to pull, without the pattern having any functional relevance (strings stuck to the cover, or a pattern painted on a board; see Figure 27.1, Compare panel). Across the two studies, chimpanzees, bonobos, orangutans, capuchin monkeys, and human children age 3 to 5 years performed significantly above chance in the causal condition but failed the arbitrary one, suggesting that learning to respond to an arbitrary visual pattern is not how they solve the broken-tool task (although interestingly, only children could solve the arbitrary version if they had first solved the causal one). Importantly, the difference does not seem to be explained by differences in the amount of visual feedback: Chimpanzees were able to solve a memory condition in which they first saw the real problem before it was obscured with a plain cover.

This approach has been used in combination with a transfer task approach. For example, in the trap-tube task (developed by Visalberghi & Limongelli, 1994), subjects need to push a piece of food out of a horizontal tube away from a trap. Capuchin monkeys and chimpanzees that learned to do so were then given another task in which the tube was inverted, and therefore nonfunctional (Povinelli, 2000; Visalberghi & Limongelli, 1994). Similar to the previous example, the interest is in comparing performance on the original task in which the discriminative perceptual cue is relevant to the outcome (because the food will fall into the trap) and one in which it is not (because the tube is inverted). Subjects continued to avoid the trap, and so it seemed that they had treated the trap as a perceptual cue but had not encoded its functional significance. However, combining these approaches might be problematic, because subjects are expected to abandon a previously successful strategy. For this reason, the compare approach is more powerful when it examines the performance of two groups of naïve subjects in two different scenarios, as in the broken tool example.

Regardless of whether a within- or a between-subjects design is used, the chief difficulty for the compare approach is making the two contexts comparable in important ways that have been shown to influence associative learning. For example, Call (2004) investigated “inference by exclusion” in a paradigm that has been used with a wide range of species: finding food inside one of two cups. In the critical condition, the subject only sees (or hears) information about the empty cup, which is shaken (silently) or shown to the subject, and the subject has to infer that the food must be in the other cup. To rule out an associative explanation (e.g., avoid silent/empty cups), Call (2004) compared this causal condition with an arbitrary condition (a recording of a rattling sound was played when one cup was touched but not the other). Great apes and capuchin monkeys solved the causal problem at a group level when the cues were embedded in the causal context, but they did not solve an arbitrary comparison (Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Call, 2004; Hill, Collier-Baker, & Suddendorf, 2011; Sabbatini & Visalberghi, 2008). In contrast, dogs did not show this difference (Bräuer et al., 2006; though see Erdöhegyi, Topál, Virányi, & Miklósi, 2007, for ways in which a bias toward social cues in dogs might mask inference performance in dogs). However, critics of the sound recording comparison have argued that subjects might have a more specific association comprising the visual and auditory elements (Penn & Povinelli, 2007). Their argument is that failure to choose an unshaken noisy cup reflects the specific nature of this association, instead of an appreciation of the causal relationship between an object and its container. Interestingly, African grey parrots (*Psittacus erithacus*) behave in an intermediate fashion—they solve the arbitrary task if there is a conjunction between shaking of a cup and a sound recording but do not use the sound recording alone (Schloegl, Schmidt, Boeckle, Weiß, & Kotrschal, 2012).

In another experiment, chimpanzees seemed to infer the location of a food reward based on the effect of its weight. They chose the lower of two cups on a seesaw balance when it tipped immediately after the (hidden) baiting of one of the cups, but not when the experimenter moved the balance by hand a short time after adding the bait to one of the cups (Hanus & Call, 2008). This experiment has been criticized because the two conditions differ in terms of the delay between the two cues, and associative learning has been shown to be highly sensitive to temporal contiguity (Povinelli & Ballew, 2011). Similarly, Hanus and Call (2011) confronted chimpanzees with a task in which they had to select a bottle containing juice from a bank of five bottles that were difficult to open. Chimpanzees opened the heavy bottle earlier in the sequence than would be expected by chance, seemingly inferring which one to open based on the weight of the juice. In contrast, they did not learn, within the same number of trials, to open one of the five bottles that was marked out with a visual cue (color) when the other four bottles were full of water. However, chimpanzees might just have found weight a more salient cue in this context, perhaps because of past experience that heavy objects contain rewards.

A final study challenged apes to locate a yogurt reward in one of two cups on the basis of trails of yogurt on the table (Völter & Call, 2014b). Apes used the trails to locate yogurt but not a dry food pellet, again showing a differential use of the same cues when embedded in a causal and an arbitrary context. When one trail appeared after the cups were moved into location (behind a barrier), and another was present before the invisible movement of the two cups, apes successfully used the temporal information to select the cup that caused the trail. Importantly, they did not always use the most recent trail: If the temporal cues were arbitrary, because the second trail was laid on a separate piece of paper after the movement of the cups, they used the proximal, causal trail rather than the more recent one. This conjunction of temporal and spatial cues to causality and the ability of apes to prioritize accordingly is a new approach and one that seems very promising for future comparative studies, perhaps in other contexts (see Chapter 29, this volume).

The compare approach has also been adopted within the framework of the Aesop's fable task. Birds that had already solved the previous discrimination tasks were given a final task in which they had to choose between two tubes marked with shape and color cues. Neither contained a food reward but one was connected to a central tube that the reward was floating in (this tube was too narrow for stones to be dropped inside). In contrast to the rapid discriminations birds made between options with causal differences, very few birds solved this arbitrary task. However, by moving the reward to a different location, not only the causal link but also the visual link between action and outcome was broken. Given the importance of visual feedback for problem solving previously described, this is problematic. A third group tested on a causal task with limited visual feedback (similar to the memory condition conducted with chimpanzees on the broken string task in Mayer et al., 2014) would be useful for examining the extent to which an alternative explanation based on feedback might explain the poor performance on this arbitrary task.

Counterintuitive tasks. Another kind of comparison has been made between conditions that differ in terms of how "intuitively" the action is related to the outcome. For example, Heinrich and Bugnyar (2005) compared the performance of one group of hand-raised ravens on the vertical string-pulling task previously described with a group tested on a counterintuitive version in which string had to be pulled down to bring a reward up via a pulley system. Most individuals in the group tested on the original task solved the task quickly, whereas none solved the counterintuitive task. However, the two conditions also differed in the amount of visual feedback provided. Cheke, Bird, and Clayton (2011) tested Eurasian jays (*Garrulus glandarius*) on a counterintuitive version of the Aesop's fable task, in which the reward moved sideways with successive stone drops, rather than toward the birds. The jays did not solve this task, in support of an explanation on the basis of causal knowledge. Although this task provides feedback for action, it is away from rather than toward the actor, which means that it might not provide the reinforcement thought to be needed to sustain action in the perceptual feedback loop hypothesis put forward by Taylor and colleagues (2012). An alternative based on a particular kind of feedback might still explain the difference between the conditions.

Taken together, these studies provide evidence that animals such as apes and corvids are better able to solve problems where the cues have causal relevance to the outcome than when their relationship with the outcome is arbitrary, even when the perceptual characteristics of the cues in the two different contexts are very similar. However, in most of the studies conducted to date, alternative explanations based on differential salience, contiguity, or visual feedback are possible. Future work will need to differentiate between the arbitrary and causal contexts in a way that is not likely to influence other hypothesized mechanisms, or include further controls that make the competing associative account less likely. Nevertheless, the weight of evidence is growing in favor of some animals such as apes (and perhaps capuchin monkeys and corvids) possessing knowledge of object properties that allows them to make inferences and decisions in a way that cannot be explained by learning of arbitrary associations based solely on first-order perceptual information. Seed and Call (2009) argued that such representations could be referred to as structural rather than perceptual: They comprise abstract information about the structure of objects and the causal role they play in certain interactions, and not just their perceivable features. But they argue that these representations should be distinguished from symbolic representations that characterize adult human concepts, such as gravity.

Exploration

In the section on insight, we described one line of theoretical reasoning that explains insight as the outcome of an ability to use experience with objects to learn something about how they can be made to function, even in the absence of reward. Animals possessing an ability to learn in this way, whatever the details of the mechanism, would benefit from exploring objects during play (see Volume 1, Chapter 34, this handbook and Chapter 28, this volume), and indeed species of primates and birds with a high proclivity for problem solving are object oriented and show high levels of object play (Bateson & Martin, 2013). Is there any evidence that they engage in the kind of actions that might enable them to learn about object properties? Of particular interest are cases in which animals combine objects with one another, or the substrate. Such combinatorial play was only described for capuchin monkeys and chimpanzees among a study of 74 primate species (Torigoe, 1985). Several species of parrots also show such play, including New Zealand kea (*Nestor notabilis*; J. Diamond & Bond, 1999) and African grey parrots (*Psittacus erithacus*; Pepperberg &

Shive, 2001). Recently, a comparative study of several species of parrots (*Diopsittaca nobilis, Pionites melanocephala, Cacatua goffini*) and corvids (*Corvus corax, C. monedula, C. moneduloides)* found the highest levels of combinatorial play in Goffin's cockatoos (*Cacatua goffini*) and New Caledonian crows (*C. moneduloides*; Auersperg et al., 2015). These two species also show the greatest proclivity for problem-solving competence, including the use and manufacture of tools (Auersperg et al., 2015). This supports the hypothesized link between combinatorial play and physical cognition. However, to our knowledge there is no direct evidence that animals learn about how objects function from play. Another open question is whether animals can use exploration strategically to seek information about how objects behave.

Children have been described as "little scientists" who intervene with the world to diagnose features or events that are causally relevant from those with which they typically covary (Gopnik & Meltzoff, 1997; Gopnik & Schultz, 2007). It has been suggested that, in contrast, nonhuman animals learn about causal relationships by association (e.g., when the wind blows, fruit will fall from a tree), but do not represent a causal framework that would support novel inferences (e.g., shaking the branch might have the same effect; Bonawitz et al., 2010; Tomasello & Call, 1997; see also Chapter 29, this volume). However, there is a lack of evidence rather than evidence of a lack: There has only been one study examining exploratory interventions with nonhumans, which compared chimpanzees with 4- and 5-year-old children (Povinelli & Dunphy-Lelii, 2001). Subjects had to place two or more blocks upright (the chimpanzees received a food reward for doing so). In catch trials, one of the blocks would not stand, because of either a visible or an invisible anomaly. All participants explored the visibly anomalous block through visual and tactile modalities, but only 5-year-old children explored the invisibly altered (weighted) block. The authors suggested that this reveals that only the older children's exploratory behavior was driven by explanation seeking, as the chimpanzees could simply have been responding to the perceptual novelty of the visibly altered block (Povinelli & Dunphy-Lelii, 2001). However, the problem had no solution. This might have limited the motivation to explore. More important, there was no way to glean whether subjects had been seeking an explanation for the anomaly or whether they had come up with one, except by analyzing verbal reports made by children. Developmental studies showing that exploratory behavior in children is motivated by explanation seeking also relied on language: analyzing spontaneous utterances made by children (Legare, Gelman, & Wellman, 2010) or framing the problem linguistically (e.g., "Which block made the machine go?"; Schulz, Gopnik, & Glymour, 2007).

The developmental evidence shows that by the age of 4 or 5 years, children do use exploration strategically. For example, Schulz and colleagues (2007) showed that children would use their own intervention to disambiguate confounded evidence: When two blocks glued together made a machine go, children spontaneously tried placing them first on one end and then the other to see which block caused the effect. Paradigms in which exploratory behavior can be used strategically to find out information within an intrinsically motivating problem solving context are needed to bridge the gap between the developmental and comparative literatures.

Behavioral Control

Despite the recent positive evidence already described, previous research concerning the tendency of nonhuman animals to reason about causality have yielded largely negative results (Penn & Povinelli, 2007). The trap-tube task is a good example: Very few chimpanzees learned to avoid the trap in the first place, and they continued to avoid an inverted trap, as if there was no more to the problem than met the eye. But changing peripheral task demands can lead to radically different results. For example, when chimpanzees were tested on the trap task without a tool, all of the subjects tested avoided the trap: They performed significantly better without a tool than those tested with one on the same problem (Seed et al., 2009; Völter & Call, 2014a). Interestingly, this was only the case when the task was novel; apes who had already learned to avoid traps when moving the reward with their fingers were able to continue to do so when given a tool (Völter & Call, 2014b). One explanation for the deleterious effect of a tool is that manipulating it is cognitively demanding: using one to solve a new task may overload executive functions (such as attention) and lead to failure (Seed et al., 2009). Another example pointing to the importance of executive functions for physical problem solving is that some chimpanzees succeeded on a task that required them to choose an intact tool over one shown to be broken in a prior demonstration, even though at the time of choice the two appeared connected (Seed et al., 2012). Previously, chimpanzees failed a version of this task with higher peripheral demands (Povinelli, 2000). Interestingly, performance on the new task correlated with one that just required subjects to attend to and remember which tool was where, suggesting that levels of executive function predicted success on this challenging physical problem (Seed et al., 2012).

In a review of the problem-solving capacities of nonhuman primates, Tomasello and Call (1997) distinguished two main aspects on which evolutionary pressures may have acted: The first aspect refers to the evolution of representational systems. This could be an understanding of functional object properties or a representation of their causal relationship to the goal. In addition, Tomasello and Call (1997) argued that "the sine qua non of cognitive adaptations is flexibility . . . that the individual organism to some degree controls" (p. 8). The flexible control of behavior, perception, and mental processes may be important for individuals to choose an appropriate action. *Executive functions* (EF) are "a set of general-purpose control processes that regulate thoughts and behaviors" (Miyake & Friedman, 2012, p. 8). Perhaps unsurprisingly given the breadth of the definition, there is some debate about which processes should fall under this umbrella and how they should be categorized. Cross-sectional studies of adults show that although there is an overall correlation in the performance of individuals across several different "executive" tasks, there is not complete overlap, and three factors can be dissociated corresponding to inhibitory control, working memory, and flexible shifting of attention (Miyake & Friedman, 2012; Miyake et al., 2000). EFs have been hypothesized by some to play a central role in the evolution of human cognition. For example, an increase in working memory capacity is thought to be implicated by manufacturing of complex tools by hominids, especially those with symbolic as well as practical functions (Coolidge & Wynn, 2001; Read, 2008). Attention shifting has been cited as important not only for tool innovation but for all skills that call for perspectival shifting, such as theory of mind (Seed & Tomasello, 2010; see also Chapter 32, this volume), another putatively derived human attribute. And inhibitory control is essential if a problem-solver is to look before it leaps. Executive function is clearly an important ingredient for flexible problem-solving behavior, but what evidence is there that it has changed across evolution?

There have been a few studies investigating the evolution of control processes, predominantly by investigating inhibitory control (Amici, Aureli, & Call, 2008; Beran & Evans, 2006; MacLean et al., 2014; Rosati, Stevens, Hare, & Hauser, 2007; Vlamings, Hare, & Call, 2009). For instance, a large number of studies have looked into *delay of gratification* in nonhuman primates, particularly chimpanzees (Beran & Evans, 2006, 2009; Evans & Beran, 2007). Delay of gratification paradigms are derived from studies with children and are thought to measure inhibitory control (Mischel, Shoda, & Rodriguez, 1989). In the original study, children were presented with two food rewards, one of which was more desirable than the other. Subjects could choose to receive the less desirable reward immediately or to wait for the more desirable reward. There is substantial improvement in delay of gratification over human development (Mischel et al., 1989) and individual differences on this paradigm predict later academic performance (Eigsti et al., 2006). Interestingly, chimpanzees delay gratification for up to 11 minutes on variations of this paradigm (Beran & Evans, 2006) and even outperform adult humans in food-related contexts (Rosati et al., 2007).

However, the delay of gratification task seems to require more than just the ability to refrain from an unwanted response (A. Diamond, 2013), as it also measures temporal discounting (see Chapter 24, this volume), or the way in which an item's value degrades according to delay-to-receipt from the subject's point of view. Indeed, the notion that the task taps directly into response inhibition has recently been challenged. In a computerized training procedure for EF, children did not improve their ability to delay gratification; however, the training was effective for selective attention (measured with the flanker task: subjects need to attend and respond to a target stimulus while ignoring irrelevant, "flanking" stimuli around it) and response inhibition (measured with a go/no-go task: subjects need to respond to a specific stimulus and inhibit a response to a second stimulus; A. Diamond & Lee, 2011). Thus, although it is interesting that chimpanzees perform well on delay of gratification procedures, this may not directly reflect their ability to refrain from unwanted responses. Other factors, such as impulsivity (e.g., a tendency to prefer immediate hedonic satisfaction over a larger, delayed reward), directly affect performance on this paradigm (see Chapters 16 and 24, this volume); and although impulsivity and response inhibition are interrelated, they are not identical (Hongwanishkul, Happaney, Lee, & Zelazo, 2005). Additionally, variations of the experimental procedure can produce very different results. For instance, although chimpanzees were prepared to wait for larger food rewards significantly longer than human adults, human adults waited significantly longer for monetary rewards as compared to food rewards (Rosati et al., 2007). Here, differences between species reflected differences in motivation: Humans are often very motivated to wait for monetary rewards, in some cases over year—simply consider the act of saving money.

Another paradigm that has been used extensively to study inhibition across primate evolution is the *reversed-reward contingency* paradigm. Here, subjects are presented with two food arrays, one containing a larger food reward than the other. However, if subjects comply with their tendency to choose the larger food reward, they receive the smaller one. Chimpanzees and other primates struggle with this particular paradigm in its classical version and choose the larger food reward even after hundreds of trials of task presentation (see Shifferman, 2009, for a review). However, in an all-or-nothing version of the problem Japanese macaques (*Macaca fuscata*) learned to overcome their initial response tendency (Silberberg & Fujita, 1996). In this version, subjects who chose the larger food array received no reward at all, and this higher cost situation revealed an ability to inhibit. Even the widely used reverse-reward contingency therefore presents interpretive problems. It is highly unnatural and does not resemble the conditions of natural foraging situations (Shifferman, 2009). Importantly, neuropsychological studies revealed that the critical brain area thought to be involved in response inhibition (the orbitofrontal cortex; Dias, Robbins, & Roberts, 1996) is not involved in reversed-reward contingency: Rhesus macaques with lesions to the PFO were just as successful as controls (Chudasama, Kralik, & Murray, 2007).

In sum, it seems likely that studies using delay of gratification or reversed-reward contingency paradigms to study the evolutionary origins of inhibitory control do not only measure the tendency to inhibit prepotent, unwanted responses. This is a difficulty that spans the study of EF processes: the problem of task impurity (i.e., specific task demands may produce individual variation that is unrelated to the process of interest; Miyake & Friedman, 2012). Importantly, in a comparative framework it is therefore difficult to make firm conclusions about what drives species differences in performance on one task.

Amici and colleagues (2008) extended the research into the evolutionary origins of inhibitory control by including several measures of the EF process of interest. The authors compared the performance of all great ape species and four monkey species on the same experimental paradigms. The measures included classical inhibition paradigms, such as delay of gratification, but also the A-not-B task, in which a subject retrieves a reward from location A in three consecutive trials; on the fourth trial the reward is first placed in location A but then switched to location B in full view of the subject. This is thought to require inhibitory control: Repeated searches in location A resulting in reward are likely to evoke a prepotent response of searching this location again, in the next trial. This tendency needs to be inhibited in the critical trial. Amici and colleagues (2008) found intriguing differences between species: It seemed that species living in stable, cohesive groups were limited in their ability to refrain from inadequate responses as compared to species living in more dynamic social systems with high fission-fusion dynamics (i.e., social groups in which animals split into subgroups of varying sizes and individuals throughout the day). Thus, in contrast to Deaner et al. (2006; 2007), Amici and colleagues (2008) did not find that larger brains predicted better performance (e.g., gorillas living in stable groups performed worse than spider monkeys on most tasks, despite their larger brain size). However, the sample sizes included were very low (e.g., only seven gorillas), limiting the generalizability of these species differences. Another problem of the study is that the authors averaged performance across the tasks, and it remained unsettled whether the different experimental paradigms tapped into the same latent variable (i.e., inhibitory control). An individual differences approach (similar to Herrmann et al., 2010), although impossible with the sample sizes used, could have revealed whether the detected differences might have been attributable to one single factor capturing the underlying process of inhibitory control or to multiple factors.

Finally, in a large-scale study, MacLean and colleagues (2014) presented 36 species (23 primate) with two measures of self-control: the A-not B task and the cylinder task. In the familiarization phase of this second task, subjects are confronted with an opaque cylinder containing a food reward. This opaque cylinder is then replaced by a transparent cylinder in the following trials. To retrieve the food reward, subjects need to refrain from reaching directly for the food and instead make a detour movement—obtaining the food from the opening of the cylinder. The authors found that the level of performance was predicted by absolute brain size, in line with the analysis of primates by Deaner et al. (2007). From the primate sample, dietary breadth but not social group size predicted performance (MacLean et al., 2014). However, although the tasks were strongly correlated on a group level, the relationship of the tasks was not investigated on the individual level. This analysis would be crucial to detect common variance of both tasks suggesting an underlying cognitive process that is required for both problems—to see if the species differences were really due to differences in inhibitory control. Ideally, a broader battery would be run to provide a point of contrast to explore if the relationships are particular to inhibitory control or reflect broader differences in executive function. However, sample size is always a limiting factor.

In sum, we are still trying to characterize skills such as insight and causal reasoning in animals. There remains a good deal of debate about the existence of such nonassociative processes in nonhuman animals, and at present these abilities have been studied mainly in large-brained species with a natural tendency toward object manipulation and problem solving, such as primates, corvids, and parrots. The endeavor is revealing exciting abilities that traditional associative learning models struggle to explain, which suggests that characterizing the cognition underpinning innovative, creative behavior is worthwhile, even if we do not yet have precise alternative models to explain the behavior (see Chapter 28, this volume). Before we can make meaningful comparisons across species, as well as have a better understanding of these nonassociative processes, it will be very important to consider executive function. This might constrain problem-solving ability by limiting the amount of information that can be held in mind (working memory), how easily an animal can inhibit prepotent responses to do something new (inhibition), or how flexibly it can deploy attentional focus to different aspects of a problem (attentional control). A better understanding of these executive processes will be important if we are to isolate the effect of one skill from another on problem-solving ability.

CONCLUSION

In this chapter, we have reviewed some of the work at the forefront of the quest to understand animal problem solving from ultimate and proximate perspectives. We have defined problem solving as a form of innovation: overcoming an obstacle to reach a goal, where the entire solution is not in the existing repertoire or socially learned. This means that the definition of problem solving has much in common with the classification of technical innovation by Overington and colleagues (2009), which serves to distinguish observations of animals performing novel techniques from observations of animals exploiting novel resources—both cases of innovation. The difference between the two is that one is a definition of the process by which the behavior occurred, and the other serves to classify the behavior itself. A reported observation of a new technique cannot establish whether this individual invented the behavior or learned it socially.

Comparative analyses of brain size have revealed that more innovative species have larger brains. Meta-analyses that compare performance on cognitive tests in primates suggests that one factor that makes one species a better problem-solver than another is intelligence—although as we have discussed, the picture might not be that simple, because there might be multiple dissociable components to intelligence. Bigger brains clearly play a role in emancipating animals from hard-wired responses and enabling flexible behavior, but an answer to the question of what socioecological pressures cause brains to evolve remains elusive.

When it comes to the noncognitive traits (such as personality, temperament, and motor skill) that evolution might have acted on many questions remain unanswered: We still do not really know what makes one animal a better problem-solver than another. However, great progress has been made in developing the tools needed to measure the noncognitive factors that are likely to influence problem solving, for example, appreciating that an animal's response to novelty reflects more than one motivation. Importantly, however, comparing a diverse array of species to try to extract general principles about how problem solving evolves might be hampered by an incomplete appreciation of the cognitive mechanisms recruited by different species.

Associative learning is unlikely to be the only route available to some animal species when it comes to putting past experience to work in a new context. Research that aims to look at the details of how animals solve problems therefore provides a complimentary line of work for understanding species differences by seeking the cognitive explanations for successful problem-solving ability. Research in this field is going through an exciting period of discovery, with theories and models for nonassociative processes of reasoning and representation on the horizon. In the future, it will be important for researchers working at the different levels of explanation to try to integrate their knowledge. For example, comparative cognitive researchers could provide researchers that compare species in their natural environments where ecological validity is highest with paradigms for measuring skills such as object exploration, causal reasoning, and executive function.

Unravelling the make-up of the problem-solving mind is a fascinating challenge, and comparative researchers have a great diversity of minds to study. Comparing species is a powerful tool for uncovering what pressures cause minds to evolve, and comparing individuals can shed light on the structure of the skills and abilities that go into problem solving, by revealing what hangs together. But interpreting these differences is made problematic by the complexity of the task, and teasing apart cause from correlation is no easier in this field than any other. It might be some time before we can answer the questions raised in this chapter, but the journey is revealing fascinating new insights into animal minds.

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CHAPTER 28

ANIMAL CREATIVITY AND INNOVATION

Stan A. Kuczaj

Creativity, curiosity, innovation, and novelty are intimately connected. Every creative act is novel in some sense for the actor, and curiosity provides the foundation for the abilities involved in apprehending novel events and purposely producing novel behaviors (Greenberg, 2003). As such, curiosity is the impetus for individual creativity and innovations (see Burghardt, 2015; Kuczaj & Eskelinen, 2014; see also Volume 1, Chapter 34, this volume). Although some forms of curiosity are uniquely human (Hauser, 2003), others exist in nonhuman animals and are manifested in a variety of ways (Berlyne, 1960, 1966; Glickman & Sroges, 1966), responses to novelty varying across individuals and species. Animals that are neophilic tend to investigate and perhaps even seek novelty, whereas neophobic animals tend to avoid novelty. An animal's initial interest may result in further exploration of the novel stimulus that first piqued the individual's curiosity, which in turn could result in innovations.

Neophilia and neophobia are not necessarily mutually exclusive (Pisula, 2009). They can occur simultaneously in an individual, the relative strength of each depending on the individual, the species, and the context (Greenberg, 2003). For example, pumpkin-seed-sunfish (*Lepomis gibbosus*) that are bold when presented with a novel object may not be as bold when exposed to a novel food (Coleman & Wilson, 1998). Similarly, Carib grackles that are curious about objects are not necessarily curious about novel foods (Reader, 2003). Findings such as these led Mettke-Hofmann (2007) to conclude that contexts that yield the most neophilia for an individual or species are those most likely to result in innovations. Human infants engage in more information seeking behaviors when events violate their expectations (Stahl & Feigenson, 2015), and the same may be true for animals. In addition, some contexts may be more likely to produce innovations that are noticed by others. Foraging contexts might be most important for some species, or for a given species at a given time. Play contexts might be ideal arenas for innovation, especially for young animals (Bateson, 2015; Burghardt, 2005, 2015; Kuczaj & Eskelinen, 2014; Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006; see also Volume 1, Chapter 34, this handbook).

In general, adult animals are less curious than young animals (Benson-Amram & Holekamp, 2012; Greenberg, 1987, 2003; Heinrich, 1995; Pellis, 1981, Pisula, 2009). Young animals may be more curious because their limited experience results in a greater proportion of their world being novel and therefore interesting. Or young animals may not have learned that novel things can be dangerous. Moreover, the relationship between age, innovativeness, and curiosity is complex. Juvenile raptors (*Milvago chimango*) that were more neophobic proved to be poorer problem-solvers, but there was no relationship between neophobia and problem-solving performance for adult birds (Biondi, Bó, & Vassallo, 2010). If this pattern holds for other species

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(see Chapter 27, this volume), it may be that curiosity in young animals facilitates problem solving, perhaps because it provides young animals more opportunities to accidentally discover solutions (Benson-Amram & Holekamp, 2012). Adults, on the other hand, have more advanced cognitive skills and a lifetime of experiences to draw on—which may cause them to be more cautious when confronted with something new, but which also may help them solve novel problems in a more purposeful manner.

Despite these general age trends, it is important to remember that curiosity varies across individuals of all ages (Budaev, 1997; Glickman & Sroges, 1966; Reader, 2003). Species and individual differences in curiosity may interact with context and age to yield individual and species differences in creativity and innovation (Budaev, 1997; Greenberg, 2003; Reader, 2003). It seems likely that personality influences these individual differences (see Volume 1, Chapters 9 and 11, this handbook), specifically the bold–timid continuum that has been studied often in animal personality research (Budaev, 1997; Gosling, 2001; Highfill & Kuczaj, 2007; Kuczaj, Highfill, & Byerly, 2012; Massen, Antonides, Arnold, Bionda, & Koski; 2013; Wilson, Clarke, Coleman, & Dearstyne, 1994).

Innovation is positively correlated with low neophobia, high neophilia, and high social learning abilities (Reader, 2003), with individual variation in each of these characteristics resulting in some individuals being more innovative than others (Kawai, 1965; Kuczaj & Eskelinen, 2014; Kummer & Goodall, 1985; Laland & Reader, 2003; Morand-Ferron, Cole, Rawles, & Quinn, 2011; Pace, 2000; Russon, 2003; Thornton & Samson, 2012). Bolder animals are more likely to explore and investigate novelty, and as a result are more likely to produce individual innovations. Bold pigeons (*Columba livia*) exhibit more innovative solutions in problem solving situations (Bouchard, Goodyer, & Lefebvre, 2007). Innovative Carib grackles (*Quiscalus lugubris*) are less neophobic, more curious, and more likely to persevere than noninnovative birds (Overington, Cauchard, Côté, & Lefebvre, 2011). Bold animals are also more likely to alter successful behaviors to challenge themselves, a phenomenon most easily observed during play (Kuczaj & Eskelinen, 2014).

Conservatism occurs when an animal finds it difficult to abandon a known successful behavior (Brosnan & Hopper, 2014). This "if it's not broke, don't fix it" bias decreases the likelihood that an individual will produce an innovation and the possibility that animals will adopt another's novel behavior. It may also explain why foraging innovations are more likely to be produced when existing strategies fail (Boesch, 2013; Brosnan & Hopper, 2014; Hopper, Schapiro, Lambeth, & Brosnan, 2011; Katzir, 1982; Kummer & Goodall, 1985; Reader & Laland, 2001). Individual patterns in play behaviors might reveal the extent to which individuals differ in conservatism, and so may predict which individuals will be innovative in novel problem solving situations. But animals that are neophilic in a play context might not be so in a foraging situation or threatening social context (Kuczaj, Highfill, & Byerly, 2012). The extent to which individuals are neophilic across ages and contexts needs additional study.

Although curiosity has been observed in many species, all curiosity is not the same. Hauser (2003) suggested that even though animals may be curious about objects and events in the sense that they explore and investigate novelty, they are not at all curious about what caused the object to appear or the event to occur. He cited the example of monkeys residing in Cayo Santiago. When humans burned trash on Cayo Santiago, home to approximately 1,000 rhesus macaques (*Macaca mulatta*), coconuts that were accidentally tossed in the fire exploded, providing monkeys with easy access to coconut meat, a food item they seemed to enjoy. The monkeys had never been observed opening coconuts and apparently did not know how to do so. Somewhat surprisingly, despite benefiting from accidental coconut explosions for years, no monkey ever placed a coconut in a fire. Hauser believed that this failure resulted from the monkeys' lack of curiosity about the causes of events, which limited the types of innovations they are able to produce.

Although some animal innovations involve the use of tools to obtain food (Berthelet & Chavaillon, 1993; Sanz, Call, & Boesch, 2014; Shumaker, Walkup, & Beck, 2011; see also Chapter 30, this volume), Hauser (2003) pointed out that it is often unclear how they come to understand the relationship between the tool and its role in achieving the goal (see Chapters 27 and 29, this volume). He noted that we do not know if the first chimpanzee to use a stick to fish for termites was playing with a stick near a termite mound and accidentally used the stick to obtain termites, noticed a stick in a termite mound and serendipitously discovered termites on the stick when she removed it from the mound, or if the chimpanzee pondered the use of a stick to feast on termites before actually using it. Hauser suggested that the first two possibilities are examples of "dumb luck," whereas the latter possibility is closer to what we usually think of as curiosity and innovation. Another example concerns a captive rough-toothed dolphin (*Steno bredanensis*) that was observed placing a human's swim fin over his rostrum, swimming to the bottom of a pool, and placing the swim fin under the lip of a gate that separated two pools. The dolphin then maneuvered the fin to raise the gate, removed the fin from its rostrum, and swam away without swimming through the open gate and entering the other pool (Kuczaj, Xitco, & Gory, 2010). This dolphin had been observed playing with swim fins before, but had never before been seen using the fin as a lever and so this appeared to be a creative use of the swim fin by the dolphin. However, it is unclear if this individually innovative behavior was insightful, an example of trial and error learning, or a serendipitous discovery. One of the other dolphins in the enclosure subsequently adopted this same strategy for opening gates and so apparently benefited by its observations of its tankmate. Although the behavior was transmitted to another dolphin, the spread of the behavior was quite limited.

Curiosity and creativity are obviously related, but curiosity alone is insufficient to produce individual innovations. The neophilic animal investigates novel aspects of its world, whereas the creative animal acts on its world to produce novelty. Thus, in addition to being curious about novelty, the creative animal modifies its behavior and assesses the effects of its behavior on the world. Innovations can result from these experiences, particularly if the animal is capable of what Call (2013) referred to as *productive thinking*, the abilities involved in creating new ways to solve problems and achieve goals.

Although some innovations can be serendipitous, Hauser (2003) argued that curiosity and innovation involve more risk taking than accidentally discovering something new. The risk taking inherent in satisfying one's curiosity may explain why animals are resistant to change (trying new things is risky) and why they may only do so when circumstances demand it. But even if an innovation occurs accidentally, an animal must be capable of benefiting from its incidental experience if it is to take advantage of its good fortune (Call, 2013).

DO CREATIVITY AND INNOVATION DIFFER?

The precise nature of the relationship between *creativity* and *innovation* is a matter of some dispute. Bateson and Martin (2013) argued that creativity and innovation should be distinguished (see also Finke, Ward, & Smith, 1992; Runco, 2014), with creativity referring broadly to the generation of novel behaviors and innovation being reserved for those creations that are adopted by other members of a group because they serve a useful purpose (see also Csikszentmihalyi, 1996; Hoppitt & Laland, 2013; Ramsey, Bastian, & van Schaik, 2007; Reader & Laland, 2003). But Epstein (2015), Feist (1998), Kaufman and Kaufman (2004), Mackinnon (1962), Russ (2014), and Simonton (1999) all suggested that creative behaviors need to be *novel* and *useful*, which blurs the distinction Bateson and Martin (and others) have made between creativity and innovation. I will use creativity and innovation interchangeably because I believe that individuals can be innovative even if others fail to adopt their inventions. I will use the term creativity interchangeably with the phrase *individually innovative* to refer to novel behaviors produced by an individual that are purposeful and meaningful to that individual. Thus, creative behaviors are those that are individually innovative and that can be distinguished from other-derived innovations. The latter are individual innovations (creations) that are adopted by members of one's group, and so might be characterized as cultural innovations (for discussion of the issues surrounding the notion of animal culture, see Avital & Jablonka, 2000; de Waal & Tyack, 2003;

Laland & Galef, 2009; Reader & Laland, 2003; Whitehead & Rendell, 2014).

The idea that creativity occurs when an individual produces a novel behavior corresponds to what Sawyer (2012) termed the *individualist definition*. Something is creative in this view if an individual produces something new, including combinations that have not occurred before. Of course, all novel behavior is not the same. Some behaviors are novel to the individual but not to other members of the group. Other behaviors may be introduced by the individual to the group (other-derived innovation). In addition, some behaviors are completely novel to the individual, but others are only slight variations on those the individual already knows. For the purposes of this chapter, novel behaviors will be considered creative if they are purposeful and meaningful to the individual.

For example, dolphin bubble play often begins with a dolphin interacting with a bubble produced by another dolphin (Kuczaj et al., 2006). If the dolphin simply reacts to bubbles in the environment by biting them for the first time, biting the bubbles is a purposeful novel behavior but one that does not involve planning or insight. But if the dolphin produces the bubbles with the intent to bite them, a primitive sort of planning is implicated. Intent is difficult to demonstrate, but consider the following example. One of the calves studied by Kuczaj et al. (2006) practiced blowing bubbles while swimming upside-down near the bottom of her pool. After releasing the bubbles, she chased and attempted to bite each bubble before it reached the surface of the water. Once she became proficient at this, the dolphin began to release bubbles while swimming closer to the surface, making it increasingly difficult to catch and bite all of the bubbles before they reached the surface. During this time, the number of bubbles the dolphin produced varied, the apparent goal being to catch the last bubble just before it reached the surface of the water. As a result, the dolphin eventually learned to emit different numbers of bubbles from different depths, the apparent ideal number being that which challenged her but also allowed her to succeed in biting all the bubbles. Her modifications of her behavior were creative and certainly appeared to be purposeful and involve planning. But her creative bubble biting behaviors were not adopted by other members of her group and so did not become other-derived innovations.

As this example illustrates, innovation can involve the acquisition of a new behavior or the use of a known behavior in a new context (Kummer & Goodall, 1985). Using a novel solution to solve a familiar problem may sometimes be more difficult for animals than solving a novel problem. Wild red-fronted lemurs (*Eulemur rufifrons*) that had learned to pull a lid to open a box containing food were able to modify this solution after the box was modified so that a barrier had to be slid away in addition to the box being opened (Huebner & Fichtel, 2015). But when the correct solution required pulling the lid with one hand and then raising a barrier that was on the outside of the box, only the most persistent lemurs were able to abandon their previously learned solutions to solve the problem.

Individuals vary in their innovative prowess and in the extent to which they can learn innovative behaviors from others. Brosnan and Hopper (2014) distinguished three phrases of innovation. *Invention* is the first phrase, which corresponds to what I am calling individual innovation, and involves an individual creating a new behavior or using a known behavior in a new context. The second phrase, *transmission*, occurs when others learn the innovative behavior first discovered by an individual, and so corresponds to other-derived innovation. The final phase, *preservation*, is significant in that it enables cultural innovations to endure, sometimes across multiple generations.

INVENTION

There are numerous examples of individual innovation among animals (Avital & Jablonka, 2000; Fragaszy & Perry, 2003; Ramsey et al., 2007; Reader & Laland, 2003), and likely many more to be discovered. Sometimes the motivation that underlies invention is unclear until sufficient observations are made. Killer whales (*Orcinus orca*) were initially observed using fish to bait and catch live seagulls (Kuczaj & Walker, 2012). If the baiting proved successful, the whale then played with the gull much as a cat plays with a mouse. The first observation of this behavior involved a mother whale that caught a gull and then gave the gull to her 18-month-old calf, after which the calf played with the gull for approximately 15 minutes before the gull perished. The next observations involved this calf trying to catch gulls herself. This proved to be difficult for the calf and required numerous attempts, during which time the young whale was only rarely reinforced by the occasional near catch of a gull. After weeks of trial and error learning, she mastered this skill. Her efforts also served as models for other whales that subsequently attempted to capture their own gulls. Each whale developed a slightly different preferred method for catching gulls after individual periods of trial and error learning, demonstrating that the social learning in these cases represented some form of goal enhancement rather than an exact duplication of observed behaviors.

Some of the whales became so adept at catching gulls that they modified their behavior to make catching gulls more difficult. For example, one whale that lurked below the surface easily caught gulls as they attempted to grab the fish floating on the surface. The whale subsequently abandoned this successful strategy and attempted an innovation. Rather than catching the gulls at the surface, the whale propelled herself out of the water in attempts to catch gulls approximately four to five feet above the surface of the water as the gulls swooped down toward the fish. This innovation was not motivated by failure—she could catch multiple gulls in a day using her old strategy and failed to catch a gull for days following her innovative change. She nonetheless persisted in attempting to catch gulls far above the surface, and eventually caught gulls using this new technique. She never achieved the degree of success with the innovative approach that she had with her original technique, but nonetheless rarely attempted to catch gulls at the surface. Her earlier successful method was evidently not enough of a challenge. Innovation sometimes results when an activity loses its stimulating value.

Foraging innovations have been observed in a number of species and are likely motivated by different factors than those that influence play innovations. For example, several Indo-Pacific dolphins (*Tursiops* sp.) in Shark Bay, Australia, lift large conch shells from the ocean floor to the surface, where they tip the shells and consume the fish that are dislodged (S. J. Allen, Bejder, & Krützen, 2011). Although this foraging strategy has been observed in more than one dolphin, the spatial distances between the observations suggest that the behaviors result from independent individual innovations.

Innovations may involve food preparation after the item has been obtained. Finn, Tregenza, and Norman (2009) observed a bottlenose dolphin catching cuttlefish by herding one to the sea floor, pinning it to the bottom, and killing it. Before eating her catch, the dolphin engaged in an elaborate series of behaviors. She first moved the cuttlefish from the sea floor and beat it with her rostrum to remove the ink. The dolphin then returned the cuttlefish to the sea floor, placed it upside down on the sand, and removed the skin and cuttlebone by pushing it along the bottom. Unfortunately, it is not known how the dolphin learned this complex series of food preparation behaviors. Nor is it clear if this innovation was transmitted to others. However, as I subsequently discuss, some food preparation innovations are adopted by others.

TRANSMISSION

Observations of others can provide information about the environment and possible behaviors (Galef, 2003; Kuczaj & Yeater, 2006; Kuczaj, Yeater, & Highfill, 2012), and animals can benefit from such experiences. For example, chimpanzees can learn different solutions to a problem from others and then transmit the solution they learned to others (Horner, Whiten, Flynn, & de Waal, 2006). So a group of chimpanzees that uses stick tools as pounders, enlargers, and collectors to extract honey or as reachers to hunt a small mammal hidden inside a log (Wilfried & Yamagiwa, 2014) provides ample opportunities for observational learning of novel uses and adaptations of tools. But tendencies such as conservatism and functional fixedness can reduce the spread of other-derived innovations (Brosnan & Hopper, 2014; Galef, 2003). Functional fixedness refers to the inability to use an existing behavior or strategy in a new way. Brosnan and Hopper (2014) pointed out that more research is needed in this area, and that the extent to which an animal exhibits functional fixedness will likely depend on whether the animal needs to use an object in a novel way or use a behavior innovatively. Some animals might find it more difficult to change their normal interactions with objects than to modify known behaviors to better suit novel contexts. But others might have the opposite tendency.

In addition to the limitations imposed by conservatism and functional fixedness, all models are not equally salient. Context and age often interact to determine the salience of a model. Dolphins, particularly dolphin calves, are quite selective in terms of who and what they imitate (Kuczaj et al., 2006; Kuczaj & Yeater, 2006; Kuczaj, Yeater, & Highfill, 2012; Yeater & Kuczaj, 2010). The mother is a salient model for calves in communicative and foraging contexts (Bender, Herzing, & Bjorklund, 2009; Guinet, 1991; Krützen et al., 2005; Kuczaj & Winship, 2015; Sargeant & Mann, 2009). However, calves attend more to slightly older and more competent peers in play contexts (Kuczaj et al., 2006). In general, young animals might find other young animals' play more interesting but rely more on older and more competent animals as models of foraging and mating strategies. For example, juvenile chimpanzees pay less attention to younger animals attempting to crack nut shells, focusing instead on the efforts of same-age and older chimpanzees (Biro et al., 2003). It is not surprising, then, that chimpanzees are more likely to copy innovative foraging behaviors produced by older high-ranking individuals (Horner, Proctor, Bonnie, Whiten, & de Waal, 2010). Low-ranking animals that produce individual innovations may not have their inventions adopted because others do not pay attention to their behavior (Biro et al., 2003; Brosnan & Hopper, 2014). In turn, low-ranking animals may not adopt the innovations of higher-ranking individuals because their low status prevents them from closely observing high-ranking animals (Brosnan & Hopper, 2014).

Why do some, but not all, individuals incorporate the behaviors they observe into their behavioral repertoire? Conformity is the tendency to behave in the same way as the majority of one's group (Brosnan & Hopper, 2014) and can facilitate other-derived innovations by motivating individuals to adopt the behaviors of others (see Chapter 19, this volume). But conformity can also inhibit innovation (Brosnan & Hopper, 2014). Individual innovation is diminished if an animal behaves as conspecifics do rather than exploring other possibilities. It can also decrease other-derived innovation if conformists are less likely to adopt the novel behaviors modeled by individual innovators. The curiosity of young animals may increase the possibility that young animals produce individual innovations and the possibility that they adopt innovations first produced by others. This may be one reason why young animals sometimes discover and introduce foraging innovations to their group, including behaviors related to food preparation. Perhaps the most famous case involves Japanese monkeys (*Macaca fuscata*) removing sand from sweet potatoes by dipping them in water and brushing the sand off before eating them (Kawai, 1965; Kawamura, 1959). Within ten years of the first observation of this behavior, many of the monkeys in the troop were washing potatoes in this way. Juvenile monkeys close in age to Imo, the 2-year-old female that discovered this behavior, were most likely to learn this new behavior. Mature adults proved less likely to adopt the new behavior, with adult males being the least likely to do so. Imo later produced another innovative food preparation technique—separating wheat from sand by tossing the sandy wheat into water and then scooping up the sand-free floating wheat. This behavior was most readily learned by 2- to 4-year-olds, monkeys in the same age class as Imo at the time she discovered this technique. These findings, together with the aforementioned studies on play (see Volume 1, Chapter 34, this handbook), suggest that young animals are selective conformists in the sense that they reproduce the behavior of peers more so than that of adults (Kuczaj, Yeater, & Highfill, 2012). Witnessing similarly aged peers innovate seems to facilitate the adoption of observed behavioral inventions (Kuczaj et al., 2006; Kuczaj & Eskelinen, 2014). Avital and Jablonka (2000) suggested that animal traditions occurred when young animals learned behaviors that were in the group repertoire, but young animals can also play important roles in the addition of new behaviors to a group's repertoire (Kuczaj et al., 2006; see also Chapter 20, this volume).

Conformity is not limited to young animals. The power of conformity was demonstrated when wild vervet monkeys (*Chlorocebus aethiops*) were exposed to artificially dyed corn, one color denoting a bitter taste and another indicating a more pleasant flavor (van de Waal, Borgeaud, & Whiten, 2013). One group of monkeys was provided blue corn that tasted bitter and pink corn that was palatable. Another group experienced bitter pink corn and tasty blue corn. As expected, each group of monkeys developed a preference for the colored corn that was not bitter, a preference that persisted even after the bitter taste was no longer added to either color of corn. These preferences were passed along to infant monkeys, demonstrating that infants paid attention to their mothers' behavior. Males that migrated from a group that preferred one color of corn to a group that preferred the other color of corn tended to change their preferences to those of their new group. Their previous experience with the two colors of corn was overridden by their observations of the opposite pattern in their new group, perhaps because of a need to adhere to the norms of the new group.

The integration of two groups of captive chimpanzees also illustrated the power of conformity. Chimpanzees from the immigrant group modified their vocalization for "apple" so that it matched that of the resident group (Watson et al., 2015). This change only occurred after members of the two groups had begun to spend significant amounts of time together, suggesting that social interaction may be the lubricant for social adaptations. In this case and that of the colored corn, immigrant animals were more likely to adapt their behaviors to match those of the resident group rather than vice versa.

Conformity can sometimes move in the opposite direction. When a few humpback whales from the west coast of Australia migrated to the east coast, the resident whales quickly changed their song to match that of the immigrants (Noad, Cato, Bryden, Jenner, & Jenner, 2000). Whale song changes over time, and the appearance of a new song somehow sparked a transition from the existing east coast song to the west coast song that was introduced by the immigrants. Determining the factors that affect the flow of conformity within and across groups is important for increased understanding of the roles of conformity on creativity and innovation (individual and other-derived).

It is often difficult to determine the processes involved in the spread of an innovative behavior. Great tits (*Parus major*) and blue tits (*cyanistes caeruleus*) learned to open milk bottles by poking a hole in the foil cap (Fisher & Hinde, 1949; Hinde & Fisher, 1951). This was first observed in 1921 and had been reported in more than two dozen sites by 1947. It is not clear exactly how this behavior spread across the U.K., but blue tits have been demonstrated to acquire other new behaviors via social learning. Birds exposed to a novel foraging task benefited from watching a demonstrator solve the task (Aplin, Sheldon, & Morand-Ferron, 2013). Juvenile females and subordinate males benefited more from social learning experiences than did adult females or dominant males. Birds that were more innovative in the novel task also proved to benefit more from social learning experiences, a positive relationship that is relatively rare (Reader & Laland, 2000; Bouchard, Goodyer, & Lefebvre, 2007). In another study, great tits showed consistent individual variation in novel foraging situations, but these differences were not reflected in birds' exploration of novel environments (Cole, Cram, & Quinn, 2011). But great tits do demonstrate consistency when exploring novel objects and novel environments (Verbeek, Drent, & Wiepkema, 1994).

Although the influence of conformity on behavior is undeniable, it rarely results in all members of a group adopting another's invention. Observations of novel behaviors sometimes result in the adoption of novel behaviors, but other times do not. For example, individual kea (*Nestor notabilis*) learned to open the lids of trash cans with their bills, an individually innovative foraging behavior that was observed by other birds (Gajdon, Fijn, & Huber, 2006). Despite these observational opportunities, only five of the 36 birds studied demonstrated this lid opening behavior, and it is difficult to discern whether the lid opening that occurred depended more on individual innovation or other-directed innovation. But observing other birds opening lids did not automatically result in the observers mimicking the behavior they witnessed.

Individual differences in observational learning were also found when six Goffin cockatoos (*Cacatua goffini*) observed a male that had discovered how to make and use wood splinters to obtain toys and food (Auersperg, Szabo, von Bayern, & Kacelnik, 2012). Three male birds (but no female birds) learned to use the tools, and two of these males learned to manufacture tools (Auersperg et al., 2014). The birds did not imitate the model's specific behaviors, so the social learning appeared to be based on goal emulation. Curiously, no female birds adopted the behaviors they observed. Given the small number of subjects, it is difficult to ascertain the significance of this apparent gender difference.

Animals are clearly selective in their choices of who to observe and what to imitate (see Chapters 19 and 20, this volume). A number of factors influence whether a human imitates another human's behavior (Bandura, 1986), and similar factors likely affect an animal's willingness to mimic the behavior of another (Kuczaj & Yeater, 2006). Behavioral context, the relative novelty of the modeled behavior, the ages of the observer and the model, and the personalities of the observer and the model all influence whether a behavior is copied (Kuczaj, Yeater, & Highfill, 2012).

Dolphin calves and juveniles that had been rated as bolder by their trainers were typically the first to examine a novel object (Kuczaj, Yeater, & Highfill, 2012), but the more cautious calves often positioned themselves slightly behind the bolder animals. The cautious dolphins appeared to use the bolder dolphins as a barrier between themselves and the frightening new object, and moved to maintain this protective and apparently reassuring shield whenever necessary. If their bold counterpart began to more actively investigate the novel object, the cautious animals typically swam away rather than move closer to the action, but not so far that they could not observe the bold dolphin's interaction with the object. These watchful cautious animals were wary of novel objects, but were nonetheless interested in them. Their neophobia prevented them from initially approaching and investigating a novel object, but their curiosity drove them to observe from afar, the presence of a bold peer allowing them to achieve a closer proximity to the novel object than would be the case otherwise. Watchful cautious animals should be distinguished from those that are so neophobic that they consistently avoid novel objects, even when a bolder companion leaves to investigate it. The more severely neophobic dolphins seemed to lack the curiosity that motivated their bolder and their watchful cautious conspecifics. Of course, it is possible that even the most neophobic animal is curious, but that its fear completely overrides its interest.

The watchful cautious dolphins benefited from their observations of their bold peers. They eventually approached the object and even tried to reproduce the bold dolphin's interaction with the object, sometimes shortly after the bold animal had done so but more typically only after days of watching the bold dolphin investigate the object. In contrast, the severely neophobic dolphins never interacted with the novel objects in the Kuczaj et al. (2012) study.

In one condition, a group of 24 dolphins were exposed to a machine that produced underwater bubble rings. The machine was completely novel to the dolphins. In addition, these dolphins had never been observed blowing bubble rings. Bold dolphins spent more time observing the machine than did timid dolphins. Bold dolphins were also the first animals to interact with the bubble rings produced by the machine. During the first two days in which the bubble machine was in the lagoon, timid dolphins never approached the bubble machine and only watched it while using a bold animal as a "safety shield." However, on the third day, two of these watchful cautious dolphins independently approached the bubble machine alone. It is possible that their interactions represented instances of what Piaget (1962) called *deferred imitation*, because each dolphin's initial interactions with the machine matched what they had earlier observed their bold partner doing. One of the watchful cautious dolphins first interacted with the bubble machine by quickly swimming by a few inches above it and repeating this behavior six times before leaving to hover nearby and watch the machine produce bubbles. The bold dolphin the cautious animal had observed had done this on several previous occasions. The other watchful cautious dolphin's initial interactions consisted of hovering approximately 1.5 meters above the machine and biting the bubbles as they approached. This dolphin's earlier bold companion was most likely to interact with the machine in this same way. At least for these two watchful cautious dolphin calves, the opportunity to observe bold peers appeared to signal that it was safe to interact with the novel machine and to provide information about how to interact with the novel object.

Another example from Kuczaj, Yeater, and Highfill (2012) involved an artificial swim leg used by an amputee. Although these dolphins had ample experience with human swimmers, this was the first time they had been exposed to an artificial leg attached to a human swimmer. Many of the dolphins were attracted to the artificial leg. Their curiosity was first manifested by frequent echolocation bouts directed toward the leg. Some of the bolder animals nudged and gently mouthed the leg. As was the case with the bubble machine, the bold dolphins were the first to actively explore the novel leg, oftentimes accompanied by cautious dolphins that watched the bolder animals' interactions with the limb. On the fifth day in which the swimmer was with the dolphins, one of the watchful cautious dolphins actually approached and gently mouthed the leg. Once again, observing a bold peer interact with a novel object resulted in a more cautious animal eventually attempting to reproduce the bold model's behavior.

Observing another model a behavior may be the most common form of transmission, but parental teaching also occurs, albeit rarely (Caro & Hauser, 1992; Hoppitt et al., 2008). Teaching has been observed in cheetah mothers that provide their cubs with prey to practice hunting skills (Caro & Hauser, 1992), meercat mothers that bring their pups scorpions to capture and kill (Thornton & Raihani, 2010), chimpanzee mothers that model nut cracking or termite fishing for their offspring (Boesch, 1991; Lonsdorf, 2006), killer whale mothers that demonstrate a variety of foraging strategies (López & López, 1985; Maniscalco, Matkin, Maldini, Calkins, & Atkinson, 2007; Visser et al., 2008), and dolphin mothers that help their calves learn to crater feed (Bender, Herzing, & Bjorklund, 2009).

PRESERVATION

Transmission and preservation are obviously related, transmission making preservation possible. The emergence of lobtail feeding in humpback whales (*Megaptera novaeangliae*) in the Gulf of Maine demonstrates how a novel foraging strategy can become widespread within a population (J. Allen, Weinrich, Hoppitt, & Rendell, 2013; Weinrich, Schilling, & Belt, 1992). A lobtail feeding whale first strikes the surface of the water with its fluke (sometimes repeatedly) before submerging and surrounding fish with bubbles it exhales. The whale then lunges open-mouthed through the confused prey, gathering large mouthfuls of fish. This behavior was first observed in one whale in 1980, and had spread to approximately 40% of the whale population in this area by 2007. This behavior does not appear to be transmitted from mothers to offspring, suggesting that horizontal or oblique transmission is involved. Additional observations are needed to determine if this behavior is preserved across multiple generations. Innovations need to be passed along from one generation to the next for preservation to occur.

Some dolphins in Shark Bay, Australia, carry sponges on their rostrums to protect themselves from injury as they forage on the ocean floor (Krützen et al., 2005; Smolker et al., 1997), a behavior that is transmitted to their calves, with female calves being more likely to acquire this behavior than male calves (Mann, Stanton, Patterson, Bienenstock, & Singh, 2012). However, the manner in which this transmission occurs is not known (Kuczaj & Winship, 2015). Does the mother's use of a sponge intrigue the calf because the sponge is a novel object, the mother's carrying of the sponge is a novel behavior, or because the sponge is used for foraging? Does the mother only provide observational opportunities? Or does she teach her calf how to forage with a sponge much like chimpanzee mothers teach their offspring to crack nuts (Boesch, 1991)?

The process involved in the transmission of tool use in New Caledonia crows (*Corvus moneduloides*) is much clearer (Holzhaider, Hunt, & Gray, 2010). Young crows benefit from observing their parents manufacture and use tools. Their observations are frequently rewarded by the parent feeding them the item obtained with the tool, which likely heightens their interest in tools. The tools that their parents discard are typically the first tools used by juvenile birds, which may influence the tool preferences they exhibit as adults.

Although other-derived innovations such as lobtail feeding and sponging have obvious adaptive significance, others are more difficult to understand. A group of chimpanzees in Zambia acquired the tradition of placing and leaving a stiff piece of grass one ear (van Leeuwen, Cronin, & Haun, 2014). This behavior was first observed in one animal in 2010, and quickly spread throughout the majority of this group of chimpanzees but not to neighboring isolated groups. Moreover, the behavior persisted in this group after the innovator died. If this behavior is preserved across generations, then even behaviors that lack apparent evolutionary benefits may be preserved.

Another unusual behavioral innovation was reported by Perry (2011). Members of a group of white-faced capuchin monkeys (genus *Cebus*) adopted an eye-poking behavior, which is apparently a method of testing the quality of a social bond by inserting the tip on a partner's finger into one's own eye socket. This behavior was initiated by one animal, spread throughout the group, and continued after the death of the innovator. Once again, the extent to which this behavior is preserved will depend on its transmission across generations.

CONCLUSION

Curiosity provides the foundation for creativity and innovation. There are species and individual differences in curiosity, which may account at least in part for individual and species differences in creativity and innovation. Personality also plays an important role. Bold individuals contribute to a group's behavioral repertoire in a number of ways. They explore and investigate novelty and in so doing provide valuable information about possible behaviors and their consequences. Morgan (1900) suggested that behaviors observers found interesting were more likely to be imitated, and it may be that interesting innovative behaviors are more often adopted than less interesting ones. Morgan (1900) also speculated that the lack of interesting models could reduce curiosity and innovation in a group of animals. If so, groups that lack bold individuals may be behaviorally stagnant compared to groups with bold animals. The timid-bold personality dimension may selectively influence the adoption of innovative behaviors produced by others in that bold animals may be more likely to be observed and copied. If bold animals are more likely to explore novel situations and test possible behaviors for achieving goals, a predisposition to attend to the behaviors of bold individuals may increase the survivability of what I have called watchful cautious animals. These less bold but still curious animals may also be predisposed to selectively reproduce modeled behavior, depending on how the model fared (Horner et al., 2010; Kuczaj, Yeater, & Highfill, 2012). Learning more about the differences between severely neophobic animals and watchful but cautious animals will significantly improve our understanding of the roles personality and social interactions play in innovation. In humans, personality characteristics such as risk taking, openness to new experiences, tolerance of ambiguity, and perseverance are associated with creativity (Lubart & Mouchiroud, 2003). Additional research is needed to determine how such factors affect animal creativity and innovation.

It is possible that timid animals adopt the innovations of bold animals to gain social acceptance. Imitation increases prosocial behavior among humans (van Baaren, Holland, Kawakami, & van Knippenberg, 2004), and timid animals might mimic bold animals' innovations as a means of increasing prosocial behavior. Human adults who wish to improve their status within a group tend to mimic the behavior of a member of the group (Lakin, Chartrand, & Arkin, 2008), and timid animals may mimic the behavior of bolder animals to facilitate acceptance by the innovative animals (Kuczaj, Yeater, & Highfill, 2012). We clearly need to learn more about the influences of social pressures and social consequences on mimicry.

Play is an important context for animals to explore possibilities and develop flexible problem solving skills (Burghardt, 2015; Kuczaj et al., 2006; Kuczaj & Eskelinen, 2014; see also Volume 1, Chapter 34, this handbook and Chapter 27, this volume). The play context provides opportunities for individuals to create novel experiences for themselves and social learning opportunities for others. The novel experiences that result from play enhance individual behavioral variability, individual creativity, and individual innovations that may spread throughout the group. It is likely that species differences in play are related to species differences in creativity and innovation. The need to challenge oneself during play has been speculated to be more likely in species for which flexible behavior and problem solving are important, but not in members of species that are more reliant on more rigid stereotypic behaviors (Kuczaj & Makecha, 2008). If this is true, then species that use play as an innovative arena may prove to be more creative problem solvers in other domains.

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CHAPTER 29

CAUSAL AND INFERENTIAL REASONING IN ANIMALS

Christoph J. Völter and Josep Call

The chimpanzee troop is traveling silently through the rainforest. All five males suddenly stop and stare intently at the canopy. Just a moment ago, a branch shook above them. One of the chimpanzees begins to climb a tree; others do the same. As the first chimpanzee is nearing the top, two monkeys quickly run along a thin branch away from him towards the edge of the tree. The chimpanzee does not follow them but climbs down slightly and begins to travel in the same direction as the monkeys on a much ticker branch right below them. As the chimpanzee is about to reach the monkeys' position, they suddenly leap into the air landing on a neighboring tree. The chasing chimpanzee cannot follow them but the monkeys have made a fatal mistake. They are now surrounded by the rest of the troop and after a short pursuit one of them is captured and brought down to the ground. Even though the male who caught the monkey shares his bounty with other chimpanzees, the chimpanzee who initiated the chase climbs up again heading for the canopy where it catches the second monkey although it had remained motionless and hidden since its companion's capture.

Confronted with a vast array of stimuli involving (among other things) moving branches, jumping monkeys and climbing conspecifics, chimpanzees in the above example must use this information to make appropriate decisions. Is a moving branch sufficient to conclude that a monkey is in the canopy? What about if the branch moves in the presence of a gust of wind? Once a monkey is caught, should the chimpanzees cease the hunt or continue searching for another monkey? Inferential reasoning is a process that allows individuals to respond adaptively to a variety of challenges both in the physical and social arena, especially when facing new, incomplete, or contradictory information.

It is conceivable that inferential abilities offer fitness benefits in contexts such as foraging or social competition, especially when conditions are unstable but predictable. Avoiding a competitor after seeing him defeat an individual that in turn has defeated the subject earlier (e.g., Grosenick, Clement, & Fernald, 2007; Paz-y-Miño, Bond, Kamil, & Balda, 2004) or choosing a tool that is more likely to crack open a nut than another one (e.g., Visalberghi et al., 2009) are just two examples illustrating this point. Under stable conditions, in contrast, trial-and-error and associative learning could be viable alternatives to inferential processes. Thus, the feeding ecology and the socioecology of a species might be important predictors of inferential abilities in nonhuman animals (Aureli et al., 2008; Milton, 1981; Parker & Gibson, 1977).

Elucidating the nature, use, and origin of knowledge in animals is one of the major endeavors of comparative psychology. Two aspects of knowledge used in inferential reasoning are particularly relevant. First, there is the question of the types of relations established between stimuli (prediction vs. causation). Are stimuli considered as mere signals or predictors (i.e., moving branches indicate the presence of monkeys), or are they also conceived as causes for the observed effects (i.e., monkeys cause branches to move). Second, there is the question

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of how this knowledge is organized. Are multiple stimuli relations considered in isolation or are they organized into a coherent and fluid network?

The goal of this chapter is to review the literature on inferential reasoning abilities of nonhuman animals paying special attention to the nature of the relations between stimuli. We begin by offering a definition of inference, some important key distinctions, and a classification of inferential abilities. The next sections will review what is known about basic inferences in nonhuman animals and explore the issue of causal maps and the evolution of causal reasoning. We will close by addressing four key issues for understanding inferential abilities in nonhuman animals: (a) which kinds of relations animals represent, (b) what kind of protological operations they apply to these representations, (c) how can the inferred relations be integrated in complex causal maps, and (d) how inferential reasoning may have evolved. Although our review will concentrate on work done in the laboratory in food acquisition, simply because this is the work that can distinguish between the various processes, we will include information about field data whenever possible.

DEFINITIONS AND KEY DISTINCTIONS

Inference has been defined as "the act or process of reaching a conclusion about something from known facts or evidence" (Inference, n.d.) or more specifically as "rules that operate on representations in virtue of their structure" (Bermúdez, 2003, p. 111). Inferences are grounded on some kind of knowledge and allow for updating beliefs in the light of novel information. In other words, inferences entail transformations of mental representations and allow for making predictions based on these mental representations. Inferential reasoning involves selective encoding, combination, and comparison of information (Davidson, 1995). Selective encoding entails that only functionally relevant information (for the solution of the problem) is extracted from the wealth of perceptually available information. Selective combination means that pieces of information that were encoded before are re-combined in an entirely new way. Finally, selective comparison occurs when new information is compared to stored information and, by doing so, new connections are discovered. This means that inferences about the world might also affect which type of information is encoded based on the perceptual input. Thus, information encoding and processing are interrelated and might depend upon inferential abilities.

Learning and Reasoning

Although inferential reasoning is one process for knowledge formation, it is not the only one. Learning is another one, and a major endeavor of comparative psychologists has been to distinguish which process underlies a particular response. Premack (1995) differentiated reasoning from learning at the level of representation by noting that learning involves associating spatiotemporally contingent, perceivable events. Reasoning, in contrast, allows for combining perceived events with imagined events or associating spatiotemporally separate events (see also Maier & Schneirla, 1935). Accordingly, we can distinguish inferences from associative learning on the basis of the type of prior knowledge necessary.

Researchers have also suggested inferential reasoning as a candidate explanation of target behaviors when animals solved problems after being provided with only partial information for the solution. For instance, predators may locate prey by seeing it disappear into a hole or by eliminating alternatives based on the presence or absence of certain indirect cues. If the prey had gone in the other direction, it would have been seen or it would have made branches move. Another criterion is that the solution is achieved spontaneously, without trial and error and direct reinforcement, or solely being based on innate predispositions. Using scent to locate the prey is not indicative of inferential abilities if the species is predisposed to do that. This does not mean that scent per se negates the possibility of inference. On the contrary, if one can show that the individual interprets the lack of scent as evidence that the prey is absent, then it would be possible to invoke inferential reasoning.

Despite these differences between learning and reasoning, knowledge engendered by learning can provide the raw material for inference. Numerous studies have shown that after learning by association, subjects can transfer this knowledge to new stimuli to make inferences (see Chapters 5, 15, and 17, this volume). However, we want to distinguish these kinds of transfer from stimulus generalization, which is a transfer that typically occurs along a particular stimulus dimension. For example, an animal might generalize in a color discrimination task to other hues. Inferences, in our view, involve transfers of relations of a more abstract nature such as structural and conceptual. Admitting that the boundaries between abstract and concrete relations may be fuzzy in some cases, inferential reasoning might be especially suited for transferring prior knowledge to structurally or conceptually similar, yet perceptually completely distinct scenarios.

Comparative psychologists typically use two methods to probe the cognitive processes underlying observable behavior (Völter & Call, in press; for examples, see Figure 29.1). One consists of a transfer (or probe) test conducted after the subjects have reached a training criterion (e.g., associating certain stimuli or stimuli relations with food delivery) or solved the initial problem (e.g., birds dropping stones to raise the water level inside a tube). Transfer tests on the basis of stimuli that are perceptually different but conceptually similar to the trained/initial tests probe to which extent the subjects can apply their current knowledge to new situations. By measuring whether subjects can go beyond stimulus–stimulus and stimulus–response associations, transfer tests provide a measure of cognitive flexibility. The other method consists of an associative learning test to assess the extent to which the performance can be explained by basic associative processes, not inferential processes. Learning tests are usually conducted with another group of subjects and provide a measure of cognitive complexity (i.e., what is the minimal type of representation required to solve the task).

Protological Operations

Two basic (proto)logical operations are needed for making inferences about the world: negation and conditional (if–then) reasoning. With regard to negation, Bermúdez (2003) suggested that nonlinguistic creatures might not be able to negate complete thoughts but that they understand their environment in terms of contraries such as absent–present, noise–silence, visible–invisible, etc. These contrary concepts might enable them to perform operations involving protonegations. The second operator needed is a conditional one. According to Bermúdez, nonhuman animals might track regularities in the environment using a simple form of conditional reasoning. That is to say, they might understand causality in terms of causal conditionals between actions and outcomes and between events in the environment. This would allow them to entertain instrumental beliefs about how a desire can be satisfied in a certain situation. The object properties to which an organism is sensitive to might then limit the content of these causal conditionals.

Causal conditionals and proto-negation enable nonlinguistic animals to perform several basic types of protoinferential operations (see Table 29.1). First, predictive or forward inference (Tomasello, 2014) entails reasoning from the antecedent to the consequent and can be understood as a causal conditional (if A then B: A, therefore B). Tool selection is a classic example for this type of predictive inference. For instance, if a stone of appropriate weight hits the nut, the nut will crack. Based on this representation, an animal should select an appropriate tool to bring about the desired effect.

Second, backward or diagnostic inference entails reasoning from the consequent (the effect) to the antecedent (the cause; if A then B: B, therefore A). This abductive inference is not logically valid but can be seen as an "inference to the best explanation" (Sober, 2012, p. 28). Coming back to our initial example, the chimpanzees need to represent here the causal conditional "if monkeys are moving in the canopy, branches start moving." The observation of moving branches might then lead the chimpanzees to infer the presence of monkeys. A special case of backward inference involves the (proto)negation of the consequent (if A then B: not B, therefore not A). Again going back to the initial example, static branches might lead the chimpanzees to infer the absence of the monkeys.

Third, inference by exclusion or reasoning by excluded alternatives (Call, 2004) is a form of disjunctive syllogism (A or B: not A, therefore B). Bermúdez (2003) describes this operation at the

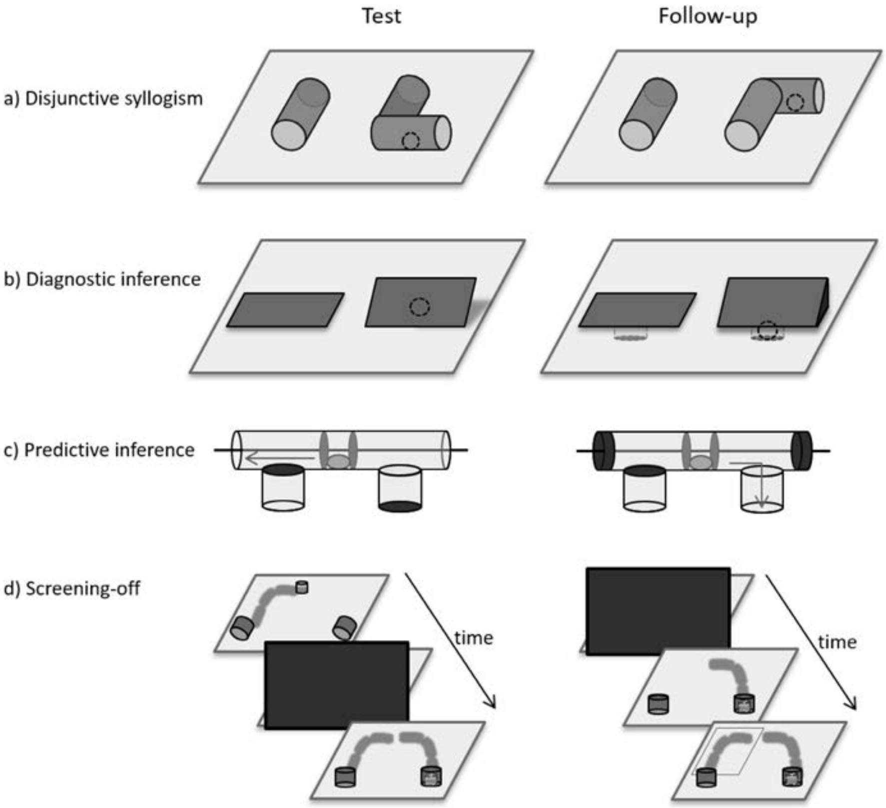

FIGURE 29.1. Illustration of different experimental paradigms aiming at inferential abilities of nonhuman animals, including test and follow-up conditions. The follow-ups serve to control for alternative explanations and examine flexibility in response to changing stimulus configurations. (a) Presented with a choice between two containers, New Caledonian crows exclude the empty straight tube as food location. To rule out avoidance of containers without visible baiting, in a follow-up there is no food visible in either of the containers (Jelbert, Taylor, & Gray, 2015). (b) Apes can locate hidden food based on its effect on the inclination of an overlying board. A general preference for slanted surfaces is controlled for by presenting them with a solid object, a wedge (food is hidden in holes covered by wedge), which resembles the slanted board in appearance (Call, 2007). (c) Rooks confronted with a two-trap apparatus anticipate the effects of the trap and, therefore, move the food away from the trap. If the rooks simply learned a stimulus-response association, their performance should decline when they receive a transfer condition in which the bait must be moved into a nonfunctional trap to extract it (Seed et al., 2006). (d) Apes spontaneously use a yogurt trail to locate a hidden yogurt cup following an invisible displacement. When confronted with a choice between containers at the endpoint of a pre-existing (i.e., causally irrelevant) trail or a trail produced during the invisible displacement, apes should prefer the latter. A simple preference for the most recent cue is controlled for by creating a situation in which the most recent trail is causally irrelevant (Völter & Call, 2014b).

nonlinguistic level as a causal conditional using the protonegation (i.e., the contrary) of the antecedent (not A). In our initial example, the chimpanzees might represent that either wind or the monkeys are causing the movement of the branches. Here, the causal conditional might be “if wind gets up while the branches start moving, there are no monkeys in the canopy.” Now there is a lull in the wind but the branches start moving (not A), therefore monkeys might be in the tree (B).

The previous forms of inference do not exhaust the types of inference that have been investigated

TABLE 29.1

Types of Inferences and Examples From the Animal Cognition Literature

Type of Inference	Definition	Example
Disjunctive syllogism	A or B: not A, therefore B	An experimenter is hiding an apple and a banana in two containers. After being distracted for a moment, the subject sees how the experimenter is eating the apple; therefore, only the banana is left (Premack & Premack, 1994).
Diagnostic inference: Affirming the consequent (abductive inference)	if A then B: B, therefore A	If the food is displaced, it produces a visual trail: the trail points to one of two cups; therefore, the food is hidden under this cup (Völter & Call, 2014b).
Denying the consequent (*modus tollens*)	if A then B: not B, therefore not A	If there is food inside a shaken cup, it produces a rattling sound: The shaken cup stays silent; therefore, food is absent in this cup (Call, 2004).
Predictive inference (*modus ponens*)	if A then B: A, therefore B	Tool use: If a stone of sufficient weight hits the nut, the nut will crack (Visalberghi et al., 2009).
Transitive inference	if A then B and if B then C: A, therefore C	An unknown conspecific is dominant to a group member that is dominant to the subject; therefore, the stranger will be dominant to the subject (e.g., Bond et al., 2003).
Relational inference (analogical reasoning)	A and B: a, therefore b	Relational matching-to-sample tasks: the stimuli of the sample pair are of the same size; therefore, select a same-sized stimulus pair as a relational match (e.g., Smirnova, Zorina, Obozova, & Wasserman, 2015).

in nonhuman animals. Although they will not be in the focus of this chapter, two other forms deserve to be mentioned briefly. Transitive inference (see Chapter 18, this volume) is a type of syllogism based on linking two premises to derive a conclusion (if A then B; if B then C; A, therefore C). Inference by analogy or second order relational categorization (see Chapters 5 and 17, volume) is based on using the relation between two elements in one set to derive the missing element in a second set (A and B: a, therefore b).

Spatiotemporal and Object–Object Relations

Before reviewing the available data, we briefly need to introduce an additional aspect regarding the representation of causal relations that is interrelated with the metaphysics of causation (see Chapter 26, this volume). More specifically, it concerns the questions whether causes and effects are spatiotemporal events, to what extent causes and effects can be individuated, and how causal relations differ from noncausal correlations (Schaffer, 2014). Spatiotemporal relations between events are fundamental for detecting causal relations in the environment. Proxies for causal relations are temporal directionality and spatiotemporal contiguity. Object–object relations are a special case of spatiotemporal relations but they are particularly relevant for organisms interacting with their physical environment. Crucially, object–object relations are governed by physical laws and organisms might benefit from their inherent predictability. The inferential abilities of animals, therefore, might depend on the object properties (e.g., solidity, weight, etc.) to which they are sensitive. Examples of spatiotemporal inferences include stage 6 object permanence (e.g., locating concealed objects, also after visible and invisible displacements, Piaget, 1954) and inferences by exclusion (e.g., inferring the location of an object by eliminating other possible locations). Object–object inferences focus on physical interactions between objects (i.e., on how one object affects the other). Here, basic notions of solidity and support play a crucial role (see Chapter 26, this volume). Object–object inferences are involved, for example, in some forms of diagnostic reasoning and tool use (see Chapters 27 and 30, this volume).

TYPES OF INFERENCE

In this section, we turn to the empirical literature on inferential abilities in nonhuman animals. In particular, we systematically review the experimental evidence for disjunctive syllogism and diagnostic and predictive inferences across a wide variety of species.

Disjunctive Syllogism

In the animal cognition literature, inferences akin to a disjunctive syllogism are usually termed exclusion or inference by exclusion. Inference by exclusion can be defined as inferring the identity of an unknown alternative by logically eliminating the other known options (Call, 2004). Researchers have used two main experimental paradigms to shed light on exclusion in nonhuman animals: food search and relation identification, which roughly correspond to spatiotemporal relations and arbitrary relations, respectively.

Spatiotemporal relations. In its simplest version, subjects are presented with two opaque cups and the experimenter hides food in one of them. In different trials, subjects are shown the content of the baited cup (baseline condition), the content of the empty cup (exclusion condition) or neither of them (control condition). Thereafter, the subject can choose between the two cups. About 30 species (see Table 29.2) have been tested in some version of this task. Great apes, several monkey species, ravens and Clark's nutcrackers have spontaneously solved the task (see Figure 29.2). Positive results have also been found for dwarf goats (*Capra aegagrus hircus*; Nawroth, von Borell, & Langbein, 2014) and African grey parrots (*Psittacus erithacus*; Mikolasch, Kotrschal, & Schloegl, 2011) but only after repeated testing, thus leaving open the possibility that subjects learned the response. Dogs (*Canis familiaris*) generally preferred the cups that the experimenter manipulated (Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Erdőhegyi, Topál, Virányi, & Miklósi, 2007) but succeeded after controlling for local enhancement. When the experimenter was touching and looking at both

TABLE 29.2

Species Investigated on Various Forms of Disjunctive Syllogism

Species	References	Two cups	Invisible displacement	Two cups/ two items	MTS	Symbol
	Primates					
Gorilla gorilla	Call, 2004	X				
	Barth and Call, 2006		X			
Homo sapiens	Call and Carpenter, 2001; Hill et al., 2012	X				
	Barth and Call, 2006		X			
	Aust et al., 2008				X	
Pan paniscus	Call, 2004	X				
	Barth and Call, 2006		X			
Pan troglodytes	Call, 2004; Call and Carpenter, 2001; Hill et al., 2011	X				
	Barth and Call, 2006		X			
	Call, 2006; Premack and Premack, 1994			X		
	Beran and Washburn, 2002; Tomonaga, 1993				X	
Pongo abelii	Call and Carpenter, 2001; Hill et al., 2011; Marsh and MacDonald, 2012	X				
	Barth and Call, 2006; DeBlois et al., 1998		X			

(Continued)

Symphalangus syndactylus	Hill et al., 2011	X				
Ateles geoffroyi	Hill et al., 2011	X				
Cebus apella	Grether and Maslow, 1937; Heimbauer et al., 2012; Marsh et al., 2015; Paukner et al., 2009; Sabbatini and Visalberghi, 2008	X				
Cebus capucinus	Grether and Maslow, 1937	X				
Cebus unicolor	Grether and Maslow, 1937	X				
Chlorocebus sabaeus	Grether and Maslow, 1937	X				
Eulemur fulvus	Maille and Roeder, 2012	X				
Eulemur macaco	Maille and Roeder, 2012	X				
Macaca mulatta	Grether and Maslow, 1937; Petit et al., 2015	X				
	de Blois and Novak, 1994		X			
Macaca nemestrina	Grether and Maslow, 1937	X				
Macaca silenus	Marsh et al., 2015	X				
Macaca tonkeana	Petit et al., 2015	X				
Papio anubis	Petit et al., 2015; Schmitt and Fischer, 2009	X				
Papio hamadryas	Marsh et al. 2015	X				
Saimiri sciureus	Marsh, Vining, Levendoski and Judge, 2015	X				
	De Blois et al., 1998		X			
Nonprimate mammals						
Canis familiaris	Brauer et al., 2006; Erdohegyi et al., 2007	X				
	Collier-Baker et al., 2004; Fiset and LeBlanc, 2007		X			
	Aust et al., 2008				X	
	Griebel and Oller, 2012; Kaminski et al., 2004; Pilley and Reid, 2011					X
Capra aegagrus hircus	Nawroth et al., 2014	X				
Elephas maximus	Plotnik et al., 2014	X				
Felis catus	Doré, 1986, 1990; Dumas and Doré, 1989; Goulet et al., 1994		X			
Ovis orientalis aries	Nawroth et al., 2014	X				
Phoca vitulina	Hanggi and Schusterman, 1995				X	
Sus scrofa domestica	Nawroth and von Borell, 2015	X				
Tursiops truncatus	Jaakkola, Guarino, Rodriguez, Erb, and Trone, 2010		X			
	Herman, Richards, and Wolz, 1984					X
Zalophus californianus	Schusterman and Krieger, 1984; D. Kastak, and Schusterman, 1994, 2002; Pack et al., 1991; Schusterman et al., 1993				X	X
Birds						
Columba livia	Aust et al., 2008; Clement and Zentall, 2003; Zentall et al., 1981				X	
Corvus corax	Schloegl et al., 2009	X				
Corvus corone	Mikolasch et al., 2012	X				
Corvus monedula	Schloegl, 2011	X				
Corvus moneduloides	Jelbert et al., 2015	X				
Garrulus glandarius	Shaw et al., 2013	X				
Nucifraga columbiana	Tornick and Gibson, 2013	X				
Cacatua goffiniana	Auersperg et al., 2014		X			
Nestor notabilis	Schloegl, 2011	X				
Psittacus erithacus	Mikolasch et al., 2011	X				
	Pepperberg et al., 1997		X			
	Pepperberg et al., 2013			X		
	Pepperberg, 1987				X	
	Pepperberg, 2006					X

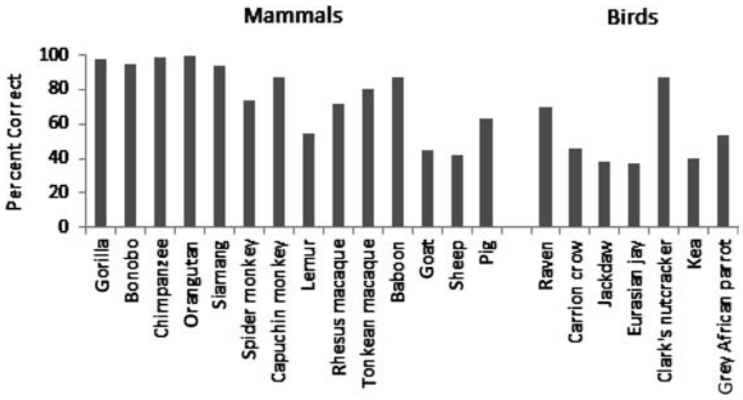

FIGURE 29.2. Mean percent of correct choices in the two-cup disjunctive syllogism task in mammals and birds. These data do not include studies using three cups or tubes to present the task. When a species has been investigated in multiple studies, we combined the data from those studies to obtain a single data point per species. We would like to emphasize that the presented results, particularly their comparative implications, should be interpreted with caution because differences in experimental design might affect the interspecies comparison to some extent (e.g., using identical or perceptually different cups might affect performance, as has been suggested for African grey parrots; see Pepperberg et al., 2013).

cups but was revealing only the content of one of them (baited or nonbaited), the dogs picked the baited cup (Erdőhegyi et al., 2007). Asian elephants (*Elephas maximus*) have also passed a version of this task using olfaction (Plotnik, Shaw, Brubaker, Tiller, & Clayton, 2014). In contrast, sheep (*Ovis orientalis aries*), squirrel monkeys (*Saimiri sciureus*), domestic pigs (*Sus scrofa domestica*), keas (*Nestor notabilis*), Eurasian jays (*Garrulus glandarius*), or jackdaws (*Corvus monedula*) have failed this task.

Positive results must be interpreted with caution because individuals might have simply avoided the empty cup. Therefore, determining what the subjects learned about the container whose content has not been revealed is vital for an inference-by-exclusion account. Using L-shaped tubes and straight tubes in an information seeking paradigm (Paukner, Anderson, & Fujita, 2006; see also Chapter 31, this volume) is one possible approach. Seeing that one arm of the L-shaped tube (see Figure 29.1a) is empty should not lead subjects to avoid it because the food could still be there. Observing that the straight tube is empty, in contrast, should lead them to abandon this hiding place. An avoid-the-empty-tube strategy does not predict a differential treatment of the stimuli, which is precisely what New Caledonian crows did, showing a marked preference for the L-shaped over the straight tube (Jelbert, Taylor, & Gray, 2015). Confronting subjects with sets of opaque cups that can be inspected from underneath (before choosing one of them) is another imaginative way to test the avoidance hypothesis. Marsh and MacDonald (2012) found that orangutans (*Pongo abelii*) were more likely seek information in trials with three cups compared with trials with one cup, suggesting that subjects inferred that the food was located in the single cup even though they had not seen any empty cup. Moreover, if avoidance of the empty container is such a trivial response, it is unclear why so many species failed to solve this task. Note that upon seeing the food, those same species solved the task without difficulty.

The invisible displacement task (Piaget, 1954) represents an elaboration of the two cup task described earlier except that subjects witness the reward being placed inside a displacement device (e.g., opaque cup) which is then moved under each of multiple alternative hiding places. Once all displacements are concluded, the displacement device is shown to be empty and the subject is allowed to search for the reward. Unlike the two cup task, this means that subjects do not see any of the target cups being empty, thus making the cup avoidance explanation mentioned earlier moot. In fact, Piaget (1954) argued that successful performance in such a task evidenced a mental reconstruction of the reward's trajectory.

Numerous species have been tested in the invisible displacement task using a scale originally developed to test human infants (Uzgiris & Hunt, 1975; see also Chapter 26, this volume). Several mammal and bird species are reported to have passed at least the single displacement task in this scale. There is controversy, however, on whether scientists took sufficient measures to guard against inadvertent experimenter-given cues and whether controls were conducted that help to disentangle associative learning and inferential explanations (Jaakkola, 2014, 2015; Pepperberg, 2015). Control tasks that take care of some of these alternative accounts involve touching all the alternative hiding places without the possibility that the food was displaced to this location. For instance, after each visit to the hiding places, the cup is lifted and its content is revealed. In this way the movements of the experimenter are identical irrespective of where the food is hidden and the animals cannot apply the heuristic "choose the hiding place that was visited by the displacement device" (Pepperberg, Willner, & Gravitz, 1997).

Based on a review of the literature, Jaakkola (2014) concluded that the best evidence for invisible displacement was found in great apes. The evidence for other species, most notably parrots, is suggestive but most studies did not include control tasks to rule out noninferential explanations. Two studies included conditions in which the displacement device visited more than one hiding place: African grey parrots (Pepperberg et al., 1997) and Goffin cockatoos (*Cacatua goffiniana*; Auersperg, Szabo, von Bayern, & Bugnyar, 2014) succeeded in locating the food. However, Jaakkola (2014) questioned the Goffin cockatoo results because a magnetic mechanism was used for the displacement of the food, which might have allowed birds to detect the food directly via magnetoreception.

Early studies provided some evidence that cats (*Felis catus*) and dogs successfully solved visible and invisible displacement tasks while controlling for olfactory cues (Dumas, 1992; Gagnon & Doré, 1992, 1993; Triana & Pasnak, 1981). However, a practical search strategy (searching for the reward at the location that was visited by experimenter) was not ruled out as candidate explanation. For cats, Doré and colleagues (Doré, 1986, 1990; Dumas & Doré, 1989; Goulet, Doré, & Rousseau, 1994) showed that they would search consistently at the last location where they had seen the reward. Also for dogs, more recent studies found little evidence that they tracked invisible displacements (Collier-Baker, Davis, & Suddendorf, 2004; Fiset & Leblanc, 2007). Rather, these studies suggest that dogs mainly use visual cues such as the location of the cup that was used as displacement device to locate the hidden food. Bottlenose dolphins (*Tursiops truncatus*) passed the standard invisible displacement task only when a human hand was used as displacement device (Jaakkola, Guarino, Rodriguez, Erb, & Trone, 2010). However, they failed control conditions in which the experimenter visited more than one potential hiding place. Like cats and dogs, the dolphins appeared to have used some kind of heuristic such as "choose the screen that was visited by the experimenter."

A more complex form of disjunctive syllogism was introduced by Premack and Premack (1994) using a two-food, two-location search task. Chimpanzees observed the experimenter hiding an apple and a banana in two different containers. While the chimpanzees were distracted, the experimenter removed one of the food items and subsequently, the chimpanzees saw the experimenter eating it. One out of five chimpanzees consistently selected the container with the fruit different from the one eaten by the experimenter. Premack and Premack, argued that the successful individual might have inferred that the experimenter had removed one of the fruits from the container out of her sight. Therefore, this piece of fruit was not available anymore which is why the chimpanzee selected the container associated with the other fruit. This result has been replicated with apes and grey parrots (Call, 2006; Mikolasch et al., 2011). One of seven parrots chose the cup that was not associated with the food item that the experimenter removed out of the parrot's view (Mikolasch et al., 2011). A follow-up condition probed whether the successful bird just learned the association between the piece of food taken by experimenter and picking the cup associated with the other piece of food. In this association control condition, the parrot saw that the experimenter was taking the piece of food out of her pocket and thus clearly not from one of the cups. Here, the parrot chose randomly.

In a replication of this study, four African grey parrots passed the inference by exclusion test but chose randomly in the association control condition (Pepperberg, Koepke, Livingston, Girard, & Hartsfield, 2013). In addition, the latter study excluded another potential behavioral rule that the parrots could have used, namely that the birds simply avoided the cup from which a reward was removed. In a second experiment, the two cups were baited with two rewards each, one with two highly preferred rewards and one with two low-value rewards. When the birds subsequently saw that the experimenter had one of the favorite rewards removed (out of their sight), the birds maintained their preference for the cup with the remaining high value reward.

Call (2006) reported that five out of 24 apes solved this task above chance levels. Moreover, group analyses revealed that apes responded above chance levels in the first trial but not in the control conditions. A follow-up test with a simplified procedure and fewer trials replicated this result and also showed an age effect. Only five out of 10 apes below 11 years of age scored 75% correct or higher whereas 11 out of 12 apes above 10 years of age reached this score. Note that this task, just like the previous ones, could be potentially solved using a conditional discrimination. If the apple is on the table, pick the banana, if not, pick the apple. Call (2006) tested this possibility (using arbitrary discriminative cues such as the color of a plastic chip or pieces of food different in type from the hidden food) and found that the same apes who could solve the original task failed to solve it in conditional discrimination. The fact that apes also succeeded on the first trial provides further evidence that conditional discrimination is unlikely to explain success in this task. So far, we have considered tasks that operate based on natural (i.e., spatiotemporal) relations. The next section also covers tasks aiming at disjunctive syllogisms operating on arbitrary (but 100% predictive) relations between stimuli.

Arbitrary relations. In matching-to-sample tasks animals learn to sort stimuli into equivalence classes. For example, C. R. Kastak and Schusterman (2002) trained California sea lions (*Zalophus californianus*) to match stimuli (10 Arabic numerals and 10 capital letters) to compatible samples (i.e., letter to letter and numeral to numeral). In the training, there was a sample and two defined stimuli (one compatible and one incompatible) and the sea lions needed to pick the compatible one. Following this training, there are two different ways how exclusion can be tested with this paradigm: For type I exclusion, subjects are confronted with a novel sample (e.g., #) and as test stimuli a familiar stimulus of a predefined class (e.g., A) and a novel stimulus (e.g., +). The stimulus of the familiar class can be excluded as a match to the novel sample, thus, the novel stimulus should be chosen. In type II exclusion, subjects are confronted with a familiar sample (e.g., 8) and as test stimuli a novel stimulus (e.g., #) and a familiar stimulus of a different equivalence class (e.g., A). Again, to rule out avoidance of the known stimulus, the learning outcome has to be examined (i.e., the critical question is whether animals form novel equivalence classes by exclusion).

With regard to type I exclusion, pigeons (*Columba livia*; Clement & Zentall, 2003; Zentall, Edwards, Moore, & Hogan, 1981), sea lions (D. Kastak & Schusterman, 1994; Pack, Herman, & Roitblat, 1991; Schusterman, Gisiner, Grimm, & Hanggi, 1993), chimpanzees (Beran & Washburn, 2002; Tomonaga, 1993), and harbor seals (*Phoca vitulina*; Hanggi & Schusterman, 1995) chose the novel stimulus when confronted with a novel sample. However, as already noted earlier, avoidance of the familiar but incompatible stimulus might explain this result. Sea lions (C. R. Kastak & Schusterman, 2002) and chimpanzees (Tomonaga, 1993) were also presented with a type II exclusion test using predefined samples and both species spontaneously selected the novel stimulus. To exclude avoidance of the familiar but incompatible stimulus as alternative explanation, the sea lions were then presented with transfer tests in which the learning outcomes were evaluated. After their initial exclusion task, the sea lions had to choose between the previously selected stimulus (#) and a novel stimulus (+) when presented with a sample of the same class as before (e.g., 8). In the second transfer test, the previously selected stimulus (#) was used as sample. In both transfer tests the sea lions treated the # as member of the equivalence class *numbers* (i.e., they chose # when the sample was a number and they chose members of the class numbers when # was the sample). Thus, the sea lions rapidly expanded stimulus classes based on the exclusion of alternatives—something that can hardly be explained by avoidance of incompatible stimuli.

Similarly, Aust and colleagues (2008) presented pigeons, dogs, and humans (children and adults) a touchscreen with a discrimination task in which some stimuli were rewarded and others were not. When the nonrewarded stimuli were then shown together with novel stimuli one pigeon, half of the dogs, and most of the human participants selected the novel stimulus. This finding replicated previous work with pigeons (Zentall et al., 1981). Crucially, when the learning outcomes were examined, dogs and humans but not the pigeon showed evidence that they had learned positive class membership of novel stimuli by excluding alternatives. The pigeon's performance, in contrast, could be explained by a preference for novel stimuli.

The evidence is mixed in chimpanzees, with some positive (Cerutti & Rumbaugh, 1993; Savage-Rumbaugh, 1986) and some negative findings (Beran & Washburn, 2002; Tomonaga, 1993) on learning new class memberships by exclusion in matching-to-sample tasks (either using food lexigram or arbitrary stimulus relations). In the latter studies, chimpanzees preferred undefined stimuli (over multiple predefined stimuli) when presented with novel sample stimuli. However, they failed to learn by exclusion associations between undefined stimuli and novel samples, raising the possibility that they were using an avoidance strategy when presented with novel samples.

In the context of language acquisition (see Volume 1, Chapter 32, this handbook), exclusion learning is sometimes termed *fast mapping*. A few studies have investigated exclusion learning using language-based paradigms in nonhuman animals. Alex, a grey parrot, was trained in vocal labeling and object categorization tasks. When presented with an array of known and unknown objects and asked to count the *thimbles* (a novel label) he would give the number of all presented objects and after negative feedback the number of the unknown objects (Pepperberg, 1987; see also Volume 1, Chapter 32, this handbook). This test was repeated four times with new objects and new labels and Alex performed like in the first trial except for the last trial in which he spontaneously answered correctly by stating the number of the unknown objects.

Bottlenose dolphins and California sea lions were trained on the comprehension of an artificial language that allowed them to perform different actions on objects in response to a sequence of computer-generated sounds (dolphins) and gestures (dolphins and sea lions) of human experimenters (Herman, Richards, & Wolz, 1984; Schusterman & Krieger, 1984). When they were presented with a novel object in the presence of familiar ones, they could quickly map a novel gesture to this novel object. However, sea lions needed a few hundred exclusion trials to learn to associate this label with the object when given a choice between two object–label pairs that were both "learned" by exclusion (Schusterman et al., 1993).

Similarly, Rico, a border collie who was trained to fetch more than 200 objects in response to verbal labels, could identify the referent of a new word by exclusion learning (Kaminski, Call, & Fischer, 2004). In the test a novel target object was placed amongst familiar ones. When Rico was asked to bring an object using a novel name, Rico fetched the novel object. In a subsequent retention test four weeks later, the target object was now placed amongst familiar and novel objects. When Rico was again asked to bring an object with this label, Rico fetched the object he had retrieved four weeks ago more often than expected by chance. The authors suggested that Rico's performance provided evidence for fast mapping of object–name associations.

This finding was replicated with another border collie (Pilley & Reid, 2011). However, in the latter study the border collie retained his knowledge only over a time interval of 10 min. After 24 h, in contrast, she did not retain the names of the target objects any more. Griebel and Oller (2012) criticized these studies as evidence of fast mapping because the retention tests did not rule out an "extended exclusion" strategy. Accordingly, the border collies might have selected the relatively novel item whose retrieval was rewarded before without remembering the word–object association. A test of fast mapping would require pitting two objects whose label has been learned by exclusion against each other. When they presented a Yorkshire terrier who could accurately retrieve more than 100 objects with the same exclusion and retention tests the terrier performed similar to the border collies in the previous studies. However, when they finally pitted the two target objects (that they introduced in the exclusion test) against each other, the terrier failed to map the previously established labels onto the objects. Thus, the possibility remains that dogs' performance in these fetching tasks can be explained by an extended exclusion of familiar and completely novel objects, as can the results of marine mammals in the artificial language tasks.

Diagnostic Inference

We now turn to diagnostic inferences that entail reasoning from the consequent (the effect) to the antecedent (the cause). Diagnostic inferences are made either based on affirming or denying the consequent. In contrast to the studies reviewed in the previous section, here we mainly focus on object-object relations.

Affirming the consequent (abductive inference). Cheney and Seyfarth (1990) presented wild vervet monkeys (*Chlorocebus pygerythrus*) and baboons with a fresh carcass in a tree or snake tracks on the ground both of which might be interpreted as a consequence of predators (leopards and pythons, respectively) being nearby. They reasoned that if the monkeys inferred the presence of danger from these indirect cues, they would give alarm calls. However, despite ample experience with leopards and pythons none of the monkey groups gave any alarm calls or showed any signs of increased vigilance to begin with in response to these indirect cues. It is possible that the stimuli used in these field experiments were not realistic enough (the python tracks were human made and the carcass was stuffed). However, vervet monkeys that encountered real python tracks did not show signs of increased vigilance either. Moreover, one might argue that the gazelle's carcass signals to the vervet monkeys that the leopard in the vicinity is satiated and, therefore, poses currently no threat to them. However, Cheney and Seyfarth (1990) reported that monkeys indeed gave repeated alarm calls when they saw a leopard dragging prey into trees and feeding on it. Finally, these cues might not be reliable signals of an immediate threat, as they remain visible for some time even when the predator is long gone. In any event, these findings do not provide any evidence for diagnostic reasoning in these monkeys.

In the lab, simpler diagnostic reasoning tasks have been designed. One of which is instantiated by a version of the two cup test described the previous section, where instead of showing that a container is baited or empty, the sought object provides an indirect cue of its presence. If instead of showing the content of the cups, one shakes them, the cup with the food inside produces a rattling noise (provided that it is both solid and loose) whereas the empty cup remains silent. Several species including gorillas, bonobos, chimpanzees (Call, 2004), capuchin monkeys (Heimbauer, Antworth, & Owren, 2012; Sabbatini & Visalberghi, 2008; but see Paukner, Huntsberry, & Suomi, 2009), and African grey parrots (Schloegl, Schmidt, Boeckle, Weiß, & Kotrschal, 2012) can spontaneously use such an auditory cue to detect its presence (see Table 29.3). Other species such as orangutans (Call, 2004; Hill, Collier-Baker, & Suddendorf, 2011) failed this task. Although some species including pigs (Nawroth & von Borell, 2015), and baboons (*Papio hamadryas anubis*; Schmitt & Fischer, 2009) can learn to use this cue to locate the food, this is not necessarily the same as spontaneous performance because associative processes might well account for it. Furthermore, dogs, in contrast to apes, did not discriminate between causally relevant rattling noises

TABLE 29.3

Species Investigated on Various Forms of Diagnostic Inference

Species	**References**	**Noise**	**Absent noise**	**Board**
	Primates			
Gorilla gorilla	Call, 2004	X	X	
	Call, 2007			X
Homo sapiens	Hill et al., 2012	X	X	
Pan paniscus	Braeuer et al., 2006; Call, 2004	X	X	
	Braeuer et al., 2006; Call, 2007			X
Pan troglodytes	Call, 2004; Hill et al., 2011	X	X	
	Braeuer et al., 2006; Call, 2007			X
Pongo abelii	Call, 2004; Hill et al., 2011	X		
	Call, 2007			X
Cebus apella	Heimbauer et al., 2012; Paukner et al., 2009; Sabbatini and Visalberghi, 2008	X	X	
Eulemur fulvus	Maille and Roeder, 2012	X	X	
Eulemur macaco	Maille and Roeder, 2012	X	X	
Macaca fascicularis	Schloegl et al., 2013; Schmitt et al., 2012			X
Macaca mulatta	Petit et al., 2015	X		X
Macaca tonkeana	Petit et al., 2015	X	X	X
Papio anubis	Petit et al., 2015; Schmitt and Fischer, 2009	X	X	X
Saimiri sciureus	Marsh et al., 2015	X	X	
	Nonprimate mammals			
Canis familiaris	Brauer et al., 2006; Erdohegyi et al., 2007	X	X	
	Braeuer et al., 2006			X
Elephas maximus	Plotnik et al., 2014	X		
Sus scrofa	Albiach-Serrano et al., 2012	X	X	X
Sus scrofa domestica	Albiach-Serrano et al., 2012; Nawroth and von Borell, 2015	X	X	
	Albiach-Serrano et al., 2012			X
	Birds			
Gallus gallus	Chiandetti and Vallortigara, 2011			X
Psittacus erithacus	Schloegl et al., 2012	X		

and arbitrary auditory cues that served as a control suggesting that they were apparently not sensitive to the causal relations between the shaking of the cup and the rattling noise (Bräuer et al., 2006).

Even those individuals who solved the task in the first trial may not have used inference because the rattling noise may have simply called their attention to that cup, which is why they selected it. However, this explanation is weakened because an arbitrary noise associated to the baited cup does not elicit the same response. Even the same prerecorded food rattling sound played back on top of the baited container was not enough to ensure success. This means that the auditory cue alone dissociated from the food is not effective. Penn and Povinelli (2007) argued that subjects might have learned previously to use a combination of the sound and the cup movement as cue. Hill et al. (2011) tested this possibility with the duplicate follow-up test. After passing the original shaken cup test, two chimpanzees were presented with two sets of identical test cups. The duplicate cups were shaken one after the other (but not the test cups). When subjects chose between the test cups, they did not score above chance levels suggesting that even the combination between shaking motion and rattling sound was insufficient to explain apes' performance.

The null results with the audio recorder and duplicate cups control conditions may indicate that individuals potentially conceive the rattling sound not as mere predictor of the presence of food but as its effect. Accordingly, apes might have reasoned from this effect to its cause, the food. Inspired by the arrested motion paradigm (Baillargeon, Spelke, & Wasserman, 1985), Call (2007) presented apes with two small boards on a platform. The experimenter showed a food piece to the subject and then, behind a screen, placed it under one of two boards, which acquired a slanted orientation while the other stayed flat on the platform. When the screen was removed, monkeys and apes preferred the slanted board over the flat board (Call, 2007; Petit et al., 2015; Schloegl, Waldmann, & Fischer, 2013; Schmitt, Pankau, & Fischer, 2012). Furthermore, apes showed no preference between a flat board and a solid wedge, which mimicked a slanted board including its reinforcement regime (i.e., if they picked it they received the same rewards as with the slanted board; Call, 2007; but see Bräuer et al., 2006). This means that subjects processed a perceptually similar (but causally different) stimulus in quite a different fashion. Not all species behaved in the same way though. Whereas dogs prefer the slanted board, they also prefer the wedge stimulus (Bräuer et al., 2006). This is not surprising given that wedge and slanted board share identical reinforcement regimes.

When searching for an imprinted object hidden under one of two differently inclined boards, newly hatched domestic chicks (*Gallus gallus*) also preferred the steeper inclined board whose slant was consistent with the size of the hidden object (Chiandetti & Vallortigara, 2011). Their preference was to some extent modulated by the size of the imprinted object but they did not show a significant preference for the less inclined board when imprinted with a smaller object. Chicks did not receive the solid wedge control condition and consequently, it remains to be seen whether their performance is driven by a general preference for perceptual features. One could argue that the slanted board is not treated as the effect of the supporting food reward but that it is merely a better place for an object to hide compared to a flat (or less inclined) board. Although invoking relevant properties of objects as hiding places eliminates any causal connection between the board orientation and the food as its cause, the wedge by virtue of its volume could also work as a hiding place, but apes did not prefer it.

A series of tasks devoted to the question of weight further investigated this issue. Hanus and Call (2008) presented chimpanzees with a balance beam with two cups on opposite sides. When both cups were empty the beam stayed in equilibrium, but lost it when one food item was placed inside one of the cups. Chimpanzees who could not witness which container was baited preferred the bottom cup but only in the experimental condition, and they did so in the first trial. In the control condition, the beam was already slated prior to baiting any of the cups. Even though the bottom cup was always baited (to mirror the reinforcement regime of the experimental condition), chimpanzees did not prefer it. One possibility is that the bottom position was preferred but only when associated with movement, something that the control condition lacked. However, a follow-up test showed that when the experimenter (not the food) was responsible for the movement (because he pushed the beam after baiting it had left it stationary), the preference for the bottom location disappeared. Hanus and Call (2008) interpreted this result as an indication that when the experimenter intervened (i.e., acted as an external cause of the movement), apes did not attribute the cause of the movement to the food inside one of the two cups. Povinelli (2011), in contrast, interpreted the null result following the experimenter's intervention on the basis of disrupted Michottean causal perception (see section on Causal Maps).

Other paradigms also suggest that chimpanzees can infer the location of food based on its weight. Schrauf and Call (2011) found that they learned to use weight but not color, even though previous studies established that weight per se is not a more powerful cue than color (e.g., Schrauf & Call, 2009). Hanus and Call (2011) found that when searching for an opaque bottle filled with juice among several other empty opaque ones (all bottles were difficult to open), chimpanzees first checked by lifting the bottles until they found the heavy one before opening it. In contrast, they were unable within the given number of trials to learn to use a visual cue that reliably indicated the bottle filled with juice compared with bottles filled with water.

Finally, a recent study found that apes (chimpanzees, bonobos, and orangutans) spontaneously make use of a trail left by a leaking yogurt cup (which was displaced out of their sight) to locate its source. In contrast, they ignored the same trail when it did not match the displaced food type, even though it was 100% predictive of the food location (Völter & Call, 2014b). Just like the recording of rattling or the slanted wedge, a perceptually very similar or identical cue that was not caused by the food lost its effectivity. This suggests that apes infer the cause of the observed effect and do not just learn a conditional discrimination.

Denying the consequent. Previously, we saw that a cue can predict the presence of food and in some cases even its cause. Under some conditions, the absence of a cue can also predict the absence of its cause. Here subjects must infer the food location based on the absence of a cue that, if the food had been present, would have occurred. In the shaken cup task, this translates into the following: If the food is in the cup, it produces a rattling noise when shaken. Now, the shaken cup does not produce a noise, therefore, the food is absent, and therefore, the food should be in the remaining hiding place, the other cup. An alternative explanation is again avoidance of the silent cup acquired through prior reinforcement. Control tasks that have been developed to account for avoidance of the silent-shaken cup is the silent-rotated or silent-stirred cup condition. If the food was in the cup, rotation of the cup should produce a noise whereas stirring should not. Therefore, subjects should prefer the silent stirred cup but not the silent-rotated cup to the silent-shaken cup.

Compared to the visual version of the task, fewer individuals and species and have succeeded in the acoustic version when only negative information is available. Among the species that have been reported to succeed this task are gorillas and bonobos (Call, 2004), chimpanzees (Hill et al., 2011; but see Call, 2004), capuchin monkeys (Sabbatini & Visalberghi, 2008), grey parrots (Schloegl et al., 2012), and pigs (after some training with the rattling sound; Nawroth & von Borell, 2015). Control conditions showed that gorillas, bonobos, and capuchin monkeys were not merely avoiding the silent shaken cup (Call, 2004; Sabbatini & Visalberghi, 2008). When compared to a silent-rotated cup condition, subjects did not avoid the silent shaken cup. Moreover, when compared to the silent-stirred cup condition, apes preferred the stirred to the shaken cup. Similarly, the performance of one out of three domestic pigs that passed the silent shaken cup condition can also hardly be explained by avoidance of the empty cup (Nawroth & von Borell, 2015).

Species that failed to select the baited cup when the empty one was shaken are orangutans (Call, 2004; Hill et al., 2011), tonkean macaques (*Macaca tonkeana*; Petit, Call, & Thierry, 2005), dogs (Bräuer et al., 2006), and Asian elephants (Plotnik et al., 2014). Three out of seven elephants, however, succeeded in an olfactory version of the task when they could smell at the empty food container only. It remains ambiguous, however, whether the elephants just avoided the empty container or whether they inferred the location of the food by exclusion.

Predictive Inference

The counterpart to diagnostic inferences are predictive inferences (Visalberghi & Tomasello, 1998), that is, inferring the consequent from the antecedent. Predictive inferences are especially relevant for action planning. The common theme of tasks aiming at predictive inferences is that animals need to anticipate the effect that their actions will have on the trajectory or status of a food item (see Chapter 27, this volume). The most widely used tasks in this area include tool selection, trap tasks, string pulling, and water displacement tasks. Here we will cover only briefly tool selection and trap tasks. Recent reviews, including some in this volume, covered these and other tasks in detail (Jacobs & Osvath, 2015; Seed, Hanus, & Call, 2011; see also Chapters 27 and 30, this volume).

Tool selectivity. Although tool-use is not rare in the animal kingdom, flexible tool-use is (see Chapter 30, this volume). One important aspect of this flexibility is tool selectivity. Prior to using a tool, individuals have to choose, and in some occasions make, tools whose features are suitable for solving the task at hand. Thus, capuchin monkeys and chimpanzees select stones with suitable weight to crack open hard-shelled nuts (Boesch & Boesch, 1983; Visalberghi et al., 2009). Apes and New Caledonian crows select tools of an appropriate length to obtain rewards (Chappell & Kacelnik, 2002; Mulcahy, Call, & Dunbar, 2005; Wimpenny, Weir, Clayton, Rutz, & Kacelnik, 2009), and apes tend to choose tools of optimal length when choosing longer tools entails an additional cost (Martin-Ordas, Schumacher, & Call, 2012). Orangutans, chimpanzees and capuchin monkeys select appropriate tools as a function of their pliability (Manrique, Gross, & Call, 2010; Manrique, Sabbatini, Call, & Visalberghi, 2011). Orangutans select tools that can be used as a straw and do even modify nonfunctional tools to turn them into functional ones (Manrique & Call, 2011). In many of these cases, such performance is observed from the first trial. Chimpanzees and New Caledonian crows make tools prior to their use, including construction of certain features such as brushes or hooks, which improve their efficiency (e.g., Sanz, Call, & Morgan, 2009; Weir, Chappell, & Kacelnik, 2002).

Trap tasks. The classic trap tube task consists of a horizontally mounted Plexiglas tube with a hole in the center. Underneath this hole there is a container that captures everything that is moved into the hole. Originally designed to test capuchin monkeys and children (Visalberghi & Limongelli, 1994), this task was used also with chimpanzees (Limongelli, Boysen, & Visalberghi, 1995; Reaux & Povinelli, 2000) and woodpecker finches (Tebbich & Bshary, 2004). The initial results indicated that this was a remarkable difficult task (for reviews, see Call, 2010; Tebbich, 2013). In light of these results, some authors argued that individuals were seemingly incapable of predicting the consequences of their actions because they failed to anticipate the trap as an obstacle impeding the progression of the food. Two main developments took place since then. First, several versions of this task have sought to reduce potential hidden constraints. Some of the changes introduced to the original task included presenting two tubes simultaneously oriented in opposite directions (Martin-Ordas, Call, & Colmenares, 2008), moving the trap from a tube to a table (Povinelli, 2000), increasing the options available for extracting the food (Girndt, Meier, & Call, 2008; Mulcahy & Call, 2006), and in some cases, even entirely eliminating the need for using a tool (Seed, Call, Emery, & Clayton, 2009; Völter & Call, 2014a, 2014c). In most cases, the task became easier and subjects were avoiding the trap even in the first trial (e.g., Girndt et al., 2008). Moreover, Martin-Ordas, Jaek, and Call (2012) found that after having learned to solve a trap task, apes transferred their knowledge to a different type of obstacle (i.e., barrier) and vice versa, thus suggesting that subjects had acquired knowledge based on a structural representation, not a purely perceptual one.

Second, the task has been adapted to test birds. In the two-trap tube (Seed, Tebbich, Emery, & Clayton, 2006; Tebbich, Seed, Emery, & Clayton, 2007) the birds moved the food located in a horizontal tube by pulling or pushing a pre-inserted stick with two discs attached to it that enclose the food reward. Along the tube there were two traps, one functional (i.e., capturing the food when it is moved over the trap) and one non-functional (i.e., the reward can be retrieved if the reward is moved towards this fake trap, see Figure 29.1c). Rooks quickly learned to solve the initial task. All of the birds that passed the initial task also transferred their solution to a variant of task with the same functional traps but a novel, visually distinct nonfunctional trap. When these birds were subsequently presented with two further transfer tasks, only one out of seven rooks passed these transfer tasks. Thus, most of the rooks seemed to have learned in the course of the study to avoid the functional trap. One individual, however, showed evidence that the she might have learned a more abstract rule taking the surface continuity and solidity of the barriers into account to predict the trajectory of the reward.

New Caledonian crows were tested with a similar version of the two-trap tube that required tool use (Taylor, Hunt, Medina, & Gray, 2009). Three out of six birds mastered the initial task and they also continued to avoid the functional trap when the visual appearance of the functional trap changed (e.g., when the color of the trap changed).

They failed, however, when the correct option was to move the reward inside a nonfunctional trap without a base. Crucially, these birds also mastered a functionally similar but perceptually distinct problem, the trap table task. In this task the crows needed to rake one of two rewards by means of a stick within reach. One of the two rewards was located behind a gap in the table which would capture the reward if it was moved into the gap. The three successful birds, unlike the ones that failed the two trap tube task, rapidly solved this functional transfer task. Thus, three out of the six New Caledonian crows appeared to be sensitive to surface continuity and not merely on perceptual cues such as the base of the traps.

The experiments on the trap task paradigms shows how task constraints can mask the ability that the paradigms are seeking to assess. Moreover, this line of research illustrates how transfer tests (using different perceptual cues; e.g., Seed et al., 2011; Völter & Call, 2014a) and functional transfer tests (using completely different set-ups that only share functional features, e.g., gaps in surfaces; e.g., Martin-Ordas, Jaek, & Call, 2012; Taylor et al., 2009) help to differentiate between stimulus-bound associative learning explanations and inferential explanations based on abstracted rules (e.g., not to move the reward over a gap in a surface). These studies show that rigid stimulus-response contingencies are insufficient to explain the performance of great apes and corvids.

CAUSAL MAPS

Thus far, we have seen how animals make inferences about single causal relations in various situations. The question arises whether they can also represent more complex causal structures involving multiple relations. The key challenge for learning causal structures is that the perceptual input that organisms receive from their environment is correlational. Different causal structures, however, can underlie the same correlational input (which has been termed the causal inverse problem; Gopnik et al., 2004). For instance, a correlation between two events, A and B, might reflect a direct causal relationship between the two events (A→B or B→A), an indirect causal relationship via a common cause for example (A←C→B), or just a spurious correlation without any detectable causal relationship. With increasingly complex patterns of correlation, the causal ambiguity increases, which in turn make causal inferences more difficult. In this section, we will explore what kind of strategies animals might adopt to reduce this ambiguity.

Discounting Alternative Causes

The first steps toward more complex causal structures are situations in which animals need to differentiate between multiple causes of an effect. The moving branches that the chimpanzees are witnessing in the initial example might be the effect of wind, conspecifics, or their target. Inferential reasoning might entail discounting alternative explanations or, to use a term coined by the philosopher Hans Reichenbach (1956), *screening off* alternative causes (see Chapter 27, this volume). In our example, if the chimpanzees observe that the branches start moving when the wind picks up, they should not expect monkeys in the canopy. In formal terms, this means that, for candidate causes A and B, if the probability that effect E is occurring is completely depended on the presence of A (i.e., $P(E|A\&B) = P(E|A)$), then A is screening off B from E (Hitchcock, 2010).

Beside such conditional probabilities, temporal information and prior knowledge help to constrain the number of possible causal structures (Waldmann, Cheng, Hagmayer, & Blaisdell, 2008). Causal relations, unlike associations, are directed. The prime indicator of causal directionality is temporal directionality. Causes precede their effects in time; remembering which of two correlated events was prior, therefore, helps to reduce ambiguity. Finally, in the case of object–object relations, prior knowledge (e.g., about geometrical-mechanical relations) offers another way to reduce the number of possible causal structures. We will first consider studies in which animals are required to differentiate between multiple candidate causes for an effect. These studies are usually conducted as follow-up experiments when organisms appear to infer the presence of a hidden cause (A), given its effect (E). In the follow-up condition, a second, visible candidate cause (B) is added to the situation. In the presence of this second candidate cause B, it is unnecessary to assume that A is also present (i.e., evidence for A is absent), even though it entails no evidence for A's absence.

In the slanted board paradigm (Call, 2007), great apes located food (A) underneath a slanted board (E). After initial success, apes were presented with two inclined boards; one of which, however, was supported by a visible wooden block (B). In principle, food could be under either board but given the presence of the wooden block as a potential cause, the rational choice is to select the slanted board without an alternative cause for its inclination. Great apes chose randomly here. Similarly, in another follow-up, apes were presented with two pieces of food (e.g., a large piece of carrot and a small piece of banana). Pretests established that apes preferred banana to carrot irrespective of the size. However, when both pieces of food were hidden (out of view) under the two boards, apes preferred the steeper board, even though this resulted in the less-preferred piece of carrot. These findings do not provide evidence that apes use screening-off information to discount alternative causes. Tested with the same basic setup, long-tailed macaques (*Macaca fascicularis*) also failed to discount alternative causes (Schloegl et al., 2013).

Similar findings were obtained in a tool selection paradigm (Seed, Seddon, Greene, & Call, 2012). After having shown sensitivity to the relation between a moving stick tool (A) and the movement of a connected food reward (E), chimpanzees received a follow-up. Here, the experimenter simultaneously moved a piece of banana with her hand (B) while she was moving a broken stick tool with her other hand. When she moved the connected tool (A), the piece of banana moved as before but without the experimenter's intervention. Again, the apes should make the inference that, if the experimenter is moving the banana directly, there is no evidence for the simultaneously moving stick being causally related to it. And again, apes failed to select the candidate cause not screened-off by an alternative cause (see Chapter 27, this volume).

In the balance task (Hanus & Call, 2008), chimpanzees spontaneously selected the lower container (A) that tilted the balance (E). However, when the experimenter in a follow-up pressed one side of the balance down (B) 3 s–5 s after the baiting of the containers, apes chose randomly. This finding may indicate that apes discount the food reward as cause of the tilted balance in the presence of an alternative cause (i.e., the experimenter's hand). However, Povinelli (2011) disputed this interpretation because the delayed intervention would have disrupted their causal perception of the situation (cf. Michotte, 1963). We note, however, that the proposed Michottean launching events typically involve visible contact between the colliding objects, something that is not the case in the balance task. Moreover, Michottean causal perception would not explain their preference for the bottom cup.

Even though causal perception might not provide a good explanation for these findings, temporal information about the sequence of events certainly plays an important role here. It may facilitate the discounting of alternative causes by adding temporal structure to the input. In the previous screening-off studies that apes failed, temporal structure was missing. In the slanted board paradigm, apes were simultaneously presented with two inclined boards, one visibly supported by a wooden block (Call, 2007). Similarly, in the tool selection task the experimenter moved the broken tool and the reward simultaneously (Seed et al., 2012).

Other studies that did find evidence for discounting of alternative causes included information about the temporal structure of events. In another version of the slanted board, both boards were inclined in the beginning of the trial but one board was falling flat to the platform (Call, 2007). Here, apes preferred the inclined board to the flat board. It would be interesting to see whether apes would succeed in the wooden-block condition if they initially saw how one of the boards was supported only by the wooden block. This latter procedure has been administered with macaques (Schloegl et al., 2013) but it did not help them to solve the task. For great apes, however, this is an open question.

One study specifically aimed at great apes' capacity to discount alternative causes on the basis of temporal information (Völter & Call, 2014b). Here, apes spontaneously followed a visual trail to locate a yogurt cup that had been invisibly displaced and hidden under one of two containers while leaving a trail. In a follow-up, chimpanzees were presented with a pre-existing yogurt trail pointing to one of the two hiding places before the experimenter could hide the reward. After the invisible displacement, the apes saw two symmetrical trails, each one pointing to one of the two containers. To locate the reward, the apes were required to discount the pre-existing trail. Chimpanzees preferred the container marked by the most recent trail without any indication of learning. Control conditions ruled out that features of the trail itself led them to the baited cup or that apes generally preferred the most recent trail they encountered. These findings suggest that the chimpanzees took the temporal directionality between yogurt displacement (cause) and trail (effect) into account and discounted alternatives based on this information.

Finally, the blicket detector paradigm, a method borrowed from the developmental literature (Gopnik & Wellman, 2012), was recently adapted for nonhuman primates. The blicket detector is a reward dispenser that is controlled by certain objects, the so-called *blickets*, which are placed on top of the device. A key question with this paradigm is whether primates discount alternative causes by differentiating between confounded and unconfounded interventions. An intervention is confounded if multiple variables are altered at once. In the blicket detector case, multiple objects are placed on the detector simultaneously, which activates the detector. The causal status of each object remains ambiguous after such a demonstration. Only unconfounded interventions (i.e., each object is placed on top of the detector by itself) allow for disentangling the effects of each candidate cause. In a first adaptation of this paradigm for nonhuman primates, capuchin monkeys seemed to differentiate between confounded and unconfounded interventions, at least after significant exposure to the task contingencies (Edwards et al., 2014). The extent of training, however, is key for the interpretation of these results. From the associative learning literature, cue competition effects such as forward blocking are well known phenomena that may result in a very similar outcome (e.g., Kamin, 1969). In another adaptation of this paradigm, great apes observed the unconfounded intervention only once before they chose between two candidate objects (Völter, Sentís, & Call, 2016). Nonhuman apes, like preschool children, preferred objects whose effect on the detector was independent of a second object. Associative cue competition effects are less likely here because the relevant contingency was presented only once.

Transitive Inferences

To what extent nonhuman animals acquire more complex, map-like causal representations is subject to ongoing debate. Transitive inferences (A>B, B>C, therefore A>C) are a first step towards causal maps. Transitivity allows for making inferences about the relation between stimuli that never occurred together. Of course, transitivity is not only important for causal cognition but also for numerical cognition, another domain providing compelling evidence for inferential abilities in animals (see Volume 1, Chapter 32, this handbook and Chapters 18 and 25, this volume). For example, Alex, the grey parrot, spontaneously inferred the ordinality of new numerals (7 and 8) after having learned the ordinal relations of the numerals 1 to 6 and 6 to 8 (7>6, 6>1–5, therefore, 7>1–5). Strikingly, Alex also identified the cardinal value of these new numerals from their ordinality (Pepperberg & Carey, 2012), something that has not been demonstrated in any other animals, at least in the absence of explicit training (e.g., Matsuzawa, 2009).

For the purpose of this chapter, however, we will focus now on transitivity of causal relations. When learning causal chains, such as A→B, B→C, one might make the inference that A is causing C (Menzies, 2014). What makes the situation more complicated for causal relations is that, unless B necessarily follows from A and C necessarily follows from B, intransitivity may result (which is not true for other transitive relations based on quantities). Other variables that are causally related to B and interventions might affect the validity of the inference, A→B, B→C, therefore, A→C.

In the associative learning literature, similar findings have been termed second-order conditioning (Yin, Barnet, & Miller, 1994). Associative models of transitive judgments (such as value transfer theory) seek to explain the transitive responding as a property of the reinforcement history (e.g., von Fersen, Wynne, Delius, & Staddon, 1991), a debate that we will not address here (see Chapter 18, this volume). Instead, we will focus exclusively on transitivity in causal relations, as, for example, in social group hierarchies.

Playback experiments provided evidence for primates' and corvids' inferences about social interactions and the structure of their social group. Chimpanzees, for instance, looked longer to playbacks of agonistic calls that violated the social group hierarchy (Slocombe, Kaller, Call, & Zuberbühler, 2010). Similar effects have been found with baboons (*Papio cynocephalus ursinus* and *Papio hamadryas ursinus*; Cheney, Seyfarth, & Silk, 1995; Kitchen, Cheney, & Seyfarth, 2005) and ravens (Massen, Pašukonis, Schmidt, & Bugnyar, 2014). These findings raise the possibility that some animals make transitive inferences to learn the dominance hierarchy of their social group (Cheney & Seyfarth, 1990). Alternatively, animals might learn over time the dominance relationship of every single dyad in their group. However, the number of dyadic relations that they would need to learn grows quadratically with increasing group size. Transitive inference might help animals to learn dominance relations more efficiently by taking advantage of indirect evidence and without necessarily keeping track of every dyadic relationship in the group. In line with this, experimental studies with highly social animals such as pinyon jays (*Gymnorhinus cyanocephalus*; Paz-y-Miño et al., 2004) and fish (*Astatotilapia burtoni*; Grosenick et al., 2007) provided evidence that they can infer their own dominance position relative to unknown conspecifics based on observed interactions of unknown individuals with known group members.

Complex Causal Structures

So far, we have considered evidence in accordance with the view that some animals can use temporal information to discount alternative causes, represent causal chains, and perform in certain contexts transitive inferences about causal relations. Now we turn to the question to what extent animals can make different predictions about complex causal structures such as causal chains (A→B→C) and common cause models (A←B→C). In particular, something that is difficult to explain by standard associative accounts is the special treatment of (own or other agents') interventions. An intervention is defined as "an exogenous unconfounded experimental manipulation which puts the variable intervened on under the control of whatever causes the manipulation" (Woodward, 2011, p. 25). Interventions, thus, entail that the manipulated variable is independent of its other causes. Moreover, interventions are reliable indicators of causal directionality (Waldmann et al., 2008). An animal that is sensitive to the special status of interventions should, therefore, differentiate between events associated with own interventions and merely observed events. Blaisdell and colleagues (Blaisdell, Sawa, Leising, & Waldmann, 2006; Leising, Wong, Waldmann, & Blaisdell, 2008) provided evidence that rats (*Rattus norvegicus*) are indeed sensitive to this difference. In their experimental paradigm, rats got the opportunity to learn during a preconditioning procedure that a light stimulus (L) was the common cause of food (F) and an auditory stimulus (T; F←L→T). To establish this causal structure, the rats learnt both contingencies (L→T and L→F) separately. Following this training procedure, Blaisdell and colleagues (2006) removed the light bulb and presented the rats in the observation condition with the acoustic stimulus. In the intervention condition, the rats were given the opportunity to press a lever, which, in turn, was followed by the tone. Crucially, the rats expected food when they were presented with the tone but only in the observation condition (i.e., when they did not produce the stimulus themselves by intervening on the lever). Thus, Blaisdell and colleagues argued, the rats in the observation phase acted as if they had made the backward inference that the light (which was not visible because the light bulb was removed) must have caused the acoustic stimulus.

A second predictive inference would entail that the (unobserved) light also had caused the food. In the intervention condition, however, the rats acted as if they were reasoning that their own interventions, that is, the lever pressing, had caused the acoustic stimulus. Thus, the intervention should have affected only the acoustic stimulus but neither the light nor the food reward. When Blaisdell et al. (2006) changed the preconditioning procedure so that the rats were to learn a causal chain, with the acoustic stimulus causing the light cue which, in turn, was causing the food (T→L→F), the rats did not show such a difference between the intervention and observation condition. In both conditions of the causal-chain structure, the acoustic cue should lead to light, which should result in food. In line with this, the rats expected food in both observation and intervention conditions. These findings support the notion that rats can make inferences about complex causal structures and that they differentiate between the effects of own interventions and observed events. This interpretation has provoked a lot controversy (see Penn & Povinelli, 2007), with some arguing that response competition might be sufficient to account for the findings (Dwyer, Starns, & Honey, 2009). However, as pointed out by Blaisdell and Waldmann (2012), response competition would make predictions (e.g., a negative correlation between lever pressing and checking for food) that are not supported by the data. According to the single-effect learning model (Waldmann et al., 2008), the rats in this paradigm learn single causal relations (by using temporal cues to differentiate between cause and effect) and make sequential link-by-link inferences based on shared events of these relations (e.g., in a causal chain, A→B→C, B is inferred from A and then, C is inferred from B). In this way, rats may make inferences about complex causal structures without explicitly integrating multiple relations into coherent causal maps.

ON THE EVOLUTION OF INFERENCE

Several theories have been proposed to explain the evolution of inference. Perhaps the most well-known is transitivity and sociality. Schusterman, Reichmuth, and Kastak (2000) suggested that inference may serve the social domain. This hypothesis has been tested by directly comparing species that live in complex, hierarchically organized groups with nonsocial animals on tasks measuring transitivity using lists of arbitrary stimuli. Species living in complex social groups like pinyon jays and ring-tailed lemurs (*Lemur catta*) outperform nonsocial animals like scrub jays (*Aphelocoma californica*) and mongoose lemurs (*Eulemur mongoz*) regarding transitive inference (Bond, Kamil, & Balda, 2003; MacLean, Merritt, & Brannon, 2008). Aureli et al. (2008) proposed that species with higher fission-fusion dynamics (FFD) would possess more advanced inferential abilities than those with lower FFD, but this idea still awaits empirical verification.

Other theories have emphasized nonsocial aspects. Schloegl et al. (2009) hypothesized that food caching species might be especially prepared for exclusion as this ability might help them to locate cached food more efficiently. Food-caching specialists such as ravens, Clark's nutcrackers, and carrion crows perform well on the visual two-choice exclusion paradigm (at least when controlling for local enhancement) whereas other noncaching species such as keas or jackdaws perform poorly (Mikolasch, Kotrschal, & Schloegl, 2012; Schloegl, 2011; Schloegl et al., 2009). However, other species do not fit the predictions. Eurasian jays, a highly specialized food-caching species, showed little evidence for exclusion (Shaw, Plotnik, & Clayton, 2013) whereas African grey parrots, a noncaching species, can solve exclusion tasks (e.g., Mikolasch et al., 2011; Pepperberg et al., 2013). Thus, the relation between food caching and exclusion, even when focusing on corvids, is far from straightforward. Feeding selectivity has also been proposed to explain the fact that dwarf goats outperformed grazing sheep in the visual two-choice exclusion task (Nawroth, von Borell, & Langbein, 2014). Likewise, domestic pigs, which can also be characterized as selective foragers, solved a variant of the visual exclusion task (Nawroth & von Borell, 2015), but note that success was not spontaneous, which means that associative learning may have also been implicated.

It would be premature to attempt to decide which of these hypotheses is correct. The data available are simply too patchy to reach conclusive answers. Nevertheless, the data highlight that inferences may be advantageous for making predictions both about the ecological and social environment. Seyfarth and Cheney (2003; see also Dunbar, 1998) have made a compelling argument for why processes based on rote learning and memory may not be sufficient to explain how nonhuman primates deal with social complexity in a flexible manner. A similar argument could be made for some ecological problems involving complex foraging decisions. Furthermore, it is currently unclear whether inferential reasoning is a domain general ability that evolved to solve ecological and social problems or whether animals have evolved specialized inferential abilities to solve specific problems (e.g., dominance hierarchies), but that can be applied to other situations.

CONCLUSION

Making inferences entails relating disparate pieces of information. Animals of various taxa are capable of encoding spatiotemporal, arbitrary, and object–object relations, and using them to carry out various protological operations. The use of the disjunctive syllogism seems widespread in the animal kingdom, even though its complexity is likely to vary across species. To date, diagnostic and predictive inferences, especially about object–object relations, appear exclusive to great apes, corvids, and parrots, but more research is needed on other species. For species with a less developed object–object relation psychology, temporal structure of events may be the primary source of information about causal structures. Also for great apes, temporal information seems to be crucial when discounting alternative causal relations. Despite substantial progress in this area much more research is required to understand how inferential abilities develop, what is their structure and function, and how they may have evolved.

From an ultimate level perspective, mapping the distribution of inferential abilities across the animal kingdom is a crucial task, paying special attention to certain pivotal species by virtue of their phylogenetic position and/or their socioecological adaptations. With regard to the former, work with invertebrates is sorely needed. With regard to the latter, more data on species with diverse socioecologies would be highly desirable to examine the relation between socio-ecology and cognition. Although this question has received some research attention (e.g., Amici, Aureli, & Call, 2008; Bond et al., 2003; Stevens, Rosati, Ross, & Hauser, 2005; see also Volume 1, Chapter 10, this handbook), the data are still too patchy to construct a comprehensive picture about the timing and the socioecological determinants in the evolution of inference.

From a proximal level perspective, it is unclear whether all inferential abilities (e.g., disjunctive syllogism, transitive inference, diagnostic inference) are part of a domain general ability or whether each of them constitutes a separate module specialized and dedicated to solve particular problems (e.g., speeding up the mastery of dominance hierarchies). If the focus on multiple species is the key to map the evolution of inference, the focus on individuals, more specifically individual differences, is crucial to discover whether inference is a single process or can be segregated into multiple components. Although inferential tasks such as the slanted board and the shaken cup task cluster together, and set themselves apart from discrimination learning tasks (Herrmann & Call, 2012), this result needs to be consolidated by studies with larger samples both in terms of subjects and tasks. It is important that large scale studies include control conditions, because as we indicated throughout the chapter, noninferential solutions might be a viable alternative that needs to be ruled out.

The ontogeny of inference is largely unknown except for data on object permanence, but being based on the Uzgiris-Hunt scale makes its interpretation problematic (see Collier-Baker et al., 2004; Jaakkola, 2014). Future research should map how the boundaries of animals' causal representations develop. Field studies so far are underrepresented but crucial in this context for gauging how different upbringings may affect inferential reasoning. Finally, while we have reviewed evidence in this chapter showing how animals make inferences about their environment, it is still unclear to what extent they seek causal explanations. Future research may illuminate whether animals can deliberately produce interventions or, more generally, seek information to proactively uncover the causal structure of their environment.

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CHAPTER 30

COGNITIVE INSIGHTS FROM TOOL USE IN NONHUMAN ANIMALS

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Humans' daily life is dominated by, and depends on, the use of tools. Because we are so skilled at using tools, and attribute a pivotal role in human evolution to tool use, the existence of similar phenomena in nonhumans has always attracted attention. However, precisely defining which behaviors constitute tool use and manufacture in nonhuman animals is difficult. According to Shumaker, Walkup, and Beck (2011), tool use is

> the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool. (p. 5)

According to St. Amant and Horton (2008), tool use is the exertion of control over a freely manipulable external object (the tool) with the goal of (1) altering the physical properties of another object, substance, surface or medium (the target, which may be the tool user or another organism) via a dynamic mechanical interaction or (2) mediating the flow of information between the tool user and the environment or other organisms in the environment. (p. 1203)

Therefore, some behaviors, such as the use of food as bait to attract a prey, are considered to be tool use according to Shumaker et al.'s definition, but are not tool use according to St. Amant and Horton's definition because a dynamic mechanical interaction is not involved. Neither definition considers tool use to include behavior such as nest building because the relations among the objects constituting the nest are static. Finally, tool manufacture, according to St. Amant and Horton, "involves the fashioning or modification of objects in the environment to improve their suitability as tools" (p. 1206) and, according to Shumaker et al., is "any structural modification of an object or an existing tool so that the object serves, or serves more effectively, as a tool" (p. 11). Tool use has been classified according to the modes in which tools are used (e.g., dropping, pounding, inserting, etc.) and manufactured (e.g., detaching, subtracting, reshaping, combining; Shumaker et al., 2011).

Despite the debate about how to define tool use and manufacture, it is clear that these behaviors are exceedingly rare across the animal kingdom. Tool use has been documented in less than 1% of the animal genera currently identified, and a much smaller percentage of species manufacture tools. However, even though these behaviors are rare, they have a broad phylogenetic spread, with tool using being identified in many animal taxa (namely sea urchins, insects, spiders, crabs, snails, octopi, fish, birds, and mammals) and tool manufacture being identified only in some animal taxa (namely ants, crabs, birds, and mammals). Thus, tool use and tool manufacture has evolved multiple times across the animal kingdom.

Given the wide phylogenetic spread of tool use, it is clear that this behavior is not restricted to a

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particular level of cognitive ability (Beck, 1980). However, explaining the rarity and phylogenetic spread of tool use is difficult. Hansell and Ruxton (2008) suggested that tool use is rare because of few ecological contexts in which this behavior is advantageous. This idea implies that species only known to use tools in captivity would use them in the wild if it was beneficial and they had the opportunity to do so. This "lack-of-utility" explanation also predicts that wherever nutrient rich food resources occur that can be exploited with tools, such as termite mounds and dead logs containing wood boring grubs, species should use tools. However, this is not the case (Hunt, Gray, & Taylor, 2013). Given there are ample foraging opportunities when tool use could provide substantial benefits, the lack-of-utility hypothesis poorly explains the rarity of tool use.

The frequency of the independent occurrence of tool use across taxonomic groups suggests that important cognitive constraints are involved. Invertebrates and fish have the lowest frequency (one occurrence of tool use for every 98,090 species) compared to birds (one occurrence for every 165 species) and primates (one occurence for every 38 species; see Hunt et al., 2013). The earliest documentation of tool use in birds refers to Egyptian vultures using stones to break open ostrich eggs (Alexander, 1838). Since then, many bird species have been reported to use tools. The first report of tool use by chimpanzees (*Pan troglodytes*) was in 1843 (by Savage & Wyman, cited in Shumaker et al., 2011). In their catalogue of tool use, Bentley-Condit and Smith (2010) reported that 43 primate species used tools and most of the cases reported come from captivity. As with primates, many bird species have only been seen to use tools in captivity (44% of the 167 species documented by Bentley-Condit & Smith, 2010). According to the definitions we adopted, tool use is absent in reptiles and amphibians. These frequency data suggest (a) that tool use has arisen independently in birds and mammals at a far higher rate than in invertebrates and fish, and (b) an obvious positive correlation across the animal kingdom between the frequency of the independent occurrence of tool use and cognitive ability. Comparative work has correlated different measures of primates' and birds' brain size (see Volume 1, Chapter 24, this handbook) with continuous operational measures of cognition such as tool use (birds: Lefebvre, Nicolakakis, & Boire, 2002; primates: Reader & Laland, 2002), innovation (birds: Lefebvre, Whittle, Lascaris, & Finkelstein, 1997; primates: Reader & Laland, 2002), and social learning (primates: Reader & Laland, 2002). Results showed a strong positive relation between the frequency of flexible tool use and relative brain size in birds (Lefebvre et al., 2002; see Lefebvre, 2013 for a review) and relative neocortex size in primates (Lefebvre, 2013; Reader & Laland, 2002), with tool-using species having larger brains and possibly greater cognitive skills that may enable goal-directed use of tools. Moreover, the taxa that rank high on innovation, tool use, and social learning tend to be those that pass sophisticated cognitive experiments.

Tool use in invertebrates and fish appears to be rather stereotyped with a strong genetic basis, but a much more flexible behavior in birds and mammals (Alcock, 1972). Hunt et al. (2013) speculated that stereotyped tool use required an appropriate pre-existing inherited behavior that could evolve into tool use with minimal genetic tweaking. This process would severely restrict the evolution of tool use. Once evolved though, adaptive tool use with its large inherited component would quickly become ubiquitous within a species, as is characteristic of stereotyped tool use. These forms of tool use represent narrow specializations to solve particular problems and will not be further discussed.

RESEARCH ON FLEXIBLE TOOL USE IN ANIMALS

We focus on flexible tool use, which is the use of different tools possibly in different contexts to reach different types of goals (Boesch, 2013). Flexible tool use also implies the production of innovative solutions to respond to challenging or new situations (Call, 2013). Among the many features that indicate flexibility in tool use are (a) the number of different tools used to reach a goal and whether the order in which they are used is crucial (e.g., Wimpenny, Weir, Clayton, Rutz, & Kacelnik, 2009); (b) the complexity of the overall decisional process when using tools (e.g., Carvalho, Cunha, Sousa, &

Matsuzawa, 2008; Matsuzawa, 2001); (c) the number and kind of spatial relations (static vs. dynamic) among objects, surfaces, and movements that must be recognized or produced to achieve a goal (e.g., Fragaszy & Cummins-Sebree, 2005; Visalberghi & Fragaszy, 2012); (d) whether and when the tool is modified; (f) the extent to which tool use is a developmental acquisition; (g) the extent to which tool use repertoires differ across populations because of social influences; and (h) the ecological challenge solved with tools (Boesch, 2013).

Flexible tool use requires behavioral predispositions as well as cognitive abilities. Call (2013) proposed that the propensity to explore and manipulate objects, the ability to learn from the environment even without reinforcement and to recombine information acquired independently in terms of space and time are necessary ingredients to acquire this skill. Moreover, flexible tool use may imply active inhibition of prepotent and past responses, shifting and focusing attention from the irrelevant to the relevant features of the task, and selecting and planning the sequences of actions to be performed (Coolidge & Wynn, 2005; see also Chapter 27, this volume). Therefore, information from short-term and long-term memory systems is fundamental and the larger the capacity of working memory (see Chapter 10, this volume) the better the ability to maintain the integration of information (e.g., plans of actions, short- or long-term goals, or task relevant stimuli) in an active state despite interference and/or response competition (Kane & Engle, 2000, 2002). In fact, proficiency in flexible tool use seems related to the previously mentioned abilities (Bechtel, Jeschonek, & Pauen, 2013; Sabbatini et al., 2012; Seed & Byrne, 2010; Taylor & Gray, 2014).

Besides birds and primates, only a few species use tools with some flexibility (Mann & Patterson, 2013; Shumaker et al., 2011). Veined octopus (*Amphioctopus marginatus*) off the coast of Northern Sulawesi and Bali use coconut shell(s) for protection (Finn, Tregenza, & Norman, 2009). The behavior of carrying coconut-shell halves and assembling them into a protective shelter started when factories begun to discard shells in the ocean. It is likely that the already established use of large empty bivalve shells for protection by octopi initiated the new behavior. Interestingly, veined octopus use coconut shells to hide from predators even though carrying them around restricts locomotion. In Shark Bay, off the western Australian coast, bottlenose dolphins (*Tursiops* sp.) use their nose to stir up the ocean floor in search of food; a subset of the population (11% of adult females; Mann & Sargeant, 2003) tear off living sponges and put them over their nose to protect the skin from potential painful stimuli (Krützen et al., 2005). The sponge interferes with echolocation and grasping suggesting that the dolphins prefer to forage using sponges than having full visual and sonar information (Mann et al., 2008). Moreover, an analysis of social networks among weaned tool-using bottlenose dolphins showed that spongers preferred to associate with other spongers (Mann, Stanton, Patterson, Bienenstock, & Singh, 2012), which may be crucial to find the best sites for tools and prey. Calves of bottlenose dolphins spend thousands of hours observing maternal tool use before first performing sponging for themselves (Mann et al., 2008). As we will see following, flexible tool use has developed to a complex level only in a few bird and primate species.

Tool use across bird species occurs in diverse contexts mostly associated with foraging and physical maintenance, including pounding cached food with a hard object held in the bill and using diverse material such as sticks to assist in extracting otherwise difficult-to-access food (Bentley-Condit & Smith, 2010; Shumaker et al., 2011). A greater diversity of tool use has been reported in free-living birds compared to captive ones. However, diversity of tool use within a species in the wild remains extremely limited compared to that of primates such as chimpanzees (McGrew, 2013) and capuchin monkeys. In other words, tool use in birds is a much more specialized behavior compared to the generalist behavior seen in primates. We can only speculate why this is so, but it probably has a cognitive explanation.

Two bird species living on tropical pacific islands have evolved the habitual (i.e., repeatedly shown by several members of a group; see McGrew, 1992) and flexible use of tools in the wild to extract mostly invertebrate prey: the Galapagos woodpecker finch (*Camarhynchus pallidus*) that uses stick and thorn tools (Gifford, 1919), and the New Caledonian crow (*Corvus moneduloides*) that uses stick and leaf tools (Hunt, 1996). Other species that may have flexible tool use include the Australasian palm cockatoo (*Probosciger aterrimus*) that uses sticks to drum on hollow trunks in only a small area of its range and the American brown-headed nuthatch (*Sitta pusilla*) that uses bark scales to lever off bark to obtain invertebrates (see Shumaker et al., 2011, for more details). However, little is known about the flexibility of tool use in these two species.

Tool use in woodpecker finches was first reported in 1919 by Gifford. Early observations showed that finches safeguard tools and carry them between probe sites for repeated use (Bowman, 1961; Hundley, 1963). Tool users also make simple tools by detaching sticks and cactus spines. In captivity, tool using woodpecker finches modify tools by shortening them or removing troublesome side extensions (Eibl-Eibesfeldt & Sielmann, 1962; Millikan & Bowman, 1967). Tool use is a highly seasonal activity, being used to obtain around 50% of prey in the dry season (Tebbich, Taborsky, Fessl, & Dvorak, 2002). This suggests that dry-season-related food constraints could have been the crucial selection pressure for the evolution of tool use in woodpecker finches. Tool use by woodpecker finches developed in hand-raised juveniles without them observing conspecifics using tools (Tebbich, Taborsky, Fessl, & Blomqvist, 2001). Thus acquisition of their basic tool use involves a large genetically inherited component. Subsequent experiments with captive woodpecker finches investigated the cognition underpinning their tool skills. Tool-using woodpecker finches performed similarly to non–tool-using Galapagos small tree finches (*Camarhynchus parvulus*) and woodpecker finches, but below the level of New Caledonian crows with more complex tool skills (Tebbich & Bshary, 2004, Teschke, Cartmill, Stankewitz, & Tebbich, 2011; Teschke et al., 2013). Teschke et al. (2011) suggested that the similar performance of tool-using woodpecker finches compared to non–tool-using small tree finches supported the idea that nonhuman tool use does not require specialized cognition. However, this conclusion does not take into account the degree of learned behavior involved in the acquisition of tool skills or the complexity of the skills. For example, woodpecker finch-like tool skills that are rather simple and largely genetically inherited may require a minimal level of cognitive specialization.

Non–tool-using keas and rooks are examples of bird species that are good at solving physical problems in the wild without tools (Diamond & Bond, 1999; Hunt, 2014b), even though they are capable of flexible tool use in captivity. Hand-raised rooks have shown the most impressive tool skills among captive birds that do not use tools in the wild (see Chapter 27, this volume). For example, they are able to solve the Aesop's fable task, in which floating food inside a tube can be brought within reach if the water level is raised, if they have had prior experience in dropping stones to obtain a goal (Bird & Emery, 2009a, Taylor & Gray, 2009). The hand-raised rooks also bent the ends of nonfunctional straight wire into functional tools to extract a bucket with food from a tube (Bird & Emery, 2009b). The authors suggested that the wire-bending was insightful problem solving (Call, 2013; Seifert, Meyer, Davidson, Patalano, & Yaniv, 1995), that is, rapid recognition from experience that a bent tool was much more efficient. Although all four rooks bent the wire on every one of their 10 trials, Hunt et al. (2013) suggested that the rooks bent the inserted straight wire over the tube rim possibly by chance when they tried to pull it out of the tube. Nevertheless, the rooks were highly adept at handling objects and rapidly repeated actions associated with success. The hand-raised rooks show that certain non–tool-using, large-brained birds like *Corvus* species probably have the cognitive ability to use tools in the wild. However, the cognitive leap required to develop flexible and habitual tool use in the wild by a non–tool-using species is likely to be demanding (Hunt et al., 2013). Captive keas use tools in simple ways, including inserting sticks or balls into a box to move food so that it could be obtained (Auersperg, Huber, & Gajdon, 2011, Auersperg, von Bayern, Gajdon, Huber, & Kacelnik, 2011). A wild kea has recently been filmed using sticks as tools to probe into stoat traps (O'Connor, 2014), suggesting that novel problems may somehow help so-called clever, non–tool-using birds in the wild to overcome the cognitive demands of innovating tool use.

As with birds, tool use across primate species occurs in diverse contexts mostly associated with foraging and physical maintenance (Bentley-Condit & Smith, 2010; Shumaker et al., 2011). Interestingly, the published reports on tool use in captivity outweigh those in the wild (Shumaker et al., 2011), and a larger repertoire of tool behaviors have been described for captive groups than for wild populations, as highlighted by Fragaszy, Izar, Visalberghi, Ottoni, and de Oliveira (2004) and Fragaszy, Visalberghi, and Fedigan (2004) for capuchin monkeys. In addition, captive individuals also exhibit a larger variety of tool combinations and modifications than their wild counterparts (see Haslam, 2013, for a detailed discussion).

Before Goodall's (1963) report of tool use by wild chimpanzees, nonhuman tool use was commonly viewed as behavior that could say little about intelligence and cognitive evolution and "man the toolmaker" was considered the only one to make and use tools intelligently (Oakley, 1956). The discovery of flexible tool skills in chimpanzees provided more than a philosophical shift in human thinking. It offered the opportunity to investigate the role of tool behavior in cognitive evolution initially in our closest living relative and afterwards in many other species.

Termite-fishing (Goodall, 1963, 1964) was the first habitual tool use described for wild chimpanzees, at Gombe in Tanzania. Termite fishing involves inserting a stem into a termite nest to extract termites biting the invading object. Since then, countless other reports of tool use have been described. Shumaker et al. (2011) lists 60 different populations using tools and new findings on the technology of chimpanzees continue to emerge (Luncz, Mundry, & Boesch, 2012; McGrew, 2013; O'Malley, Wallauer, Murray, & Goodall, 2012; Sanz, Call, & Boesch, 2013). Habitual tool use has been documented in wild Sumatran orangutans *(Pongo pygmaeus abelii*) to extract the *Neesia* seeds without touching the prickly matrix of the fruit (Meulman & van Schaik, 2013; van Schaik, Fox, & Sitompul, 1996). In contrast, tool use is very rare in gorillas (*Gorilla gorilla*; Breuer, Ndoundou-Hockemba, & Fishlock, 2005; *Gorilla beringei beringei*; Kinani & Zimmerman, 2015) and even rarer in bonobos (*Pan paniscus*), though in captivity all the great ape species use tools spontaneously in flexible and diverse ways (e.g., Call, 2010; Gruber, Clay, & Zuberbühler, 2010; Haslam, 2013; for a review see Shumaker et al., 2011). Habitual stone tool use was also reported in 2007 in wild Burmese long-tailed macaques (*Macaca fascicularis aurea*) to access encased foods (Malaivijitnond et al., 2007). These macaques select stone tools of different size, shape and hardness to exploit different prey: pounding hammers are used to crush shellfish and nuts on anvils and axe hammers are used to pick or chip at oysters attached to boulders or trees (Gumert, Kluck, & Malaivijitnond, 2009; Gumert & Malaivijitnond, 2013). Finally, habitual tool use in wild tufted capuchins (*Sapajus* sp.) was reported about ten years ago (Fragaszy, Izar, et al., 2004; Moura & Lee, 2004; see Figure 30.1).

The systematic study of selection and use of tools in primate species has a long tradition in comparative psychology (e.g., Klüver, 1933; Köhler, 1925/1976; see also Tomasello & Call, 1997). The amount of data on tool use in primates is so vast that we will focus on the ability of chimpanzees to (a) select tools on the basis of functional features and use tool kits (i.e., the repertoire of tools used habitually by a group; Sanz & Morgan, 2007), (b) use tool sets (i.e., different tools one after the other in the correct functional order), (c) modify tools, and (d) use tools in sequence (i.e., use a tool to obtain another tool, which subsequently will serve to obtain an out-of-reach goal).

Tool Selection and Use of Tool Kits

Captive and wild chimpanzees treat functional and nonfunctional tool features differently and flexibly adapt to the requirements of the task at hand (e.g., Boesch & Boesch, 1990; Herrmann, Wobber, & Call, 2008; McGrew, 1992; Sanz & Morgan, 2010; see also Chapter 29, this handbook). Most of the studies on tool selection focused on visually accessible properties such as length (e.g., Mulcahy, Call, & Dunbar, 2005), shape (e.g., Povinelli, 2000), continuity, and support (e.g., Herrmann et al., 2008). More recently, nonvisually accessible properties, such as pliability have been also studied (e.g., Manrique, Gross, & Call, 2010). Moreover, the tool kits used by most chimpanzee populations for foraging,

FIGURE 30.1. An adult female bearded capuchin monkey carrying an infant on her back is using a quartzite stone to crack open a palm nut that weighs almost as much as she does (about 2 kg). Photograph by Elisabetta Visalberghi. Reprinted with permission.

sociality, sex, physical maintenance, etc. consist of about 20 different types of tools (McGrew, 2010). At Goualougo Triangle, Republic of Congo, the most commonly used tools are for extractive foraging, whereas at Ngogo (Kibale National Park, Uganda), they are for hygiene and courtship (Sanz & Morgan, 2007; Watts, 2008). Finally, whereas some tool-using behaviors are performed by all chimpanzee populations (e.g., leaf sponges to obtain drinking water, aimed throwing of objects) others are not. Nut-cracking (i.e., opening nuts by pounding or hammering them on hard objects) is performed by chimpanzees living in western Africa and not by the populations living east of the Sassandra-N'Zo river despite the presence of suitable nuts and stones; therefore, nut cracking is considered a cultural behavior (Whiten et al., 1999).

Tool Sets

Chimpanzees also use tool sets to achieve a single goal. The most impressive case concerns a population in Gabon using a tool set of five objects (pounder, perforator, enlarger, collector, and swab) to obtain honey from underground hives (Boesch, Head, & Robbins, 2009). Throughout the year the chimpanzees living in the Goualougo Triangle use two different tools to obtain termites from underground nests (Sanz, Morgan, & Gulick, 2004). To extract termites from subterranean (as opposed to elevated) nests chimpanzees have to insert the stout stick into the ground to create a long, narrow tunnel. Then, on its removal, chimpanzees insert the fishing probe, a second flexible stem with a frayed end, into the tunnel to collect the termites. Selecting the tool with the correct features for each of the two tasks is essential to solve this problem, because the flexible tool cannot perforate the ground and the rigid tool cannot catch the termites. Furthermore, the chimpanzees seemed to anticipate the task by arriving at termite nests with the puncturing stick and the herbaceous fishing tools that they would need.

Modification of Tools

Another interesting aspect of the Goualougo Triangle chimpanzees is that they gather stems from plants located near the termite nest to manufacture fishing probes. In particular, they

> uproot the stem or use their teeth to clip the stem at the base and then remove the large leaf from the distal end by detaching it with their hand or mouth before transporting the stem to the termite nest, where they complete tool manufacture by

> modifying the end into a “paint brush” tip by pulling the stem through their teeth, splitting the probe lengthwise by pulling off strands of fibre or separating the fibres by biting them. (Sanz, Call, & Morgan, 2009, p. 294)

Brush tools are more effective in gathering insects than unmodified ones (Sanz et al., 2009).

Sequential Tool Use

Chimpanzees also perform sequential tool use involving two or more tools. Sequential tool use differs from the use of a tool set because in the former the first tool acts on the second one to reach the goal, whereas in the latter the different tools are used one after the other. Nevertheless, in both cases the order in which each tool is used is not independent from the use and function of the other tool(s) and there is a time delay between tool use onset and the achievement of the goal. Sequential tool use is challenging because the subject must (a) recognize that tools can be used on a nonfood item, (b) resist the immediate motivation to use the tool to attempt to reach the food directly, and (c) be able to organize her/his behavior hierarchically (Taylor, Hunt, Holzhaider, & Gray, 2007). In captivity, spontaneous use of two tools in sequence has been reported in chimpanzees (Köhler, 1925/1976), gorillas, and orangutans (Mulcahy et al., 2005). More recently, spontaneous use of up to five stick tools in sequence has been reported for chimpanzees, bonobos, and orangutans (Martin-Ordas, Schumacher, & Call, 2012).

The two following sections provide case studies on species associated with our research: the New Caledonian crow and tufted capuchin monkeys. Choosing examples of tool behavior that evolved independently, and that we know well, should provide a basis for valuable comparative insight into the evolution of rudimentary technology and associated cognition.

NEW CALEDONIAN CROWS: ECOLOGY, BEHAVIOR, AND SPECIALIZATION FOR TOOL BEHAVIOR

New Caledonian crows are endemic to New Caledonia, situated in the tropical south-west Pacific Ocean. They live and forage in a wide range of habitats including mangroves, scrubland, and rainforest. They are a smallish black crow and males are generally larger than females (Kenward, Rutz, Weir, Chappell, & Kacelnik, 2004). Their unusually straight bill together with widely spaced and forward-facing eyes may be morphological adaptations for the efficient manipulation of tools (Troscianko, von Bayern, Chappell, Rutz, & Martin, 2012; Martinho, Burns, von Bayern, & Kacelnik, 2014). New Caledonian crows are also reported to have relatively large brains and enlarged associative forebrain regions (Cnotka, Güntürkün, Rehkämper, Gray, & Hunt, 2008; Mehlhorn, Hunt, Gray, Rehkämper, & Güntürkün, 2010), but these findings need to be confirmed (Medina, 2013).

Like other *Corvus* species, New Caledonian crows are opportunistic omnivores and eat a wide range of plant food and mostly invertebrate prey (del Hoyo, Elliott, & Christie, 2009; Dutson, 2011; Hannecart & Letocart, 1980). Like humans, they exploit candlenuts and longhorn beetles, the rich year-round food sources associated with candlenut trees (*Aleurites molucanna*), with flexible and novel techniques (Bluff, Troscianko, Weir, Kacelnik, & Rutz, 2010; Hunt, 2000b; 2014b; Hunt, Sakuma, & Shibata, 2002; Rutz & St. Clair, 2012). Their longhorn larvae “fishing” is an excellent example of their dexterous manipulation skills. Experienced birds first irritate a grub by using the tool tip to touch sensitive areas around its head, then position the tool tip at the large mandibles for the annoyed prey to grab on to it (Hunt, 2000b; Rutz et al., 2010). Larvae are then expertly extracted attached to the tool tip (see Figure 30.2).

An obvious adaptation for tool use in New Caledonian crows is a genetic predisposition to develop basic tool skills (Hunt, Lambert, & Gray, 2007, Kenward, Rutz, Weir, & Kacelnik, 2006; Kenward, Weir, Rutz, & Kacelnik, 2005). Such a disposition, however, does not exclude learning and innovation in the development and transmission of their tool behavior (Hunt, Abdelkrim, et al., 2007; Hunt & Gray, 2007a). Indeed, their impressive foraging techniques in the wild suggest that they have special cognitive abilities for developing innovative foraging solutions.

FIGURE 30.2. **Adult New Caledonian crow dexterously extracting a longhorn larva clamped onto the end of its stick tool. From *Crow Smarts*, by P. S. Turner, 2016, Boston, MA: Houghton Mifflin Harcourt. Copyright 2009 by Andy Comins. Reprinted with permission.**

The Use and Manufacture of Tools

New Caledonian crows make and use tools year-round and are one of the few bird species in which habitual tool use can be found in every population to some degree (Hunt et al., 2013). They use two distinctly different types of tools: living and dead tree twigs and similar stick-like material (Le Goupils, 1928; Hunt, 1996; 2000b; 2008; Hunt & Gray, 2002; 2004a; Troscianko, Bluff, & Rutz, 2008) and those made from the barbed edges of *Pandanus* spp. leaves (Hunt, 1996; Hunt & Gray, 2004b; see Figure 30.3). Within each type of tool, the crows manufacture simple and complex varieties. The degree of complexity for stick tools is largely to do with whether or not they are hooked implements. Crows manufacture the most complex stick tool by crafting crochet hook-like implements out of fresh forked twigs (Hunt, 1996; Hunt & Gray, 2004a; see Figure 30.4).

New Caledonian crows also use thorny vines and fern stolons to make hook tools that take advantage of naturally occurring hooks (Hunt & Gray, 2002). The degree of complexity of tools made from *Pandanus* spp. has to do with shape as all varieties of these tools incorporate hooks (Figure 30.3). *Pandanus* spp. leaves are long and narrow with strong parallel fibers and the leave edges are lined with strong, sharp barbs (Figure 30.3). Crows shape three distinct varieties of *Pandanus* spp. tools: simpler designs ripped along leaf edges that are either wide or narrow, and a complex tapered, or stepped, design (Hunt, 1996, 2014a; Hunt & Gray, 2003; Figure 30.3). Each of these three designs is an arbitrary shape unconstrained by characteristics of the raw material and tools are not retouched once removed from the leaf (Hunt, 2000a). Thus experienced crows manufacture *Pandanus* spp. tools to a pre-existing design. The manufacture of a range of designs for each type of hooked implement (i.e., stick and leaf type), and their use in orientations that enable birds to hook prey toward themselves, shows that New Caledonian crows are the only species besides humans to have incorporated hook technology into their tools (Hunt, 1996). On the island of Maré, adult crows generally specialize in using either the wide *Pandanus* spp. tools that they make there or (nonhooked) stick tools, and even mated pairs can have different preferences (Hunt & Gray, 2007b). How this parallel manufacture of two distinct tool types within a local population is maintained remains unknown.

Other studies have also found evidence of behavioral flexibility in the natural tool use of New Caledonian crows. In forest they repeatedly use tools at many probe sites, usually safeguarding them

FIGURE 30.3. Left: A young *Pandanus* spp. tree with mature leaves around 2 m long. Photograph by Vero Monjo. Reprinted with permission. Center: the artifactual evidence on a *Pandanus* spp. leaf of the manufacture of a two-stepped *Pandanus* spp. tool. Right: Examples of the each of the three distinct *Pandanus* spp. tool designs made by New Caledonian crows—a wide tool, a narrow tool, and a stepped tool. The working ends on all tools are at bottom (note the sharp barbs facing away from the working tip).

FIGURE 30.4. The common sequence of actions to manufacture a hooked twig tool from a fresh forked twig. The crow first breaks off and discards the left fork, leaving a blunt stump. Then it breaks off the right fork just below the fork join and removes the leaves from the unrefined tool. The crow finally refines the blunt stump into a pointed hook by removing small pieces of wood with its bill. The finished tool made by a New Caledonian crow is 13.1 cm long.

between foraging sessions (Hunt, 1996; Klump, van der Wal, St. Clair, & Rutz, 2015). Moreover, like chimpanzees (Povinelli, Reaux, & Frey, 2010), crows are capable of context-dependent tool use. When faced with a potentially hazardous object, such as a model spider or snake, they prefer to use a tool rather than their bill to interact with the object (Taylor, Hunt, & Gray, 2012; Wimpenny, Weir, & Kacelnik, 2011). Thus crows appear to understand that tools can be used to reduce the risk of physical harm, so they can use tools flexibly when faced with hazardous situations. This capability also suggests that they have separate representations of bill and tool during active tool use. That is, when using a tool crows, like chimpanzees, do not simply incorporate it into their body schema but instead appreciate that it remains an inanimate object even though it is being used to directly extend their body's reach.

At this point, we examine the degree to which New Caledonian crows (a) select tool on the basis of functional features and use tool kits, (b) modify tools, (c) move rewards with tools across irregular surfaces, and (d) use tools in sequence.

Tool selection and use of tool kits. New Caledonian crow populations studied so far have tool kits. As stick tool use exists in all populations, tool kits consist of stick and *Pandanus* spp. tools where the latter tools are made (Hunt, 1996). However, as crows make a range of stick and *Pandanus* spp. tools there is considerable variation in the exact makeup of tool kits. On the island of Maré, crows use nonhooked stick tools and wide *Pandanus* spp. tools (Hunt & Gray, 2007b). On mainland Grande Terre, tool kits can consist of (a) stepped *Pandanus* spp. tools and nonhooked and hooked sticks, (b) stepped and narrow *Pandanus* spp. tools and nonhooked and hooked sticks, or (c) all three *Pandanus* spp. tool designs and nonhooked and hooked sticks (Hunt & Gray, 2003). Further variation also exists in the kind of nonhooked and hooked sticks that are included in tool kits. On Maré, crows specialize in making nonhooked sticks out of fresh twigs and use the narrow, distal end for probing (see Hunt & Gray, 2002). In candlenut tree areas crows commonly use leaf stems from candlenut trees to try and extract longhorn beetle prey (Hunt, 2000b). Thus the common type of stick tools in their tool kits can depend on available raw material. In contrast, the particular *Pandanus* spp. tool designs in their tool kits are unrelated to the raw material and may be associated to some degree with task-specific probing requirements (Hunt, 2014a; Hunt & Gray, 2003). Furthermore, the considerable length variation in each *Pandanus* spp. tool design that occurs mostly between sites may also be related to function as well as traditional behavior (Hunt & Gray, 2003).

The degree varies considerably to which New Caledonian crows take into account functional features of the tools they use and make. Some of the best evidence that they make functional choices comes from studies where they have had to learn a new type of tool use. They have not been able to solve the Aesop's fable task spontaneously. However, after being trained to drop stones, they performed very well at a number of discrimination tasks where they had to choose between functional and nonfunctional objects. They show preferences, often from the first or second trial, to drop stones into water rather than sand-filled or empty tubes and prefer to drop large heavy or solid objects over small floating or hollow ones to access the floating food (Jelbert, Taylor, Cheke, Clayton, & Gray, 2014; Logan, Jelbert, Breen, Gray, & Taylor, 2014; Taylor et al., 2011). These performances are similar to those of children between the ages of 5 and 7 (Cheke, Loissel, & Clayton, 2012). Arbitrary tasks, where the previously rewarded stimuli were set up as cues in a search task, did not lead to the same discriminations (Taylor et al., 2011). This finding suggests that crows have an understanding of the task and that this understanding is used to guide their choices. These performances also show that, just like capuchins, the crows are able to take into account nonvisual features such as weight when selecting tools. In the floating versus sinking condition the crows were faced with white blocks that varied only in weight. They not only chose the heavy block over the light block, they actually discarded the floating block before observing how it interacted with the water.

Studies examining what wild New Caledonian crows understand about their tools led to more ambiguous findings. Recent work on Grande Terre demonstrated that crows that made hooked twig tools preferred to probe with the hooked end of the stick rather than the straight end, even when tool curvature and bark removal at the hooked end were experimentally manipulated (St. Clair & Rutz, 2013). However, on Maré, crows selected at random when offered one wide *Pandanus* spp. tool with leaf-edge barbs and one wide *Pandanus* spp. tool without leaf-barbs (Holzhaider, Hunt, Campbell, & Gray, 2008). Also, when choosing between one *Pandanus* spp. tool with the barbs in a nonfunctional orientation (facing downwards) and another with the barbs in a functional orientation (facing upwards), they select randomly. Therefore, the Maré crows did not take into account the presence or direction of barbs. Thus selectivity of ready-made tools by these crows may depend on the type of tool.

A similar pattern emerges when New Caledonian crows have to select tools on the basis of length and diameter. Chappell and Kacelnik (2002, 2004) reported that two wild-caught crows (a) selected tools that matched above chance level distance to food and (b) selected twigs for tool making with diameters that tracked, but did not exceed, hole width. One of the birds, Betty, had strong preferences for long and thin tools, characteristics which are highly functional in the wild (see Hunt & Gray, 2002). Also, when these preferences were taken into account these crows matched tool length to food distance and tracked hole width (Bluff, Weir, Rutz, Wimpenny, & Kacelnik, 2007). These findings suggested that they were taking into account the hole and the tool characteristics before selecting or making a tool. These results contrasted with those in Hunt, Rutledge, & Gray (2006), which showed that two free-living crows initially selected or made tools of “average” length, and if these tools did not work they then selected or made tools more suited to hole depth. This suggests that the strategy of New Caledonian crows was initially based on a heuristic, or default, approach, which was rapidly modified when it did not work. One possibility for the differences in these findings may be the captive versus naturalistic experimental approach adopted by the previous studies (Bluff et al., 2007). The crows in the Hunt et al. study could also forage away from the experimental site and they might have initially made tools functional at nearby foraging sites. Another possibility is that the matching and tracking found by Chappell and Kacelnik may be an artefact of their experimental designs (Silva & Silva, 2010, 2012). In similar tool length experiments, Silva and Silva (2010, 2012) found no evidence that human subjects tried to select tools that matched the distance to food. Also, woodpecker finches and New Caledonian crows in subsequent studies did not match tool length to distance to food (Bluff et al., 2010; Tebbich & Bshary, 2004; Wimpenny et al., 2009). Moreover, the matching of tool length is inconsistent with crows generally preferring to position the nonworking ends of tools along one side of their heads to hold tools more securely than to hold the nonworking end in the tips of their bills (Hunt, 2000b; Rutledge & Hunt, 2004), and the tracking of hole diameter is inconsistent with crows’ preference for thin tools.

Modification of tools. Although New Caledonian crows are famous for modifying natural material to make tools, experimental study of their tool modification skills has largely focused on the use of novel tool materials. Weir, Chappell, and Kacelnik (2002) reported that a crow named Betty had spontaneously shaped a novel material (straight wire) by bending it to extract a bucket containing food from a vertical tube. Whether or not Betty’s first wire-bending was a deliberate attempt to make a more efficient tool, rather than the accidental outcome of probing outside the tube, she subsequently repeated this behavior on nine further trials. It is currently unclear exactly how Betty generated this novel behavior. It is possible that the repeated wire bending was insightful problem solving. However, it is unclear whether Betty either understood or planned out her actions because in nine trials out of 10 she bent the wire only after trying to extract the bucket with the straight piece of wire. When she was subsequently tested on tasks where she had to reshape bent or unbent aluminum strips, she showed impressive skills at manipulating the new material in ways appropriate to the task (Weir & Kacelnik, 2006). Nevertheless, the authors concluded that she failed to provide conclusive evidence that she understood and planned her actions.

Moving rewards with tools across irregular surfaces. One widely used paradigm for testing physical cognition in animals is the trap-tube designed by Visalberghi and Limongelli (1994; see also Chapters 29 and 30, this volume). In this task a transparent horizontal tube has a hole in its middle connected to a trap whose content cannot be reached by the subject. A reward is placed into the tube nearby the trap and the subject could displace it only by using a stick to push it out. Depending on which side subjects insert the stick, the reward is either pushed out of the tube or into the trap. Once an animal has learned to successfully avoid pushing food into the trap researchers then present transfer problems where a critical feature of the problem is changed. In early versions of the trap-tube paradigm in the transfer task the trap-tube had been flipped upside down, rendering the trap non-functional (Visalberghi & Limongelli, 1994). An associative learning account predicts animals should continue to avoid the trap, regardless of its position, because of its association with loss of the food. In contrast, if this association is not affecting the strategy of solution, subjects should not take into account the trap. When presented with the trap-tube task birds used the tool to pull the food toward themselves (instead of pushing it as the original trap-tube task required to do), and New Caledonian crows and tool-using woodpecker finches ignore the inverted trap (Taylor, Hunt, Medina, & Gray, 2009; Taylor, Roberts, Hunt, & Gray, 2009; Tebbich & Bshary, 2004).

More recent transfer tasks have examined the response of animals when cues associated with the trap are removed, or reversed. The trap-table paradigm involves an animal avoiding a trap embedded into a table, rather than a hole in the bottom of a tube. This test can therefore be used to assess if an animal can continue to solve a problem when the cues associated with success have been removed. As the problem has a similar structure to the trap-tube task, an animal that has learned to solve the trap-tube can solve the trap-table task by transfer. New Caledonian crows can successfully solve by transfer the trap-table task from the first trial when using tools (Taylor, Hunt, et al., 2009), as can the great apes (Girndt, Meier, & Call, 2008; Martin-Ordas, Jaek, & Call, 2012; but see Martin-Ordas, Call, & Colmenares, 2008). When New Caledonian crows were presented with a trap-tube transfer task where they had to choose between an effective trap (with a base) and an ineffective trap (without a base), they chose at chance level. Given that the crows failed to predict that food would fall out of a tube if they pushed it into the baseless trap, it seems likely that their understanding of the problem has some limitations (Taylor, Hunt, et al., 2009).

Sequential tool use. A number of studies have examined if New Caledonian crows are capable of sequential tool use in which one tool is used to gain access to another. Crows used a small stick placed in front of a toolbox to pull within reach a longer stick that could then be used to gain access to out of reach food (Taylor et al., 2007). This behavior might have been underpinned by their natural tendency to attempt to retrieve attractive objects that are out of their reach (Clayton, 2007). This hypothesis is supported by the finding that in a sequential tool task crows continued to use a short tool to get a longer tool even when no food was present (Wimpenny et al., 2009) as if long sticks were attractive objects in their own right, most likely because of their past association with food. To examine if this conditional reinforcement hypothesis is sufficient to explain sequential tool use in New Caledonian crows, Taylor, Elliffe, Hunt, and Gray (2010) created a three stage task where crows had to pull up a string to obtain a short tool, which could then be used to get the long tool and thereby get the food by using it. This short tool was an unattractive object, because it had previously been associated only with failure because crows could not use this tool to get food. According to the condition reinforcement hypothesis the crows should not solve this problem, as they would have to act to gain access to a negative, unattractive object. However, the crows solved this problem, thus showing the ability to hierarchically organize tool behavior.

Acquisition of Tool Use

Mated pairs of New Caledonia crows live in long term monogamous relationships and there appears to be only limited dispersal of crows between populations (Abdelkrim, Hunt, Gray, & Gemmell, 2012, Rutz, Ryder, & Fleischer, 2012). On the island of Maré, pairs stayed together year round on permanent home ranges that overlapped with the home ranges of neighboring pairs (Holzhaider et al., 2011). An interesting aspect of the breeding system is that juveniles generally stay on their parents' home range up to the next breeding season, and sometimes longer (Holzhaider et al., 2011). During this time parents provide the opportunity for juveniles to learn complex foraging skills in two ways. First, mated pairs are extremely tolerant of their offspring and provide the social scaffolding over juveniles' first year that channels their learning in a particular direction (Holzhaider, Hunt, & Gray, 2010a; Holzhaider et al., 2011). For example, they tolerate juveniles at close quarters when using tools, even when juveniles sometimes "steal" their parents' extracted food and tools. Second, the exceptionally long period of parental care given to juveniles in the form of parental feeding may play a crucial role in the effectiveness of this scaffolding (Hunt, Holzhaider, & Gray, 2012). Continued feeding by parents means juveniles stay close to them when they are foraging, giving juveniles the opportunity to obtain information about tool making and how the tools are used. Thus extended parental care might be a life-history adaptation to ensure offspring acquire and perfect their tool-related foraging skills (Hunt et al., 2012).

Moreover, the learning component may be substantial in the ontogeny of tool-oriented behavior in New Caledonian crows (Kenward et al., 2006; Holzhaider et al., 2010a, 2010b) and their persistence in performing somewhat plastic object combinations (Bluff et al., 2010) facilitates learning of the tool manufacture techniques (Kenward et al., 2011). This pattern is consistent with that proposed for the acquisition of tool use in primates (Fragaszy & Adams-Curtis, 1991; Lockman, 2000).

TUFTED CAPUCHIN MONKEYS: ECOLOGY, BEHAVIOR, AND PREREQUISITES FOR TOOL BEHAVIOR

Capuchin monkeys are robust, medium-size Neotropical primates, with a semi-prehensile tail. A large ratio of brain size to body size also distinguishes capuchins from other monkey species (Fragaszy, Visalberghi, & Fedigan, 2004) and the neural substrate controlling capuchins' hand movements has a high number of sensorimotor fibers that are crucial for manual dexterity (Rilling & Insel, 1999). Recent molecular analysis has revealed that capuchin monkeys, formerly identified as the single genus *Cebus*, are two genera, with the robust (tufted) forms (including *libidinosus*, *xanthosternos*, *apella* and several other species) now recognized as the genus *Sapajus*, and the gracile forms retained as the genus *Cebus* (Lynch Alfaro, Boubli, et al., 2012; Lynch Alfaro, Silva, & Rylands, 2012). Tufted capuchins are widely distributed in South American countries with the exception of Chile and Uruguay (Lynch Alfaro, Boubli, et al., 2012; Lynch Alfaro, Silva, & Rylands, 2012). Tool use has been reported in *Cebus* and *Sapajus* species, but thoroughly investigated in captive settings and recently in the wild only in the latter genus (Visalberghi & Fragaszy, 2012).

Capuchin monkeys are omnivorous; their main food source is the pulp of mature soft fruits, complemented with invertebrate prey and other plant parts, such as seeds, flowers and stems. Occasionally they prey on small vertebrates, like birds, rodents and even small primate species (Fragaszy, Visalberghi, & Fedigan, 2004; Sampaio & Ferrari, 2005). Their diet can include anthropogenic food sources and they are able to survive in modified environments, including areas adjacent to agricultural fields, parks set aside for ecotourism and urban areas (e.g., Freitas, Setz, Araújo, & Gobbi, 2008; Sabbatini, Stammati, Tavares, & Visalberghi, 2008). Capuchins are renowned as extractive foragers, meaning that they exploit hidden and encased foods. Their foraging behavior is distinctive for its inclusion of a large variety of strenuous actions as well as precise ones. Among New World monkeys, capuchins stand out because of their high degree of manual dexterity (Fragaszy, Visalberghi, & Fedigan, 2004; Lacreuse & Fragaszy, 1997; Spinozzi, Laganà, & Truppa, 2007; Spinozzi, Truppa, & Laganà, 2004). They are able to perform relatively independent movements of the digits and to use a variety of precision grips (Christel & Fragaszy, 2000; Costello & Fragaszy, 1988; Spinozzi et al., 2004, 2007). They are particularly explorative and engaged with objects (Fragaszy, Visalberghi, & Fedigan, 2004). Captive capuchins of all ages devote considerable attention, time, and energy to manipulating objects (Visalberghi, 1988); moreover, they frequently combine objects and surfaces in actions (e.g., bang objects on surfaces and poke them into surfaces; Fragaszy & Adams-Curtis, 1991). These characteristics are important prerequisites of tool using skills and explorative tendencies and combinatorial manipulation are likely to lead to spontaneous discoveries and innovations.

The Use of Tools

The systematic studies on tool use in captive capuchin monkeys, which started at the beginning of the 20th century, show that they use many different types of tools to reach a wide variety of different goals (for a review of more than 70 studies, see Visalberghi & Fragaszy, 2012). At the beginning of the present century a few populations of wild tufted capuchins have been discovered to use stick and stone tools (Fragaszy, Izar, et al., 2004; Moura & Lee, 2004).

Although capuchin monkeys use tools mostly to obtain food, they do it also in situations not related to food acquisition. For instance, capuchins use stones and sticks during aggressive inter- and intraspecific interactions or toward predators, in captivity (Vitale, Visalberghi, & De Lillo, 1991) and in the wild (Boinski, 1988; Moura, 2007). In these cases, their throwing is rarely well aimed and the movement is not ballistic. Chimpanzees also throw stones in charging displays (Nishida, Zamma, Matsusaka, Inaba, & McGrew, 2010). Stone and stick throwing have also been used by females as part of their proceptive display (Carosi & Visalberghi, 2002; Falótico & Ottoni, 2013). Male chimpanzees of Mahale, Tanzania, use leaf-clipping to attract females during courtship (Nishida, 1980), whereas those in the Ngogo community (Kibale National Park, Uganda) use leaf-clipping and branch-waving for the same purpose (Watts, 2008).

At this point, we examine the degree to which capuchin monkeys (a) select tools on the basis of functional features, (b) modify tools, (c) move rewards with tools across irregular surfaces, and (d) use tool kits, tool sets and tools in sequence.

Selection of tools on the basis of functional features. Capuchins treat functional and nonfunctional tool features differently and flexibly adapt to the requirements of the task at hand (e.g., Visalberghi & Fragaszy, 2012). For example, they extract food with probing sticks (captivity: Fragaszy, Visalberghi, & Fedigan, 2004; wild: Mannu & Ottoni, 2009; Souto et al., 2011) and, in captivity, they select the functional stick to push food out of a horizontal tube from among four different objects and avoid using the nonfunctional ones (Visalberghi, 1993).

Capuchins can also take into account nonvisual features when selecting tools. They select stones, best suited to crack nuts open, on the basis of weight and/or the sound produced when tapped (Fragaszy, Greenberg, et al., 2010; Schrauf, Huber, & Visalberghi, 2008). When Visalberghi et al. (2009) tested wild bearded capuchin stone tool users by providing them new artificial stones that looked identical, they learned to acquire information about their weight by tapping with a finger on the surface and by using the sound produced to inform their choice (see Figure 30.5). Capuchin monkeys are also able to efficiently detect the rigidity of objects (Manrique, Sabbatini, Call, & Visalberghi, 2011). In this experiment the subject faces an out-of-reach reward whose recovery is possible only with a rigid tool (task 1) or only with a flexible tool (task 2). In one condition the subject could manipulate the tools and then choose which one to use; whereas in the other condition an experimenter repeatedly bent (or tried to bend) each tool in front of the subject. In both conditions, capuchins efficiently used the information previously gathered (in task 2, by inference) about tool affordances and selected the functional tool above chance levels. In this experiment, capuchins were able to obtain information by directly manipulating the tools as well as by inferring tool characteristics while observing the object's behavior when manipulated by the experimenter. Also, when a tool provides counterintuitive information (e.g., a big stone lighter than a small stone, so that size is not predictive of weight; see Figure 30.5), nut-cracker capuchins relied on the relevant feature (weight) that makes the tool functional and disregarded the irrelevant feature (size; Visalberghi et al., 2009).

FIGURE 30.5. The capuchin monkey has to select which stone to transport to the anvil to crack a palm nut. In this counterintuitive experimental condition the bigger artificial stone (right) is much lighter than the small one (left). To evaluate whether the stone has sufficient mass to be functional the capuchin taps it so to generate acoustic and haptic information concerning the density of the stone. Photograph by Elisabetta Visalberghi. Reprinted with permission.

Modification of tools. Recognizing an object as functional and using it is easier for capuchins than modifying an object appropriately before using it (Visalberghi & Trinca, 1989). Captive capuchins were presented with a transparent horizontal tube with a reward in the middle and with tools that were too thick (sticks taped together forming a bundle too wide to fit in the tube), too short (three short sticks, and at least two had to be inserted one after the other to dislodge the reward), or blocked (a stick with thin wooden blocks on either end). Subjects solved these conditions by dismantling the bundle, inserting one stick after the other, and removing the blocking pieces, respectively. Despite being always successful, they attempted to use the original object without modifying it and to use parts of the object that did not have the necessary properties to displace the food from the tube. These errors suggest that with limited exposure to the task (10 trials) there is still a poor comprehension of the necessary properties of the stick to displace the reward (Visalberghi & Trinca, 1989; Visalberghi et al., 1995). Apes and children performed better than capuchins as their error rates decreased across 10 trials (Visalberghi, et al., 1995; Visalberghi & Limongelli, 1996), suggesting a quicker appreciation of the role of the functional properties. It would be interesting to assess whether more experience with this type of problem would allow the monkeys to gain such an appreciation. Given our knowledge on how experience is vital for learning we predict this to be the case. In fact, experienced wild capuchins modify probing stick tools by resizing and trimming them to remove leaves and side branches; in a few cases the thinning of the distal extremity was also observed (Mannu & Ottoni, 2009).

Moving rewards with tools across irregular surfaces. Visalberghi and Limongelli (1994) tested four capuchin monkeys in the trap-tube task, previously described, and one of them was highly successful. This capuchin received a set of control conditions designed (a) to assess her comprehension of the functioning of the trap and (b) to single out the elements she used to solve the task. The results indicate that the strategy of avoiding the trap was used also when unnecessary (e.g., when the trap was above the tube and, therefore, ineffective) and the strategy was based on the distance rule of "inserting the stick into the opening of the tube farthest from the reward." Note that in all conditions (with and without the trap) the reward was always positioned slightly left or right from the tube center and the subject had to push the reward out of the tube. A subsequent experiment, in which the distances of the reward from the tube openings were controlled by modifying the lengths of the tube arms, proved that this capuchin was indeed using a distance-based associative rule, whereas the successful chimpanzees also tested with the trap tube did not (Limongelli et al., 1995).

In another study with a trap-tube task in which apes could rake the reward or push it out of the tube, only some chimpanzees and orangutans ignored the inverted trap when they could rake the reward; in contrast, bonobos and gorillas did not even learn to solve the trap-tube (Mulcahy & Call, 2006). Other experiments (e.g., Povinelli, 2000; Seed, Call, Emery, & Clayton, 2009) provided contrasting results. Some showed that chimpanzees fail to attend to the substrate on which pulling tools operated and ignore the location of a hole that could trap the food along its path; other experiments support the view that chimpanzees have an appreciation of the relation among the elements involved but have difficulties to manage the cognitive load imposed by tool use in this task. Although capable of causal reasoning, humans can also use undemanding heuristics and unnecessary biases to solve trap-tube problems. In fact, adult humans consistently inserted the stick into the end of the tube farthest from the reward and avoided the tube side with the trap also when it was above the tube and, thus, ineffective (Silva, Page, & Silva, 2005). The similarity of humans' and primates' behavior suggests that the use of simple heuristic procedures does not preclude the capacity for more sophisticated strategies.

Finally, captive capuchins are successful in using a hoe/rake to retrieve a reward placed on a surface presenting a hole or an obstacle (Fragaszy & Cummins-Sebree, 2005; Fujita, Kuroshima, & Asai, 2003; Fujita, Sato, & Kuroshima, 2011). Apes perform better in the trap-platform task than in the trap-tube task where they can push or rake the rewards (Martin-Ordas et al., 2008). Most likely when the hoe strikes the hole the subject can see/feel objects falling into the hole; this feedback from action can be very important for learning to move the reward past the hole and not into it (Visalberghi & Fragaszy, 2012).

Tool kits, tool sets, and sequential tool use. At the Parque Nacional da Serra da Capivara (Brazil) wild capuchins use sticks as probing tools (e.g., to access honey, vertebrate prey, insect nests, water) and stones as digging tools (to access roots and tunnel spiders; Falótico & Ottoni, 2011; Mannu & Ottoni, 2009; Ottoni & Mannu, 2001). This tool kit favors the emergence of tool sets (e.g., the use of one stone to excavate soil and of a second stone to strike the embedded plant tuber) and sequential tool use (e.g., the use of small stones to loosen bigger quartz pebbles embedded in conglomerate rock). Captive capuchins use tool sets, such as a stone to crack a nut, and then a stick to pry out pieces of nut kernel (Westergaard & Suomi, 1993). They also spontaneously use a short rigid stick to obtain a longer rigid stick (Anderson & Henneman, 1994), or a rigid stick to obtain a flexible one that could be used to dip into a 90° angled tube (Sabbatini et al., 2014). Finally, trained capuchins use up to eight rake tools in sequence (Warden, Koch, & Fjeld, 1940). As previously described, apes use tool sets and are proficient in using tools sequentially also without training.

Stone Tool Use

S. libidinosus and *S. xantosternos* are the only species known to use stone tools in the wild to crack open nuts (Canale, Guidorizzi, Kierulff, & Gatto, 2009; Fragaszy, Izar, et al. 2004; Mendes et al., 2015; Moura & Lee, 2004; Ottoni & Izar, 2008; Waga, Dacier, Pinha, & Tavares, 2006). The reports on stone tool use come from seasonally dry Cerrado and Caatinga habitats in the north-east and center of Brazil. Four wild populations of *S. libidinosus* were seen using stone tools (Parque Nacional de Brasília, Distrito Federal: Waga et al., 2006; Fazenda Boa Vista, Piauí: Spagnoletti et al., 2012; Parque Nacional da Serra da Capivara, Piauí: Ottoni & Izar, 2008; Serra Talhada, Pernambuco: De Moraes, Da Silva Souto, & Schiel, 2014). The food items exploited with tools vary across populations. At Fazenda Boa Vista, Piauí, stones were used to process palm nuts

(*Astrocaryum campestre*, *Attalea barreirensis*, *Orbignya* sp. and *Attalea* sp.) and other encapsulated food items such as cashew nuts (Sirianni & Visalberghi, 2013; Spagnoletti, Visalberghi, Ottoni, Izar, & Fragaszy, 2011); at the Parque Nacional de Brasília stones were used to process *Hymenea courbaril* fruit and *Acrocomia aculeata* nuts (Waga et al., 2006); at Parque Nacional da Serra da Capivara, Piauí, stones were used not only to access encapsulated fruit, as observed at the other sites, but also to dig for tubers (*Cobretum* sp. and *Spondia tuberosa*) and roots (*Astronium* sp.) and to cut wood to extract insects and larvae (Mannu & Ottoni, 2009); at Serra Talhada stone tools were used to access hard and encapsulated food (*Manihot epruinosa* seeds; fruit of *Syagrus oleraceae*; *Commiphora leptophloeos* seeds) and to process plant parts protected by thorns (Cactaceae: *Pilosocereus pachycladus* and *Tacinga inamoena*; De Moraes et al., 2014).

These differences in tool use across capuchin populations can result from differences in the availability of stones types and food items and to the degree of terrestriality (i.e., opportunities to encounter nuts and stones; Meulman, Sanz, Visalberghi, & van Schaik, 2012; Ottoni & Izar, 2008; Visalberghi et al., 2005). Variation in tool use and tool manufacture in response to environmental characteristics is reported in wild chimpanzees, however cultural factors and local traditions have also been demonstrated (Boesch & Boesch, 1990; Luncz et al., 2012; Schöning, Humle, Möbius, & McGrew, 2008; Whiten et al., 1999). The relatively very few systematic studies of tool use by wild capuchin monkeys severely hinder a proper understanding of tool use variation in these primates (Mannu & Ottoni, 2009; Sirianni & Visalberghi, 2013).

At Fazenda Boa Vista, Piauí, researchers have carried out field observations and many field experiments to investigate how skillful bearded capuchins are when using stone tools and making decisions concerning tool use (for a review see Visalberghi & Fragaszy, 2013). Pounding nuts and other encapsulated food items on a hard surface involves two spatial relationships between objects concurrently (Visalberghi & Fragaszy, 2012). In this situation the nut must not only be placed in relation to the hammer, but, at the same time, must also be correctly placed on a hard anvil for the pounding to be successful. Apart from managing more relationships, the tool user has to correctly select the hardness of the hammer and the anvil accordingly to that of the nut and needs to bring the elements together before being able to act (Boesch & Boesch, 1984; Spagnoletti et al., 2011).

Bearded capuchins are sensitive to the physical properties of hammers, such as weight and material, and choose or use the "functional" tools on the basis of the hardness of the food item they want to crack (Spagnoletti et al., 2011; Visalberghi et al., 2009; Fragaszy, Greenberg, et al., 2010). To crack palm nuts stone tools should be resistant and heavy. Heavier stones are more expensive to lift and use but produce more kinetic energy than smaller stones. Capuchin monkeys have marked sexual dimorphism in body mass, with adult males weighing 57% more than adult females (3.7 kg vs. 2.1 kg; Fragaszy, Pickering, et al., 2010). Field observations showed that when females crack high resistance nuts they use heavier stones (median 1250g) than when cracking low resistance nuts (median 873g; Spagnoletti et al., 2011). In contrast, the resistance of nuts did not affect the weights of hammers used by males, likely because of their higher body masses. Therefore, capuchins take into account the mass of the stone and the resistance of the nut and their own strength.

Nutcrackers have a strong preference for placing nuts into the pit of the anvil in a stable position, rather than on its flat surface, and by doing so they decrease the percentage of times in which the nuts are displaced after the strike and efficiency is increased (Fragaszy, Liu, et al., 2013; Liu et al., 2011). Massaro, Liu, Visalberghi, and Fragaszy (2012) investigated the role of stone mass and stone distance from the anvil on capuchins' selection. When stones are of equal mass capuchins prefer to transport to the anvil the closer stone rather than the one further away. When the heavier stone is 3 m from the anvil and the light stone is 6 m away, all capuchins select the heavier stone because it is more effective to crack nuts, that is, the nut can be cracked open with few strikes. On the contrary, if the heavy stone is far from the anvil individuals vary in their sensitivity to distance of transport. Small-bodied individuals perceive that transporting the heavy stone for 6 m is too costly and select the lighter stone closer to the anvil, even if it requires many more strikes. In contrast, large-bodied individuals always chose the most effective tool, regardless of distance. Finally, when provided with a heavy stone far from the anvil and a light stone on the top of the anvil capuchins transported the heavy stone only when given high resistance nuts, and not when given low resistance nuts (Massaro, 2013). Therefore, they performed optimal choices that took into account the mass of the stone, its distance from the anvil and the resistance of the nut.

Acquisition of Tool Use

The possibility to generate feedback from actions is crucial for learning when using tools (Visalberghi & Fragaszy, 2012). Learning to use tools involves managing the multiple degrees of freedom involved in generating the correct forces, trajectories and orientations that the tool makes with objects and surfaces, and to do this skillfully takes considerable practice (Bril, Rein, Nonaka, Wenban-Smith, & Dietrich, 2010). In capuchins the acquisition of tool use skills is a developmental process that lasts years. Simply observing another individual using a tool is not sufficient for even an adult novice to acquire these skills, and youngsters face much steeper challenges than adults. Proficiency in using common hand tools, such as a spoon or a pair of scissors, takes human infants months or years of practice (Lockman, 2000). Situational features that motivate individuals to manipulate the relevant materials in the right place support the acquisition of tool use; combinatorial exploration produces information that guides subsequent activity and may lead to the acquisition of tool use. For example, learning how to crack nuts with stones begins with capuchin infants manipulating objects, including stones, by beating them against a substrate. One-year-olds often attempt to crack nuts. However, the proper coordination of movements and positioning of nuts, "hammer" stones, and "anvils" (any hard and level substrate) is not usually reached until about 3 years of age (de Resende, Ottoni, & Fragaszy, 2008). Also adult capuchin that are naive learn stone tool use by trial-and-error (Visalberghi, 1987).

Interestingly, young capuchins differ from young chimpanzees in the probabilities of performing the two essential actions of tool use, placing the nut and striking it with a stone. Young chimpanzees readily place objects on a surface and then release their grasp, but they do not often strike one object with another. Capuchins show the reverse pattern, striking readily but placing and releasing less often. From an age earlier than 3 years old, though, capuchins are very interested in nut cracking by other individuals. Observers are typically younger than the observed nutcrackers who can be the mothers as well as other adults and juveniles. The food-related activities of the dominant males tend to attract much attention. Some scrounging by young observers is also allowed. Scrounging, as a proximate motivation, optimizes the conditions for social learning of nut cracking techniques (Ottoni & Izar, 2008). Enduring artifacts associated with tool use, such as previously used tools, partly processed food items and residual material from previous activity, aid chimpanzees and capuchins to learn to use tools, and to develop expertise in their use, thus contributing to traditional technologies in nonhumans (Fragaszy, Biro, et al., 2013). This expands the contribution of social context to learning a skill beyond the immediate presence of a model nearby.

CONCLUDING REMARKS ON ECOLOGY, COGNITION, AND TECHNOLOGY

Studies carried out in captive and wild settings demonstrate that a few bird and several primate species perform flexible tool use. Experimental studies showed that birds and primates (although with certain variability and limitations among and within the species tested so far) are able to attend and encode the task relevant features to achieve success, and to select and hierarchically organize the sequences of actions to be performed. Moreover, it can be argued that experience is fundamental to acquire tool using skills; birds and primates do not form a simple association between tool type and reward to be obtained. This raises the intriguing possibility that finding new solutions to physical problems involves not only background knowledge about object properties, but also an ability to use that information to predict how a tool will behave when acted on. However, results also suggest that birds and primates have difficulties in taking into account the multiple features of the elements of the task and in monitoring the spatial relations among these elements. These difficulties probably emerge when the problem-solution distance and the relational complexity inherent in tool use increase, and thus also increasing the associated working memory requirements (Haidle, 2010, 2014).

In the wild, New Caledonian crows are only known to use tools in a foraging context, but in captivity they have used tools in a different context to examine a potentially dangerous object. In the wild and in captivity, they skillfully manufacture different types of complex tool designs. In contrast, in both settings capuchin monkeys and chimpanzees perform many different behaviors to use many types of tools in many contexts; however, they modify tools at a lower frequency than the crows. Therefore, tool use is more versatile and multipurpose in primates than in New Caledonian crows (and other birds as well). This might be due to the greater behavioral repertoire/flexibility of primates compared to birds, their greater manipulative skills (the primate hand is better designed at grasping/holding/moving objects than the bird beak) and, possibly, their more complex learning skills.

Hunt et al. (2013) proposed that the differences between birds and primates might be due by different processes and mechanisms of transmission. Once tool use in New Caledonian crows appeared, strong selection probably drove their suggested adaptive complex for this behavior (Hunt & Gray, 2007a). In fact, the widespread occurrence of basic tool skills in New Caledonian crows and woodpecker finches has a strong genetic basis (Tebbich et al., 2001; Kenward et al., 2005). In their scenario, an inherited disposition for a specific kind of tool use combined with limited social learning facilitates the vertical transmission of adaptive tool use within species. Minimising horizontal transmission also facilitates the standardization of tool skills and therefore their potential enhancement (Sterelny, 2006). The context-specific tool use and probable diversification and cumulative change of tool designs in New Caledonian crows (Hunt, 2014a; Hunt & Gray, 2003) are consistent with this scenario. In contrast, lack of a disposition for a specific type of tool use and an increased reliance on social learning (providing horizontal and vertical transmission of tool skills) facilitates greater contextual diversity of tool use within species, including non-adaptive tool use (see Chapters 19 and 20, this volume). Moreover, tool use in primates may have arisen even without strong selection pressures. In fact, the adaptive value of tool use in terms of individual fitness in primates has not yet been demonstrated (Biro, Haslam, & Rutz, 2013) and the relation between tool use and food scarcity is not supported by recent research whereas tool use rate correlates with the abundance of foods to be exploited with tools (Koops, McGrew, & Matsuzawa, 2013; Sanz & Morgan, 2013; Spagnoletti et al., 2012).

Koops, Visalberghi, and van Schaik (2014) proposed a more general scenario in which three sets of factors, namely environment, sociality and cognition, influence invention, transmission, and retention of material culture. First, the environment provides ecological opportunities, in terms of resource density and likelihood to encounter them, which prompt innovation, transmission and retention of tool use. Second, social opportunities for tool use in terms of social tolerance, gregariousness and leftover artefacts from tool-use activities influence transmission and retention of tool use. Third, cognitive capacities for tool use in terms of individual and social learning abilities are also important. Individual learning plays a crucial role to prompt innovation, whereas socially biased learning is essential for transmission of tool use among group members.

The differences between New Caledonian crows and tool-using primates may be important for understanding early technological progress. There is little evidence to date that primates which habitually use tools have adaptations associated with their tool behavior or have enhanced their tool designs in cumulative-like way. In contrast, New Caledonian crows appear to have a range of adaptations associated with their tool behavior and seem to have enhanced their tool designs in a rudimentary, cumulative-like way (Hunt & Gray, 2003). Although the latter claim remains contentious

(Hunt, 2014a; Lewis & Laland, 2012), New Caledonian crows provide the best evidence for such technology. This raises the question about whether specialization via an adaptive complex associated with tool behavior is a crucial requirement for the evolution of technological progress. If we wish to learn how cumulative technology and its associated underlying cognition evolve, comparative investigation using primate and avian models is necessary because technological progress is likely to be underpinned by adaptations supporting fixed phenotypes and flexible mechanisms (Biro et al., 2013; Meulman, Seed, & Mann, 2013).

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CHAPTER 31

THE COMPARATIVE PSYCHOLOGY OF METACOGNITION

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Metacognition—the monitoring and control of one's cognitive processing—is an important research area in cognitive psychology and cognitive neuroscience (Dunlosky & Bjork, 2008; Flavell, 1979; Fleming & Frith, 2014; Nelson & Narens, 1990). It is a human capacity central to learning, comprehension, and communication. It is a sophisticated capacity possibly linked to consciousness and self-awareness (Koriat, 2007; Nelson, 1996). It emerges late in development (Balcomb & Gerken, 2008). It might be uniquely human (Metcalfe & Kober, 2005).

Given metacognition's importance, one naturally asks whether nonhuman animals share aspects of metacognition (Kornell, 2009; Metcalfe, 2008; Smith, 2009). If so, it could reveal their reflective minds. It could provide animal models for metacognition and nonverbal ways to foster it in populations with language impairments. Thus, researchers have actively explored animal metacognition (e.g., Basile, Schroeder, Brown, Templer, & Hampton, 2015; Beran, Smith, & Perdue, 2013; Call, 2010; Couchman, Coutinho, Beran, & Smith, 2010; Foote & Crystal, 2007; Fujita, 2009; Kornell, Son, & Terrace, 2007; Paukner, Anderson, & Fujita, 2006; Roberts, McMillan, Musolino, & Cole, 2012; Smith, Coutinho, Church, & Beran, 2013; Suda-King, 2008; Sutton & Shettleworth, 2008; Templer & Hampton, 2012; Washburn, Smith, & Shields, 2006; Zakrzewski, Perdue, Beran, Church, & Smith, 2014). Primates especially show seemingly metacognitive performances in tasks of perception, memory, foraging, and information seeking.

However, as in all areas of behavioral research, interpretative issues arise. Different psychological interpretations of metacognitive phenomena are possible. One could emphasize associative or higher-level cognitive processes. We do not prejudge where animals' performances lie on this continuum. Instead, we summarize the field's empirical and theoretical progress to date. The animal metacognition literature presents an illuminating mosaic of theoretical perspectives in comparative psychology, concerning when and why different psychological descriptions of animals' uncertainty performances are warranted.

The basic problem in this field is that studying animal metacognition presents patent methodological issues. One cannot just borrow the techniques of human research (e.g., introspective self-reports). Animals cannot make these reports. Therefore, researchers must foster behavioral responses that might indicate metacognition. One standard uncertainty-monitoring paradigm uses a two-alternative forced choice (2AFC) task (e.g., categorizing a pixel box as sparsely or densely populated). The animal also is given an optional uncertainty response (UR) that can be used to opt out of the trial without penalty and sometimes without reward (a sparse-uncertain-dense task). The UR lets animals manage their uncertainty and declare it behaviorally and observably. If animals do monitor internal states of confidence, they should decline difficult trials selectively because these trials foster doubt selectively. Humans (*Homo sapiens*) and some animals (rhesus macaques [*Macaca mulatta*], a bottlenosed dolphin [*Tursiops truncatus*], and rats [*Rattus norvegicus*]) have used the UR adaptively, skipping harder

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trials near the animal's discrimination breakpoint, despite sacrificing a possible reward for responding correctly with a primary perceptual-classification response (Foote & Crystal, 2007; Smith et al., 1995; Smith, Shields, Schull, & Washburn, 1997).

The UR has a long history in psychophysics (see Chapter 1, this volume)—humans were often allowed to respond "uncertain" on difficult classification trials (Watson, Kellogg, Kawanishi, & Lucas, 1973). Some psychophysicists thought that URs were qualitatively different from primary perceptual responses because they are a metacognitive report. If animals' URs have this status, they are important behavioral ambassadors. The uncertainty paradigms also have connections to studies of animal consciousness. Weiskrantz (1986, 1997) considered studying consciousness behaviorally. His thought experiment provided animals two discrimination responses and a commentary key with which to report on the status of their knowledge or perception. The UR is close to this commentary key, thus Weiskrantz was an influential original voice in this area. We agree that this approach could—pending careful theoretical work—ground explorations of animal consciousness. Toward this possibility, Cowey and Stoerig (1995) showed that macaques will use a commentary key to declare behaviorally that they think they haven't seen a stimulus.

Nonetheless, there are possible low-level explanations of the macaques' metacognitive performances. They might be explained associatively if animals' URs are cued by stimuli or shaped by reinforcement (see Chapter 18, this volume). Therefore, an associative concern is natural, appropriate, and constructive. This is why the associative-metacognitive debate has dominated the area (Basile & Hampton, 2014; Basile et al., 2015; Carruthers, 2008, 2014; Hampton, 2009; Jozefowiez, Staddon, & Cerutti, 2009a, 2009b; Le Pelley, 2012, 2014; Smith, 2009; Smith, Beran, Couchman, & Coutinho, 2008, Smith, Beran, Couchman, Coutinho, & Boomer, 2009a, 2009b; Smith, Couchman, & Beran, 2012, 2014a, 2014b; Smith, Zakrzewski, & Church, 2015; Staddon, Jozefowiez, & Cerutti, 2007).

For example, the use of concrete stimuli in the early studies to cause animals difficulty and uncertainty could clearly be problematic. Error-causing stimuli could be associatively aversive and avoided for this reason—not based on any metacognitive judgment. Accordingly, Metcalfe (2008) made stimulus absence in metacognitive tasks a benchmark in her operational definition of animal metacognition, and we can ask whether animals meet this invisible-stimulus criterion.

Uncertainty tasks could also induce response competition and produce behavioral-cue associations of hesitation and vacillation. Accordingly, Hampton (2009) distinguished performances that were based on public mechanisms (publicly visible cues) from private mechanisms, revealing the animal's privileged access to internal cognitive states.

A third concern is raised by studies that give animals concrete rewards for their metacognitive responses (Foote & Crystal, 2007; Fujita, 2009; Hampton, 2001; Inman & Shettleworth, 1999; Kornell et al., 2007; Suda-King, 2008; Sutton & Shettleworth, 2008). This approach might increase the low-level response strength of the UR, making it attractive in some contexts even though it expressed nothing metacognitive.

A fourth concern arose as some fit associative models to animals' uncertainty-monitoring performances (e.g., Jozefowiez et al., 2009a, 2009b; Le Pelley, 2012; Smith et al., 2008, 2015; Staddon et al., 2007). Generally, these models assume that animals store the reinforcement histories associated with different stimuli and respond with aversion–avoidance (not metacognitive) responses when they encounter error-causing stimuli. These models have played an influential role in fostering our literature's presumption of associationism. As we will discuss, we must delimit carefully the contribution that formal models can and cannot make to theory in this area.

The general problem remains, though. One must give animals indeterminate trials to produce the uncertainty they may monitor. This will lead to errors and lean rewards. Associative-learning processes could sense these contingencies, entraining avoidance responses that seem metacognitive but are not. This is the challenge for the animal metacognition *researcher*. However, metacognition might be present, as in humans, though stimuli are visible and there is behavioral hesitation and reinforcement information. So the problem is to interpret the findings judiciously, leaving room to see an important facet of animal minds that might be there. This is the challenge for the animal metacognition *theorist*.

RECENT CONTRIBUTIONS TO ANIMAL METACOGNITION RESEARCH

This area has seen strong empirical progress. In this section, we present a range of important and especially recent findings in the area, in a straight up and theoretically neutral manner, so readers can ground themselves empirically in the area. Some early studies are not covered, as they were reviewed in other places (Kornell, 2009, Metcalfe, 2008; Smith, 2009; Smith et al., 2012, 2014a; Smith, Shields, & Washburn, 2003). See Table 31.1 for a summary of the animal results described in this section.

Hampton (2001)

Hampton (2001; also Kornell et al., 2007) explored macaques' metamemory. Rhesus macaques performed a matching-to-sample (MTS) task. The UR let monkeys accept a less preferred reward by declining the memory test. Monkeys selectively declined memory tests at long delay intervals when they had forgotten the sample. Note that the sample (the memory target) applied for a single trial. Animals couldn't condition to avoid particular stimuli. They might need to "friend" those stimuli on the very next trial. Moreover, the UR was made when there was no stimulus present that could trigger

TABLE 31.1

Recent Contributions to Animal Metacognition Research

Reference and task	Nonhuman species	Metacognitive measurement	Main result
Hampton (2001): MTS task	Rhesus macaques	Uncertainty response	Monkeys used URs more often for items after extended delay
Smith et al. (1998): Serial-problem recognition task	Rhesus macaques	Uncertainty response	Monkeys used URs more often for items in memory-tenuous list positions
Washburn et al. (2010): MTS task using divided visual field paradigm and transcranial magnetic stimulation	Rhesus macaques	Uncertainty response	Monkey used URs on trials for which TMS stimulation disrupted poststimulus processing and retention
Basile et al. (2015): Information-seeking and memory task	Rhesus macaques	See-the-answer response	Researchers found no evidence supporting behavioral cue association, rote response learning, expectancy violation, response competition, generalized search strategy, or postural mediation
Call and Carpenter (2001): Baiting task	Chimpanzees, Orangutans	Choosing and looking behavior	Apes visually inspect containers when baiting was not seen
Beran et al. (2013): Lexicon symbol naming task in baiting task	Chimpanzees	Naming food using lexicon symbols	Apes inspected container for food that was baited without knowledge before naming
Beran et al. (2015): Delayed memory task	Chimpanzees	Confidence "movements"	Apes selectively moved to delivery site to receive reward for correct responses
Washburn et al. (2006): Discrimination and MTS tasks	Rhesus macaques	Uncertainty response	Monkeys generalized UR without training
Zakrzewski et al. (2014): Discrimination task	Rhesus macaques	Cashout response (modified UR)	Monkeys cashed out accumulated tokens based on trial difficulty and risk
Morgan et al. (2014): MTS task	Rhesus macaques	Retrospective and prospective confidence judgments	Monkeys showed transfer of high/low bets from retrospective to prospective task
Smith et al. (2006): Discrimination task with deferred feedback	Rhesus macaques	Uncertainty response	Monkeys selectively used UR for difficult trials without immediate reinforcement
Smith et al. (2013): Discrimination with and without concurrent MTS task	Rhesus macaques	Uncertainty response	Concurrent load reduced UR but not primary discrimination responses

an avoidance response. Hampton also compared URs on sample-present trials (a memory sample presented) and blank trials (no memory sample presented). Now, with the delay interval controlled, animals made more URs on blank trials.

Smith, Shields, Allendoerfer, and Washburn (1998)

Smith, Shields, Allendoerfer, and Washburn (1998) presented a converging metamemory finding. Macaques saw picture lists and then judged whether a probe picture had been in the list. Monkeys could decline any memory tests they chose. Monkeys, on accepting tests, remembered best items that appeared early and late in the list (primacy and recency, respectively; see Chapter 10, this volume). Crucially, they made URs in the mirror image of that memory performance—they declined memory tests more when memory-tenuous list positions were queried. Monkeys also held their error rate constant at 10% as the memory lists grew longer and more difficult. They did so by increasing their URs to just the right degree. Thus, in an intriguing form of self-regulation, they established a criterion so that they accepted the memory test if they were 90% or more likely to answer correctly.

Washburn, Gulledge, Beran, and Smith (2010)

A macaque performed a specialized MTS task. Sample shapes were presented briefly—before they could be fixated—in the left or right visual periphery. This let the sample be represented more richly in the opposite cerebral hemisphere. The macaque sometimes received transcranial magnetic stimulation (TMS) to the left or right cortex during the forgetting interval. This disrupted visual working memory safely and temporarily. With no TMS, the macaque matched well and made few URs. With sample presentation and TMS opposed (stimulus left periphery, TMS right cortex), the macaque matched poorly and made many URs. With sample presentation and TMS concordant (stimulus left periphery, TMS left cortex), the result was like no-TMS trials. Therefore, it was not just the feel of TMS that caused URs. Rather, concordant TMS did not erase memory effectively, and the macaque was sensitive to that. This result, though with a single animal, provided distinctive evidence that macaques monitor memory states and manage them using URs.

Basile, Schroeder, Brown, Templer, and Hampton (2015)

Most recently in metamemory research, Basile et al. (2015) evaluated seven possible explanations of macaques' URs in MTS tasks. Monkeys performed a task in which they could take memory tests immediately or see the answer again before testing. The researchers found no support for the "hypotheses of behavioral cue association, rote response learning, expectancy violation, response competition, generalized search strategy, or postural mediation" (p. 85). But they repeatedly found results supporting the memory-monitoring hypothesis. Basile et al. concluded that monkeys "can use memory strength as a discriminative cue for information seeking, consistent with introspective monitoring of explicit memory" (p. 85).

Call and Carpenter (2001)

Call and Carpenter (2001; also Call, 2010; Suda-King, 2008) addressed the overtraining in some uncertainty paradigms that could entrain avoidance behaviors. They combined a naturalistic uncertainty task (e.g., which tube has food) with a UR (e.g., visually confirming food's location). Sometimes the apes saw food containers baited. Then, they retrieved the food without further visual inspection. Sometimes they did not see the baiting. Then, they sought information through inspection. These inspection behaviors occurred easily with scant training that could have engendered associative learning. In fact, these tasks nearly lack associative cues, because nothing in the situation signals whether inspection is warranted. These tasks may logically require animals to respond to their state of knowledge. This paradigm is also important because it produces intriguing species differences (see the section Additional Cross-Species Studies of Animal Metacognition and Information Seeking).

Beran, Smith, and Perdue (2013)

Beran et al. (2013) extended Call's paradigm to language-trained chimpanzees naming food items using lexicon symbols. For three chimpanzees, the identity of a hidden food was the information needed to obtain it. They got the food if they named it on their keyboard. They could report the food's name directly or first inspect the opaque container in which it was hidden. Sometimes the chimpanzees saw the food-item placed. Then, they often directly named it. Sometimes they did not see it placed. Then, they often inspected the container before naming. Thus, chimpanzees sought relevant information only when they had no available memory.

Beran, Perdue, Futch, Smith, Evans, and Parrish (2015)

Beran et al. (2015) considered another spontaneous metacognitive behavior. Chimpanzees performed a task in which feedback was delayed and the food rewards given for correct responses were spatially separated from the response. Crucially, if the chimpanzees did not move to the reward-delivery site before the food was dispensed, it fell out of reach and was lost. Chimpanzees were more likely to move to the dispenser's location on trials they had completed correctly than on those they had completed incorrectly. These *confidence movements* occurred before any feedback about the trial's outcome. Thus, chimpanzees apparently moved on the basis of their confidence in their responses, and their confidence movements accorded well with their task performance. These spontaneous confidence movements could suggest that chimpanzees adjusted their behavior reflecting their states of confidence and uncertainty.

Washburn, Smith, and Shields (2006)

Washburn et al. (2006) brought the UR to Harlow's (1949) learning-set methodology. Monkeys received many two-choice discriminations, each for six trials. The UR gave information about the correct choice on each series. On Trial 1, monkeys could not know the correct answer, but the UR gave that information. On Trial 2 through Trial 6, they could know the answer from Trial 1's feedback or the UR's hint. The monkeys showed an ideal uncertainty-monitoring—information-seeking data pattern. They made many URs on Trial 1, when they were useful. They made fewer URs on Trial 2 through Trial 6, when they could know the answer and when their performance showed they did. This study extended Harlow's original findings by showing that animals could develop an uncertainty-based learning set (Uncertain? Ask!) to complement their outcome-based learning set (e.g., Win-Stay; Lose-Shift). This result also showed instantaneous transfer of the UR on the first trial of a new task: a transfer effect with which associative descriptions must reckon.

Zakrzewski, Perdue, Beran, Church, and Smith (2014)

Zakrzewski et al. (2014) addressed the problem of testing metacognition under static risk–reward contingencies (e.g., timeout always 20 s; reward always 1 food pellet). This could foster inflexible, conditioned responding. So they gave humans and monkeys a discrimination task that allowed tokens (exchangeable into food pellets) to accumulate. The token economy was like that in Morgan, Kornell, Kornblum, and Terrace (2014). The monkeys also had available a modified UR that allowed them to cash out their token bank to receive pellets at any time. By cashing out, participants could receive their accumulated rewards prior to making a response that, if incorrect, would eliminate all tokens. Humans and monkeys used this modified UR optimally, cashing out prior to completing difficult trials they might get wrong. What makes this result more impressive is that humans and monkeys used the cashout response flexibly, taking risk level into account. That is, humans and monkeys cashed out differentially not only on the basis of trial difficulty but also the number of tokens at risk. They widened their cashout-response region as accumulated rewards increased, providing more protection against a costlier error. Haun, Nawroth, and Call (2011) showed a similar flexibility in ape species.

Morgan, Kornell, Kornblum, and Terrace (2014)

Morgan et al. (2014) recently illustrated the interesting contrast between retrospective and prospective confidence judgments; that is, animals' making confidence judgments prospectively in lieu of accepting a discrimination to follow, or making them retrospectively regarding a discrimination response already completed. In Morgan et al.'s study, two macaques made confidence judgments measured as *high* or *low* bets on performance in an MTS task.

When high- or low-risk responses were made, respectively, the monkey could gain three or one food tokens (or lose these from its token bank on an error). Rewards were maximized if the animal bet high before (prospective condition) or after (retrospective condition) correct responses. One monkey successfully transferred metacognitive skills from a retrospective task to a prospective task immediately; one did so to a lesser extent. These results are the first to show retrospective and prospective metacognitive judgments using the same task and monkeys. This is a strong demonstration that nonhuman animals can transfer their metacognitive abilities flexibly. Hampton (2009) discussed the possible theoretical differences between prospective and retrospective metacognitive judgments, but these judgments converged in the present case.

Smith, Beran, Redford, and Washburn (2006)

Smith et al. (2006; also Couchman et al., 2010) addressed the problem that trial-by-trial reinforcement might entrain reactive URs. They eliminated trial-by-trial feedback in a sparse-uncertain-dense task, providing summary feedback after every four trials. Then, macaques received feedback out of trial-by-trial order. Monkeys could not associate responses to stimulus-response pairs. They could not associate the UR to error-causing stimuli because they did not know which stimuli they had missed. The processes of associative learning were disrupted, but macaques could still potentially monitor uncertainty. One macaque in this study showed an important result (see also Le Pelley, 2012, 2014; Smith et al., 2014a, 2014b). Over the range of punishing to rewarding stimulus levels, there was almost no relationship between the proportion of correct responses and the proportion of URs. No associative description predicts this independence—URs (if they are low-level aversion responses) should condition to aversive, losing stimuli. So, the deferred-reinforcement paradigm successfully camouflaged the task's associative structure. The animal needed some other way to respond "uncertain." In fact, his URs were beautifully entrained to the subjective difficulty and uncertainty of the trials as the animal experienced them. In this case, subjective uncertainty and objective reward were decoupled. The animal's URs tracked the former.

Smith, Coutinho, Church, and Beran (2013)

Smith et al. (2013) explored the impact of working memory load (see Chapter 10, this volume) on uncertainty monitoring. Macaques performed a sparse-uncertain-dense task combined with a concurrent MTS task. The concurrent memory load sharply reduced URs while leaving intact the use of the primary perceptual responses (sparse, dense). An additional experiment asked whether the concurrent load would have the same effect on a third, "middle" perceptual response if it replaced the UR. The concurrent load had a very small effect on this primary perceptual response as well. This result suggests that the psychology of the UR and a task's perceptual responses are distinctively different in some way that it is important to understand.

Paul, Smith, Valentin, Turner, Barbey, and Ashby (2015)

Paul et al.'s (2015) human study provides a neuroscience basis for the result in Smith et al. (2013). Their participants performed a sparse-uncertain-dense task as already described. Using rapid event-related fMRI, the researchers demonstrated that the neural activity pattern elicited by humans' URs is qualitatively different from that recruited by humans' primary perceptual responses. URs activated a distributed network including prefrontal cortical areas, anterior/posterior cingulate cortex (ACC, PCC), anterior insula, and posterior parietal areas. Functional-connectivity results suggested that computing and responding to uncertainty recruit a network that converges on the PCC, precuneus, and dorsal ACC. These results raise the possibility, as did early psychophysicists, Weiskrantz (1986, 1997) and Cowey and Stoerig (1995) with their colleagues, that commentary keys like the UR are distinctively different psychologically from primary perceptual responses—in cognitive content and brain organization. This is a human study, yet it is an exciting possibility that animals might be tested in waking-fMRI arrangements, for in that case the generalization of this idea to other species could be directly evaluated.

ADDITIONAL CROSS-SPECIES STUDIES OF ANIMAL METACOGNITION AND INFORMATION SEEKING

As part of the rapid growth of animal metacognition research, researchers have broadened the field's empirical base by exploring its expression in other species besides macaques and apes. This research has the potential to serve many useful functions, including mapping the phylogenetic breadth of metacognition, revealing the evolutionary lines that were the source of its emergence, and thus revealing the earliest stages in the evolution of the human capacity.

Dolphin

Smith et al. (1995) tested a dolphin (*Tursiops truncatus*) in an auditory (pitch) discrimination task. The dolphin responded "high" or "low," respectively, for tones of 2100 Hz or 1200–2099 Hz, or made URs to decline trials. The task was conducted at the dolphin's pitch-discrimination limit, ensuring trial difficulty that might foster uncertainty. On low trials (up to 2070 Hz) and high trials (2100 Hz), low and high responses dominated. URs predominated in the threshold region between. The dolphin correctly assessed the difficulty of threshold trials and declined them selectively. Remarkably, his URs peaked near 2086 Hz, 1/9th of a semitone from 2100 Hz. It is doubtful this threshold task allowed for an intermediate stimulus class that controlled the UR, but it is conceivable. This was a very early animal metacognition study, and it is subject to some of the associative criticisms introduced earlier.

The dolphin showed his own spontaneous uncertainty behaviors at threshold. Smith et al. (1995) asked naive observers to describe the animal's behavior on trials of different pitch. Factor analysis isolated a hesitation-wavering class of behaviors that peaked near 2086 Hz, just as URs did. Tolman (1927) thought that these kinds of behaviors—these lookings and runnings back and forth—could become the behaviorist's definition of animal consciousness. Are these ancillary hesitation behaviors indicating uncertainty processes? Or, inverting causality, are vacillations cueing the animal to respond uncertain? It is a profoundly important point that if one does not know which way causality runs, one should wait for the empirical tie-breaker. The tie cannot be broken by associative presumption or inclination.

Rats

In a study by Foote and Crystal (2007), rats discriminated sounds of different duration (2 s–8 s). They could also decline trials, satisficing with a smaller, sure reward. Rats showed data suggestive of metacognition. They declined selectively the durations near the discrimination's breakpoint that placed them at greater risk for error. They performed more accurately when they chose to complete the discrimination trial than when they were forced to complete it (the chosen–forced advantage). As Crystal and Foote (2009) noted, these aspects of performance became a standard for animal metacognition starting from important work by Inman and Shettleworth (1999). The chosen-forced advantage might be an intuitive indication of metacognition—it could suggest the animal is monitoring a signal of knowing that has validity and justifies completing the trial—though Smith et al. (2008) discussed constraints on this interpretation.

The rat study must be interpreted cautiously. It concretely rewarded URs. It used first-order perceptual stimuli, placing it in the line of fire of associative criticisms already discussed. Crystal and Foote (2009) concluded that both aspects of the metacognitive performance pattern could reflect associative reactions to first-order perceptual representations, so that no metacognitive inference was warranted or allowed. In reaching this conclusion, they drew heavily on the formal model in Smith et al. (2008), which is unfortunate given the serious problems that attend the application of associative models in this area (as previously discussed).

Roberts et al. (2012) asked whether rats would make a voluntary information-seeking behavior, that is, rearing up on hind legs to look over a barrier in a T-maze for a cue to the correct direction to take. By doing so, they could potentially obtain reward on every trial. Or they would be guessing and obtain 50% of available rewards. Rats accurately completed the task without the barrier in place, but they did not make the novel rearing response when the barrier blocked their view. On the basis of this and other studies, Roberts et al. concluded that instances of seeming information seeking by nonprimates are a form of secondary sign-tracking that is quite different from the metacognition-like processes used by primates.

Pigeons

Teller (1989) tested pigeons' metamemory in an MTS paradigm. Birds could match a sample shape after a delay interval for a large reward or make a hint response for a smaller, guaranteed reward. Pigeons matched more poorly and made more hint responses at longer delays. But Teller concluded that the delay interval's length was exerting stimulus control over the hint response, so that pigeons were not showing any memory-monitoring capacity.

Inman and Shettleworth (1999) took a similar approach. However, their pigeons made only slightly more hint responses at longer delay intervals, indicating substantial insensitivity to the difficulty fostered by a forgetting interval. Inman and Shettleworth's results were initially controversial, because one could find slight evidence for metamemory within them. However, they interpreted their findings cautiously, concluding that pigeons had not shown they could use the strength of memory traces as a discriminative cue. Sutton and Shettleworth (2008) continued the pigeon research in multiple experiments and converging paradigms. They still found no relationship between trial difficulty and pigeons' level of uncertainty responding, or their use of low- and high-confidence responses.

Roberts et al. (2009) studied information-seeking responses by pigeons in a MTS task. One response would reveal the sample shape; another response would reveal the matching choices. Pigeons had a remarkable tendency to wake up the matching responses so they could respond, even though this choice meant that they had not seen the sample and could not possibly have the information that would allow correct response. The researchers concluded, "The findings of all of these experiments suggest the absence of metamemory in pigeons" (p. 129).

Of course, these negative results need not be the whole or final story. Pigeons might have a brittle, empirically shy capacity for metacognition only observable under felicitous conditions. Supporting this idea, Adams and Santi (2011) found following extensive training that pigeons could sometime show the chosen–forced advantage, and sometimes show higher rates of trial-decline responses for more difficult trials. Possibly, at the margin, methodological factors determine whether a metacognitive pattern of results will be obtained. Illustrating this pattern, Goto and Watanabe (2012) showed that large-billed crows showed aspects of the metacognitive data pattern when tested with a retrospective, but not prospective, methodology.

There are additional interesting studies with birds that would take this chapter beyond its allowed length (e.g., Iwasaki, Watanabe, & Fujita, 2013; Nakamura, Watanabe, Betsuyaku, & Fujita, 2011; Zentall & Stagner, 2011; see also Chapter 15, this volume). It is noteworthy that whereas primate articles have debated sharply the presence–absence of meta, the associative-cognitive nature of meta, and so forth, bird articles have focused on phenomena, methodological variations, and fostering conditions. There are considerable strengths to the latter approaches as a way of mapping the basic phenomena, especially when backlit by the qualitative debates that have not always served the primate literature well.

Capuchin Monkeys

Basile, Hampton, Suomi, and Murray (2009) tested capuchin monkeys (*Cebus apella*, a new world primate) with Call's (2010) food-concealment task. Only one monkey showed the adaptive pattern of searching actively when not knowing the food's location. Others succeeded after extensive training but when search effort increased they lost the adaptive search pattern. Basile et al. concluded their study provided minimal support for capuchin metacognition.

Paukner et al. (2006) tested capuchin monkeys similarly. Some used visual inspection prior to selecting food-baited tubes. But they futilely searched bent tubes (the bait could never be seen) and also searched clear tubes (the baited tube was obvious). Paukner et al. pointed to species differences in metacognition given capuchins' contrasting behavior to macaques and apes. In an MTS paradigm, Fujita's (2009) capuchin monkeys showed only fleeting glimpses of the metacognitive data pattern (e.g., escaping more after long forgetting intervals, showing the chosen–forced advantage), pointing to a metacognitive capacity that is tenuous at best.

Beran, Smith, Coutinho, Couchman, and Boomer (2009) tested capuchin monkeys using two related tasks. In the sparse-uncertain-dense task, they could make URs to decline the most difficult intermediate stimulus levels. In the sparse-middle-dense task, they earned rewards for making the middle response (MR) to these same stimulus levels. Capuchins made MRs at high rates but almost never URs, even when the error timeout was increased to 90 s. (One capuchin did make URs at this point in the study, but after several transitions between the two tasks had cross-contaminated the MR and UR.)

Thus, the two tasks produced a remarkable dissociation. If URs and MRs were associatively based in the same way, as has been suggested, capuchins' associative competence would have allowed MRs and URs. To be clear, if URs were a response to stimuli, conflict, aversion, avoidance, fear, competing response strengths, reward maximization, wavering behaviors, hesitation latencies, or any other first-order cue, capuchins should have read that cue and let it occasion adaptive URs. They did not. This raises the theoretical possibility that MRs and URs are underlain by different psychological mechanisms or lie on different psychological levels. Our literature must approach this dissociation and not avoid it.

Still, as with pigeons, one should not deny capuchins metacognition categorically. Other methods could successfully foster metacognitive behaviors. Illustrating this point, we have recently found (Beran, Perdue, & Smith, 2014) that capuchins make more URs when placed in a 6AFC task (with .16 correct for chance responding) than a 2AFC task (with .5 correct for chance responding). Some of the reticence in capuchins' metacognitive capacity may be linked to their generous level of risk tolerance (i.e., they are willing to try a trial with .5 chance of reward) that macaques may not share. We do not think this is all of the story, but it may be part of the story.

Finally, Beran and Smith (2011) studied information-seeking responses by capuchins and macaques in the MTS task Roberts et al. (2009) used with pigeons. Both species succeeded where pigeons failed—illuminating samples before matching, revealing necessary information appropriately. Nonetheless, given more complex information-seeking scenarios, the performance of the species diverged strongly. Most macaques showed the optimal information-seeking behaviors throughout, but no capuchin did so. There may still be real differences in the facility with which macaques and capuchins approach metacognitive and information-seeking tasks.

BEYOND ASSOCIATIVE ACCOUNTS OF ANIMALS' UNCERTAINTY PERFORMANCES

Our review of research in this area has a crucial theoretical implication: Animals' uncertainty performances have sometimes transcended traditional explanations based in associative learning. Here are specifics. Animals do not only make URs toward present first-order stimuli. They make them facing abstract same–different judgments (Shields, Smith, & Washburn, 1997), facing memory tests with no memory-relevant stimuli present (Hampton, 2001), and when TMS has temporarily erased their visual working memory (Washburn et al., 2010). Hampton (2009) pointed to other paradigms that transcend the problem of reacting to visible stimuli (Foote & Crystal, 2007; Goto & Watanabe, 2012; Kornell et al., 2007; Nakamura, et al., 2011; Son & Kornell, 2005; Sutton & Shettleworth, 2008). Thus, animals have met the invisible-stimulus criterion that Metcalfe (2008) proposed, and she does acknowledge that some macaques (though not all) have shown a kind of metacognition.

Nor do animals only make URs when they are concretely rewarded. Beran, Smith, Redford, and Washburn (2006; also Couchman, 2015; Smith et al., 2006, Smith, Redford, Beran, & Washburn, 2010) showed that they make URs even when these bring no tangible reward.

Nor is it that animals depend on trial-by-trial reinforcement to condition their use of the UR to particular stimulus-response combinations. Smith et al. (2006) showed that a macaque could make adaptive URs to subjectively difficult stimuli even when associative-learning processes were severely disrupted by deferred-delayed feedback (also Couchman et al., 2010).

Nor have latency cues and behavioral-cue associations been shown to lie behind URs. Hampton's blank trials showed that animals make URs not on the basis of the length of the forgetting interval. Shields et al. (1997) examined the relative latencies of monkeys' URs and primary perceptual responses, asking whether hesitation or dithering cues URs ("I vacillate, therefore I escape"). The hypothesis was not born out. Indeed, animals sometimes show long latencies on primary perceptual responses, because they deflect away from first almost making a UR. It is as if the monkey realized that it did know the answer after all.

URs also do not depend on intensive training to instill associative response habits. It is the elegant contribution of Call and his colleagues to have shown that animals make spontaneous, ecological metacognitive behaviors with scant training. Beran et al. (2013) showed that these behaviors extend to naming known food items using the chimpanzees' lexigram keyboard. These may be the most abstract and reflective confidence responses ever demonstrated in the literature, and the memory content that allows these responses may be explicit and resident in working consciousness. Beran et al. (2015) demonstrated another form of spontaneous uncertainty behavior—the prefeedback confidence movement to the displaced location of the reward. In fact, the food-search tasks are especially interesting because very little in the situation signals whether inspection is warranted. These tasks may logically require animals to respond to their state of knowledge (i.e., to be metacognitive) if they can.

A similar logic attends the metamemory studies. Hampton's (2001) macaques, after observing the sample and waiting through the retention interval, were presented with two abstract response icons. These icons had no trace relevance, so nothing memory-relevant was visible at that time. Yet animals had to choose to accept or cancel the memory test. To do so, they had to initiate an internal memory search for a hot or recent trace that would justify accepting the test. So the task's structure drives the animal inward to monitor memory in some way. This example illustrates the need for behavioral analysts to attend carefully to animals' real information-processing situation in uncertainty tasks, rather than invoking casually notions of stimuli and reinforcement. The casualness undermines the field's theoretical development.

In developing the metamemory paradigm further, we saw that Basile et al. (2015) ruled out additional associative explanations of their animals' memory-monitoring performances. Carruthers and Ritchie (2012)—formidable critics of animal metacognition—summarized the status of the associative debate:

> We fully accept that this body of work, taken as a whole, cannot be explained in low-level associationist terms, as involving mere conditioned responses to stimuli. A great deal of careful experimentation has been done to demonstrate that this is not the case, and we are happy to embrace this conclusion. (p. 76)

Carruthers (2014) went further: "An obsessive focus on associationist accounts of animal behavior impedes progress in comparative psychology and obstructs attempts to understand animal precursors and homologies of components of human cognition" (p. 138). These statements capture one aspect of current theory in this literature. Theory is moving toward new, nonassociative conceptions of cognitive process that appropriately frame the psychological performances animals achieve. Those conceptions may of course not encompass the full human construct of metacognition. Nonetheless, in a field with strong associative foundations and inclinations, this effort to move beyond the associative-learning model is a profoundly important contribution made by many colleagues in this field.

There is another aspect to current theory. It is the idea that some animals, in some tasks, show some forms of metacognition. Sutton and Shettleworth (2008) concluded that "metamemory, the ability to report on memory strength, is clearly established in rhesus macaques (*Macaca mulatta*) by converging evidence from several paradigms" (p. 266). Fujita (2009) concluded that "evidence for metacognition by nonhuman primates has been obtained in great apes and old world monkeys" (p. 575). Roberts et al. (2009) concluded that "substantial evidence from several laboratories converges on the conclusion that rhesus monkeys show metacognition in experiments that require behavioral responses to cues that act as feeling of knowing and memory confidence judgments" (p. 130). We agree this conclusion is justified, if one carefully delimits what animals have so far done and understands that animals may share only some facets of human metacognition.

REFINING THEORETICAL APPROACHES TO ANIMAL METACOGNITION

Overall, the animal metacognition literature has provided an illuminating cross-section of theoretical approaches within comparative psychology. Here, we describe some principles that have been beneficial in this field's theoretical development.

Disciplined Associationism

Our field has benefited from requiring associative hypotheses to be disciplined, not loose and casual. For example, one could declare loosely that URs are associative because animals use them to maximize reinforcement by declining difficult trials. But difficulty is neither a stimulus nor an associative construct. It is a derived cognitive construct. If animals monitor trial difficulty so as to decline difficult trials adaptively, that is a form of metacognition, though it need not have the trappings of consciousness and self-awareness.

The Information-Processing Situation

Second, our field has benefited from attending sharply to the animal's true information-processing situation. We have already seen that the metamemory studies force macaques inward to conduct a memory search for available traces that might be the to-be-tested sample. By carefully analyzing the animal's situation, one sees that this processing is profoundly different from associative-learning processes as traditionally understood and that it deserves a higher-level cognitive description (Smith et al., 2014a, 2014b).

Beyond Associative Models

Third, our field is benefiting from moving beyond the use of formal-mathematical models that purport to associatively describe animals' uncertainty performances (e.g., Jozefowiez et al., 2009a, 2009b; Le Pelley, 2012; Smith et al., 2008, 2014a, 2014b; Staddon et al., 2007). These models originally had substantial influence on the field, until their failures became clear. These failures were the focus of a target article (Smith et al., 2014a) with commentaries (Basile & Hampton, 2014; Carruthers, 2014; Le Pelley, 2014; Smith et al., 2014b). The models are unstable. They fail to capture important phenomena. They can require a level of mathematical power (e.g., 9 free parameters) guaranteed to turn a model into a mathematical abstraction with no psychological grounding. These models are pure mathematics, nothing more. They instantiate nonunique, arbitrary mathematical transformations to recreate a graph. These transformations have no intrinsic tie to the animal's psychology, and they cannot embody associative processing or, to be fair, metacognitive processing. Basile and Hampton (2014) found these problems persuasive and concluded that "the associative models proposed by Le Pelley et al. and Jozefowiez et al. do not currently explain the breadth of nonhuman metacognitive performance" (p. 135). This conclusion promises to energize the animal-metacognition literature. A formal model can never indicate whether an animal is privately monitoring his knowledge or uncertainty about internal representations. This will always be a cognitive-psychological question answerable only by systematic research.

Levels of Animal Mind

Fourth, our field benefits from understanding that animals may have different levels in mind, different levels of explicitness, awareness, declarativeness, and so forth. For example, Smith et al. (2013) showed that URs are particularly reliant on working-memory capacity, more so than the primary perceptual responses in the same task. We believe that our literature will progress as it incorporates more cognitive-psychological theoretical perspectives like these, wherein there is allowance for different systems of learning (procedural, rule-based), different systems of memory (implicit, explicit), and so forth. The idea of levels and systems will liberate the field from the all-or-none associative-metacognitive debate.

Associative Compression

Fifth, some in this field have taken a universalist-associative perspective (Jozefowiez et al., 2009a, 2009b; Le Pelley, 2012; Smith et al., 2014a, 2014b; Staddon et al., 2007). It supposes that all animals' performances will fit under the general rubric of associationism (reinforcement, response strengths, etc.). But this rubric is far too vague to be constructive. The problem is that it compresses all of animals' performances on one (associative) level. This compression works against the careful cognitive-psychological analyses that are crucial to our field. URs on any level, by any system—low-level reactions to aversive stimuli, even fully conscious metacognitive URs—would be emptily and vaguely mapped on the compressed associative rubric. Performances would be blurred that have profoundly different psychological characters. The idea of associationism would cease to have any meaning. It is another significant step that our literature has moved beyond this associative compression.

Empirical Parsimony

Sixth, as associative mechanisms have been challenged, some have shopped among multiple associative explanations, appealing here to reinforcement, there to stimuli, now to latency, then to vacillation behaviors. This kind of associative musical chairs has not been productive. In our view, these attempts to defend a unitarian-associative perspective have been unparsimonious and nonconstructive. In contrast, it is parsimonious to attribute animals' uncertainty performances to a basic uncertainty-monitoring utility. This encompasses all the results simply and naturally, using an adaptive capacity with which cognitive evolution would likely have endowed some species. In our view, it has been constructive to our field to take the research findings as a whole, across many species and tasks, and to accept that some nonhuman species have a basic capacity for cognitive monitoring. It gives the field license to explore that capacity and to seek its cognitive underpinnings and its level in the animal's mind. Still, this does not presume to say that this system is equal to humans' metacognitive system.

Evolutionary Parsimony

Seventh, the animal metacognition literature has gained from seeking evolutionary parsimony. Humans and monkeys often produce about the same graph in uncertainty tasks. In Shields et al. (1997), humans and monkeys produced performance profiles that correlated at .97. It is most unparsimonious to claim that nonetheless these performances were qualitatively different—that is, respectively metacognitive and associative. We know no other case in which such similar performances have been described so differently. Here, reasonable scientific parsimony would suggest some continuity—not perfect or exact—between humans' and animals' uncertainty performances and systems. Supporting continuity, humans, macaques, and chimpanzees share evolutionary histories and homologous brain organization. This also makes it unparsimonious to claim they would perform uncertainty tasks in qualitatively different ways.

All-or-None Conceptions

Eighth, our field has gained from softening its extremes. We have discussed the strong associationists in our field. But others have focused instead on humans' metarepresentational metacognition by which we reflect formally and explicitly on our own thinking (Carruthers, 2008, 2009; Metcalfe, 2008). These theorists question in principle attributing metacognition—defined as this ultimate self-reflective capacity—to animals. Illustrating well this all-or-none approach in our literature, Le Pelley (2012) pointedly framed the field's principal issue as associative animals versus metacognitive monkeys.

But this approach has frozen our field into a polarized debate that has not benefited theoretical development. Another approach is more promising. We could acknowledge that animals' cognition in some uncertainty tasks is higher-level, deliberate, decisional, and possibly metacognitive. Then, we could drop the all-or-none debate and work together to write an interesting comparative-cognitive psychology explicating these performances.

For example, there might be different types of metacognition. Metcalfe and Son (2012) ascribed Foote and Crystal's (2007) study with rats and Smith et al.'s (1995) dolphin task to a level of anoetic metacognition because both involved categorization of present stimuli and not judgments about internal representations. Or, there might be a continuum of metacognition, as monitoring becomes more explicit and conscious and the animal gains reflective access to its own mental states (Smith et al., 2013). Or, there might be species that have basic uncertainty-monitoring systems that serve them adaptively, but that have not bought the apps of self-awareness, consciousness, and meta-representation that humans have bought. The idea of different kinds of metacognition applies to humans, too. Hoffman and Schwartz (2014; also Kornell, 2014) noted that humans are not always self-reflective in their metacognitive actions. It is an extremely important point that one must not require animals to show self-reflection in tests for metacognition because humans often do not show it. More generally, we must not overlook metacognition in animals simply because our animal techniques lag human assessments (declarative self-report) that are crucial to attributing metacognition to humans.

Transcending the extremes in our field opens empirical and theoretical ground. We can ask whether monkeys have a basic uncertainty system that is the ancestral form of humans' full-fledged metacognition system. We can ask if behavioral metacognition bears on the earliest, preverbal, developmental roots of human metacognition (Balcomb & Gerken, 2008). There might be basic, nonverbal forms of cognitive regulation that could be fostered in children (e.g., in language-delayed and autistic children or children with mental retardation) who are wanting in conscious, declarative, cognitive self-regulation. This would suggest that animal models of metacognition do have significance, and that animal metacognition research has relevance to issues of education, training, and humans' self-regulation and behavioral control. It would illustrate why human cognitive psychologists should be aware of and interested in the tasks and phenomena of animal metacognition. And thus comparative science in this domain would be woven into the fabric of contemporary cognitive science—to the gain of both domains.

METACOGNITION IN RELATION TO THE SELF AND OTHERS

Animal metacognition research has important relationships to research on other facets of self-awareness, self-control, and self-perceptions of agency. It also has important relationships to research on animals' theory of mind—that is, the possibility that some animals know that conspecifics are themselves cognitive agents that can receive information and even misinformation.

Relation to Theory of Mind

Research in metacognition (knowing one's own mental states and feelings) has an important relationship to research in mindreading (knowing conspecifics' mental states and feelings; see Chapter 32, this volume). The issue of the evolutionary precedence of these capacities has been an important topic. Humphrey (1976) made the famous proposal that metacognition arose as a support for mindreading among social animals. Carruthers (2009) took the stronger view that mindreading evolved first to serve social functions and later was directed inward to ground metacognition.

This proposal predicts concordance for metacognition and mindreading. Above all, no animal should show metacognition but lack mindreading—that would break concordance and disconfirm the proposal. Macaques are metacognitive by the literature's consensus but traditionally they were considered not to mindread (but see Call & Santos, 2012). Thus, macaques could show that metacognition can have evolutionary precedence over mindreading.

Readers will see this progression's conceptual strength. If mindreading evolved first, then there were creatures that understood or represented the mental states of others without understanding or representing their own. But animals with no self-knowledge of mental states would have no basis for judging another's. How could one ever attribute anger to the other if one has no conception of it on the basis of privileged access to it in the self? It would be like trying to identify the keys in a conspecific's pocket though one lacks a conception of what keys and pockets are. But metacognition could have evolved nonsocially to serve diverse fitness functions (e.g., managing uncertainty in route-finding and predator avoidance). Then, it could have come to coserve as an emulation utility supporting mindreading. Metacognition would thus be an ideal preadaptation to mindreading, with mindreading a gentle extension of an existing capability, because now, in a sense, animals would have already come to know what keys and pockets are. This progression explains intuitively macaques' capacity for metacognition and their lesser capacity for mindreading as a phase in the overall emergence of primates' reflective mind.

Relation to Mirror Self-Recognition

Research in animal metacognition was preceded by the dyemark test (e.g., Gallup, 1982), another approach to animals' self-awareness (see Chapter 33, this volume). Some apes, but not monkeys, show mirror self-recognition by the metric that they know their own face or body in a mirror. These results grounded Gallup's influential proposal that mirror recognition indicates self-awareness linked also to consciousness and metacognition. He also proposed that this g-factor of self-reflective mind emerged only once in the ape-hominid lineage.

Gallup's technique presents methodological and interpretative difficulties (small effect sizes, anesthesia-timing confounds, etc.). The idea of unique ape self-awareness is disturbed by research showing that dolphins show analogous phenomena (Reiss & Marino, 2001). They examine a red spot on their body in a mirror as if to say, "Does this red spot make me look fat?" Gallup's approach also cannot grant the researcher access to animals' metacognition. In fact, the relationship between body recognition and metacognition remains fascinating but unknown.

Animal metacognition research contributes to this area, complementing Gallup's test and supporting his theoretical goals. First, it provides independent assays of cognitive self-awareness to broaden the study of self-awareness, though certainly metacognition paradigms have their own methodological and interpretative issues, as discussed in this chapter. Second, metacognition partially falsifies Gallup's hypothesis. That macaques show a metacognitive capacity suggests that aspects of self-reflective mind exist outside the line of apes. The macaque data contribute in this area similarly to the dolphin data. Third, metacognition research shows that the evolution of self-reflective mind could be more complex than Gallup allows. If metacognition exists without mirror awareness, then these are not the same thing and not all aspects of self-awareness have perfect evolutionary concordance. Self-reflective mind may be a patchwork of abilities, not an integral ape achievement. In our view, the patchwork conception is constructive because it lets one scrutinize separately the behavioral and functional characteristics of individual capacities.

Relation to Self-Control and Agency

Animal-metacognition research also has close ties to work on self-control and agency. In a study by Metcalfe and Son (2012), the highest level of autonoetic metacognition was reserved for cases in which metacognition is suffused with self-awareness. To Metcalfe and Son, this directly raised the question of whether animals understand the concept of their agency within a task, and of whether they can report (not) having agency within a task as they perform it. Accordingly, researchers have begun to explore declarative reports of agency by humans and animals. Metcalfe and colleagues (Miele, Wager, Mitchell, & Metcalfe, 2011; Metcalfe, Eich, & Miele, 2013) have used a video game in which mouse movements let one reach targets descending on the screen. By disrupting, fuzzing, or lagging the cursor control, one can reduce humans' effective agency in the task and they report this loss of agency sensitively.

Research with chimpanzees (Kaneko & Tomonaga, 2011) and macaques (Couchman, 2012, 2015) has suggested that animals are capable of self-agency that is comparative to that of humans. In Couchman (2015), humans and monkeys were given a task in which they moved a cursor with a joystick while different types of distractor cursors also moved on the screen. Their task was to identify which cursor they were controlling. Humans and monkeys were able to identify the self-controlled cursor, successfully monitoring the relationship between planned movement and perceived action. To date, this result may be the most persuasive evidence that Metcalfe and Son's (2012) highest level of metacognition is present in nonhuman animals.

CONCLUSION

Animal metacognition is an active area within contemporary comparative psychology. Animals' and humans' metacognitive capabilities are isomorphic and continuous with one another. Associative interpretations fail to account for this body of findings. Cognitive interpretations at some higher level are indicated. Higher-level interpretations are encouraged by the fact that some cognitively agile species nonetheless barely express a metacognitive capacity.

This research area has theoretical implications for theory-of-mind research. It provides new measures within the domain of self-awareness research. Animal metacognition paradigms extend the techniques available to child-development researchers—these paradigms are ideal for testing young humans, too. They could support the study of metacognition in language-delayed or autistic children and promote the training of metacognition in populations with educational challenges. Indeed, comparative research might establish animal models for metacognition and cognitive self-regulation that could be broadly useful.

We recommend additional research to establish the full phylogenetic distribution of metacognition, especially research with marine mammals and corvids. It is important to know whether metacognition is primarily a primate achievement or a general property of cognitively sophisticated minds. We recommend additional research to explore whether metacognitive phenomena reflect explicit and declarative cognitive states held in a working consciousness. The techniques of animal metacognition research verge on demonstrating animals' cognitive awareness, and it is possible these techniques could be extended to take the last steps in this direction. Finally, we recommend neuroimaging research as a complement to other approaches in animal metacognition research, as these techniques become more feasible with nonhuman primates.

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CHAPTER 32

MIND READING IN ANIMALS?

Juliane Kaminski

Theory of mind (ToM) refers to an individual's ability to make inferences about another individual's mental states. The term was first introduced by Premack and Woodruff in 1978, when they asked whether ToM exists in chimpanzees. Their paper has since sparked much research on the concept in nonhuman animals and humans alike. Premack and Woodruff called it a theory because mental states are not directly observable and therefore must be inferred.

THEORY OF MIND IN ANIMALS

In recent years, comparative cognitive research has focused on the question of whether nonhuman animals have a ToM as humans do. From an evolutionary perspective, it is likely that humans share some of their social cognitive skills, perhaps including mental state attribution, with other species. And recently, researchers have focused on identifying which ones. A challenge in comparative work is that researchers have to make assumptions about the animals' understanding of others' mental states on the basis of the behavioral output of the animals; therefore, research in this domain relies heavily on creative paradigms designed to identify which social cognitive skills, if any, animals possess.

In 1976, Humphrey emphasized the effect that life in complex social groups might have had on the evolution of social cognitive skills in animals. He stated that life in complex social groups should put a premium on the evolution of social intelligence, because relationships in social groups change and the individual has to have skills in place that allow for quick adaptation. Since then, several hypotheses have been put forward to explain how and why social cognitive skills in nonhuman animals and humans might have evolved. Whiten and Byrne (1988) formulated the *Machiavellian intelligence hypothesis*, which puts a premium on competition as an important driving force for the evolution of social cognitive skills in social species. The hypothesis is that life in groups, and especially competition over resources, puts a constant selection pressure on the species to evolve flexible social cognitive skills because of the constant struggle to outwit competitors to monopolize resources. Whiten and Byrne hypothesized that social cognitive skills evolved in a kind of "arms race" between the evolution of measures to manipulate others and the evolution of countermeasures to avoid manipulation by others. Based on this hypothesis, we should expect animals to display their social cognitive skills especially in competitive situations over resources, as that would be the context in which they have evolved.

Dunbar and colleagues formulated the *social-brain hypothesis* (Barton & Dunbar, 1997; Dunbar, 2002), which states that social cognitive capacities are most likely an adaptation to life in complex social groups and go together with the evolution of larger brains. Because brain tissue is very costly, we would expect large brains to evolve only when the cost of doing so is outweighed by the benefit of having a larger brain (Dunbar, 2002). The idea is that larger brains, especially a larger neocortex, allow for

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better processing of information and the more complex the social group structure, the more individuals would benefit from a greater ability to process information, social and otherwise. A greater ability to process information will allow the individual to make flexible decisions and hence adapt quickly to the constantly changing social environment. Based on this hypothesis, we should expect flexible social cognitive skills in almost all social living species, and we would expect more complex social cognitive skills the more complex the social group structure of the species.

Recently, van Schaik and colleagues formulated the *cultural intelligence hypothesis*, which states that species with improved social learning abilities will also show better asocial learning abilities and hence will have more generally advanced cognitive skills (van Schaik & Burkart, 2011; Whiten & van Schaik, 2007). This hypothesis seems to be supported by a study by Reader and Laland (2002), who found a positive correlation between reports of social learning and innovation in primates with executive brain ratio (neocortex + striatum). This hypothesis would explain why humans, as a species with outstandingly developed social learning skills, have outstandingly developed cognitive skills (van Schaik & Burkart, 2011; see also Volume 1, Chapter 13, this handbook). Tomasello and colleagues, in their version of the cultural intelligence hypothesis, argue that humans have not evolved higher general intelligence but rather a specific set of social cognitive skills, which leads to humans being "ultrasocial" (Herrmann et al., 2007). Herrmann et al. (2007) showed that at a specific age children exhibit physical cognitive skills similar to those of apes but social cognitive skills (including skills such as social learning, communication, and ToM) superior to those of apes. Herrmann and colleagues argued that this set of social cognitive skills was crucial for human evolution and most likely evolved in the context of activities that needed high levels of collaboration, such as hunting and gathering (Moll & Tomasello, 2007; Tomasello, 2008; Tomasello, Carpenter, Call, Behne, & Moll, 2005).

Although some researchers believe that reasoning about mental states is a uniquely human skill, others argue that humans share certain social cognitive skills, including mental state attribution, with other species, such as our closest living relatives, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). From an evolutionary perspective, certain social cognitive skills would be as beneficial for group living animals as they are for humans. Following the Machiavellian intelligence hypothesis, individuals with some knowledge about others and the capacity to attribute mental states to others would be in a better position to outwit their competitors; hence, group living should put a premium on the evolution of social cognitive skills that allow a more flexible understanding of others. However, there are many group living species but few, if any, are thought to have the capacity to attribute mental states to others. This raises the question of whether different processes, such as learning by association or behavior reading, are sufficient instead.

THEORY OF MIND IN HUMANS

Humans have the ability to attribute mental states to others, meaning that in some situations they can make inferences about others' knowledge, desires, beliefs, and so forth. For example, people infer what objects others can and cannot see, or have and have not seen, on the basis of others' visual access to those objects (Flavell, Shipstead, & Croft, 1978). In Western cultures, children develop an understanding of others' visual perspective relatively early in life. During their first year, children start following others' gaze direction and tracking others' lines of sight, apparently understanding the function of the eyes while doing so (Brooks & Meltzoff, 2002; Butterworth & Jarrett, 1991; Lempers, 1979; Tomasello, Hare, Lehmann, & Call, 2007). Recent research suggests that by the end of their first year, children also can make predictions about others' goals and intentions (Woodward, 1998); additionally, by this time children understand that when another person's line of sight is obstructed by an object, his or her visual access beyond the object is blocked (Moll & Tomasello, 2004). Around 2 years of age, children seem to start differentiating knowledge from ignorance (Dunham, Dunham, & O'Keefe, 2000; Moll & Tomasello, 2006; O'Neill, 1996; Tomasello & Haberl, 2003) and start appreciating that others have desires that can deviate from their own (Rakoczy, Warneken, & Tomasello, 2007).

Ontogenetically, however, ToM understanding is considered fully fledged only when the individual understands that others can have *false beliefs*, a stage children in Western cultures normally reach around 3.5 years of age (Wellman, Cross, & Watson, 2001). In appreciating others' false beliefs, humans understand that other people's mental states can contradict their own, as well as contradict reality. Therefore, understanding that others have false beliefs requires a fully representational ToM (Wellman et al., 2001). The standard test for this ability is the Sally-Anne test (SAT; Baron-Cohen, Leslie, & Frith, 1985). In variations of this test, participants are presented with a hypothetical or reenacted scenario in which two characters, Sally and Anne, interact over a set of two containers. In the original version, Sally has a basket and Anne has a box. Participants witness or listen to a description of a simple scene, in which Sally puts a marble in her basket and then leaves the room. While Sally is away and cannot watch, Anne takes the marble out of Sally's basket and puts it into her box. Sally then returns and the children are asked where they think she will look for her marble. Children are said to have false belief understanding if they answer that Sally will likely look inside her basket before realizing that her marble isn't there but rather in Anne's box.

One criticism of the standard SAT is that it relies heavily on language; the interaction between Sally and Anne is described to the children verbally, and the children then give verbal responses. This is one of the reasons why researchers believe that the use of the SAT has produced such variable results across different cultures. Although children from Western cultures pass the test at around 3.5 years, cross-cultural studies have shown great variation. For example, teenage Tainae of Papua New Guinea fail the SAT (Vinden, 1999). The Mofu of Cameroon also fail the SAT, unless they receive standardized schooling, as a result of which they pass the SAT by 7 years of age (Vinden, 1999). Among indigenous cultures that pass the SAT eventually, the age at which most children do so varies massively across groups—from as early as 4 years old in the Baka of Cameroon (Wellman et al., 2001) to as late as 7 years old in the Tolai of Papua New Guinea (Vinden, 1999). The age of SAT mastery further depends on the level of schooling (Vinden, 2002) and differing parenting styles (Ruffman, Slade, & Crowe, 2002; Vinden & Astington, 2000). This variability is most likely the result of the SAT not being applicable in cross-cultural settings because adult language describing mental states varies extensively across different populations (Lillard, 1998), which may result in translation errors and other difficulties that affect performance in the test. In recent years, new, nonverbal paradigms have been developed, which have the advantage of not only being applicable in cross-cultural settings but also enabling us to conduct cross-species comparisons.

From a developmental perspective, these nonverbal paradigms have changed the traditional view that false belief understanding develops in children at the age of 3.5 years, and they have produced evidence suggesting that 13- to 18-month-old children might already have a fully operational understanding of others' false beliefs (Buttelmann, Carpenter, & Tomasello, 2009; Onishi & Baillargeon, 2005; Sodian, 2011; Southgate, Senju, & Csibra, 2007). Onishi and Baillargeon (2005) developed a nonverbal false belief paradigm that used looking time as an indicator of whether 15-month-old infants' expectations were violated. The infants observed a sequence of events, which resulted in an object being placed in a certain location and an actor watching the scene having either a true or false belief about the location of the object. The results showed that infants expected the actor to search for the object on the basis of that person's belief, rather than their own knowledge of the location (Onishi & Baillargeon, 2005).

THE COMPARATIVE APPROACH

To study the evolutionary history of a certain skill it is essential to compare the cognitive capacities of different species (see Volume 1, Chapters 1, 10, and 12, this handbook). The comparative approach in many ways is the best method for investigating to what extent human cognition relies on particular adaptations that are specific to human. For example, Liberman (1996) suggested that the ability to engage in categorical perception is unique to humans and a critical adaptation that allows for human language. Subsequently, however, it was found that a number of nonhuman species seem to share this ability with humans (Hauser, 1997), which suggests that this ability probably evolved for more general-purpose discrimination rather than specifically in relation to human language.

When making comparisons, one approach is to compare species that shared a common, relatively recent ancestor with humans (e.g., the *Hominidae*, nonhuman great apes) to identify homologous traits as well as traits that are derived and unique to humans. The argument is that if a certain trait exists in all genera of a close phylogenetic family, the trait must have been present in their common ancestor, hence the trait is a homology. Ideally, one would compare all extant genera of a maximally large family with a single common ancestor. Today, four genera of the *Hominidae* are still in existence: *Homo*, *Pan*, *Gorilla*, and *Pongo*. If all these genera share a particular cognitive preference or ability, it is most likely a part of the evolutionary inheritance of the family, at least ever since the last common ancestor of the genera. In this way, behavioral continuities across genera are used to understand evolutionary past. Another ability might only be present in *Pan* and *Homo*. In that case, adding what we know about the timescale of phylogenetic divergences of the different ape genera, this ability would have been an evolutionary innovation that occurred sometime after the last common ancestor of *Homo*, *Pan*, and *Gorilla* (app. 10 million years ago). Yet another ability might only exist in *Homo*. This pattern would indicate an innovation sometime after the time of the last common ancestor between *Homo* and *Pan*, roughly 5 to 6 million years ago. In this example, *Homo* might have undergone special evolutionary adaptations unique to its evolutionary past and distinct from those of the other members of the family.

The second approach when comparing species is to compare humans with more distantly related species (e.g., birds). The question here is whether the species evolved functionally equivalent (analogous) cognitive traits as a result of similar selection pressures during their evolution. A species' cognitive adaptations, like its morphological adaptations, reflect the ecological contexts in which it has evolved as well as the species' phylogenetic inertia. To identify selection pressures during the evolution of a species, it is important to identify which aspect of the species' ecological context was important for its evolution. There are several aspects of the ecological context that may affect a species' cognitive abilities, including the complexity of the social environment (Dunbar's social-brain hypothesis), competition over resources (Machiavellian intelligence hypothesis), and adaptation to complex social collaborative challenges (e.g., hunting; cultural intelligence hypothesis). One approach that researchers have therefore used is to look at species distantly related to humans but facing similar selection pressures because of similar challenges in the surrounding habitat (e.g., complexity of social environment, level of resource competition).

In an attempt to systematically study what social cognitive skills can be found in different animals, researchers have focused on different domains: animals' understanding of others' attentional states; animals' ability to follow others' gaze, detect others' line of sight, and understand others' visual perspective; and knowledge of intentions, goals, desires, and false beliefs. Researchers also have looked at different species in each domain to see how widespread the trait is in the animal kingdom and determine whether it has evolved in certain species but not others. The idea is that by focusing on these issues we will (a) gain important insight into the evolutionary roots of social cognition and (b) learn about the mechanisms involved.

ANIMALS' UNDERSTANDING OF OTHERS' ATTENTIONAL STATE

Eye-shaped stimuli are important signals in the animal kingdom. A good example of this is the Peacock butterfly (*Aglais io*), which has eye-shaped spots on its wings to scare away potential predators. The eyespots are an effective morphological antipredator adaptation that significantly increases the individuals' chances of survival (Vallin, Jakobsson, Lind, & Wiklund, 2005), suggesting that attention to eye-like patterns is widespread and can be exploited. However, individuals from this species are most likely not aware that they have this signal. They also have very limited control over its presentation to potential predators. They cannot modify the signal, depending on whether the potential predator is in a position to actually see it. The interaction between the prey and predator can therefore best be explained as a sender–receiver relationship, in which one individual (the sender) presents a certain signal to which the other individual (the receiver) responds (see Volume 1, Chapters 30 and 40, this handbook). The sender's signal as well as the receiver's response are fixed patterns, shaped by selection processes during evolution: The Peacock butterfly likely has no understanding whatsoever of the predator's mental states.

For other species, however, there is evidence that the eyes signal something about others' attentional states (see Chapter 7, this volume). All great ape species (chimpanzees, bonobos, gorillas [*Gorilla gorilla*], and orangutans [*Pongo pygmaeus*, *P. abelii*]) adjust their gestural communication to the attentional state of a human experimenter (Kaminski, Call, & Tomasello, 2004; Liebal, Call, Tomasello, & Pika, 2004, Hostetter, Russell, Freeman, & Hopkins, 2007). When the human is attentive (e.g., has her head turned toward the subject) they use more visible gestures (such as pointing or reaching) than when the human is not attentive (e.g., has her head turned away). Chimpanzees also use different types of gestures depending on the attentive state of the receiver. They use audible (e.g., hand clapping) instead of visible gestures if others are nearby but not in a position to see them (Liebal, Call, & Tomasello, 2004; Liebal, Call, Tomasello, & Pika, 2004), and they use visible gestures (e.g., pointing) when the other is in the position to see them and the other's eyes are visible (Hostetter, Russell, Freeman, & Hopkins, 2007).

Sensitivity to the eyes, as an important signal for others' attention, seems to be spread throughout the primate family. Rhesus monkeys (*Macaca mulatta*) and ring-tail lemurs (*Lemur catta*), for example, steal less food from a human experimenter whose eyes are open or directed toward them than from one whose eyes are closed or oriented away (Flombaum & Santos, 2005; Sandel, MacLean, & Hare, 2011).

Differentiating others' attentional states is not restricted to primates and seems to be present in species more distantly related to humans as well. Dolphins (*Tursiops truncatus*) produce more "pointing" (i.e., the alignment of the body while remaining stationary for over 2 s) when a human is in a position to see them (e.g., oriented toward them) than when he or she is not (Xitco, Gory, & Kuczaj, 2004). Even Caribbean reef sharks (*Carcharhinus perezi*) seem to be sensitive to a person's body orientation, preferring to swim outside a person's visual field (Ritter & Amin, 2014).

Dogs (*Canis lupus familiaris*) also show a high sensitivity to human eyes. When tested in a competitive situation in which a human forbade them to take a piece of food, dogs took more food when the human was oriented away from the food than toward it, when the human's eyes were closed as opposed to open, and when the human was distracted as opposed to attentive (Call, Bräuer, Kaminski, & Tomasello, 2003). This was true not only in competitive but also more cooperative contexts, in which the dogs had to decide which human to beg from. Here, the dogs directed their begging more toward a human whose eyes were visible than toward a human whose eyes were covered (Gácsi, Miklósi, Varga, Topál, & Csányi, 2004).

There is also evidence that different bird species are sensitive to a human's attentional state. Starlings (*Sturnus vulgaris*) and jackdaws (*Corvus monedula*) attend to the presence of the eyes as well as the gaze direction of a human in a competitive situation related to food: When the human's eyes were closed or averted, starlings resumed feeding earlier and at a higher rate, thus consuming more (Carter, Lyons, Cole, & Goldsmith, 2008), whereas jackdaws were responsive to subtle cues of attention, depending on the social context (i.e., whether the individual was a stranger or familiar to them; von Bayern & Emery, 2009).

So a certain level of sensitivity to the status of the eyes seems relatively widespread in the animal kingdom, including among species very distantly related to each other. This could be seen as an indicator for an evolutionary ancient and relatively hard-wired behavior with an urgent evolutionary function (Emery, 2000). Rather than understanding that the status of the eyes alters an individual's perception, a recipient's reaction to eye-shaped stimuli could be rather automatic and unrelated to understanding others' psychological states. Alternatively, the trait might not be homologous in all species but might have evolved as an analogous trait separately and several times in the animal kingdom. Looking at one trait alone cannot address the question of mental state attribution in animals—other domains need to be investigated as well.

GAZE FOLLOWING IN ANIMALS

Another question on which researchers have focused is whether animals, like humans, follow each other's gaze. This would indicate that at the very least gaze direction and line of sight are as relevant for animals as they are for humans. Many species from different taxa attend to where others are looking. For social living animals, following the gaze of others would be beneficial in gaining information about outside entities. By following another's gaze the individual can get valuable information about different resources (e.g., food, predators; Tomasello, Call, & Hare, 1998). One way to test this idea is to see whether one individual follows the gaze direction of another individual to a specific target outside its own view. Various primate species follow the gaze direction of other individuals. All great ape species readily follow the gaze direction of a human experimenter (Bräuer, Call, & Tomasello, 2005; Tomasello et al., 1998; Tomasello, Hare, & Agnetta, 1999). In the Bräuer et al. (2005) study, the human experimenter suddenly shifted her gaze toward the ceiling after feeding the animal for several seconds. Gaze-following behavior in this situation was compared to a control condition during which the experimenter looked straight at the opposite side of the room. Apes looked at the ceiling significantly more often when the human had looked up than when she had not, indicating that they were sensitive to human gaze direction (Bräuer et al., 2005).

The ability to follow another's gaze is present not only in apes but also various monkey species more distantly related to humans. Emery, Lorincz, Perrett, Oram, and Baker (1997) showed that rhesus macaques were able to locate an object according to the gaze direction of a conspecific depicted on a TV monitor. Tomasello et al. (1998) tested several monkey species (e.g., sooty mangabeys [*Cercocebus atys torquatus*], rhesus macaques, stumptail macaques [*Macaca arctoides*], pigtail macaques [*Macaca nemestrina*]) for their ability to follow gaze of their group members. An experimenter, located in an observation tower, attracted the attention of one individual by presenting food to her. Once this individual had shifted her gaze toward the food, it was recorded whether a nearby subject (that had not seen the food itself) would respond with co-orientation to the conspecific's gaze shift. All monkey species tested in this setting followed the gaze direction of their conspecific. There is also evidence that different New World monkey species, including cotton-top tamarins (*Saguinus oedipus*), common marmosets (*Callithrix jacchus*), and different lemur species are responsive to the gaze direction of others (Burkart & Heschl, 2007; Sandel et al., 2011).

Gaze following is thus widespread among the primates. As with attention reading, however, gaze following also has been demonstrated in a wide variety of other mammals, such as dolphins, seals (*Arctocephalus pusillus*), goats (*Capra hircus*), dogs, and wolves (*Canis lupus*). Dolphins and seals spontaneously attend to the gaze direction of humans (indicated by head direction) in a food search game (Scheumann & Call, 2004; Tschudin, Call, Dunbar, Harris, & van der Elst, 2001). Goats, like primates, follow the gaze of their conspecifics, and dogs seem to be especially sensitive to a human's eyes and gaze direction (Kaminski, Riedel, Call, & Tomasello, 2005). Apart from the mammalian species tested, there also seems to be evidence that species even more distantly related to humans are sensitive to others' gaze direction. Ravens (*Corvus corax*) and rooks (*Corvus frugilegus*) have been shown to follow others' gaze direction (Bugnyar, Stöwe, & Heinrich, 2004; von Bayern & Emery, 2009). Ravens have been shown to co-orient with the gaze of a human experimenter from an early age. In this test, a human experimenter shifted gaze (head and eye direction) up to a distant location to which the ravens responded with co-orientation (Schloegl, Kotrschal, & Bugnyar, 2007). Recently, it was also found that the red-footed tortoise (*Geochelone* *carbonaria*), a solitary living species, follows the gaze of conspecifics (Wilkinson, Mandl, Bugnyar, & Huber, 2010). This is especially interesting because another line of research suggests that gaze following skills may be more sophisticated in species with more complex social structures compared to less socially complex species from the same family. Gibbons (*Hylobates pileatus, H. moloch, H. lar*) and siamangs (*Symphalangus syndactylus*), for example, seem to have less sophisticated gaze-following skills than those of great apes, possibly a result of their lack of social complexity as a monogamous species (Liebal & Kaminski, 2012). Additionally, ring-tailed lemurs (*Lemur catta*) show more gaze-following skills compared to other members of the strepsirrhines, possibly as an adaptation for living in the most complex social groups (Sandel et al., 2011).

Taken together, this evidence shows that gaze and gaze direction seem to be important stimuli for a number of species throughout the animal kingdom. This again suggests a very urgent evolutionary function of gaze following and a high adaptive value for different species. Most likely, gaze following helps individuals to exploit others for information about important resources, including food, mating opportunities, and so forth. As with attention reading, the fact that gaze following has emerged in very distantly related species may suggest that this trait is not homologous in all species and instead evolved as an analogous trait separately and several times in the animal kingdom.

One important question is to what extent the classical gaze-following behavior (i.e., shifting one's gaze in response to seeing another individual's gaze shift) is a more or less learned or inherent automatic response. Alternatively, gaze following could be an indicator of one individual's attention to another individual's line of sight, thus indicating the individual's attention to what the other is seeing and hence the other's psychological state. If an individual interprets gaze as an indicator of another's line of sight, the individual should, if necessary, relocate to a position from which it can see at what the other is looking.

There is evidence that at least some species seem to not just automatically follow others' gaze but truly attend to what others are looking at. Specifically, those species take some effort to track other's gaze direction to a specific target (e.g., by moving toward it) instead of automatically looking in the same direction. Tomasello et al. (1999) showed that chimpanzees walk around a barrier to track a human's gaze who had just looked behind this barrier. Bräuer et al. (2005) showed that all great apes follow the gaze of a human experimenter behind a barrier by walking around the barrier, presumably to track the human's line of sight (see Figure 32.1). There is also evidence that marmosets follow a human's gaze past distracting objects, suggesting that they understand the human's line of sight (Burkart & Heschl, 2006).

Additionally, there is evidence for nonprimate species being able to track a human's line of sight. Wolves seem to follow other individuals' gaze around barriers (Range & Viranyi, 2011) and ravens, like apes, will also move around a barrier, presumably to see at what a human is looking (Bugnyar, Stöwe, & Heinrich, 2004). Interestingly, some species fail to follow others' gaze around barriers. Northern bald ibises (*Geronticus eremita*) follow another's gaze when the other looks up, but when the other looks behind a barrier ibises look at the barrier too but do not walk around it (Loretto, Schloegl, & Bugnyar, 2010).

Yet, following gaze around barriers does not necessarily indicate a deeper understanding of seeing in others. Subjects do not have to interpret the other individual's mental state to be successful in gaze following. Instead of mentally representing that the other individual is seeing something differently from her perspective, animals may simply have the motivation to look at the same spot the other individual is fixating (Bräuer et al., 2005). Following gaze around barriers may thus indicate representations of spatial relationships but not necessarily of other minds.

DO ANIMALS TAKE THE PERSPECTIVE OF OTHERS?

Another question is whether animals understand anything about another individual's perspective, particularly that it can differ from one's own. Here, researchers distinguish between understanding

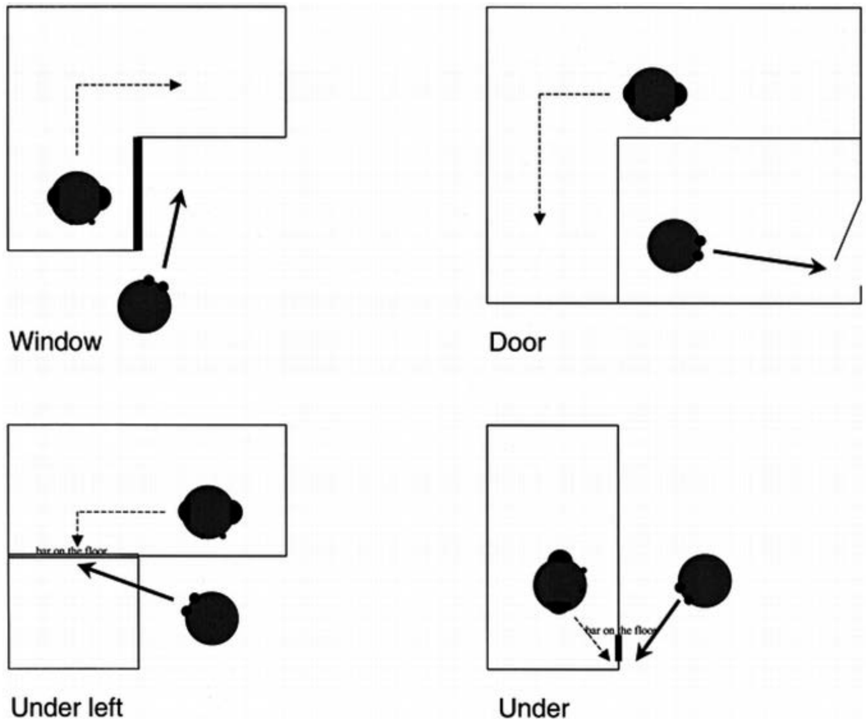

FIGURE 32.1. Gaze around barriers. Reprinted from "All Great Ape Species Follow Gaze to Distant Locations and Around Barriers," by J. Bräuer, J. Call, and M. Tomasello, 2005, *Journal of Comparative Psychology, 119,* p. 150. Copyright 2005 by the American Psychological Association.

another individual's visual and auditory perspectives. Visual perspective taking can be defined as *Level 1 perspective* taking (Flavell et al., 1978) when the individual understands that another's lines of sight is blocked (e.g., by an object), and as *Level 2 perspective* taking when the individual understands that from her or his perspective the other sees an object differently.

Some mammalian species seem to understand when others' visual access to an object or event is blocked. To test whether chimpanzees reach Level 1 perspective taking, researchers set up a situation in which two chimpanzees, one dominant over the other, have to compete over two pieces of food. The subordinate chimpanzee, which would normally not have had a chance to gain food with the dominant present, had an advantage in that it had visual access to both pieces of food whereas the dominant individual could see only one piece, the other piece being hidden by a wooden barrier. When given the chance to make a choice, the subordinate chimpanzee preferred to approach the piece of food behind the barrier, the one the dominant could not see, to the piece that was in the open and visible to the other individual. When the chimpanzees were alone, they chose randomly between the two pieces, indicating that their preference for the hidden piece was not merely based on a preference for eating behind an obstacle. In another control condition, the researchers showed that chimpanzees did not prefer a piece of food behind a transparent object, which potentially protected them from the competitor physically (Hare, Call, Agnetta, & Tomasello, 2000). One could argue that the obstacle used in this control condition was significantly smaller than the barriers used in the other conditions, weakening the argument that the chimpanzees might have seen those as physically protecting them. Bräuer et al. (2007) later controlled for the possibility that chimpanzees might use the barrier as protection by setting up a situation that was in principle identical to the one used in Hare et al. (2000) but had two obstacles between the subordinate and the dominant chimpanzees. One piece of food was then placed behind one obstacle, such that only the subordinate chimpanzee could see that piece of food, while the other piece was placed on top of the other obstacle, such that both individuals could see it. Subordinate chimpanzees still preferred the piece of food only visible to them even though they would have been protected physically from the dominant individuals on either side.

Chimpanzees' behavior cannot be explained by their perception of others' eyes as aversive stimuli. This was shown by Melis, Call, and Tomasello (2006), who demonstrated that chimpanzees prefer to reach through an opaque rather than a transparent tunnel for food. In the Melis et al. study, the chimpanzees are in competition with a human whose eyes they cannot see while deciding whether to reach through an opaque or a transparent tunnel for food. Because the chimpanzees cannot see the human's eyes while reaching, their decision has to be based on whether the human can potentially see their hand reaching through the transparent tunnel. In the competitive situation with the human, chimpanzees preferred to reach through the opaque tunnel but they did not show the same preference when they were alone and not in competition over the food. These results suggest that chimpanzees based their behavior on some sensitivity to the visual perspective of the other individual (Melis et al., 2006) and did not follow a simple rule such as "avoid the piece of food associated with the eyes of the competitor" (see Figure 32.2; but see Gretscher, Haun, Liebal, & Kaminski, 2012, for evidence that orangutans might use a simple rule to solve the same problem).

There is also evidence that other mammalian species may have some understanding when others' line of sight is blocked. Goats and domestic dogs seem to distinguish between two pieces of reward on the basis of whether another individual has visual access to it (Kaminski, Bräuer, Call, & Tomasello, 2009; Kaminski, Call, & Tomasello, 2006). Domestic dogs, for example, distinguish which toy to bring on the basis of the human's visual access to those toys. In this paradigm, the human and the dog sat opposite each other with two toys between them. One toy was placed behind an opaque barrier, such that the experimenter had no visual access to it. The other toy was placed behind a transparent barrier, such that the experimenter and the dog had visual access to the toy. On a request to fetch, dogs preferentially retrieved the toy that was visible to the experimenter. They fetched the visible toy significantly more in this condition than in a control condition where the dog and the experimenter sat on the same side of the barriers and thus had

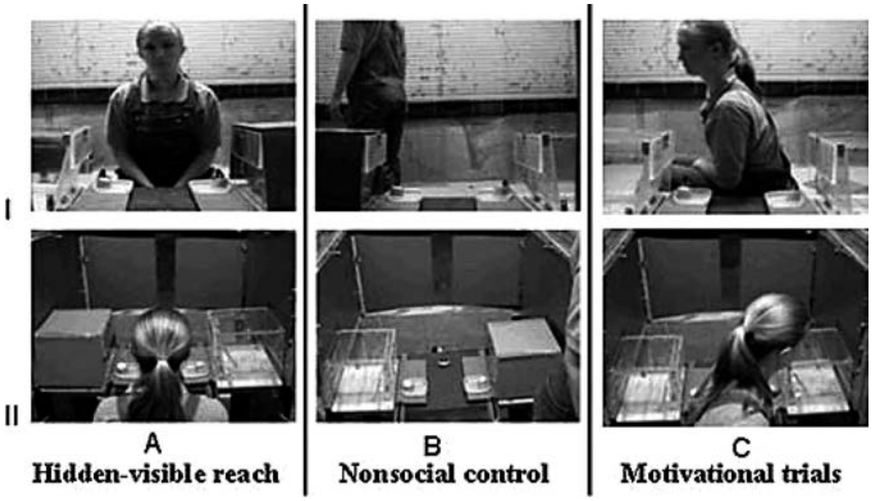

FIGURE 32.2. Reaching through opaque container. Reprinted from "Chimpanzees (*Pan troglodytes*) Conceal Visual and Auditory Information From Others," by A. P. Melis, J. Call, and M. Tomasello, 2006, *Journal of Comparative Psychology, 120,* p. 156. Copyright 2006 by the American Psychological Association.

comparable visual access to both toys (Kaminski et al., 2009). Whether this behavior is based on a true understanding of others psychological state or is based on more simple mechanisms (e.g., associative learning or simple behavioral rules) is the topic of debate (Povinelli & Vonk, 2003; Tomasello, Call, & Hare, 2003).

From an evolutionary perspective, it is interesting that birds—more specifically corvids, a group of species very distantly related to primates—seem to possess a flexible understanding of others' visual perspective very similar to that of primates. Evidence suggests that these birds have a flexible understanding of others' psychological states that allows them to form flexible strategies to reduce the probability others will steal their hidden food (caches; see Volume 1, Chapter 12, this handbook and Chapter 11, this volume). Scrub jays (*Aphelocoma californica*) and ravens differentiate situations during which they have been observed hiding food from situations where they were able to cache privately (Bugnyar, 2010; Emery & Clayton, 2001). For example, in a situation involving a choice of where to cache while a conspecific is observing, scrub jays prefer caching in locations relatively far from the observer to those nearby. They also prefer to cache behind an opaque barrier or in a tray that is located in the shade to caching out in the open or in a tray located in the light (Dally, Emery, & Clayton, 2004, 2005). The sophisticated cognitive abilities of members of the corvid family, which are comparable to those of primates, are considered a good example of analogous evolution resulting from similar selection pressures in the environment. One hypothesis is that the complexity of the social environment put the same premium on the evolution of social cognitive skills in corvids as it did in primates (Emery & Clayton, 2009).

Interestingly, when it comes to animals' understanding of the auditory perspective of others, results are different. Chimpanzees and rhesus macaques seem to understand when their actions (see Chapter 31, this volume) might produce a noise that the competitor could perceive (Melis et al., 2006; Santos, Nissen, & Ferrugia, 2006). For example, the chimpanzees in the Melis et al. (2006) study had the choice to reach through a noisy or silent tunnel for a piece of food. Although they did not distinguish both options when they were alone with no competitor around, they preferred the silent option when a competitor was present (see also Kundey et al., 2010, for evidence that dogs behave similarly in a similar paradigm). There is also evidence that when in competition with others, scrub jays prefer to hide their caches in substrates that do not produce a noise but they do not distinguish when caching alone (Stulp, Emery, Verhulst, & Clayton, 2009).

Interestingly, chimpanzees behave differently when the noise is produced rather than by themselves. In a study by Bräuer, Call, and Tomasello (2008), a subordinate chimpanzee was in a competitive situation with a dominant chimpanzee over two pieces of food. Both pieces were hidden by an opaque barrier in such a way that the subordinate, but not the dominant, chimpanzee could see them. The placement of the food then happened either noisy or silently and the subordinate chimpanzees then had to decide which piece of food to approach. If the subordinate understood that on the basis of hearing the noise the dominant chimpanzee would know the location of one piece of food (the noisy piece) but not the other (the silent piece), the subordinate should prefer the silent piece, because the dominant will most likely head for the noisy piece. In this situation, however, the chimpanzees did not distinguish between the two pieces, presumably because they did not actually produce the noise themselves (see Chapter 29, this volume). It is possible that chimpanzees have simply learned the consequences of making sounds in some situations and how to refrain from doing so, especially when in competition with others. A learned behavioral rule would explain why, as soon as the noise is produced externally, the chimpanzees do not seem to understand the connection between hearing and knowing in others and do not show evidence of understanding others' auditory perspective (Bräuer et al., 2008).

Additionally, there is evidence from other primate species that taking the auditory perspective of others might not be as straightforward as taking the visual perspective. For example, Tonkean macaques (*Macaca tonkeana*) do not distinguish a silent from a noisy box when reaching for food in a competitive situation (Costes-Thiré, Levé, Uhlrich, De Marco, & Thierry, 2015) and neither do ring-tailed lemurs (Bray, Krupenye, & Hare, 2014).

DO ANIMALS ATTRIBUTE KNOWLEDGE TO OTHERS?

Thus, there is plenty of evidence that different animal species understand something about others' current visual perspective. There is evidence for attention reading, gaze following, and even perspective taking. There is also evidence that a few species, mainly apes and corvids, understand not only something about others' current but also past visual access. One well-known paradigm is the *guesser–knower paradigm*, first introduced by Povinelli, Nelson, and Boysen (1990; see also Povinelli, Rulf, & Bierschwale, 1994). The authors conducted a series of experiments in which they wanted to test whether chimpanzees could take into account what a human had seen in the immediate past. To do so, they confronted chimpanzees with a situation in which they had to distinguish between two human experimenters who informed them about the location of hidden food. One of the experimenters (the knower) witnessed food being placed in one of several containers while the other experimenter (the guesser) waited outside the room. After the guesser reentered the room, the humans (the guesser and the knower) pointed to different containers. The chimpanzee was then allowed to choose between the containers and could potentially base his or her choice on the information coming from the most reliable source, the knower. In this setting, chimpanzees could only differentiate between humans after several hundred trials, which was most likely the result of discriminating between whether the human was present or absent during baiting. However, one general critique of this paradigm is that it is rather unnatural for chimpanzees. A human indicates the location of food in a very cooperative manner, something that would not occur in a group of chimpanzees. It is highly unlikely that one chimpanzee would indicate the location of food to another chimpanzee with the intention of letting him or her have it.

Hare et al. (2000, 2001) introduced a radically changed paradigm on the basis of chimpanzees' natural tendency to compete over food and showed that chimpanzees have quite a sophisticated understanding of others' perspective. Kaminski et al. (2008) took this paradigm further by introducing a setting in which chimpanzees took turns to pick food and the *evil eye hypothesis* could not account for chimpanzees' success. In this paradigm two individuals, subject and competitor, sat opposite one another; between them was a board, which the human could slide back and forth between both individuals. Each trial began with a hiding event, in which food was hidden under one of three cups while both chimpanzees were watching. Another piece of food was hidden under a second cup while only the subject was watching. Hence, although the locations of both pieces of food were known to the subject, only one of them was known to the competitor. In some trials the competitor was given the first choice. Subjects were unable to see the competitor's choice but knew they chose something because of their experience during an initial familiarization phase. After the competitor had made a choice, it was the subject's turn. The chimpanzees in this situation preferred the piece of food unknown to the competitor presumably because they understood that the other piece, the one the competitor had information about, was likely to be gone by the time of her or his choice. Chimpanzees' success was similar to that of 6-year-old children and adult humans (Kaminski, Call, & Tomasello, 2008). This finding therefore supports previous studies showing that chimpanzees may take into account what others have seen in the immediate past (Hare, Call, & Tomasello, 2001; see Figure 32.3).

Scrub-jays, like chimpanzees, seem to understand others' knowledge states. Dally et al. (2006) presented subjects with a situation in which they had to decide from which tray to recover hidden food. Earlier, the birds were allowed to hide food in one tray in the presence of observer A, with a second tray present but inaccessible. After a delay, the subject was allowed to cache in the other tray with observer B present. After another delay the subject was then given the opportunity to recover caches from both trays and had to decide which cache to

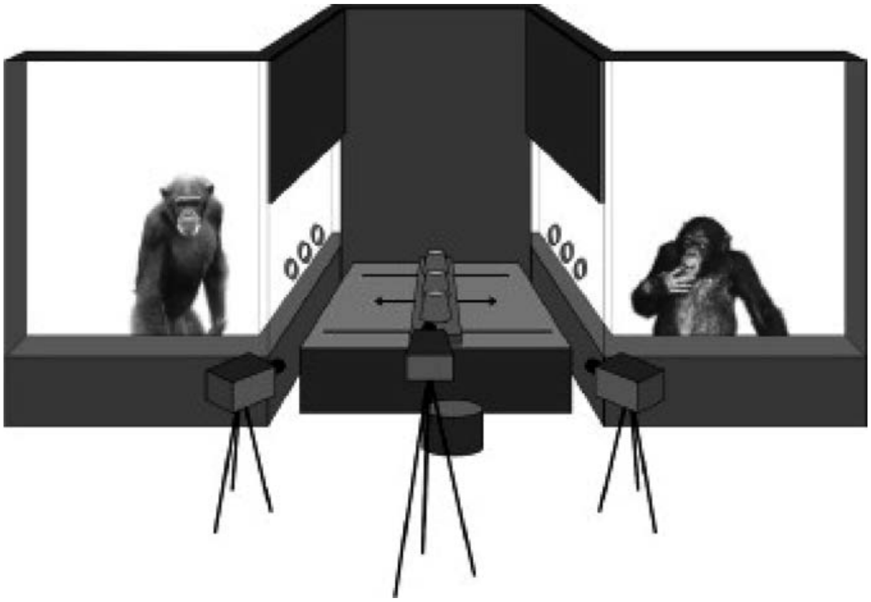

FIGURE 32.3. Knowledge ignorance. From "Chimpanzees Know What Others Know, But Not What They Believe," by J. Kaminski, J. Call, J., and M. Tomasello, 2008, *Cognition, 109,* p. 226. Copyright 2008 by Elsevier. Reprinted with permission.

recover on the basis of which observer was present. Interestingly, the birds specifically recovered the caches that observers had seen them make and did not recover any cache if observed by a completely naive individual, suggesting that it was not simple presence or absence guiding their behavior (Dally, Emery, & Clayton, 2006). Similar evidence comes from ravens, who seem to be able to predict others' behavior on the basis of what the ravens had observed others observing (Bugnyar, 2010).

DO ANIMALS UNDERSTAND OTHERS' INTENTIONS, GOALS, AND DESIRES?

Being able to attribute intentions, goals, and desires to others is considered a key step toward a fully-fledged ToM in humans. In humans, there is evidence that children understand the intentionality of others' actions around the age of 1 year old (Carpenter, Akhtar, & Tomasello, 1998; Woodward, 1998). In a seminal paper, Woodward (1998) showed that when 5-month-old infants are habituated to observing an actor interact with an object, and then the actor switches to handling a different object but in the same location, they look longer than when the actor handles the former object but in a new location. Infants' lengthier looking time is considered a sign that they were more surprised by one outcome than the other. This is seen as evidence that the infants in this study interpreted the action of the actor as being directed toward one specific object. There is also evidence that infants as young as 12 months of age interpret the intentionality of others' communicative actions (Behne, Carpenter, & Tomasello, 2005; Gräfenhain, Behne, Carpenter, & Tomasello, 2009). Behne et al. (2005) showed that children distinguish a pointing gesture given with a communicative intent from an action that resembled the pointing gesture (extended arm, head movements) but was not produced with communicative intent. Instead, the person just extended an arm and finger to check a wristwatch. Although children followed the intended communicative gesture, they ignored the unintended movement (Behne et al., 2005). Children also understand others' preferences and desires from quite early in life. In the *broccoli task*, Repacholi and Gopnik (1997) gave 18-month-old children the choice between a cracker and a piece of broccoli. Though children themselves preferred the cracker, they had no difficulties assigning the opposite preference to another person who they had witnessed show signs of dislike over the cracker and excitement over the broccoli (see also Rakoczy et al., 2007, for evidence that 3-year-old children understand that people can have incompatible desires).

In animals, there is some evidence that different species understand the goals, intentions, and possibly the desires of others. Nonhuman primates seem to understand goal-directed actions. Chimpanzees and capuchin monkeys differentiate between a person being unwilling or unable to give them food (Call, Hare, Carpenter, & Tomasello, 2004; Phillips, Barnes, Mahajan, Yamaguchi, & Santos, 2009). In that series of studies, a human constantly fed the animal. During these feeding sessions, the human was then either unable to give the food (the human acted clumsily and dropped the food) or was unwilling to give the food (the human pretended to hand over food but then, in a teasing way, withdrew the food). The human's behavior followed the same general motor pattern in both conditions but both chimpanzees and capuchins differentiated between both situations, showing that they presumably interpreted the goal of the person and not the outcome. Chimpanzees also hand over objects to humans or conspecifics when seeing them reach out for something, presumably because they identified their partners' goal (Warneken & Tomasello, 2006; Yamamoto, Humle, & Tanaka, 2009), and there is evidence that different ape species make goal-directed eye movements while observing others' actions (Kano & Call, 2014). Indeed, while observing others' actions, the apes' eyes already fixate the predicted outcome of that action (e.g., the object for which the other will most likely reach). Using eye-tracking technology, Kano and Tomonaga (2013) showed that a chimpanzee looked at an object before he or she saw a human reaching for it. The researchers argued that this showed that the chimpanzee anticipated the human's behavior and hence understood the human's goal to reach for the object.

Chimpanzees also seem to interpret the goal of others' actions while watching video sequences. Myowa-Yamakoshi, Scola, and Hirata (2012) showed that chimpanzees watching videos looked at the predicted outcome of the action before the video sequence presented it. Following Woodward (1998), Kano and Call (2014) habituated different ape species to a video sequence in which they saw a human hand reaching for one of two objects. After the habituation period, apes then watched the actual test sequence during which they saw the same human hand make an incomplete reach between the same two objects, which were swapped in location (modeled after Cannon, Woodward, Gredebäck, von Hofsten, & Turek, 2012). The apes seemed to predict the goal of the human as they predictively looked at the familiar object but not at the familiar location and did not differentiate at all in a control condition during which they witnessed an artificial claw reaching in between both objects. Specially trained circus chimpanzees were also shown to imitate rationally, which means they imitated a human's unusual actions (e.g., pressing a button with the foot instead of the hand) only when those actions seem to be intended (i.e., freely chosen) but not when the unusual action was the result of some constraint (e.g., that the hands of the human were occupied; Buttelmann, Carpenter, Call, & Tomasello, 2007). Chimpanzees seem to also differentiate between intended and unintended actions, because they copy intended actions but ignore unintended ones (Myowa-Yamakoshi & Matsuzawa, 2000; Tomasello, Carpenter, & Hobson, 2005).

There is also evidence that different monkey species attend to the goals of others. Cotton-top tamarins (*Saguinus oedipus oedipus*) use head orientation to predict the outcome of others' future actions (e.g., they predict for which object a human will be reaching; Santos & Hauser, 1999). Rhesus macaques also interpret others' actions as goal directed but only if the action itself is familiar to them, not when it is unfamiliar (Rochat, Serra, Fadiga, & Gallese, 2008).

As for nonprimate species, there is evidence that dogs seem to differentiate whether a humans' communicative gestures are intended or not (Kaminski, Schulz, & Tomasello, 2012). Like human infants, dogs distinguish between a human pointing with a communicative intent or not. If communicative intent was not established (through eye contact between the human and the dog), dogs ignored the human's actions when making a choice between two cups. It was also claimed that dogs, like chimpanzees, imitate other dogs' behavior rationally and, like chimpanzees, only copy actions that seem intended (Range, Viranyi, & Huber, 2007). However, Kaminski et al. (2011) argued that rather than being the result of observing different demonstrations, the observer dogs' behavior depended on the presence (or absence) of an uncontrolled stimulus, the visibility of a ball. Their data showed that the dogs behaved differently when the ball was visible compared to when it was not, and once this stimulus was controlled for, the initial effect vanished, showing that dogs do not seem to take into account whether an action is intended while copying others' behavior (Kaminski et al., 2011; but see Huber, Range, & Viranyi, 2012, for a different view).

A recent study, however, using the classic object habituation-dishabituation paradigm used with infants and chimpanzees, showed that dogs also seem to be surprised (suggested by their longer looking time) after repeatedly observing a person interact with an object and then seeing the same person handle a different object. This was again compared to dogs' looking time when watching the person handle the former object but in a new location. An additional control condition showed that the "actions" of an inanimate object (a black box) did not elicit the same result, suggesting that the dogs might attribute goals to people and not follow a simply associative rule (Marshall-Pescini, Ceretta, & Prato-Previde, 2014).

DO ANIMALS UNDERSTAND OTHERS' FALSE BELIEFS?

As described earlier, there is evidence for certain social cognitive skills in some animal species, including evidence that some species might take others' psychological states into account. However, there is one ability that is seen as a benchmark for ToM: understanding that others have beliefs and that those beliefs can be true or false. This is because understanding that another individual's belief is false requires an understanding that another person's mental states can be contradictory to one's own mental states and, more important, contradictory to reality. To understand that another individual's beliefs are false, one has to appreciate that there is a distinction between the inner state (or the mind) and reality and then be able to process that mental representation.

Thus, in the decades since the seminal paper by Premack and Woodruff (1978), researchers have tried to find ways to test whether animals, like humans, can understand that others' beliefs can be false, and so far there is no evidence suggesting that any nonhuman animals can make this distinction. In one version of a false belief task, Kaminski et al. (2008) compared chimpanzees with 3- and 6-year-old children in a competitive task. In the chimpanzee version of the tasks, two chimpanzees sat opposite each other with a sliding board between them, on top of which were three identical cups. One chimpanzee, however, had exclusive access to an additional cup, placed sideways to her. Two different types of reward were hidden: a high-quality, preferred reward, which was placed in one of the cups on the table between both chimpanzees; and a low-quality, less preferred reward which was always placed in the additional cup next to the subject. After the initial baiting, which both chimpanzees observed, the high-quality reward was manipulated a second time. During this manipulation, the human either lifted the reward and placed it back in its original location or shifted it to a new location. This second manipulation was either witnessed by both chimpanzees or only witnessed by the subject, who had access to the additional cup. Hence, in one of the conditions (the shift unwitnessed condition), the competitor now has a false belief about the location of the high-quality reward. The competitor was always the first to choose and the subject did not see the competitor choosing but had to base her decision on what she guessed the competitor had done. In this setting, the chimpanzees did not make the distinction between situations in which the others' belief was true or false, whereas the 6-year-old children clearly made the distinction (Kaminski et al., 2008). This is one study out of several indicating that despite the fact that chimpanzees (and other animals) understand knowledge and ignorance in others, they might not fully appreciate that others have inner thoughts (Call & Tomasello, 1999; Kaminski et al., 2008; Krachun, Carpenter, Call, & Tomasello, 2009; see Table 32.1).

TABLE 32.1

Summary of Species Tested

Category	Species tested	Main findings
Differentiating attentional states	Chimpanzee (*Pan troglodytes*); Bonobo (*Pan paniscus*); Gorilla (*Gorilla gorilla*); Orangutan (*Pongo pygmaeus, P. abelii*); Rhesus monkeys (*Macaca mulatta*); Ringtail lemurs (*Lemur catta*); Dolphins (*Tursiops truncatus*); Caribbean reef sharks (*Carcharhinus perezi*); Domestic dogs (*Canis lupus familiaris*); Starlings (*Sturnus vulgaris*); Jackaws (*Coloeus monedula*)	Sensitivity to the status of the eyes of others seems relatively widespread in the animal kingdom. Species from various taxa adapt their behavior to the attentional state of others, either by adjusting their communicative gestures accordingly or by adjusting their behavior strategically in competitive situations over resources.
Gaze following	Chimpanzee (*Pan troglodytes*); Bonobo (*Pan paniscus*); Gorilla (*Gorilla gorilla*); Orangutan (*Pongo pygmaeus, P. abelii*); Rhesus monkeys (*Macaca mulatta*); Sooty mangabeys (*Cercocebus atys torquatus*); Stumptail macaques (*Macaca arctoides*); Pigtail macaques (*Macaca nemestrina*); Cotton-top tamaarins (*Saguinus Oedipus*); Common marmosets (*Callithrix jacchus*); Dolphins (*Tursiops truncatus*); Seals (*Arctocephalus pusillus*); Goats (*Capra hircus*); Dogs (*Canis lupus familiaris*); Wolves (*Canis lupus*); Ravens (*Corvus corax*); Rooks (*Corvus frugilegus*); Red-footed tortoise (*Geochelone carbonaria*); Pileated Gibbon (*Hylobates pileatus)*; Silvery gibbon (*Hylobates moloch*); Lar Gibbon (*Hylobates lar*); Siamang (*Symphalangus syndactylus*); Northern bald ibises (*Geronticus eremita*)	Gaze following seems to be widespread in the animal kingdom and is found in species from various taxa, including rather solitary living species (e.g., the red-footed tortoise).
Geometrical gaze following	Chimpanzee (*Pan troglodytes*); Bonobo (*Pan paniscus*); Gorilla (*Gorilla gorilla*); Orangutan (*Pongo pygmaeus*); Common marmosets (*Callithrix jacchus*); Wolves (*Canis lupus*); Ravens (*Corvus corax*); Northern bald ibises (*Geronticus eremita*)	Geometrical gaze following is found in different species, including primate and some nonprimate species. Some species fail to follow others' gaze around barriers, though they follow others' gaze when they look up (e.g., the Northern bald ibis).
Perspective taking	Chimpanzee (*Pan troglodytes*); Orangutan (*Pongo pygmaeus*); Tonkean Macaques (*Macaca tonkeana*); Ringtail lemurs (*Lemur catta*); Capuchin monkeys (*Cebus apella*); Goats (*Capra hircus*); Dogs (*Canis lupus familiaris*); Scrub Jays (*Aphelocoma californica*); Ravens (*Corvus corax*)	Some species seem to take the visual perspective of others, whereas others do not seem to take others' perspective into account (e.g., Capuchin monkeys).
Understanding past visual access (Knowledge attribution)	Chimpanzee (*Pan troglodytes*); Scrub Jays (*Aphelocoma californica*); Ravens (*Corvus corax*)	Evidence for an understanding of others' past visual access exists only for a few species. Those few seem to take into account what others have or have not seen and also who has seen what.
Understanding others goals, intentions, and desires	Chimpanzee (*Pan troglodytes*); Capuchin monkeys (*Cebus apella*); Cotton-top tamarins (*Saguinus oedipus oedipus*); Rhesus monkeys (*Macaca mulatta*); Dogs (*Canis lupus familiaris*)	Some species differentiate between actions on the basis of the actor's goal and intention.
False belief understanding	Chimpanzee (*Pan troglodytes*)	There is of yet no evidence for false belief understanding in nonhuman animals.

CONCLUSION

Certain social cognitive skills, such as reading others' attentional states and following others' gaze direction, seem to be relatively widespread throughout the animal kingdom. This shows that gaze direction and the status of others' attention are a meaningful cue for many social living animals. Some of those skills (e.g., gaze following), however, appear to be automatic reflexive responses that do not necessarily involve any flexible understanding of others' psychological states. The fact that some of those traits are widespread in the animal kingdom suggest that they possess a high survival value, for example, by aiding in the rapid location of predators or avoiding conflict. Other skills, such as the ability to take another's perspective or understand what others have seen in the immediate past, do not seem to be so widespread and thus may be based on more complex cognitive operations.

Yet, whether any of these studies show that animals truly attribute mental states to other individuals is still a highly controversial issue. One criticism of all the studies mentioned previously is that the animals in those studies may simply base their strategies on associations formed during the experiment or in earlier life or simply read others' behavior and act on the basis of that information (Penn & Povinelli, 2007). Instead of having some concept of seeing, animals may simply learn to associate the eyes of their competitor with one piece of food and not the other (see Chapter 5, this volume). The stimulus "eye" may be seen as an aversive stimulus, which the subject then associates with the food and therefore avoids (the evil eye hypothesis). This explanation, however, has been made very unlikely by recent studies, which show that chimpanzees develop strategies of outcompeting their competitors that cannot be explained by the evil eye hypothesis (e.g., Kaminski et al., 2008; Melis et al., 2006; Schmelz et al., 2011, 2013). Even though most recent studies have ruled out some of the earlier explanations on the basis of associative accounts, it remains a question whether subjects in those studies need to refer to the mental states of others to solve the problem.

Another, nonmentalistic interpretation of the results is that animals do not form concepts of others' mental states but rather about others' behavior, and that this is sufficient to succeed in all paradigms used with animals so far (Povinelli & Vonk, 2003). This line of thinking suggests that animals follow certain behavioral rules that they have learned over time—for example, "every time I do X, my conspecific reacts by doing Y." The weakness of this approach is that it is not the most plausible explanation across all of the very different studies and paradigms which exist and which provide evidence for animals' understanding of others' psychological states (see Call & Tomasello, 2008, for a discussion of this point). However, all evidence to date also shows that there are strong limits to animals' understanding of others. Although some species represent other's knowledge states, such as what they may have seen in their immediate past, no nonhuman animal has yet demonstrated the ability to attribute false beliefs to others. This suggests that a truly representational ToM may be a uniquely human cognitive capacity. Call and Tomasello (2008) suggested that although animals might have what we can call a perception-goal psychology, they might lack a human-like belief–desire psychology (Call & Tomasello, 2008). Butterfill and Apperly (2013), however, suggested the existence of a *minimal ToM*, which in their definition does not involve what they call *ToM cognition*. Although ToM cognition requires true mental representation, minimal ToM does not. Instead, it involves representing goal-directed actions, which are defined as "outcomes as functions of bodily movements" (p. 614) and which do not require true representation. Butterfill and Apperly would further argue that rather than having a concept of seeing and understanding others' perspectives, animals (and in some situations humans as well) might simply register when others encounter an object (e.g., food) that is the precondition for them to perform goal-directed actions targeting that object. Again, registering that others encountered an object and adapting a behavioral strategy on the basis of that object does not require a full representation of the others' mental or psychological state, therefore explaining most, if not all, of the evidence found in animals so far.

From an evolutionary perspective, it is interesting that the most convincing evidence for flexible social cognitive skills comes from two very distantly related groups of species: apes and corvids (Clayton, Dally, & Emery, 2007; Emery & Clayton, 2009). Because the morphology of mammalian and bird brains is so substantially different (see Volume 1, Chapters 12 and 24, this handbook), their skills are almost certainly convergent rather than homologous processes (Emery & Clayton, 2009). Similar social cognitive skills therefore may be an adaptation to similar socioecological challenges in the social life of these species, such as navigating competition over resources and otherwise interacting in a complex society.

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CHAPTER 33

REFLECTING ON MIRROR SELF-RECOGNITION: A COMPARATIVE VIEW

Diana Reiss and Rachel Morrison

A year and a half after Charles Darwin completed his voyage on the *Beagle* and 21 years before he was to publish his theories of evolution, he experienced another animal encounter that further compelled him to ponder the continuity between humans and other species—even beyond that of physical evolution. It was a day late in September 1838 when Darwin was visiting the London Zoo and first met Jenny, a young orangutan being temporarily housed in the heated giraffe house. Because of his elevated social status in England, Darwin was actually permitted to enter her cage. Darwin was impressed by the ape's human-like behavior and returned twice more to visit Jenny. During one of his visits, he watched as Jenny gazed into a small mirror, contorting her face as a child would. In his notebook Darwin wrote that Jenny appeared to be "astonished beyond measure" on seeing her reflection in the mirror (Keynes, 2002).

BACKGROUND

Since ancient times, humans have used mirrors as a tool to view themselves. The first mirrors available to humans and nonhuman species were most likely naturally occurring reflective surfaces (see Figure 33.1), such as still pools of water and natural depressions in rocks that could collect water (Enoch, 2006). The earliest artifacts of manufactured mirrors date back to 6200 BCE and were found in graves in Anatolia, in the region of the Neolithic settlement of Çatal Hüyük, in what is now south central Turkey (Enoch, 2006). They were made from ground and polished obsidian, a highly reflective black volcanic glass. The proclivity, interest, and motivation of humans to use mirrors rests on their cognitive ability to understand that what is seen in the mirror is oneself—that the information in the mirror is an external representation of self. But beyond its use as a tool for self-viewing, the mirror has functioned as a simple yet valuable research tool in a myriad of comparative and developmental studies of mirror self-recognition (MSR) in humans and nonhuman species. Mirrors have also proven to be effective tools for eliciting social behavior in many species and have been used in many ethological studies as well.

MSR was long considered unique to humans, a hallmark of human self-awareness and human intelligence. However, in 1970, Gordon Gallup conducted a groundbreaking study in which he exposed four preadolescent, mirror-naive chimpanzees (*Pan troglodytes*) to a mirror and demonstrated that our closest relatives also shared this capacity. Gallup (1982) referred to MSR as "the ability to become the object of your own attention" (pp. 242–243) and the demonstration of MSR is generally considered to be a reliable index of a facet of self-awareness in humans and nonhuman animals (Amsterdam, 1972; Anderson, 1984; Gallup, 1970; Rochat, 2003). In humans the emergence of MSR is thought to coincide with the emergence of other advanced cognitive abilities and growing social awareness, including perspective-taking (seeing things from another's perceptive) and empathy (see Chapters 32 and 34,

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FIGURE 33.1. A juvenile male chimpanzee at the Arnhem Zoo. Photo by F. B. M. de Waal. Reprinted with permission.

this volume). Developmental studies with children have confirmed this connection (Bischof-Köhler, 2012; see following section Mirror Self-Recognition in Humans). Gallup (1982) was the first to suggest a phylogenetic link between the emergence of MSR and empathy. The coemergence hypothesis suggests the emergence of MSR, perspective-taking, and empathy are linked in evolution and development (de Waal, 2008).

Gallup developed and used an elegant paradigm for testing MSR in nonhuman primates: the mirror test. The basic approach exposed individual chimpanzees to a full-length mirror and their behavior at the mirror was observed and documented over time. In developmental psychology a similar approach is used to test the behavioral responses of children to mirrors. The mark test or rouge test (Amsterdam, 1972) is used as an indicator of the emergence or presence of this stage of cognitive development in children (see following section Mirror Self-Recognition in Humans). In isolation from one another, these chimpanzees were exposed to a mirror over a 10-day period (80 hr total) and their behavior was observed. Gallup (1970) reported that the chimpanzees initially exhibited social behaviors (e.g., bobbing, vocalizing, threats) at the mirror, but then these responses declined rapidly over a period of 2 days and were replaced by self-directed behaviors. Gallup stated,

> Such self-directed responding took the form of grooming parts of the body which would otherwise be visually inaccessible without the mirror, picking bits of food from between the teeth while watching the mirror image, visually guided manipulation of anal-genital areas by means of the mirror, picking extraneous material from the nose by inspecting the reflected image, making faces at the mirror, blowing bubbles, and manipulating food wads with the lips by watching the reflection. (p. 86)

According to Gallup, the observed performance of self-directed or self-exploratory behavior at the mirror was evidence of MSR in chimpanzees, but he devised and used a direct experimental procedure, the mark test, generally considered to be the litmus test of MSR to additionally confirm this ability. After observing self-directed behavior in the chimpanzees, the mark test was conducted. The chimpanzees were anesthetized and then marked with a dye that lacked tactile or olfactory properties. The marks were placed above their protruding brow ridge and on the top edge of the opposite ear, areas not visible to the chimpanzee without a mirror (Gallup, 1970). After a 4-hour recovery period from the anesthesia, the chimpanzees were observed for a 30-minute period to determine the number of mark-directed responses they exhibited in the absence of a mirror. The mirror was then reinstated and the chimpanzees were observed for 30 minutes to determine the number of mark-directed responses in the presence of the mirror. Passing the mark test required that the animal touch the marked area while attending to the mirror and do so more frequently than it did in the absence of the mirror. At the mirror, all of the chimpanzees exhibited mark-directed responses and "there was a dramatic increase in viewing time, and several noteworthy attempts to visually examine and smell the fingers which had been used to touch these facial marks" (Gallup, 1982, p. 238). During mirror exposure, chimpanzees that demonstrated MSR showed different stages of behavior at the mirror: social behavior (e.g., reacting as if viewing a conspecific), mirror exploratory behavior (e.g., attempting to look over, under, or behind the mirror), and self-directed behavior (e.g., viewing parts of their bodies or monitoring actions they perform that are unobservable in the absence of the mirror; Gallup, 1970).

Gallup (1970) tested two additional mirror-naive chimpanzees of comparable ages, who were anesthetized and marked using the same procedures. He reported that no self-directed or mark-directed behavior was observed and that these individuals responded to the mirror as if viewing a conspecific. Mirror-naive animals appear to have to learn the contingencies of mirror use and they exhibit different stages of behavior in the process. In the same study, Gallup also tested three species of monkeys—stump-tailed macaques (*Macaca arctoides*), rhesus monkeys (*M. mulatta*), and cynomolgus monkeys (*Macaca fascicularis*)—for MSR. The monkeys exhibited and persisted in showing social responses toward the mirror; no evidence was observed of self-directed behavior or of MSR. Gallup suggested that the striking difference in the mirror-oriented responses by chimpanzees and monkeys could be evidence of "a qualitative psychological difference among primates" (p. 87).

The mark test has been criticized with the claim that the increase in mark-directed touches observed in chimpanzees were artifacts of normal levels of face touching by chimpanzees after recovery from anesthesia and the marking procedure (Heyes, 1995). However, the analysis of the temporal occurrence of mark-directed versus non–mark-directed behavior in chimpanzees in mirror and nonmirror conditions further supported the conclusions of Gallup (1970) and did not support Heyes's hypothesis (Gallup et al., 1995; Povinelli et al., 1997).

Research on the capacity for MSR and the process involved in its emergence is one path to understanding the development and perception of self in humans and nonhuman species. The mirror test examines the cognitive capacity of an individual to spontaneously learn the affordances of a mirror and understand that it reflects an external representation of oneself. MSR is contingent on several other perceptual cognitive processes that at the very least include selective attention, the interpretation of visual stimuli, and proprioception (Sherrington, 1906; see also Chapters 6 and 9, this volume). Mirrors have the unique and unusual property of providing viewers with immediate and identical behavior synchronized to their own responses, different than naturally occurring social responses. Their every movement is simultaneously replicated in the mirror and therefore learning the contingencies of mirror use may require proprioceptive awareness and kinesthetic feedback (Gallup, 1968). The mirror presents the individual with potential information, in the sense that it is only available if an individual selectively attends to the mirror.

In the 4.5 decades since Gallup's seminal study, numerous studies of MSR have provided comparative data regarding self-awareness and the subjective experiences of nonhuman minds when exposed to mirrors (for a review, see Anderson & Gallup, 2011; Gallup, Anderson, & Shillito, 2002; Parker, Mitchell, & Boccia, 1994). A prodigious literature has accumulated on the phylogenetic distribution of MSR and the responses of dozens of species to their mirror reflection. To date, despite hundreds of animals tested, only a limited number of species have demonstrated this capacity. Only chimpanzees, orangutans (*Pongo pygmaeus*), gorillas (*Gorilla gorilla gorilla*), bonobos (*Pan paniscus*) and a few nonprimate species—bottlenose dolphins (*Tursiops truncatus*), Asian elephants (*Elephas maximus*), and the Eurasian magpie (*Pica pica*)—have spontaneously exhibited MSR. Notably, these self-recognizers share a suite of characteristics. They are highly social species, they have large brains (or in the case of the magpie, an exceptionally large forebrain), and they have encephalization quotients (EQ; the ratio between actual brain mass and predicted brain mass for an animal of a given size; see Volume 1, Chapters 12 and 24, this handbook) that are higher than those of species that fail to show MSR. Specifically, in humans the EQ = 7.4–7.8, in bottlenose dolphins the EQ = 4.14, in great apes the EQ = 1.5–3 (Boddy et al., 2012; Marino, 2002), in elephants the EQ = 1.13–2.36 (Herculano-Houzel et al., 2014; Shoshani, Kupsky, & Marchant, 2006), and magpies have especially high EQs (Rehkämper, Frahm, & Zilles, 1991). Humans, great apes, dolphins, and elephants also show evidence for perspective-taking and empathy (e.g., caregiving, targeted consolation/helping-behavior toward others; de Waal, 2008; Marino et al., 2008; Plotnik & de Waal, 2014; Plotnik, de Waal, & Reiss, 2006; Reiss & Marino, 2001).

In this chapter, we review the literature on the behavioral responses of human and nonhuman species to mirrors but by no means do we present an exhaustive review of the extant research on self-awareness in humans. We review the comparative literature on MSR studies, beginning with early descriptions of animal responses to mirrors. We address the following questions: If an individual attends to the mirror, how is the information interpreted? What type of behavioral responses do mirrors elicit?

Given that most species fail to show self-recognition at a mirror and respond with social behavior, mirrors have been commonly used in ethological studies to induce and document animal social responses (for a review see Gallup, 1968; Rowland, 1999). In the following section, we briefly review some of the many studies that have been conducted with fish, birds, and mammals that respond with social behavior as if reacting to a conspecific.

MIRROR-IMAGE STIMULATION

Gallup (1968) used the term *mirror-image stimulation* (MIS) to refer to “situations in which an animal is confronted with its reflected image” and stated that “such stimulation constitutes an unusual part of the environment in the sense that it enables an organism to see itself as it is seen by other organisms” (p. 782). Mirror-elicited social behavior has been reported in many fish and bird species and in some mammals (see Gallup, 1968, for a review). For example, Lissmann (1932) was one of the first to observe that mirrors elicited an unconditioned aggressive display in Siamese fighting fish (*Betta splendens*) and Tinbergen (1951, as cited in Gallup, 1968) reported that mirror exposure elicited stereotyped threatening postures in sexually aroused male sticklebacks (*Gasterosteus aculeatus*). Birds generally respond to their mirror images as if they are conspecifics, and as early as 1916, Dickey reported aggressive behavior by a male towhee (*Pipilo juscus petulans*) to its mirror reflection (as cited in Gallup, 1968). Schusterman, Gentry, and Schmook (1966, as cited in Gallup, 1968) observed that captive California sea lions (*Zalophus californianus*) exhibited social behavior toward the mirror that included the production of underwater click-type vocalizations and attempts to bite the mirror and slap it with their front flippers.

MIS responses in nonhuman primates have been well documented (see reviews in Anderson & Gallup, 2011; Gallup, 1968; Yerkes & Yerkes, 1929). Lesser apes and Old World and New World monkeys generally react to MIS as if viewing a conspecific, often exhibiting aggressive responses that may subsequently be followed by indifference to the mirror (see following section Mirror Self-Recognition in Nonhuman Primates for a few exceptions). In contrast, in their studies with great apes, Kohler (1959) and Gallup (1968) reported that the initial responses of chimpanzees to mirrors were aggressive but were replaced by more exploratory responses toward the mirror. Schmidt (1878) and Yerkes (1927) reported that orangutans and gorillas exhibited initial interest in mirrors, infrequent aggressive behavior, and increased attachment to mirrors.

MIRROR SELF-RECOGNITION IN NONHUMAN ANIMALS

The majority of species tested for MSR only exhibit social and exploratory responses (see Volume 1, Chapter 34, this handbook and Chapter 28, this volume) to mirrors. In contrast, mirror-naive individuals of species that have shown MSR may initially show social and exploratory responses toward mirrors, but these behaviors diminish and are replaced by self-directed behavior. This marked change from social or exploratory to self-directed or self-exploratory activities has been considered a positive indicator of self-recognition (Anderson, 1994; Gallup, 1970; Povinelli et al., 1993). Great apes, dolphins, elephants, and magpies progress through the same stages of behavior prior to demonstrating MSR (Gallup, 1968, 1970, 1977; Plotnik et al., 2006; Povinelli et al., 1993; Prior, Schwarz, & Güntürkün, 2008; Reiss & Marino, 2001). These phylogenetically divergent species exhibit striking similarities in the process of learning the affordances of mirrors.

Mirror Self-Recognition in Nonhuman Primates

MSR and spontaneous self-directed responses at mirrors have been well documented in chimpanzees (Gallup, 1970; Lin, Bard, & Anderson, 1992; Povinelli et al., 1993), bonobos (Hyatt & Hopkins, 1994; Walraven, van Elsacker, & Verheyen, 1995; Westergaard & Hyatt, 1994), orangutans (Lethmate & Dücker, 1973; Miles, 1994; Suarez & Gallup, 1981), and gorillas (Allen & Schwartz, 2008; Patterson & Cohn, 1994; Posada & Colell, 2007; see reviews in Gallup et al., 2002; Parker et al., 1994).

An individual's developmental level, age, or previous familiarity with mirrors can determine the amount of time they exhibit behaviors from each stage (Priel & de Schonen, 1986; see also following section Mirror Self-Recognition in Humans). In some studies, it has been reported that animals may exhibit relatively short stages of social behaviors before exhibiting self-directed behaviors. For example, Gallup (as cited in Povinelli et al., 1993) noted that in some cases the chimpanzees' behavior changed from social to self-directed after 3 to 4 min of mirror exposure. Similarly, in Povinelli et al.'s (1993) study in which 105 chimpanzees (age 10 months–40 years) were tested, some chimpanzees exhibited self-exploratory behaviors within 10 to 20 min of mirror exposure.

Developmental studies of MSR in chimpanzees have documented that social behavior is exhibited toward the mirror between 7 and 9 months of age and contingency testing begins at about 10 months of age (Robert, 1986). Self-directed behavior has been reported to first emerge at 4.5 years according to some studies (de Veer, Gallup, Theall, van den Bos, & Povinelli, 2003; Povinelli et al., 1993; see Figure 33.2) and between 28 and 30 months of age according to other studies (Bard et al., 2006; Lin et al., 1992). The use of different criteria in these studies when judging if self-directed behavior is being displayed and when determining mark test results may be partly responsible for this discrepancy in age of onset for chimpanzees.

Bard et al. (2006) provided a detailed discussion of the different criteria used in MSR studies with humans and chimpanzees. Studies with chimpanzees have historically used more rigorous criteria for what constitutes evidence of self-recognition and a passing mark test. For example, to be considered a self-recognizer Povinelli et al. (1993) and de Veer et al. (2003) required that the chimpanzees exhibit five bouts of self-exploratory behavior at the mirror for at least 30 s, and passing the mark test required that the chimpanzee have more mark-directed touches at the mirror than in the absence of the mirror. In contrast, Lin et al. (1992) and Bard et al. (2006) considered a behavior to be self-directed if the chimpanzee was looking in the mirror and touching or directing a behavior toward its own

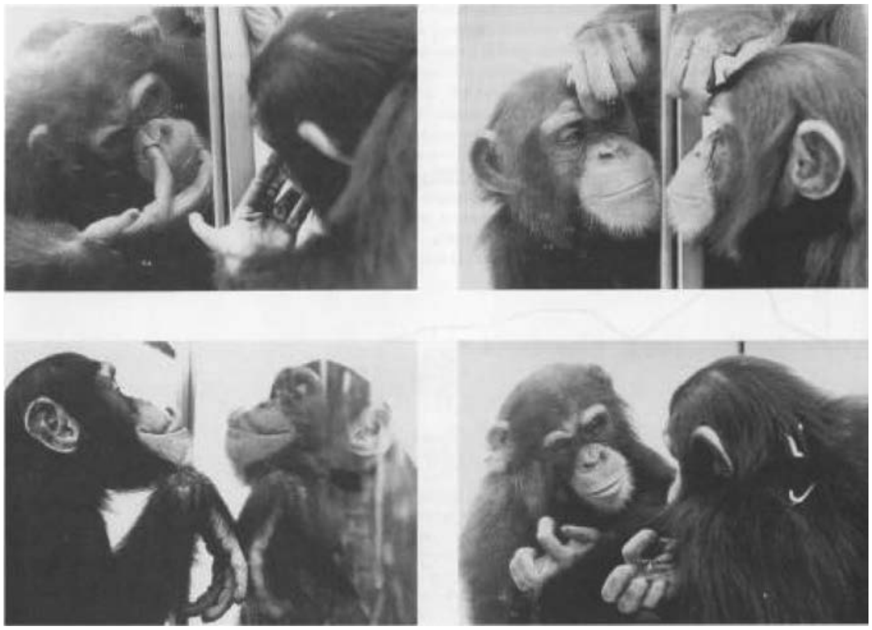

FIGURE 33.2. Examples of self-exploratory behavior by chimpanzees at a mirror. Photos by D. Povinelli. Reprinted with permission.

body, and mark-directed behavior required the chimpanzee to at least once, while looking in the mirror, direct a behavior toward and make contact with the mark. To facilitate direct comparisons between chimpanzees and humans Bard et al. (2006) conducted MSR studies using a similar approach with nine different chimpanzees (ages 24–32 months) and nine different children (ages 15–24 months). The chimpanzees were not anesthetized and the children were told they were going to be marked and similar criteria were used for judging self-directed and mark-directed behaviors. Bard et al. (2006) argued that when they used the rigorous criteria from Povinelli et al. (1993) and other prior comparative studies, none of the infant humans or chimpanzees in their study were considered self-recognizers.

Similar to Gallup's (1970) findings in his original study with chimpanzees, a mirror study with two male orangutans reported that during the course of mirror exposure, there was a decline in social behavior followed by an increase in self-directed behavior, and on testing, both animals passed the mark test (Suarez & Gallup, 1981). In this same study four gorillas (one male and three females age 13–19 years old) were also tested but did not demonstrate self-directed behavior nor did they pass the mark test (Suarez & Gallup, 1981). However, three other studies have demonstrated the capacity for MSR in three different adult gorillas (one female and two males). Patterson and Cohn (1994) reported that a female gorilla passed the mark test (she touched the mark 47 times), she also exhibited self-directed behavior, and when marked, her viewing time at the mirror increased. Posada and Colell (2007) reported an absence of social behavior when a male gorilla was first exposed to the mirror, an increase in "self-referred" behaviors over sessions, and that the gorilla passed the mark test. Allen and Schwartz (2008) reported that a male gorilla they tested touched the marked area more when in front of the mirror than in the absence of the mirror, which traditionally has been an indicator of MSR. In a study with bonobos, although mark tests were not conducted, Westergaard and Hyatt (1994) reported that four of nine bonobos who were given mirror exposure used the mirror as a tool to inspect parts of their bodies (e.g., mouth, eye, genitals) that they are unable to see otherwise. In support of the previous findings, subsequent evidence was published reporting that four additional bonobos were capable of "spontaneous" self-recognition; when exposed to their mirror image these animals engaged in similar investigative self-directed behaviors (Walraven et al., 1995).

Notably, not all individuals that show self-directed behavior at a mirror pass the mark test (Swartz & Evans, 1991; see de Veer & van den Bos, 1999, for a review of methodology and interpretation of MSR in nonhuman primates). In an early comparative study of the development of MSR, an orangutan exhibited self-directed behavior at the mirror but did not successfully pass a mark test (Robert, 1986). In their extensive developmental study with chimpanzees, Povinelli et al. (1993) demonstrated that only 50% of the chimpanzees that exhibited compelling self-directed behavior and were classified as self-recognizers passed the mark test. In a later developmental study, 12 chimpanzees (age 8–15 years old) from the Povinelli et al. (1993) study were reevaluated 8 years later and only 67% of the animals previously classified as self-recognizers were given the same classification (de Veer et al., 2003). These findings indicate that caution should be taken when assuming that mark test results are the essential ingredient of MSR (Povinelli et al., 1993).

Furthermore, not all chimpanzees exhibit MSR when tested under similar conditions. Notably, chimpanzees reared in social isolation did not show mirror self-recognition and it has been suggested that early social experience or lack thereof may influence an individual's capacity for MSR (Gallup, 1977; Gallup, McClure, Hill, & Bundy, 1971). Povinelli et al. (1993) reported disparities in the demonstration of MSR in the chimpanzees in their study and posited that early social experience could play a role in this ability, but because the degree of early social deprivation or social interaction for the majority of the individuals was unknown, no firm conclusions could be drawn. Povinelli et al. (1993) also stated that a low percentage of older chimpanzees showed MSR and suggested that this ability may decline in adulthood. Age-related differences were not attributed to rearing conditions because the animals were housed in stable breeding units. However, de Veer and van den Bos (1999) pointed out that some of the chimpanzees in the Povinelli et al. (1993) study were reported to exhibit behavioral stereotypes that are often associated with social deprivation and, therefore, differential rearing conditions may play a role in the emergence of this capacity.

In contrast with these findings in great ape species, in the numerous studies with lesser apes and Old World and New World monkeys, none have shown evidence of spontaneous MSR, although there are a few reports of possible self-directed responses (see review in Anderson & Gallup, 2011; Gallup & Suarez, 1991; Povinelli, 1987). Although siamangs (*Hylobates syndactylus*), a lesser ape species, have not passed the mark test, one study claimed that there was possible evidence for self-directed behavior in both individuals of a mated pair (Heschl & Fuchsbichler, 2009). One study reported that capuchin monkeys show differential behavioral reactions to their mirror image as seen in real time videos than to unfamiliar conspecifics in videos (de Waal, Dindo, Freeman, & Hall, 2005). These authors proposed their findings may indicate that the perceptions of self versus other in a mirror vary along more of a continuum than previously thought (de Waal et al., 2005).

Another study reported that rhesus monkeys (*Macaca mulatta*), in atypical conditions in which they had undergone surgical head implants for electrophysiological recordings, demonstrated self-directed behavior at a mirror that included observation of the implant and their genital regions (Rajala, Reininger, Lancaster, & Populin, 2010). The authors suggested that the implant or "super mark" may have served to sufficiently motivate the monkeys to use the mirror to view the implant in the post-surgical context and perhaps dampened their gaze aversion toward the mirror (Rajala et al., 2010). However, these monkeys never showed self-directed behavior toward mirrors prior to the surgical implant and this raises many interesting questions regarding the importance of motivation and the saliency of the mark on the initiation of mirror-guided behaviors (see Anderson & Gallup, 2011). In a more recent study, it was reported that after extensive training on a task involving visual and somatosensory feedback, rhesus monkeys passed mark tests and spontaneously exhibited mirror-induced self-directed behaviors (Chang, Fang, Zhang, Poo, & Gong, 2015; see a more thorough discussion in the following section

Mirror Self-Recognition: Spontaneous Emergence Versus Explicit Training). Whether the rhesus monkeys' behavior in both of these studies constitutes evidence for MSR remains unclear.

Mirror Self-Recognition in Nonprimates

During the 30 years following Gallup's initial report of chimpanzees demonstrating MSR, the capacity for MSR remained confined to humans and the great apes, fueling scientific interest and speculation regarding the evolutionary significance of MSR. Was MSR rooted in common aspects of primate social ecology, neurobiology, and cognition? In an early paper, Gallup (1979) suggested that other large-brained mammals (e.g., dolphins, other cetaceans, elephants) would be likely candidates for future tests of MSR.

Mirror self-recognition in dolphins and other cetaceans. Many years after Gallup's suggestion to conduct mirror tests with dolphins and elephants, he and his colleagues exposed two mirror-naive, 7-year-old, captive-born, male bottlenose dolphins to a mirror and used a modified version of the mark test to accommodate the nonhanded dolphin (Marino, Reiss, & Gallup, 1994). Gallup's basic procedural approach for testing MSR in apes was followed; however, a few key aspects were different: The dolphins were not isolated but instead remained with their social group when exposed to mirrors, each dolphin was marked and tested individually within the social context, and the dolphins were not anesthetized during mark applications. The dolphins showed evidence of similar stages of behavior during mirror exposure as reported in mirror studies with great apes (e.g., social, mirror exploratory, contingency-testing, self-directed behavior). These findings, although suggestive of MSR, were inconclusive because of methodological issues and difficulties in implementing adequate controls requisite to obtain robust evidence of MSR in a species unable to touch a marked part of their body with a hand. Similar suggestive yet inconclusive findings in other tests of MSR with bottlenose dolphins were also reported (Marten & Psarakos, 1994, 1995).

The first conclusive evidence for MSR in dolphins was reported when two captive-born, male bottlenose dolphins, age 13 and 17 years old, exhibited self-directed behavior and passed the mark test by using the mirror to investigate parts of their bodies that were marked (Reiss & Marino, 2001). This study used similar procedures as those previously reported by Marino et al. (1994), but conducted the requisite combination of control and test situations to produce specificity effectively equivalent to hand use. The dolphins were socially housed during mirror exposure and testing and were not anaesthetized prior to the application of the mark. To control for possible tactile cues during the marking procedure and due to the mark itself, mark and sham test control trials were conducted. During the mark test, a black nontoxic marker was used to place a mark on an area of the dolphin's body that was not visible to the animal in the absence of the mirror; during the sham marking, an identical marker filled with water was used to mark the dolphin (see Reiss & Marino, 2001, for further details on testing procedures; see also Figure 33.3). Given the fact that dolphins lack forelimbs, precluding their ability to touch a mark,

FIGURE 33.3. **A male bottlenose dolphin with a nontoxic mark above his right eye. From "Mirror Self-Recognition in the Bottlenose Dolphin: A Case of Cognitive Convergence," by D. Reiss and L. Marino, 2001, *Proceedings of the National Academy of Sciences, USA, 98,* p. 5939. Copyright 2001 by the National Academy of Sciences of the United States of America. Reprinted with permission.**

an alternative criterion for passing the mark test was used. It was predicted that if dolphins understood that they had been marked, in the post-mark condition the dolphins would likely go directly to the mirror and immediately orient the marked area of their body toward the mirror surface.

The dolphins' responses to the mirror affixed to their pool wall were consistent with the behavioral stages as reported in chimpanzees. During mirror exposure and testing, neither dolphin exhibited social behavior toward the mirror. This was not surprising because one of the dolphin pools had three reflective glass walls and therefore these animals were not truly mirror-naive at the onset of the study. When initially presented with a mirror, the dolphins exhibited repetitive contingency-testing and self-directed behaviors (Reiss & Marino, 2001). Importantly, both dolphins exhibited self-directed behaviors at the mirror (i.e., repetitive body movements, open mouth, close eye viewing, and bubble production) that were strikingly similar to self-directed behaviors previously described in the great apes and humans (Reiss & Marino, 2001; Sarko et al., 2002). Both dolphins passed multiple mark tests and their initial behavior was oriented to the mark in nine out of 11 sessions. Dolphins, unlike chimpanzees, are not social groomers and did not exhibit interest in the marks on each other, yet oriented to marks on their own bodies when seen in the mirror.

This demonstration of MSR in the bottlenose dolphin was the first convincing evidence for this capacity in a nonprimate species. These findings provide a compelling case for cognitive convergence in large brained primates and dolphins, species that have been phylogenetically distant for approximately 95 million years and show significant differences in neuroanatomical characteristics (Reiss & Marino, 2001). Furthermore, these findings suggest that the capacity for MSR is not a byproduct of factors specific to humans and their close relatives the great apes, but may instead be due to a high degree of encephalization and cognitive ability more widely distributed than previously thought (Reiss & Marino, 2001).

A subsequent study of MSR with false killer whales (*Pseudorca crassidens*) and killer whales (*Orcinus orca*) reported that killer whales exhibited contingency-testing and possibly self-directed behaviors but did not pass the mark test (Delfour & Marten, 2001). Groups of wild Atlantic spotted dolphins (*Stenella frontalis*) on 14 different occasions were presented with a handheld mirror underwater (Delfour & Herzing, 2013). The dolphins reportedly showed little interest in the mirror and rather than positioning in front of the mirror, they circled it and no contingency-checking behaviors were observed (Delfour & Herzing, 2013). Mirror studies with wild dolphins present many challenges that include maintaining a stable mirror image in the open ocean environment and being able to systematically observe the behavioral responses during mirror exposure with specific individuals. Fleeting glimpses toward mirrors by dolphins in the wild may be insufficient for learning the affordances of mirrors and thus the lack of contingency-testing and self-directed behavior in wild individuals may be due more to the methodology used rather than a true reflection of their ability for MSR.

Mirror self-recognition in elephants. As previously discussed, elephants share a suite of attributes with great apes and dolphins that made them the next logical species for a study of MSR. Plotnik et al. (2006) investigated MSR in three captive adult female Asian elephants by exposing them to a jumbo-sized (244 cm × 244 cm) acrylic mirror affixed to a wall of their outdoor holding yard. The elephants had some previous limited experience with small mirrors leaned against a tree as part of an enrichment program but had not had exposure to mirrors during the year prior to the onset of the study. During the period of mirror exposure all three elephants showed a similar progression of behavioral stages during mirror exposure as those documented in chimpanzees (Gallup, 1970; Povinelli et al., 1993) and dolphins (Reiss & Marino, 2001). During the initial two days of mirror exposure the elephants did not show evidence of social behavior but rather actively explored the mirror itself and made several attempts to look behind the mirror. Mirror exploratory behavior diminished and ended after the second day of exposure and was replaced by more repetitive contingency-testing movements, such as the performance of unusual repetitive nonstereotypic trunk and body movements when at the mirror and rhythmic head movements in and out of mirror view. Following this, all three elephants exhibited self-directed behavior at the mirror and only when at the mirror. These behaviors included close eye viewing and the inspection and touching of the inside of the mouth when standing in close proximity to the mirror (see Figure 33.4).

A series of mark and sham-mark tests were conducted after repeated occurrences of self-directed behavior were documented in the elephants. During the mark test, a visible white mark, using nontoxic children's face paint, was applied to the right side of the elephant's head and a nonvisible sham mark (a transparent version of the same paint without the color pigment) was applied to the left side of the head. The sham mark controlled for possible olfactory and tactile cues, resulting in only a visual component to differentiate between the mark and sham mark (see Plotnik et al., 2006, for more details of the procedures and materials). The elephants were marked in their barn in the absence of a mirror and their behavior was observed prior to them being released into the yard with the mirror. It was plausible that after being marked an elephant might try to explore and touch the mark and sham mark areas; once at the mirror, however, if the elephant saw itself, it should only touch the visible mark. Applying the same criterion for passing the mark test as used with chimps, one out of the three elephants tested passed the test. "Her rate of touching the mark, on the right side of her head, deviated from her general head touching during all previous conditions in its higher frequency and its bias toward the side with the visible mark" (Plotnik et al., 2006, p. 17055). Finding parallels in the progression of behavioral stages that emerge during mirror exposure, and the similarities in the specific types of behavior exhibited at the mirror by apes, dolphins, and elephants, provides further evidence in support of convergent cognitive evolution in these large brained and highly social mammals.

FIGURE 33.4. An adult female elephant orienting in close proximity to a large mirror during a study of mirror self-recognition at the Bronx Zoo. From "Self-Recognition in an Asian Elephant," by J. M. Plotnik, F. B. M. de Waal, and D. Reiss, 2006, *Proceedings of the National Academy of Sciences, USA, 103,* p. 17054. Copyright 2006 by the National Academy of Sciences of the United States of America. Reprinted with permission.

A prior study was conducted to test for the presence of MSR in Asian elephants residing at the Smithsonian's National Zoo (Povinelli, 1989). Two adult female Asian elephants were exposed to a smaller (105 cm × 241 cm) mirror that was mounted to a plywood stand and positioned outside of the bars of the elephants' enclosure just beyond the reach of the elephants' trunk. It was reported that after 2 weeks of mirror exposure, neither elephant exhibited self-directed behavior and both failed to pass the mark test. However, both elephants in this study demonstrated spontaneous mirror-guided behavior to gain access to carrots that could only be seen in the mirror (see the following section Mirror-Guided Behavior). This disparity between the findings reported by Plotnik et al. (2006) and Povinelli (1989) may be due to methodological differences between these two studies. In the Plotnik et al. study the elephants had exposure and access to a large mirror that afforded them a view of their bodies from head to toe. Because the mirror was mounted on the wall of their enclosure, they could control and adjust their proximity to it according to their optimal viewing distance and the target of their attention. The ability to touch and explore the mirror itself, and the ability to look behind the mirror, may provide individuals with information and feedback requisite to learning the contingencies and affordances of mirrors. It appears that in the majority of studies demonstrating MSR in apes, dolphins (Reiss & Marino, 2001), elephants (Plotnik et al., 2006), and magpies (Prior et al., 2008), the animals had direct access to mirrors that allowed them to see and explore the mirror itself and their own bodies.

Mirror Self-Recognition in Avian Species

The first evidence of MSR in a nonmammalian species was reported in the Eurasian magpie, a songbird species of the crow family (Prior et al., 2008). Magpies—similar to other corvid species, including jackdaws, ravens, crows, nutcrackers, and jays—lack a neocortex but possess a relatively large forebrain pallium. Five birds were tested and they exhibited similar stages of behavior to those previously described in chimpanzees (Prior et al., 2008). In the five sessions prior to being marked, three of five birds tested showed social behavior that diminished over time and cases of contingency-testing behavior. Mark tests using colored stickers and sham marks with black stickers, less likely to be visually perceived by the birds, were conducted (Prior et al., 2008). Of the five birds tested in the mirror condition, three produced mark-directed behavior toward only the colored stickers, not the sham. On the basis of these findings, the study's authors claimed this to be the first evidence for MSR in a nonmammalian species, suggesting that the "essential components of human self-recognition have evolved independently in different vertebrate classes with a separate evolutionary history" (Prior et al., 2008, p. 1). The authors further pointed out that their findings suggest that the neural capacity required for MSR has independently evolved in mammals and birds, and the demonstration of MSR in magpies indicates that a laminated cortex is not a necessary requirement for MSR.

Using the same experimental paradigm and nine adult jackdaws (*Corvus monedula*), Soler et al. (2014) attempted to replicate the findings from Prior et al.'s (2008) study. On initial mirror presentation, the jackdaws demonstrated high interest in the mirror (pecked at it and looked behind it) and exhibited self-contingent behaviors (Soler et al., 2014). Notably, social behavior was not exhibited during the initial mirror exposure. It was reported that none of the jackdaws passed the mark test because there was no difference in the number of mark-directed behaviors between the mirror and control (cardboard, no mirror) conditions. In both conditions the birds touched and tried to remove the sticker, which Soler et al. (2014) suggested represents a methodological flaw in using stickers as a mark—because of the sensitive nature of the birds' feathers, the sticker may give them tactile feedback.

One difference and potential flaw in both the Prior et al. (2008) and Soler et al. (2014) studies is that the mark test was administered prior to the observance (or report of) mirror-mediated self-directed behaviors. In the standard approach used with other species, the mark test is used to confirm MSR once self-directed behaviors have emerged. Given the potential methodological issues regarding the efficacy of the mark test with avian species as cited by Soler et al. (2014), it would be important in future studies with avian species to document mirror-mediated self-directed behavior as one indicator of MSR and then proceed with the mark test for further confirmation.

Spontaneous Emergence Versus Explicit Training

As previously discussed, most mammalian and avian species do not spontaneously, without explicit training, exhibit self-directed behavior. However, some studies have reported that explicit training of specific subroutines can induce self-directed behavior at a mirror in pigeons (*Columbia livia domestica*; Epstein, Lanza, & Skinner, 1981; Uchino & Watanabe, 2014) and rhesus monkeys (Chang et al., 2015). Epstein et al. (1981) claimed that pigeons demonstrated self-directed behavior when the contingencies of mirror use were made more explicit through training. They trained three pigeons using food reinforcement to (a) perform self-directed pecking at a blue dot on their body in the absence of a mirror, (b) peck at blue dots visible on the walls of their training chamber in the absence of a mirror, and (c) use a mirror to guide them in locating and pecking blue dots on the walls of their chamber that could not be viewed otherwise. Without further training, a blue dot was placed on the pigeon's breast under a bib so that the dot could only be seen in the mirror. Tested in the mirror and no mirror conditions, the pigeons only pecked at the dot in the mirror condition. Epstein et al. pointed out that the pigeons, as with apes in previous mirror studies, used the mirror to locate marks on their bodies but suggested the behavior resulted from their prior reinforcement histories rather than attributing it to them having self-awareness or a self-concept, as claimed in MSR studies with apes.

Thompson and Contie (1994) attempted to replicate and extend the Epstein et al. (1981) study. Six pigeons were trained and tested using similar procedures but Thompson and Contie reported that the birds failed to show self-directed behaviors in the presence of mirrors. In contrast to the findings of Epstein et al. (1981), they claimed that explicit training of the pigeons to the contingencies of mirror use was insufficient to induce self-directed behavior at a mirror. The authors stated, "These birds may have discovered something about the affordances of reflecting surfaces for locating objects from a geocentric perspective; nevertheless, they failed to generalize this information to an egocentric perspective involving body dots" (Thompson & Contie, 1994, p. 400). More recently, Uchino and Watanabe (2014) conducted another study similar to that of Epstein et al. (1981), in which two pigeons were explicitly and extensively trained in three subroutines: (a) to peck a blue dot on the front wall of their chamber, (b) to peck a blue dot on their body (self-directed pecking), and (c) to use a mirror to detect a blue dot behind them on a rear wall of their chamber (mirror-guided behavior). Later training sessions included the interdigitation of the three subroutines within one session. A similar mark test to that used by Epstein et al. (1981) was conducted, in which a blue dot was placed under a cowl (bib) on the pigeon so that it could only be detected in a mirror. The authors reported results consistent with those reported by Epstein et al. (1981) and stated that the pigeons "spontaneously integrated the learned self-directed and mirror-use behavior and displayed self-directed behavior in a mark test" (Uchino & Watanabe, 2014, p. 327). However, Uchino and Watanabe (2014) acknowledged that pigeons lack the innate ability for MSR and do not show self-directed behavior without explicit and extensive training on a prerequisite set of behaviors.

Monkeys have also been trained to use a mirror as a tool to guide their own actions and locate an otherwise undetectable object (Itakura, 1987). In the absence of training, most monkeys do not exhibit spontaneous mirror-guided behavior (Anderson & Roeder, 1989), although Anderson (1986) reported a case in which two macaques did demonstrate spontaneous mirror-guided behavior (see the following section Mirror-Guided Behavior in Nonhuman Animals). Chang et al. (2015) extensively trained seven rhesus monkeys via associative learning to use a mirror to locate and touch a colored light beam that was shone on their face. The light source gave the monkeys somatosensory information about where to touch because it was initially irritating to the skin. Once trained, the marks used no longer provided somatosensory information. The authors reported that five of the seven trained rhesus monkeys, while in their home cages, passed mark tests by touching a mark (odorless dye) on their face and a mark on their ear (new location) and that they spontaneously exhibited mirror-induced self-directed behaviors (Chang et al., 2015).

The approach used in these studies, although important for our understanding of how behavioral subroutines may be spontaneously combined and synthesized into novel behaviors, ignores a critical aspect of the MSR studies. In tests of MSR in humans and the other self-recognizing species, self-directed behavior emerges spontaneously and often after a relatively short period of mirror exposure. Learning the contingencies of mirror use as well as using the mirror to view oneself appears to be self-motivated and self-reinforcing. Importantly, the object of attention in the mirror is the self. In contrast, the self-directed behavior reported in pigeons and rhesus monkeys (Chang et al., 2015) does not occur spontaneously. Importantly, in these cases, the object of attention in the mirror is a blue dot or another stimulus that, when touched, results in an extrinsic food reward. It is not the self. Chang et al. (2015) reported that monkeys exhibited mark-directed and other spontaneous self-directed behaviors; however, the self-directed behaviors actually are not spontaneous because the monkeys had already been explicitly trained on the contingencies of mirror use not just to touch a mark. Notably, the untrained control monkeys did not exhibit spontaneous self-directed behaviors. However, Chang et al.'s (2015) findings suggest that explicit training may provide increased motivation or saliency, which may lead animals to learn the contingencies of mirror use.

MIRROR-GUIDED BEHAVIOR IN NONHUMAN ANIMALS

Although some species do not appear to demonstrate MSR, they are capable of mirror-guided behavior—using mirrors as tools to explore their environment, such as by using a mirror to locate hidden conspecifics, food, or other objects. Mirror-guided behavior suggests that individuals are capable of learning that a relationship exists between the features of their surrounding environment and the information they see in the mirror (Broom, Sena, & Moynihan, 2009). Studies of this behavior provide important information about how different species perceive and process mirror information (Pepperberg, Garcia, Jackson, & Marconi, 1995). Mirror-guided behavior has been reported in pygmy marmosets (*Cebuella pygmaea*; Eglash & Snowdon, 1983), macaques (*Macaca tonkeana*, *Macaca fascicularis*, and *Macaca fuscata fuscata*; Anderson, 1986; Itakura, 1987), Asian elephants (Povinelli, 1989), African grey parrots (*Psittacus erithacus*; Pepperberg et al., 1995), New Caledonian crows (*Corvus moneduloides*; Medina, Taylor, Hunt, & Gray, 2011), pigs (*Sus scrofa*; Broom et al., 2009), and dogs (*Canis familiaris*; Howell & Bennett, 2011; Howell, Toukhsati, Conduit, & Bennett, 2013).

Mirror-naive pygmy marmosets, given 28 days of mirror exposure, initially responded with social threats, but this behavior quickly declined and researchers observed them following their reflection and playing peek-a-boo (Eglash & Snowdon, 1983). They used the mirror to locate conspecifics from other groups that were not visible without the mirror. Rather than exhibiting threat responses toward the mirror, they went to the location of the conspecifics and produced threat displays.

Anderson (1986) compared mirror and no mirror trials conducted with three different species of nine macaques to determine if the presence of a mirror would aid them in finding a hidden raisin. Notably, two juvenile monkeys demonstrated improvement during the mirror condition and this mirror-guided behavior was in the absence of explicit training (Anderson, 1986). In another study, two male mirror-naive Japanese macaques, age 5 and 6 years old, were extensively trained to use a mirror to locate food (a piece of apple) or to hit illuminated keys that could not be seen without the aid of a mirror (Itakura, 1987). Both monkeys successfully performed the tasks, using the mirror to observe and guide their hand movements toward the object in the mirror.

In a study conducted to test for the presence of MSR and mirror-guided behavior in two adult female Asian elephants (Povinelli, 1989), neither elephant demonstrated self-directed behavior and both failed the mark test. When subsequently tested, however, both elephants demonstrated spontaneous mirror-guided behavior to gain access to carrots that could only be seen in the mirror. When the mirror was not present or was angled, the elephants were unable to locate the hidden carrots.

Pepperberg et al. (1995) conducted a study with two juvenile grey parrots (age 7.5 and 11 months) to determine how they respond to the presence of a mirror and how they process mirror information. The birds demonstrated some behaviors similar to those described in MSR studies with humans and other species, such as social (e.g., aggression, head bobbing, vocalizing) and exploratory (e.g., look behind mirror) behavior. Although neither bird exhibited self-directed behavior, they were the first nonmammalian species shown to successfully use the mirror to discriminate and locate hidden objects, providing evidence that they are capable of processing mirror information (Pepperberg et al., 1995). In a more recent MSR study with 10 mirror-naive New Caledonian crows, social and exploratory responses toward a mirror persisted throughout exposure (Medina et al., 2011). Two of the 10 mirror-experienced crows were then compared with two additional mirror-naive crows on a mirror-mediated spatial location task. All four of the crows successfully used the mirror to locate a hidden food source, suggesting that extensive prior experience with a mirror may not be required for mirror-guided behavior (Medina et al., 2011).

Broom et al. (2009) gave eight young, mirror-naive pigs (age 4–8 weeks old) 5 hr of mirror exposure and then showed them a food bowl visible only by using the mirror. Seven out of the eight pigs were able to quickly (average 23 s) find the food bowl using cues only visible in the mirror, whereas mirror-naive pigs looked for the bowl behind the mirror. The researchers suggested that these results are evidence for assessment awareness in pigs (Broom et al., 2009). A more recent study (Gieling, Mijdam, van der Staay, & Nordquist, 2014) attempted to replicate the Broom et al. (2009) study with 22 slightly younger piglets (age 4–6 weeks old). They reported that mirror-experienced pigs did better than mirror-naive pigs; however, only two out of 11 pigs were able to find the hidden food using the mirror, suggesting that the pigs were not attending to the mirror. The methods were modified to physically guide a second group of 11 pigs to a mirror and findings demonstrated that only one mirror-experienced pig could locate the hidden food and none of the 11 mirror-naive pigs could. The authors claimed that these results suggest that the pigs lack an understanding of the affordances of a mirror (Gieling et al., 2014). The disparities in findings reported by Gieling et al. (2014) and Broom et al. (2009) are curious and suggest further tests need to be conducted.

In an initial study, only two of 40 dogs were able to use a mirror to find the location of their owners (Howell & Bennett, 2011). In a follow-up study using similar methodology as Broom et al. (2009), researchers tested the ability of 44 dogs (22 experimental/mirror condition, 22 control/covered mirror condition) to use a mirror to find a bowl containing a treat (odor cues were controlled for) that was located on the opposite side of an opaque barrier (Howell et al., 2013). Results demonstrated that significantly more dogs in the experimental condition (17 of 22 vs. 9 of 22 in the control condition) successfully located the treat within the 3 min time period.

MIRROR SELF-RECOGNITION IN HUMANS

As previously stated, this section is not intended to be a comprehensive review of the substantial developmental MSR literature in humans; instead, we highlight some studies that allow for comparisons with the MSR studies in nonhuman animals. Most studies of MSR in infants and young children have documented their behavioral responses to mirrors and conducted rouge or mark tests to determine the age of emergence of MSR (reviewed extensively in Anderson, 1984). Although many studies with humans consider touching the mark or using the mirror to examine the mark on the face as definitive for the presence of self-recognition, the criteria actually used for scoring a passing mark test are inconsistent between studies. Children have also been described as passing the mark test if they touch their face near the mark, say their name when prompted with the question “who is in the mirror,” or point to themselves (Anderson, 1984; Bard et al., 2006), which brings into question the validity of some findings. It has been suggested that using verbal self-referents as evidence of MSR in infants age 18 to 24 months, especially when prompted, may not be appropriate because they may be used arbitrarily (Anderson, 1984).

Developmental studies of MSR in children have reported that children typically first exhibit social behavior between 4 and 6 months of age (Amsterdam, 1972; Dixon, 1957) that peaks between the 6th and 8th month, and exploratory behavior is exhibited between 7 and 14 months of age (Amsterdam, 1972). The next stage of behavior, repetitive or contingency testing, is typically seen in children by the end of the first year (Amsterdam, 1972), although Dixon (1957) reported the emergence of repetitive behaviors around 6 to 7 months. In most studies, self-directed behavior has been reported to emerge in children between 18 and 24 months of age; however, some report that it has been observed as early as 15 months (Amsterdam, 1972; Anderson, 1984).

It has been suggested that the development of MSR in humans coincides with the development of the capacity for making secondary representations and other indices of self-awareness, such as embarrassment, empathy and prosocial behavior, pretend play, and socially imitated or synchronous behaviors (Bischof-Köhler, 2012; Nielsen & Dissanayake, 2004; Rochat, 2003). In a longitudinal study of MSR in 10 children tested biweekly starting at the age of 15 months and continuing to 23 months, Courage, Edison, and Howe (2004) reported that MSR, personal pronoun use, and photo self-identification appeared to emerge in this sequence over 3 months and they suggested that MSR may be a prerequisite for the other abilities. Rochat (2003) suggested, "self-awareness is a dynamic process not a static phenomenon" (p. 728) and he described five different levels of self-awareness that infants experience from birth to 4 or 5 years of age. Level three is when children first start demonstrating explicit self-awareness and when MSR is thought to emerge.

Notably, just as seen with nonhuman animals, not all children pass the mark test even when they demonstrate self-directed behavior at the mirror. In Amsterdam's (1972) original study, only 13 (54%) of the 18 to 24 month old children passed the mark test. Developmental studies with infants and children also indicated intraindividual differences; some individuals initially pass the mark test but then fail subsequent tests. Reports from a longitudinal study (Nielsen & Dissanayake, 2004) described the age of emergence of several cognitive abilities, including MSR, by testing 98 infants (age 12–24 months) every 3 months. Results of the MSR tests demonstrated that some infants did not pass all of the mark tests. Notably, one infant passed the initial two mark tests at 18 and 21 months of age, but then failed the subsequent test at 24 months. Similarly, Courage et al. (2004) reported intraindividual differences in a longitudinal study with 10 children tested biweekly. Only one child passed the first and subsequent trials using the strict criteria (touching his or her nose while looking at the mirror), whereas the other nine children's responses varied across sessions (sometimes passing using strict criteria, other times using lenient criteria, or not passing at all).

Unlike most nonhuman species tested for MSR, it is typical for humans to have regular mirror exposure beginning very early in life. There are, however, rare instances where mirrors are not prevalent or accessible in certain cultures and children are essentially mirror-naive. Priel and de Schonen (1986) conducted a study of MSR comparing the mirror-directed behavioral responses of 60 children (age 6–26 months) who were mirror-naive to 60 children (age 6–26 months) with prior mirror experience. Prior experience with a mirror did not appear to impact MSR results, as both mirror-naive and mirror-familiar children began showing mark-directed behavior in the 13- to 19-month-old group, with most children between 20 and 26 months old passing (Priel & de Schonen, 1986). These findings suggest that having prior experience with mirrors may be important for learning how to use the information in the mirror to help locate an object (mirror-guided behavior); however, prior mirror experience does not impact a child's capacity for MSR (Priel & de Schonen, 1986).

CONCLUSION

The discovery that other species as well as humans recognize themselves in mirrors has provoked much discussion and speculation by psychologists about the significance of this capacity and what level or type of self-awareness or self-consciousness it represents. The confirmation that other large-brained, highly social species—from our closest relatives the great apes to a small number of evolutionarily divergent species (i.e., dolphins, elephants, and magpies)—has profound implications for our ideas about self-awareness in humans and our place in the biological and psychological spectrum.

The realization and interpretation by an individual, be it a human or nonhuman animal, that the mirror reflection is oneself emerges from a process of self-organized exploratory learning. The child, chimpanzee, dolphin, elephant, or magpie appears to explore, test, and learn about the affordances of mirrors in the absence of explicit training or guidance. The outcome of this cognitive processing is MSR, and we might think about it as a product of self-organized learning in the human and nonhuman animals that show it. The learning process prior to the realization of self in a mirror appears to be self-motivated and self-reinforcing and the same can be said for the act of using a mirror to view oneself.

Self-awareness as measured by MSR may rely on or be scaffolded on other forms of awareness, such as proprioceptive awareness, social awareness, and spatial awareness, at the very least. Is MSR an outcome of brain size, EQ, number of neurons, brain organization, level of sociality, or a mixture of these and other factors? The recipe for MSR remains unclear. In humans, the perception of self is multifaceted and pluralistic. Although we are gaining important glimpses into the subjective states of self-awareness in nonhuman minds, we remain at the border of understanding its dimensions.

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CHAPTER 34

EMPATHY THROUGH THE AGES: A COMPARATIVE PERSPECTIVE ON RODENT MODELS OF SHARED EMOTION

Jules B. Panksepp and Jaak Panksepp

At a recent annual meeting of the International Behavioral Neuroscience Society in Victoria, British Columbia, a keynote speaker (J. Panksepp, 2015) asked an audience to affirm one of the following statements:

1. Animals have emotional feelings and they can be scientifically studied.
2. Animals have emotional feelings but they cannot be scientifically studied.
3. Regardless of their existence, emotional feelings are irrelevant to a scientific understanding of behavior.

A resounding majority agreed with the first statement; in fact, only one person agreed with one of the other statements. In our opinion, this represents a scientific sea change for behavioral neuroscience, and the first statement will require neuroscientific perspectives. The principal working hypothesis for elucidating emotional feelings in mammalian species can be summarized in a truth table, as depicted in Figure 34.1. Without neuroaffective perspectives, comparative studies of empathy in animal models may not easily inform understanding of empathy in humans (*Homo sapiens sapiens*).

Owing to the preneuroscientific perspectives of Watson, Thorndike, and Skinner, as well as other behaviorists during the first half of the 20th century (see Volume 1, Chapter 2, this handbook and Chapter 1, this volume), the emotional lives of animals were largely marginalized in neuroscience research during the second half of the century. During this era, behavioral experiments were designed to elucidate how the learning of environmental contingencies (as they related to a handful of homeostatic "drives") could provide causal accounts of behavior, with little discussion about affect (J. Panksepp, 1990; also see de Waal, 2011). However, it appears that the conceptual tide has changed in the 21st century, and many of the intrinsic emotional systems of the mammalian brain are now viewed as fundamental to understanding animal behavior in general and in particular, laboratory models of psychiatric illnesses (J. Panksepp, 2011; J. Panksepp, Wright, Döbrössy, Schlaepfer, & Coenen, 2014).

A large push for this change was the development of *affective neuroscience* during the 1970s and 1980s (J. Panksepp, 1982), with increasing interest in such research into the late 1990s (J. Panksepp, 1998). Affective neuroscience attempts to elucidate the emotional lives of animals by triangulating neuroethological studies of behavior, comparative psychology, and evolutionary (particularly Darwinian) theory. Seven primary and primal affect systems have been postulated (J. Panksepp, 1998; J. Panksepp & Biven, 2012). Our goal in this chapter is to highlight how these affective systems may be involved in the empathic abilities of animals. We provide a brief description of these primary-process emotional systems in the following section (for a more detailed discussion of the organization and function of these systems, see Volume 1, Chapter 23, this handbook). A majority of the studies reviewed here focus on the manner by which laboratory mice (*Mus musculus domesticus*) and rats

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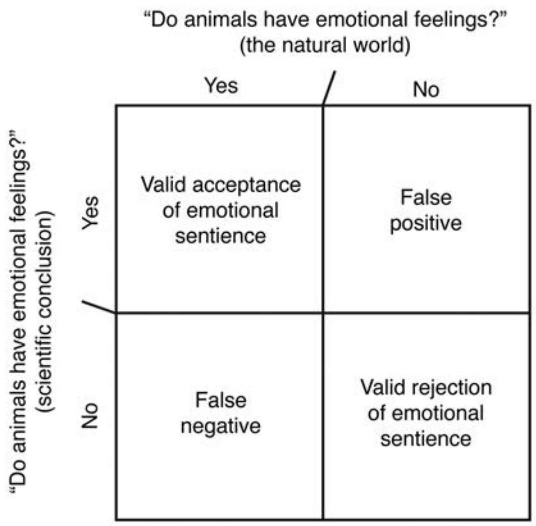


FIGURE 34.1. An affective truth table. The willingness of neuroscientists to assess the possibility of emotional feelings in mammalian species (other than in humans) requires rigorous analysis of evolutionary theory along with philosophical considerations (the natural world) relative to informed, systematic (quantitative and qualitative) observations of animal behavior (scientific conclusions).

(*Rattus norvegicus*) can experience emotional feelings similar to those of nearby conspecifics, but we also underscore several pertinent studies in other nonprimate species. We attempt to provide a coherent account of how considering affective experiences in nonprimate animals can inform behavioral scientists about how empathic capacities have emerged evolutionarily and throughout development in mammals.

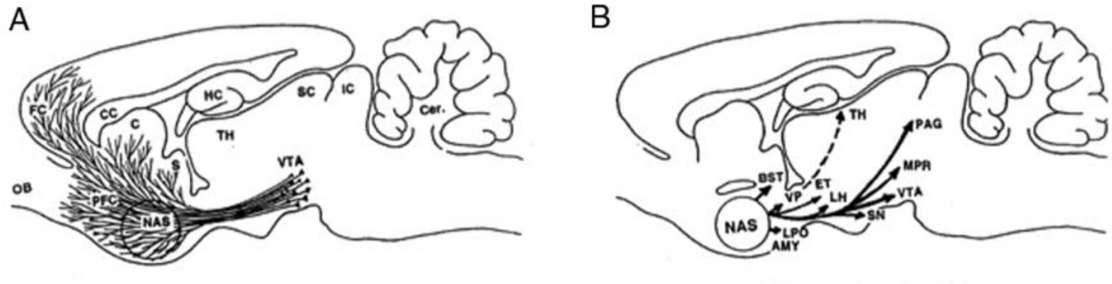
THE PRIMARY-PROCESS EMOTIONAL SYSTEMS

We use the terminology for primary-process emotional systems proposed by J. Panksepp (1998), highlighting terms that had a fundamental role during the evolution of brain–mind organization. The ascription of emotional feelings to animals is based on the fact that these brain states, as evoked by deep brain stimulation, are routinely rewarding and punishing. When combined with the results of studies on neurochemically induced conditioned place preference and avoidance, this fact provides direct evidence for affective brain states in animals (for overviews, see J. Panksepp, 1981, 1982, 1998, 2011).

SEEKING refers to activities of the mesolimbic dopamine system (with associated neurochemistries), which projects from the ventral tegmental area into the nucleus accumbens (see Figure 34.2). This system is still commonly referred to as the *brain reward system*, without a coherent discussion of its psychological aspects: It is engaged when mammals vigorously approach or avoid salient stimuli, as in the procurement of any reward or the alleviation of any punishment (see Chapter 13, this volume). It invigorates the body to act unconditionally, as well as conditionally, when there are opportunities for adaptive outcomes. This system is thus fundamental to efficient functioning of the other six emotional systems described in this chapter. Subjective phenomena (i.e., the feeling aspects of emotion) mediated by this system, as during self-stimulation behaviors, are manifest in the urge to pursue rewards of all kinds (e.g., the thrill of the hunt; feelings of enthusiasm during positive environmental and social pursuits, including sexual activities).

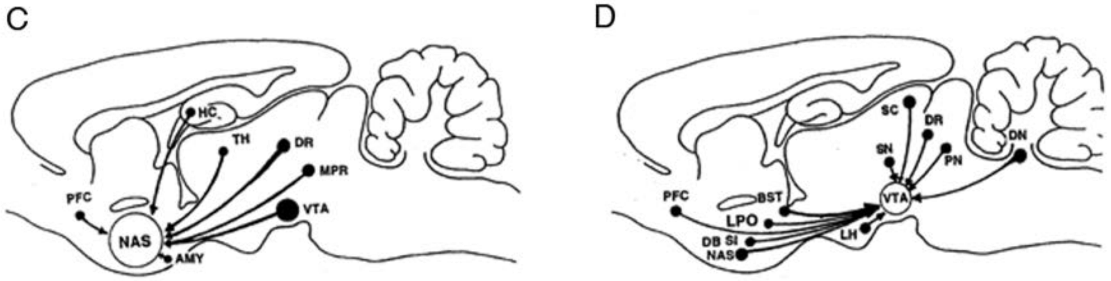
RAGE refers to the primal subcortical system that mediates affective attack, as highlighted by anger attack-type action patterns (see Volume 1, Chapter 41, this handbook). Such activations are aversive and hierarchically controlled: (a) Attack provoked from the corticomedial amygdala is dependent on lower aspects of the circuitry, and (b) attack provoked from the ventral hypothalamus is evoked at lower levels and is dependent on the integrity of the periaqueductal gray (PAG), where attack can be evoked (especially from dorsal PAG) at the lowest intensities of deep brain stimulation.

FEAR refers to subcortical systems that provoke anxiety-type behavior (e.g., freeze, flight; see Volume 1, Chapter 39, this handbook). This system extends from the dorsal PAG through the ventrolateral hypothalamic regions to the central amygdala (for an extensive review, see J. Panksepp, Sacks, Crepeau, & Abbott, 1991), where learned fear behaviors are guided by cognitive or sensory cues, especially via the basolateral amygdala (LeDoux, 2012). Fearful states can be alleviated in humans by gestures of concern and reassurance.



Mesocorticolimbic dopamine system

Efferents from the NAS



Afferents to the NAS

Afferents to the VTA

FIGURE 34.2. Neuroanatomy of the mammalian SEEKING system. (A) Sagittal view of the major projections from the ventral tegmental area (VTA), which is a primary location of (dopamine) DA synthesizing neurons. (B) Projections out of the nucleus accumbens septi (NAS), a principal innervation site of the VTA DA neurons. (C) Neural projections into the NAS. (D) Neural projections into the VTA. AMY = amygdala, BST = bed nucleus of the stria terminalis, C = caudate nucleus, CC = corpus callosum, DB SI = diagonal band/substantia innominata, DR = dorsal raphe, FC = frontal cortex, HC = hippocampus, IC = inferior colliculus, LH = lateral hypothalamus, LPO = lateral preoptic area, OB = olfactory bulb, PAG = periaquiductal grey, PFC = prefrontal cortex, PN = parabrachial nucleus, S = septum, SC = superior colliculus, SN = substantia nigra, TH = thalamus, VP = ventral pallidum.

LUST refers to neuroanatomical systems similar to those associated with rage, but which are strongly modulated by sex steroids so as to promote appetitive actions and consummation of sociosexual activities. Empathy can promote sexual sensitivities that, at times, are not common, especially in males.

PANIC, which has been illuminated by studying the distress vocalizations of young animals separated from their parents (see Volume 1, Chapter 21, this handbook), can be distinguished from FEAR neuroanatomically, as well as neurochemically; for example, opioids (which stimulate μ-opioid receptors) are exquisitely effective in reducing panic responses in the form of separation distress, whereas these efficacies are reversed for fear responses (J. Panksepp, 1998). By promoting feelings of social need—from loneliness to panic attacks—this system can generate prime signals for recruiting the supportive attention of others.

CARE promotes maternal nurturance (see Volume 1, Chapters 35 and 36, this handbook) and is heavily dependent on aspects of the SEEKING circuitry, which contains abundant oxytocin and prolactin receptors, promoting maternal feelings. Although animal data are scarce, in humans this emotion promotes empathic resonances. Interactions between the CARE and PANIC systems may be a principal substrate underlying the evolution of empathy.

PLAY is a characteristic form of positive social engagement that often takes the form of mock fighting, which animals find rewarding (see Volume 1, Chapter 34, this handbook). The neuroanatomy of this system is not as well understood as that of the others, but a clear role exists for thalamic reticular regions (Siviy & Panksepp, 2011). We assume that this system promotes development of friendships, including juvenile social bonds, and thereby helps identify individuals who are more likely to be recipients of empathic social concern.

Much remains to be learned about these systems, especially within the context of empathy. Nevertheless, acceptance of diverse and primal emotional feelings in animals, on the basis of the rewarding and punishing properties of emotional circuits, allows for more sophisticated empathy studies to proceed in animals. Thus, investigators of empathy in animal models generally welcome the transition from the Watson/Thorndike/Skinner-type view of behavior-only causation that governed 20th-century animal learning and behavioral neuroscience to a focus on affective neuroscience. We are now able to openly consider the evolutionary-conserved brain circuits for generating positive and negative affective experiences in mammals, which have implications for preclinical empathy studies (J. Panksepp & Panksepp, 2013). The cross-species affective neuroscience approach is in essence a taxonomic framework of instinct-type (unconditional) emotional expressions, wherein affect is inferred by the capacity of electrical stimulation of these brain systems to support reward and punishment learning effects.

The seven basic affects arise from primary-process emotional systems located predominantly in subcortical regions of the mammalian brain. As described elsewhere (J. Panksepp, 2011), the affective output of these primary-process emotional systems interacts with limbic and cortical networks (termed *secondary-* and *tertiary-process systems*). It is empirically tractable for animals to learn about their primary-process emotions via deeply unconscious secondary-process systems (Solms & Panksepp, 2012), which have been the focus of more traditional behavioral neuroscience research that does not acknowledge affective states in animals (e.g., LeDoux, 2012). Unfortunately, it is not yet possible to link tertiary-process (cortico-cognitive) elaborations of such states to phenomenological levels of analysis in animals (i.e., the positive and negative affect that engenders brain reward and punishment). It is also worth noting that there are other diverse forms of affect (e.g., sensory affects that generate the aversions of pain; perceptual pleasures of taste, smell, touch, etc.; Berridge, 2009; Craig, 2015), as well as homeostatic affects such as hunger and thirst (Denton, 2006).

THE MULTIPLE DIMENSIONS OF EMPATHY

With this point of view in hand we now turn to the main focus of this chapter: empathy and the possibility of its evolutionary roots in rodents. *Empathy* generally refers to how an organism shares affective states with social partners. We adhere, however, to the more specific definition of emotional empathy provided by Hoffman (2001) as “an affective response more appropriate to another’s situation than to one’s own” (p. 4). Doing so allows for a highly operational, objective, and immutable definition, one that requires an emotional repertoire (see Volume 1, Chapter 23, this handbook) and communication modalities that allow affects to resonate between individuals. Combining an affective neuroscience approach with studies of animal communication allows for neuroconstitutive (i.e., causal) studies of empathy in rodents. However, as is the case with nearly all studies of empathy in primate species, definitional ambiguities need to be confronted at the outset.

Nearly axiomatic among scholars is the view of empathy as a multidimensional psychological construct. Depending on species, context, and developmental stage, empathy can be implemented by a collection of perceptual, affective, cognitive, and motor processes. It has become popular to represent these component processes (i.e., endophenotypes) with Venn diagrams (Preston & deWaal, 2002) or with organizational models, which arrange the subprocesses of empathy relative to their situational antecedents and potential outcomes (Davis, 1994). These approaches are useful because they help scientists hone definitions of the bio-psycho-social phenomena that are involved in empathy, a necessary step for clarity in laboratory studies. In this respect, concepts such as emotional contagion, imitation, and theory of mind (see Chapters 19 and 32, this volume) are prominently represented in emotional and more cognitive-based accounts of empathy (Davis, 1994; de Guzman, Bird, Banissy, & Catmur, 2016; Grecucci et al., 2013; Jankowiak-Siuda, Rymarczyk, & Grabowska, 2011; Korkmaz, 2011; J. B. Panksepp & Lahvis, 2011; Singer & Lamm, 2009). Given the pervasive usage of these and related terms it is essential to underscore precisely the scope of each empirical study. Particularly important for the studies reviewed in this chapter are the concepts of *emotional contagion* and *emotional empathy*. Emotional contagion refers to the rapid activation of an emotional or behavioral state based on perception of the same experience in a nearby conspecific. Classic examples of emotional contagion include crying among babies in nurseries (Geangu, Benga, Stahl, & Striano, 2010), yawning (Platek, Mohamed, & Gallup, 2005), vigilance toward threats (Krause & Ruxton, 2002), smiling (Wild, Erb, Eyb, Bartels, & Grodd, 2003), and laughter (Provine, 2001). By definition these experiences must co-occur within a close temporal proximity to be considered contagious; however, it is also apparent that some contagious behaviors, such as yawning, do not have an unambiguous, affective component. Moreover, it is thought that the ability to discriminate the source of affect (i.e., one's own experience vs. another's experience) is integral for distinguishing between contagion and empathy-based explanations of vicarious feeling states. This ability is therefore necessarily based on the capacity to discriminate between (physical) representations of one's self versus others. On the basis of the primary-process emotional systems, a core self-concept has been hypothesized for all mammalian species (J. Panksepp, 1998, 2009; J. Panksepp & Northoff, 2009; for a related view, see Craig, 2015). Although provocative, empirical studies of self-recognition have been mainly limited to assessment via the mirror self-recognition (MSR) test in species that include humans, apes, cetaceans, elephants, and some monkeys and birds (Suddendorf & Butler, 2013; see also Chapter 33, this volume). This test is based almost exclusively on possessing a high level of visual acuity, which most rodents typically lack. Accordingly, it is thus difficult to determine the extent to which experimental assessments of self-recognition are biased by visual perception.

Humans can recognize their own handwriting versus that of others, supporting the concept of an implicit action self-identity (Knoblich & Flach, 2003). Golden hamsters (*Mesocricetus auratus*) self-inspect their own odor profile to discriminate between kin and unrelated individuals (Mateo & Johnston, 2000). Mice harboring the same genetic background have signature vocal repertoires (Holy & Guo, 2005), which may be one way to instantiate individuality (Lathe, 2004). We underscore these various examples to make clear that vision processing is by no means a requirement for a sense of self. Experimental tests of the self–other construct—other than the MSR test—can be (and have been) developed, and deserve further attention in animals that are more attuned to their olfactory and auditory senses. It is also noteworthy that species historically thought not to possess the capacity for MSR can pass the MSR test when procedural modifications are used (Chang, Fang, Zhang, Poo, & Gong, 2015; Rajala, Reininger, Lancaster, & Populin, 2010; but see Anderson & Gallup, 2011, 2015). For the purpose of reviewing the studies of shared affect in rodents, we adopt the working hypothesis that all mammals possess a core self (J. Panksepp, 1998, 2009), an implicit rather than explicit sense of being (Davidov, Zahn-Waxler, Roth-Hanania, & Knafo, 2013), that is capable of emotional feelings and empathy. Nevertheless, for clarity we organize the following relevant studies along the conceptual boundaries of emotional contagion and emotional empathy (e.g., vicarious fear) on the basis of whether the behavioral responses of individuals are closely coordinated in time (i.e., contagion).

Strict focus on the affective component of empathy frees us from considering more cognitively advanced forms of empathy, which are typically addressed in human studies. Concepts such as theory of mind (understanding that others can have a distinct perspective compared to one's own), sympathy (having a cognitive appreciation for another's emotional state without necessarily affectively sharing it), and the various other empathy-related constructs related to imagination, cultural tradition, and language are commonly considered in the human literature. Indeed, the remarkable cognitive aspects of animal decision-making have been well documented elsewhere (Autier-Dérian, Deputte, Chalvet-Monfray, Coulon, & Mounier, 2013; Budiansky, 1998; Massen, Szipl, Spreafico, & Bugnyar, 2014; Masson, 1999; see also Chapters 15 and 16, this volume), some of which have been experimentally modeled in rodents (Blaisdell, Sawa, Leising, & Waldmann, 2006; Foote & Crystal, 2007; Steiner & Redish, 2014). The emotional foundations of social interaction are by-and-large the most well studied phenotypes in nonprimate empathy research. Moreover, empathy's affective (vs. cognitive) roots are bound to be the most "harvestable" for further development in biological psychiatry, largely because of advances in affective neuroscience (J. Panksepp et al., 2014; J. Panksepp & Yovell, 2014). For more extensive coverage of the cognitive as well as uniquely primate aspects of empathy and its neuroimaging correlates, with cross-species perspectives, readers are referred to several other excellent reviews (Decety & Jackson, 2004; Decety, Norman, Berntson, & Cacioppo, 2012; Decety & Svetlova, 2012; de Waal & Ferrari, 2010; Keysers, Kaas, & Gazzola, 2010; Seymour, Singer, & Dolan, 2007; Singer & Lamm, 2009).

We also will not extensively discuss behavioral phenomena related to imitation. This is a critical point as imitation has a long history of investigation in animal behavior research (see Chapter 19, this volume) and more recently has become a major focus in empathy research, because of the discovery and characterization of mirror neurons (Gallese, Gernsbacher, Heyes, Hickok, & Iacoboni, 2011; see also Volume 1, Chapter 14, this handbook). Given the popularity of investigating mirror neurons during the past decade, it is important to briefly underscore the notion that has implicated them in the origins of empathy. The prototypical mirror neuron fires during the execution of an action and observation of the same movement in another. There is evidence that such neurons respond to the sounds of actions, such as lip smacking, and there also are similar neurons in the somatosensory cortices that activate during the perception of touch in others (Keysers et al., 2010). These experimental observations have been used to argue that mirroring the actions of others underlies a psychological substrate for learning about and understanding others' perspectives, and this in turn could foster the development of empathy. For additional coverage regarding the potential role of mirror neurons in empathy and affective synchronization, readers are referred to the comprehensive arguments provided by Gallese (2007), Iacoboni (2009), and Keysers and Gazzola (2009). At this point, however, we simply do not know whether mirror neurons are necessary or sufficient for understanding the evolutionary origins of emotional empathy. They have not yet been studied extensively in species that share some homologous brain regions with primates (however, see Mooney, 2014, for a review of recent work in birds and Ushakov et al., 2013, for emerging work in rodents), nor are they typically assessed in situations that are imbued by the primary-process emotional systems (see Volume 1, Chapter 23, this handbook). A lack of primary-process emotional system engagement is also true for studies of imitation in nonprimate animals. For example, although there are some intriguing studies of mate choice in fish (Dugatkin, 2007), the majority of experimental investigations of imitation involve a hungry animal successfully acquiring a foodstuff either via learning a novel behavioral procedure or by avoiding illness through copying food choices (see Galef, 2007, for a review of exemplary phenotypes). Emotional contagion and terms such as *behavioral mimicry* increasingly have been used interchangeably and thus are conflated in the rodent empathy literature. It is precisely the presence of an affective experience that differentiates contagion from mimicry. Importantly, emotional contagion is a particularly robust evolutionary strategy (relative to behavioral mimicry) when social observations tend to be error-prone or difficult (Nakahashi & Ohtsuki, 2015).

EVOLUTIONARY ORIGINS OF EMPATHY: THE CARE AND PANIC SYSTEMS

It is well known that one hallmark of mammalian development is in utero gestation; this biological trait appears to be associated with mothers actively taking care of their offspring after birth, often for prolonged periods (see Volume 1, Chapter 35, this handbook), with various shared and divergent controls (Lonstein, Lévy, & Fleming, 2015). Parent–offspring bonding is thought to be a fundamental developmental landmark in the emergence of mammalian empathy (Preston, 2013; Rilling, 2013; see also Volume 1, Chapters 21 and 36, this handbook). When left alone or distressed, newborn rodents cry in the ultrasonic frequency range (Hofer, 1987), a response that has also been modeled in birds (Edgar, Lowe, Paul, & Nicol, 2011) to understand its underlying neurochemical substrates (J. Panksepp, Meeker, & Bean, 1980). The primal nature of maternal responsiveness to infant crying has been underscored by a study in deer (*Odocoileus hemionus* and *Odocoileus virginianus*), where females approached distress calls (but not predatory or control sounds) of not only fawns but also infant bats (*Lasionycteris noctivagans*), domestic cats (*Felis catus domesticus*), and humans, as well as other mammalian species, as long as the vocalizations fell within the range of their respective species-specific fundamental frequency (Lingle & Riede, 2014).

The infantile PANIC response is rapidly quelled when a mother reunites with her offspring (see Volume 1, Chapter 21, this handbook). The CARE system then promotes active nurturing behaviors from the mother, including social grooming, refreshing of the nest, and arched-back nursing in rodents. Given the affective and ancient nature of this interaction, it may be the emotional interplay between mother and offspring that serves as the developmental as well as evolutionary substrate for the emergence of empathy. This is by no means a new concept (e.g., Decety et al., 2012). It is important, however, to consider some of the more recent findings regarding parenting in rodents, as there are some important parallels to human behavior.

First, it should be realized that maternal rodents aggressively protect their offspring (Lonstein & Gammie, 2002). They will rapidly enter an area containing the scents of an unknown, potentially infanticidal male to retrieve their pups (D'Amato, Scalera, Sarli, & Moles, 2005). Interestingly, there also is a genetic influence on maternal behavior that is similar to a strain difference in the vicarious fear responses as will be described later in this chapter (i.e., the C57BL/6 [B6] strain is more responsive than the BALB/c strain). Notably, driven by a mother's behavior toward her pups (Caldji, Diorio, Anisman, & Meaney, 2004), anxiety-related behavior is influenced via epigenetic mechanisms that interact with a female's gestational milieu (Francis, Szegda, Campbell, Martin, & Insel, 2003; see also Volume 1, Chapters 11 and 22, this handbook). Thus, the mother–offspring bond in rodents is intense: Rat mothers will exhibit a preference for her offspring over a rewarding dose of cocaine (Mattson, Williams, Rosenblatt, & Morrell, 2001), which is mediated through activity in the medial preoptic area (M. Pereira & Morrell, 2010). Moreover, μ-opioid receptors modulate a mother's care for her pups (D'Amato et al., 2005), which in turn influences the attachment of pups to their mother (Moles, Kieffer, & D'Amato, 2004; see also Volume 1, Chapter 21, this handbook). Indeed, there is robust activation of the mesolimbic reward circuitry in rat mothers when nursing pups (Ferris, Kulkarni, Sullivan, Harder, Messenger, & Febo, 2005). Many avian species also vehemently defend their offspring, such as the piping plover (*Charadrius melodus*), which feigns injury to lead predators away from their brood (Ristau, 1991).

In humans, activity in social brain networks of parents becomes coordinated, a phenomenon termed *biobehavioral synchrony* (Atzil, Hendler, & Feldman, 2014), when mothers and fathers observe their own children playing but not when observing unknown children (Atzil, Hender, Zagoory-Sharon, Winetraub, & Feldman, 2012). During too much solitude, infants will cry and a calming response, induced by active maternal carrying, occurs in humans and mice, which is characterized by a reduction in crying, mobility, and heart rate (Esposito et al., 2013). In mice, this immobility appears to have a function as mothers are more successful in returning their offspring to the nest if the pups cooperate and become immobile with the appropriate postural changes (Esposito et al., 2013). Maternal mice can also coax fathers to become more parental via emission of a specific vocalization (Liu et al., 2013). In some rodent species, such as the vole (*Orchogaster socialis*), mothers and fathers are biparental and enforce offspring care on each other (Libhaber & Eilam, 2002).

These studies involving the affective experiences of mothers and their offspring are highlighted because most of the studies reviewed later in this chapter are exclusively focused on emotional resonance within the FEAR system. Interpretations invoking the subprocesses of empathy can be applied to other affective systems, such as CARE and PANIC, as well as to the development of new behavioral procedures like those previously highlighted (e.g., Esposito et al., 2013; Liu et al., 2013). Additionally, across all affective systems experimental approaches to empathy would benefit from including and comparing rodent species that express higher levels of parental or biparental care relative to mice and rats (see Volume 1, Chapters 35 and 36, this handbook), as well as selective mother–infant bonding such as *Octogon degus* (Fuchs, Iacobucci, MacKinnon, & Panksepp, 2010). Studies of emotional empathy should also consider the various positive affective systems.

We next review a series of recent studies that demonstrate laboratory rodents can be robustly influenced by the negative affective state of their companions via the primary-process FEAR system. With respect to studies of parent–offspring behavior, infant rats can learn to avoid neutral odorants that were sensed when their mothers were expressing fear (Debiec & Sullivan, 2014; see also Chapter 19, this volume). Control experiments demonstrated that such infantile learning is not attributable to a change in maternal nurturance, but rather to the direct experience of witnessing their fearful mother. This type of intergenerational fear transfer is mediated by chemosignaling in the vomeronasal organ, with corresponding activation in basal (lateral) regions of the amygdala (Debiec & Sullivan, 2014). By contrast, newborn foals (*Equus ferus caballus*) express blunted fear responses if they have experienced the fear-invoking stimuli concurrently (i.e., social buffering) with their habituated mother (Christensen, 2016).

In the following sections, studies regarding socially mediated fear responses are organized into three major domains. We hope learning theorists will view these experimental categories relative to the order in which the unconditioned stimulus (US) and conditioned stimulus (CS) were administered to target rodents while in the presence of companions (see J. Panksepp & Panksepp, 2013), and the intensity, duration, and frequency of the US (J. B. Panksepp & Lahvis, 2011). We first discuss studies that are relevant to emotional contagion, the near-contemporaneous matching of affective states between conspecifics (Figure 34.3A). Second, as an example of emotional empathy, we review studies that illustrate instances of a phenomenon termed *vicarious fear*. The primary difference between the first and second group of studies is that the latter entails situations in which an individual exhibits changed behavioral responsiveness at a time point well after its companion(s), which were the original source of affective resonance, have been removed from the environment (Figure 34.3B). Thus a process additional to, or distinct from, emotional contagion has come to play in such situations. In other words, individuals in the latter group respond via secondary-process learning mechanisms as if they have been influenced by a partner's primary-process emotion even though the companion has not been present for an extended period of time. Third, we present studies where witnessing social distress has subsequent influences on how individuals can learn about their own affective experiences and the environment. In these studies, it appears that an individual's experience of fearful companions unconditionally primes them for extended periods such that they respond more strongly to fear-learning contingencies in their environment (Figure 34.3C). We additionally categorize the studies relative to whether the subjects were laboratory mice (*Mus musculus domesticus*) or rats (*Rattus norvegicus*), the two main species in which such work has been conducted. There are notable differences between the behavioral repertoires of rats and mice (e.g., Whishaw, Metz, Kolb, & Pellis, 2001). Note too that although we point out the possibility of species differences, well-documented strain differences exist in mice and should be expected for rats as well. Although a great majority of the experimental empathy work in nonprimates has been performed in these two rodent groups, findings in other species are underscored in sections where the respective experimental approach most closely aligns with that used in the studies of rodents.

EMOTIONAL CONTAGION

The studies discussed in this section broadly fit under the definitional auspices of emotional

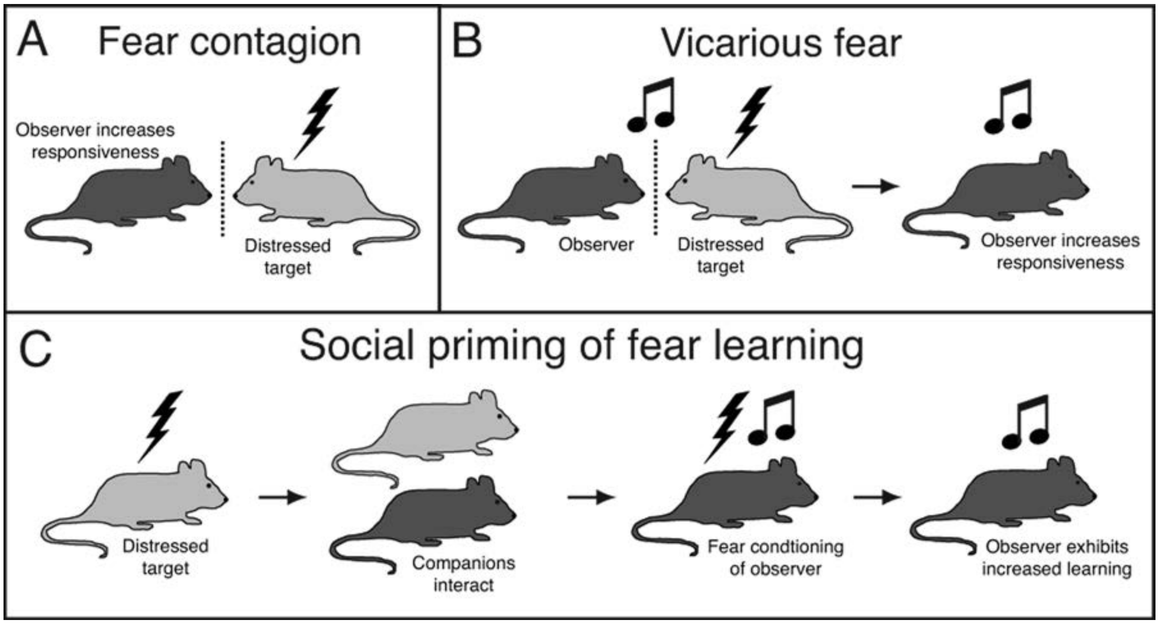


FIGURE 34.3. Rodent models of shared affect. (A) Emotional contagion is illustrated as an observer witnessing a companion receiving a shock (depicted as a lightning bolt). Responsiveness is increased in observers. Similar findings have been illustrated when rodent companions are simultaneously exposed to other noiciceptive stimuli. (B) Vicarious transfer of fear is illustrated as an observer companion witnessing a target companion receiving a shock associated with a tone (depicted as a musical note). Observers subsequently freeze to the tone. (C) Social priming of conditioned fear. After interacting with a distressed conspecific, observers that have been fear conditioned express increased fear learning.

contagion (see Chapter 19, this volume). That is, these experiments evaluate the pain or fear behavior of laboratory rodents while (a) they undergo an aversive sensory stimulus contemporaneously with a social partner, (b) they witness another partner be subjected to a painful or fearful experience (Figure 34.3A), or (c) their learning ability is assessed directly following exposure to the companion's distress.

Mice

A seminal study by Langford et al. (2006) demonstrated multiple signs of emotional contagion in mice. For example, when individual mice were in pain, associated behaviors (e.g., body contortion, paw licking) were increased and co-occurred if their companion was also in the same pain state. Notably, mice not in pain will approach and inspect a companion licking its paws (S. Watanabe, 2012) or writhing in pain (Langford et al., 2010), and this social proximity to companions appears to sensitize subsequent nociceptive processing (Langford et al., 2006). Mice cohoused with a cage mate subjected to chronic pain also exhibit heightened nociceptive responding, as well as increases in anxiety related behavior (Baptista-de-Souza et al., 2015). Moreover, companions bidirectionally alter their pain-related behavior to more closely match the pain state of others (e.g., a mouse experiencing relatively high levels of pain reduces its pain-related behavior if its companion is experiencing less pain; Langford et al., 2006). When tested, these effects are sensitive to the familiarity and sex of companions (e.g., females are more responsive than males), which appears to be communicated via visual cues (Langford et al., 2006, 2010, 2011).

Mice also express signs of contagious freezing in response to the application of shocks to their companion's paws, and this affective response is strongly modulated by familiarity between animals (Gonzalez-Liencres, Juckel, Tas, Friebe, & Brüne, 2014; Jeon et al., 2010). Depending on the experimental conditions, different sensory modalities appear to play a more or less important role in this form of emotional contagion between mice. For instance, visual cues emitted from shocked mice play a predominant role in inducing freezing in companions (Jeon et al., 2010), whereas distress vocalizations result in behavioral orientation toward target mice with partial eye closure (Chen, Panksepp, & Lahvis, 2009). When the strength, duration, and frequency of shock delivered to a target mouse are increased (similar to the protocol used by Jeon et al., 2010), distress vocalizations (i.e., squeaks) also engender prolonged freezing in companions (J. B. Panksepp, 2015), but such contagious freezing habituates with repeated experience (similar to what has been found in rats). As assumed by Chen et al. (2009) and in accord with studies in rats, Sanders, Mayford, and Jeste (2013) found that contagious freezing by mice is dependent on a specific, prior experience with pain-inducing stimuli. Moreover, a recently fear-extinguished mouse expressed renewed fear when cotested with a familiar partner expressing conditioned fear responses (Nowak, Werka, & Knapska, 2013).

Pharmacological inactivation studies implicate medial intralaminar thalamic regions, the lateral amygdala (LA), and the anterior cingulate cortex (ACC), but not more lateral thalamic nuclei, as key anatomical substrates underlying contagious freezing in mice (Jeon et al., 2010). Interestingly, these influences are right lateralized at the level of the ACC but not the thalamus (S. Kim, Mátyás, Lee, Acsády, & Shin, 2012). Companions (from the B6 strain) witnessing target mice receiving foot shocks exhibit heart rate deceleration (Chen et al., 2009) and synchronized theta rhythm activity between the LA and ACC (Jeon et al., 2010). Regulation of ACC activity by monoamines may play an important role in contagious freezing, as enhancement of dopamine-receptor 2 stimulation or serotonin levels in this brain region respectively increases or decreases contagious freezing (B. S. Kim et al., 2014). Brain studies conducted thus far (Jeon et al., 2010; B. S. Kim et al., 2014; S. Kim et al., 2012) have yet to examine whether the described neural processes are specific to contagious freezing or apply more generally to distress-induced freezing behavior (i.e., it is not known if the neural mechanisms underlying pain-induced freezing are the same as those underlying contagious freezing). In another study, heightened inducible transcription factor activity in the pre- and infralimbic cortex, and basolateral amygdala of B6 target mice, were also detected in the companions with whom they were reunited, which was associated with an increase in nose-to-nose social contacts (Meyza et al., 2015). Interestingly, these behavioral and neural responses were not found in targets or companions from the BTBR “mouse model of autism” (e.g., Ellegood & Crawley, 2015).

Noteworthy are similarities between the mouse studies and studies in other species. For example, pigs (*Sus scrofa*) express increased attention to and contact with companions that are stressed, as well as increased freezing (Goumon & Špinka, 2016). Consistent with mouse studies these responses are enhanced if the observer has previously experienced the same stressor. Pigs are also more likely to stand alert with their ears pinned back when reunited with pen mates that have undergone aversive treatment (Reimert, Bolhuis, Kemp, & Rodenburg, 2015) and exhibit prolonged heart rate deceleration after listening to conspecific distress vocalizations (Düpjan et al., 2011). Importantly, heart rate reduction via parasympathetic activation is a core feature of one prominent theory regarding the evolution of social engagement (Porges, 2007), and is predictive of empathic concern in human adolescents (Zahn-Waxler et al., 1995).

Rats

When target rats are subjected to restraint stress they emit 22 kHz-ultrasonic vocalizations (USVs) and their freely moving companions spend more time in close proximity (Bartal, Decety, & Mason, 2011). Moreover, recently shocked rats are groomed about 10 times more often by their companions than are non-shocked rats (Knapska, Mikosz, Werka, & Maren, 2010). Surprisingly, rats in contrast appear to avoid pictures of other rats receiving a foot shock (Nakashima, Ukezono, Nishida, Sudo, & Takano, 2015). Companion rats will also freeze to observations of a target rat receiving foot shocks (Yusufishaq & Rosenkranz, 2013) and the target rat’s conditioned fear responses (Bruchey, Jones, & Monfils, 2010), whereas target rats increase their conditioned fear responses if there is an experienced companion rat in close proximity, a scenario described as a *social loop* (Atsak et al., 2011). Contagious freezing in rats also dissipates on repeated experiences with distressed targets (Carrillo et al., 2015). As with mice, rats exposed to others in pain exhibit increases in subsequent nociceptive responding (Li et al., 2014), an effect that only occurs in familiar partners. Moreover, nonstressed rats also appear to pick up on the stress levels of their cage mates, especially as indicated by elevated circulating corticosterone (Akyazi & Eraslan, 2014). Illustrating the cross-species relevance of this phenotype, elevated cortisol is also observed in humans and domestic dogs (*Canis familiaris*) when listening to human infants cry (Yong & Ruffman, 2014).

Rats emit USVs within a variety of aversive contexts (Blanchard, Blanchard, Agullana, & Weiss, 1991; Knapp & Pohorecky, 1995; Kroes, Burgdorf, Otto, Panksepp, & Moskal, 2007). Companions will freeze to these sounds (E. J. Kim, Kim, Covey, & Kim, 2010) and the level of freezing is positively correlated with the extent of vocalizing by the target rat (Wöhr & Schwarting, 2008). Although rats do not appear to produce such USVs to actively alert conspecifics (Wöhr & Schwarting, 2008), they nevertheless can serve as a strong communication signal of negative affect (Burgdorf et al., 2008; Knutson, Burgdorf, & Panksepp, 2002). Similar to the mouse studies, E. J. Kim et al. (2010) demonstrated that companions freeze to their partners' USVs only if they have had prior experience with the pain-inducing stimulus. Such experience dependence could be a prerequisite to perceiving the affective content of others' vocal emissions, and this idea has been addressed by Parsana, Moran, and Brown (2012), who demonstrated that rats freeze to USVs produced by novel conspecifics only when they have been previously exposed to foot shocks that engendered USVs in themselves. Inactivation of the ascending auditory system disrupts the influence of USVs on companion fear behavior (E. J. Kim et al., 2010), confirming that hearing is a necessary sensory modality for this phenotype. An additional line of evidence also demonstrated a role for prior experience with a painful stimulus in the expression of fear behavior by companion rats, but in contrast to the previous findings (E. J. Kim et al., 2010; Parsana et al., 2012), Atsak et al. (2011) did not find that USVs induced freezing in companions. Rather, it was found that some other (unidentified) acoustic signal engendered companion freezing, and they speculated that it might be the sounds made by the target rat's body when it was shocked. Although this has never been formally evaluated in rats, it could also be that the audible distress vocalizations (i.e., squeaks) emitted by rodents during shock administration can play a role in communicating distress, which would be consistent with mouse studies. By contrast, a subsequent study (A. G. Pereira, Cruz, Lima, & Moita, 2012) showed that it was the lack of (bodily) sound made by freezing focal rats that signaled fear to their companions. The reason for the difference in findings between these two studies remains unknown.

In summary, the Atsak et al. (2011), E. J. Kim et al. (2010), and Parsana et al. (2012) studies all proposed a Pavlovian scenario in which the companion's prior experience with a pain-inducing stimulus (e.g., paw shock) and associated 22-kHz USVs becomes an internally generated conditioning cue such that USV emission by others can subsequently induce freezing. In future experiments, the companion rat's hearing should be blocked before exposure to foot shocks so as to distinguish between the contributions of the nociceptive experience, vocalizations during the pain experience, or an interaction between both. In other words, is pre-exposure to distress vocalizations (without a pain experience) or a pain experience (without the perception of distress vocalizations) sufficient to influence companion freezing from USVs?

Companion rats exposed to partners that recently experienced fear conditioning exhibit robust activation of the amygdala. Indeed, central amygdala (CA) activation appears to be specific to companions investigating target rats in general, whereas preferential activation of the medial amygdala and lateral amygdala regions occurs in companions when their partners have been shocked versus control rats (Knapska et al., 2006). By contrast, spinal-nociceptive sensitivity following social interaction with a partner in pain appears to be modulated by the medial prefrontal cortex (Li et al., 2014).

The finding that a companion rat will increase social contact and grooming of a recently distressed companion has parallels in other species. For example, prairie voles (*Microtus ochrogaster*) also groom their mates substantially after they have been exposed to shock (Young, 2014). Ravens (*Corvus corax*), distressed after an agonistic encounter, are more likely to be the recipients of affiliative contacts from bystanders, especially if they share a close social tie and the aggression was severe (Fraser & Bugnyar, 2010; also see Seed, Clayton, & Emery, 2007, for an example of third-party affiliation after agonistic behavior in monogamous rooks [*Corvus frugilegus*]; see Volume 1, Chapter 42, this handbook). Distressful experiences, such as agonistic behaviors, in the day-to-day lives of Asian elephants (*Elephas maximus*) recruit reassurance from bystanders in the herd, including vocalizations and tactile engagement (Plotnik & de Waal, 2014). Domestic dogs attend to the expression of feigned crying versus humming by approaching their owners or even complete strangers submissively, which includes sniffing, nuzzling, and licking (Custance & Mayer, 2012). Some of these findings have been interpreted as a form of emotional contagion, but they may also be relevant to the concept of consolation behavior.

There are some indications that birds are remarkably sensitive to the emotional state of conspecifics. Thus, avian species may also share some empathy-related substrates with mammals. Female zebra finches (*Taeniopygia guttata*) respond to the calls of stress-induced, separated males with vocalizations and increased corticosterone, an influence apparent for mates but not unfamiliar males (Perez et al., 2015). Hens (*Gallus gallus domesticus*) respond to offspring distress with increased alertness and vocalizations as well as changes in systemic physiology (Edgar et al., 2011). Interestingly, such differences are not manifest in hens observing familiar adult conspecifics in distress (Edgar, Paul, Harris, Penturn, & Nicol, 2012), suggestive perhaps of a phylogenetic basis for the mother–offspring bond in the emergence of emotional contagion.

There are also remarkable, albeit qualitative, examples of contagion within the context of birds utilizing their wings. Wing flapping can clearly mediate contagious flight in conspecifics (ViralHog, 2014) away from predator attacks (FWSPacificSouthWest, 2014) and can be used to maintain dynamics of the flock (ConceptsVid, 2014). In one study (J. Panksepp & Panksepp, 2013), social contagion was evaluated in groups of three to four juvenile chickens that were administered the "social peptide" vasotocin, which is similar to its mammalian homologs oxytocin and vasopressin. Rates of two distinct behaviors (i.e., yawning and lateral head shaking) exhibited no contagion effects; in contrast, wing flapping was dramatically elevated when birds were tested in groups rather than alone (J. Panksepp, 1992). We suspect that this may occur because the peptide increases social confidence (with diminished aggression), an effect that was previously described in quails, *Coturnix japonica* (Riters & Panksepp, 1997). This kind of nonflight wing flapping may be a social signal reflecting confidence within a social group, which may be an infectious state (J. Panksepp, 2009).

VICARIOUS FEAR

The previous studies regarding emotional contagion all refer to a general affective context in which a companion reacts directly (or immediately following) the expression of pain or fear by the target individual. In this section, we describe experiments in which companions are responsive well after their social experience with a distressed target individual (see Chapter 19, this volume), thereby behaving as if they had directly experienced the pain-inducing stimulus themselves (Figure 34.3B).

Mice

When the social distress of a target mouse is coupled with a neutral auditory cue, companions will freeze to the presentation of that cue (now a CS) at a later time (Chen et al., 2009). This vicarious response can be reproduced by associating the tone with playback of distress vocalizations of target mice, even though target mice are not present. Interestingly, this vicarious fear phenotype is substantially influenced by the genetic background of the companion (Chen et al., 2009; J. B. Panksepp, Ryabinin, & Lahvis, 2013) and is also sensitive to the adolescent social environment, with socially deprived companions exhibiting depressed expression of vicarious fear (J. B. Panksepp & Lahvis, 2016). Companions will also exhibit freezing when placed back into an environmental context where they witnessed a distressed conspecific (Jeon et al., 2010; Kavaliers, Colwell, & Choleris, 2003), and N-methyl-D-aspartate receptor signaling (Kavaliers, Colwell, & Choleris, 2001) and LA activation (Jeon et al., 2010) appear to be crucial to underlying neural substrates. Like cued conditioning, contextual vicarious fear is also influenced by genetic factors (e.g., Keum et al., 2016). Regarding the paradigms previously described, it should be noted that vicarious learning of pain states and fear in humans is associated with trait-measures of empathy (Colloca & Benedetti, 2009; Kleberg, Selbing, Lundqvist, Hofvander, & Olsson, 2015), indicating that these studies may tap into the fundamental basis of empathy.

Rats

Companion rats also show signs of vicarious fear. After witnessing a target rat receiving foot shocks that were paired with a neutral tone (a CS), companions will freeze 24 hr later to the presentation of the CS alone, and this response is depressed in companions that were raised in isolation during adolescence (Yusufishaq & Rosenkranz, 2013). Operant behaviors of companion rats are more severely disrupted by a fear-evoking CS if the associated foot shocks were experienced contemporaneously with a target rat rather than sequentially (Church, 1959). Monfils and colleagues (Bruchey et al., 2010; Jones, Riha, Gore, & Monfils, 2014) found that social exposure to a target rat expressing a conditioned fear response resulted in freezing by a companion exposed to the same CS 24 hr later. This vicarious response is modulated by familiarity between partners, at least in females (Jones et al., 2014).

MODULATION OF FEAR LEARNING AND EXTINCTION BY SOCIAL FACTORS

There is an additional series of studies demonstrating that social interactions can have a profound effect on how rodents individually acquire, express, and extinguish fear memories (Figure 34.3C).

Mice

Pre-exposure to a fearful mouse reduces subsequent acquisition and expression of conditioned fear in companion mice, and facilitates extinction (Bredy & Barad, 2008). This influence of social exposure on subsequent fear learning is communicated via β-phenylethylamine, a pheromone present at high concentrations in the urine of stressed mice (Bredy & Barad, 2008).

Companion mice also display a form of learned safety if they have visually observed a nonfearful conspecific prior to contextual fear conditioning. Companions exhibit a profound reduction in freezing after being conditioned themselves (Guzmán et al., 2009)—a form of social buffering that lasts for up to 10 days postobservation (Guzmán et al., 2009) and is mediated by oxytocin receptor activation in the lateral septum (Guzmán et al., 2014).

Chen et al. (2009) demonstrated that companions who undergo fear conditioning and have had prior observation of target mice undergoing fear conditioning subsequently exhibit enhanced fear learning, whereas two target mice that experience cued fear conditioning simultaneously express reduced conditioned freezing responses (J. B. Panksepp et al., 2013). Namely, co-conditioned target mice express social buffering of fear. By contrast, Lipina and Roder (2013) found that expression of cued and contextual fear conditioning is generally enhanced when learning co-occurs with a social partner. The reason for these differences remains unknown.

Rats

Mori and colleagues have conducted an extensive set of studies assessing social buffering of fear in rats. Two types of social buffering can influence a target rat's subsequent CS-induced freezing following cued-fear conditioning: (a) social housing for 24 hr following conditioning and (b) exposure to the CS with a nonfearful social partner during testing (Kiyokawa, Takeuchi, & Mori, 2007). The later manifestation of social buffering does not require physical contact with a social partner and is mediated by olfactory signals (Kiyokawa, Takeuchi, Nishihara, & Mori, 2009; Takahashi, Kiyokawa, Kodama, Arata, Takeuchi, & Mori, 2013). Moreover, this type of social buffering is stronger when olfactory signals of a familiar social partner are present (Kiyokawa, Honda, Takeuchi, & Mori, 2014). Buffering may result from social factors dampening activation of the HPA stress-axis when re-exposed to the CS (Kiyokawa, Hiroshima, Takeuchi, & Mori, 2014), and the underlying biological substrate involves a neural circuit linking the main olfactory bulb to the CA/LA via the posterior-medial region of the olfactory peduncle (Kiyokawa, Wakabayashi, Takeuchi, & Mori, 2012).

By contrast, when rats are exposed to a fearful partner, they subsequently exhibit enhanced contextual fear conditioning and avoidance learning (Knapska et al., 2010). Observations of a target rat's conditioned responses to an auditory CS can also increase subsequent fear learning in companions (Bruchey et al., 2010).

BEYOND EMPATHY AND SOCIAL MODULATION: PROSOCIAL BEHAVIOR IN RATS

One hallmark of empathy is that it can lead to behaviors directed toward an individual in need, such as consolation and helping. Prosocial behavior refers to the allocation of time and effort in aiding another without direct benefit to oneself, and there is some evidence for this capacity in laboratory rats (see Volume 1, Chapter 44, this handbook). For instance, if a target rat is left dangling uncomfortably in the air, a companion will act to lower it to safety (Rice & Gainer, 1962). Importantly, this helping behavior increases in frequency if companions have had prior experiences with physical pain.

Rats rapidly learn to relieve the distress of restrained companions by opening a door with their own head to free them (Bartal et al., 2011). This helping behavior depends on prior experience with the rat (i.e., 2 weeks of co-housing) that is being helped (Bartal, Rodgers, Bernardaz Serria, Decety, & Mason, 2014) and it appears to be more rapidly expressed in females (Bartal et al., 2011). Within this experimental context, rats free trapped companions at a similar rate to acquiring a palatable reward, and they also appear to share these desirable foodstuffs with their liberated companions (Bartal et al., 2011).

In a related a study (Sato, Tan, Tate, & Okada, 2015), rats learned to rescue their cage mates from confinement to a water pool—a context found to be aversive to rats. This helping behavior was sensitive to the companion's prior experience: When the roles were reversed, and previously confined rats could liberate the individual that freed them, expression of the helping behavior was greatly enhanced. Similar to the Bartal et al. (2011) study, rats with helping experience were more likely to free their cage mate relative to acquiring a palatable reward and would share the food reward with their companion.

Observation of rodents in a colony can quickly lead to the conclusion that feeding is a social (and perhaps contagious) behavioral activity. For instance, rats will coordinate their behavior to acquire palatable rewards, and they prefer to do this (consuming the reward together) when also given the option of acquiring and consuming it in solitude (Schuster & Perelberg, 2004). In this study, individual rats chose via a T-maze to "shuttle" with a partner in a runway to access a sweetened liquid rather than perform the action alone.

Rats are also known to actively allocate food rewards to a partner (see Volume 1, Chapter 44, this handbook). For example, rats who have had prior experiences with such sharing will actively provide food to unfamiliar conspecifics, with no benefit to themselves (Rutte & Taborsky, 2007). This helping behavior was more likely to be directed toward those that were the most compromised by food deprivation (Schneeberger, Dietz, & Taborsky, 2012) and may be influenced by the extent of experience with helpful partners (Dolivo & Taborsky, 2015). A related study using a double T-maze demonstrated that rats prefer to earn rewards with a conspecific rather than acquire them alone (Hernandez-Lallement, van Wingerden, Marx, Srejic, & Kalenscher, 2014), a social bias that appears to require integrity of the basal lateral amygdala (Hernandez-Lallement, van Wingerden, Schäble, & Kalenscher, 2016). Márquez, Rennie, Costa, and Moita (2015), also utilizing a double T-maze, confirmed that rats exhibit prosocial choices to allocate food rewards to their partners, a behavioral decision dependent on observing the food seeking behavior and delivery of reward to the helped partner. Thus, the previously mentioned findings of food sharing among rats (e.g., Bartal et al., 2011; Sato et al., 2015) are not without precedent (also see Krafft, Colin, & Peignot, 1994). There is also evidence that jays (*Garrulus glandarius*) exhibit advanced forms of sensitivity to their partner's current food preference (Ostojić, Shaw, Cheke, & Clayton, 2013) and that crows (*Corvus monedula*) will similarly allocate food rewards to conspecifics in a cooperative fashion, particularly if the recipient is first observed trying to procure the foodstuff itself (Schwab, Swoboda, Kotrschal, & Bugnyar, 2012). Grey parrots (*Psittacus erithacus*; Péron, John, Sapowicz, Bovet, & Pepperberg, 2013), and rooks (Seed, Clayton, & Emery, 2007) can also learn to share foodstuffs with conspecifics in a cooperative problem-solving task. Additional examples of food sharing across the animal kingdom include blood regurgitation in vampire bats, *Desmodus rotundus* (Carter & Wilkinson, 2015), and sequential fish sharing in bottlenosed dophins (*Tursiops truncates*; Fedorowicz, Beard, & Connor, 2003). It should be noted that many of the experimental approaches for assessing cooperative food sharing were inspired by the various paradigms that have been extensively developed in nonhuman primates (de Waal, Leimgruber, & Greenberg, 2008; Horner, Carter, Suchak, & de Waal; 2011; Silk & House, 2011).

A recent critique of prosocial behavior in rats (Vasconcelos, Hollis, Nowbahari, & Kacelnik, 2012) noted that prosociality without empathy is possible, citing as evidence the extensive helping behaviors of the *Hymenopteran* insects. In the tradition of English behaviorist Anthony Dickinson, they suggest that two psychological concepts, goal-directedness and instrumental action, are crucial to consider within this context. We generally agree with their point of view insofar that it can stimulate new experimental approaches in the rodent empathy field, particularly with regard to determining the conditions that lead to empathically driven helping behavior in nonhumans. However, it also seems to us that one important point not mentioned by these authors needs to be highlighted: Although there can be prosociality without empathy, we suggest that there can also be empathy without prosociality. In other words, one of these phenomena can be present without the other being manifest and vice versa. This is presumably true for all animals capable of emotional empathy, including humans. In some scenarios, prosociality without empathy may occur, driven by kin selection processes (Vasconcelos et al., 2012), for instance, or the apparent instinctual urge in humans to help others (Davis, 1994). By contrast, empathy without prosociality may occur if an organism has intact emotional neurocircuits and communication domains, but perhaps is lacking the cognitive or physical capacities needed to express prosocial behavior. For example, birds may have the neural circuitry required to control movement of hands without possessing them (Budiansky, 1998); it is therefore likely that some animals may be able to express empathy, but because of ecological, physical, or cognitive constraints they do not help others.

Bartal et al. (2011) found that helper rats would free their restrained companions even when subsequent social contact was prevented, which was taken to indicate that the helping behavior was motivated by an attempt to alleviate the companions' distress rather than a desire for social contact. In a previous review, J. Panksepp and Panksepp (2013) suggested that it is important to control for the possibility of helper rats contributing aid because of visual stimulation or reward by adding an opaque barrier that separated the helper rat from freed rat. Sato et al. (2015) subsequently confirmed that helper rats were primarily motivated to relieve a companion because of its distress by demonstrating that helpers rarely open doors to gain social access to nondistressed companions.

However, it is also important to highlight another recent study that has produced an experimental account seemingly contradictory to the interpretations of helping behavior forwarded by Bartal et al. (2011) and Sato et al. (2015). In this study (Silberberg et al., 2014), free rats could touch a sensor that would open a door and release a physically restrained companion from a tube into the same area as the helper or into a separate area. The authors reported that helping behavior was initially robust, with fast latencies and high levels of responding to release the restrained companion into a separate area, but these behavioral responses waned across trials. Response latencies decreased again, however, when the conditions were alternated and the restrained companion could be released into the same area as the free rat. In a separate phase of testing, the amount of time that the free rat and the formerly restrained rat spent in social proximity was measured (e.g., free rat touching the restraining tube or door, companion willingly placing itself within the tube near the door). The authors reported that three of six free rats and four of six formerly trapped rats spent a majority of their time in this social zone. On the basis of their collective findings, Silberberg et al. (2014) thus concluded that it was a desire for social contact (not empathy) that motivates rat helping behavior, with the touch sensor perhaps serving as an operant that maintains social proximity between rats.

The Silberberg et al. (2014) study offers an important alternative hypothesis to explain rodent helping behavior (similar to concepts discussed by Vasconcelos et al., 2012). At this point, we feel that several issues should be discussed to help clarify how this work contrasts with the other studies, which we hope will provide additional insight into the *social-contact versus empathy* accounts of rat helping behavior.

First, our own analysis of Silberberg et al. (2014) demonstrated that the free rats spent 857 s ± 387 s (mean ± *SD*) in contact with the restraining tube and freed rats spent 808 s ± 644 s in the tube during the 1800 s experimental period. (It should be noted that initial latencies to free the trapped rats during this phase of the experiment were not provided by the authors, but we assume it was near the 100 s median they provided for the previous part of the experiment.) Although they surmised that many of the rats spent their time in pursuit of social contact, we question this conclusion on the basis of our own calculations. One way to definitively assess this would be to take on a statistical approach to the data analysis, comparing these values to a group of control rats where social contact was not a factor. In other words, what is the baseline staying-time for rats in this part of the experimental arena without the presence of a companion in the adjacent compartment? Moreover, noteworthy is that the helper rats were not offered a second inactive sensor nor were yoked controls used, both of which are classical requirements for demonstrating a behavior is under operant control.

Second, a stronger measure in support of the social-contact hypothesis would be to report the amount of time rats spent in the social zone of the area simultaneously. We performed a simple test for correlation on the data reported in Silberberg et al. (2014) and found that time in contact with the restraint tube by the free rat was negatively correlated with the time the recently freed companion willingly spent within the tube (Pearson's correlation, $R = -0.88$, d.f. $= 5$, $P = 0.021$). Thus, rats that spent a substantial amount of time in the social zone had companions that spent little time there, a finding seemingly at odds with the social-contact hypothesis and not discussed by Silberberg et al.

Third, social isolation in rodents is by far the most potent modulator of social contact in rodents (Douglas, Varlinskaya, & Spear, 2004; J. Panksepp & Beatty, 1980; J. B. Panksepp & Lahvis, 2007; J. B. Panksepp, Wong, Kennedy, &, Lahvis, 2008). The obligate prediction that arises from a social-contact hypothesis is that longer durations of social isolation would be positively associated with the desire for social contact and should therefore facilitate helping behavior. Separating companions for set periods of time prior to testing is a routine experimental approach in studies of social motivation. On the basis of the majority of published studies focusing on laboratory mice and rats it is not clear why Silberberg et al. (2014) expected their 6 pairs of (socially-housed and socially-tested) rats to have a strong desire for social contact in the first place. Nevertheless, the conclusion of the Silberberg study brings up another fundamental point about animal behavior: The emotional/motivational systems of the mammalian brain are dynamic and interactive. In many instances, we would not expect an individual's behavior to be driven by a single psychological process. Moreover, sociability and empathy appear to have common within-individual origins (Eisenberg, Spinrad, & Knafo-Noam, 2015), making it unsurprising that these processes may interact within certain contexts.

Fourth, the Silberberg et al. (2014) study cited as one of their own experimental goals the need to reproduce behavioral findings. We agree, and particularly in the behavioral/psychological sciences, it is the weight of evidence across studies that must guide research into the future. Silberberg et al. provided a thoughtful, psychologically driven interpretation of their data, yet one that we think does not nullify the role of empathy in rat helping behaviors. At this time, across three relatively distinct procedures for assessing helping behavior, two studies support the empathy hypothesis (> 82 rat pairs: Bartal et al., 2011; 28 rat pairs: Sato et al., 2015) whereas another argues for a social-contact hypothesis of rat helping behavior (6 rat pairs: Silberberg et al., 2014), and so the weight of evidence continues to grow. In principle, the fact that these rodent phenotypes are sensitive to familiarity with the distress invoking situation (Rice & Gainer, 1962; Sato et al., 2015), occur without shared kinship (Sato et al., 2015), are modulated by familiarity between partners (Bartal et al., 2014), can be biased toward higher expression by females (Bartal et al., 2011), and demand precedence over direct rewards for oneself (Bartal et al.; 2011, Sato et al., 2015) are all suggestive that these helping behaviors are driven by a mechanism other than kin selection or high-level cognition. The likely psychological process at play here is emotional empathy. One way to test this would be to evaluate whether the expression of helping behavior covaries with strain-dependent or experience-dependent differences in measures of emotional empathy, similar to the examples described in the prior sections of this chapter. Taken together, these studies—guided by pioneering work on the consolation and helping behaviors of nonhuman primates (de Waal & Suchak, 2010)—support the view of empathy as underlying motivator of prosocial behavior in mammals.

DOES EMPATHY FUNDAMENTALLY REFER TO NEGATIVE AFFECTIVE STATES OR IS THERE A ROLE FOR POSITIVE EMOTIONS?

Historically, the term empathy has been used within the context of negative emotional situations. Individuals sense that others undergo a painful, fearful, or major stress (i.e., aversive) experience, and then “take on” a behavioral state consistent with that social observation. However, adoption of an emotional state by witnessing a companion should not be constrained by emotional valence. In other words, an alternative idea is that positive as well as negative emotional states can be shared empathically between individuals. Although this is a working hypothesis, our own emotional lives as humans provide support for this idea. It goes without saying that positive affect engenders positive affect at social gatherings such as parties, sporting events, and musical performances, and recent studies in laboratory rodents provide some support for positive emotional resonance in animal groups.

Studies into the social neurobiology of drug reward (for excellent recent reviews, see Bardo, Neisewander, & Kelly, 2013; El Rawas & Saria, 2015) indicate that laboratory rodents adopt an emotional state commensurate with their drug-rewarded companions even though they lack the requisite experience with the drug. For instance, *pseudosensitization* has been shown in mice who simply interacted with morphine-injected companions. In other words, drug-naive companions expressed behavioral sensitization to a challenge dose of morphine if they had prior experiences with social partners given morphine (Hodgson, Hofford, Roberts, Wellman, & Eitan, 2010). Prior shared, social experiences with morphine also appear to exacerbate its rewarding properties (Cole, Hofford, Evert, Wellman, & Eitan, 2013; also see Kennedy, Panksepp, Runckel, & Lahvis, 2012). In another study, mice preferred conspecifics that had a common rewarding experience with methamphetamine (Watanabe, 2015). Moreover, rats prefer to self-administer cocaine with partners who are also self-administering (M. A. Smith & Pitts, 2014), and they prefer the company of conspecifics who have a similar history of cocaine (M. A. Smith, Strickland, Bills, & Lacy, 2015). Furthermore, social interactions appear to enhance the rewarding effects of cocaine (Thiel, Okun, & Neisewander, 2008). Collectively, these studies are suggestive of rewarding experiences that can permeate into other individuals, which may be one way by which positive affective experiences are shared among laboratory rodents (see T. Watanabe et al., 2014, for a potential example in humans).

Another piece of evidence indicating that rodents can share positive affect is the remarkably playful activities of laboratory rats. Rats reduce play and do not show preference for socially inactive companions (Calcagnetti & Schechter, 1992; Varlinskaya, Spear, & Spear, 1999), but they prefer to be in the company of individuals who emit positive affective vocalizations (Burgdorf et al., 2008). Moreover, the social abnormalities of BTBR mice can be ameliorated when they are cohoused with companions from the more gregarious B6 strain (Yang, Perry, Weber, Katz, & Crawley, 2011). It should also be noted that the well-known play behaviors of domestic dogs, including the play bow, have been shown to be contagious (Palagi, Nicotra, & Cordoni, 2015). Domestic pigs also play with each other substantially more after they have observed pen mates receiving a rewarding experience (Reimert, Bolhuis, Kemp, & Rodenburg, 2013). It generally goes without saying that positive social moods are infectious (Provine, 2001) and the previous studies indicate that some positive affective states of rodents can be shared among conspecifics. The evidence that animals can adopt or prefer the positive emotional states of their companions is nevertheless preliminary. Experimental approaches using other species with well-described play systems, such as nonhuman primates (E. O. Smith, 1978) and birds (Diamond & Bond, 2003), will help to establish the extent to which empathy can become involved in play. Nevertheless, studies of empathy for negatively valenced emotions, particularly the FEAR system, are much more established and continue to pave the way for understanding the continuity and divergence of empathic abilities across species.

CONCLUSION

We hypothesize that the types of affective resonance described herein are subserved by the neural mechanisms on which higher order empathic tendencies emerge in human development. This is not to say that empathic attitudes cannot simply be assumed at a cold cognitive level in humans, but to highlight that at the foundational affective level, human empathic tendencies may still be heavily dependent on primary-process emotional systems shared by all mammals. On the basis of the studies in rodents that have been reviewed here it becomes clear that this animal group is capable of shared affect, the most fundamental feature of empathy. This conclusion is strengthened by the fact that many factors known to influence empathic responsiveness in humans (e.g., social bonds, prior experience, sexual identity) are similarly affected in rodents. Moreover, findings in other mammalian species also concur with the existence of a primal form of empathy. The continued study of empathy in nonprimates offers an opportunity to develop experimental models that may be less influenced by cultural factors. Nevertheless, irrespective of the effect of experiential factors, experimental manipulations can still be systematically and robustly used in the animal behavior laboratory, more so than in the human clinical context. Thus, utilization of an affective neuroscience approach begets a perspective where incorporation of the seven basic emotion systems can help elucidate the basic mechanisms of empathy in the mammalian brain.

The finding that humans exhibit a racial bias in empathy for pain (Contreras-Huerta, Baker, Reynolds, Batalha, & Cunnington, 2013) illustrates the complex (biological and environmental) nature of empathy development, especially because it can be reversed by social experience (Cao, Contreras-Huerta, McFadyen, & Cunnington, 2015), similar to rodents that have been socialized with companions expressing genetically based physical differences (e.g., Bartal et al., 2014). Experimental studies of rodents may therefore provide insights into how empathy originates and matures via development and experience. Likewise, irrespective of the role of behavioral mimicry in empathy, there is still a question as to how mirror neurons originate (Heyes, 2010): To what extent is the mirroring system influenced by genetic variation? What is the degree to which such systems develop on the basis of social experience? Although this remains a very open question, there are established genetic and genomic strategies in mice that can be used to approach this issue more systematically than the currently used electrophysiological and imaging techniques in primates.

Finally, the connection between empathy and prosocial behavior can be further explored in rodents, as can the subcomponents (or endophenotypes) of empathy, which have been dissected further more recently in humans (Kanske, Böckler, Trautwein, & Singer, 2015).

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CHAPTER 35

ANIMAL WELFARE SCIENCE

Michael Mendl, Georgia J. Mason, and Elizabeth S. Paul

Humans control the lives of many millions of animals. In 2012, we farmed more than 24 billion birds, mainly chickens, and consumed more than 158 million tons of fish (Food and Agriculture Organization, 2014, 2016). We also use animals in research, sport, zoos, and entertainment, and as companions. As exemplified by a 2006 European Union survey, many people are concerned about animal wellbeing: 34% rated the protection of farm animal welfare as being highly important to them (European Union, 2007). Perhaps as a consequence, debates on animal welfare can be emotive and antagonistic. Objective information is thus required to inform these arguments, and supplying this information is one role of animal welfare science. Here, we consider the challenges of scientifically studying animal welfare.

Animal welfare science has its roots in the mid-20th century. Around that time the work of Swiss biologist Heini Hediger (1950) promoted interest in how captivity affects the behavior and wellbeing of zoo animals, and Ruth Harrison's (1964) book *Animal Machines* provoked the British government into setting up the Brambell committee to investigate modern intensive farming methods. The result was the 1965 Brambell Report, *The Welfare of Animals Kept Under Intensive Livestock Systems*, which included an insightful appendix by the ethologist William Thorpe that raised prescient questions about the assessment of animal pain and distress and called for scientific research on animal welfare.

Today, animal welfare science is a thriving, international field ranging from fundamental studies of animal behavior, cognition, and emotion to applied studies aimed at solving specific welfare problems. It covers farm, laboratory, zoo, and companion animals and is multidisciplinary, drawing on theory and methods from behavioral biology, experimental and cognitive psychology, physiology, veterinary science, genetics, and other fields. It has evolved in a context characterized by the complexities and conflicts inherent in animal use (Herzog, 2010). Can we justify keeping animals in particular ways to provide us with food, new drugs, entertainment, and companionship? What are we prepared to tolerate and why? For example, if it improved the welfare of captive carnivores, should we allow them the freedom to express hunting behavior by feeding them live prey?

Resolving these types of question is immensely difficult and colored by the interplay of personal attitudes and values, ethical stances, and economic and political considerations—factors that are the focus of social science and philosophical research on animal welfare, but which we do not have space to consider here (see, e.g., Paul & Podberscek, 2000; Sandoe, Christiansen, & Appleby, 2003). However, it also requires a deep understanding of the animals themselves, and how exactly they are affected by the ways in which we keep them. It is this question that is at the core of animal welfare science and which we focus on here. In contrast to the abolitionism of animal rights, animal welfare science thus seeks

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to objectively evaluate and improve how animals are treated, for example, by comparing the welfare impact of different housing systems or the welfare benefits of different analgesics, and by tackling questions such as how to impose procedures such as handling, transportation, castration, and de-horning in the most humane way.

The findings of animal welfare science may be used to support arguments that systems or procedures, or the use of particular species for particular purposes, are unethical, or to drive improvements in welfare within the constraints of existing practices. Some may view the latter approach—probably more common in research on farm animals—as implicitly supporting an industry that they consider unethical, whereas others argue that it generates real welfare improvements within systems that are unlikely to change rapidly because of societal, economic, and political obstacles. In both cases, research findings inform laws, industry codes, and guidelines, such as those published by the National Academy of Sciences on laboratory animal pain and distress. Animal welfare research also raises fascinating fundamental questions, such as which species or stages of development are sentient? And what is the function of emotion?

The broad scope of animal welfare science is covered in textbooks by Broom and Fraser, (2007) and Appleby et al. (2011), and a recent review by Walker et al. (2014). However, here we concentrate on the varied behavioral and psychological questions that it raises. We consider what animal welfare actually is, how we can measure it, and the likely generic causes of good and bad welfare. We end by highlighting some current and future challenges. Rather than reviewing findings, we focus on conceptual issues. To some, the term *animal welfare science* is an oxymoron, so we try to explain how it can be studied in a logical and structured way.

WHAT IS ANIMAL WELFARE? FEELINGS, FUNCTION, AND FREEDOM

Fraser and colleagues (1997) have identified three conceptual approaches to defining animal welfare. The first approach places the putative subjective experiences and *feelings* of animals at its center. The second approach emphasizes the intact and healthy *functioning* of the animal. The third approach focuses on the *freedom* of animals to live natural lives and perform "normal" behavior.

A rationale for the freedom approach is given by Kiley-Worthington (1989): "If we believe in evolution . . . then to avoid suffering, it is necessary over a period of time for the animal to perform all the behaviours in its repertoire" (p. 333). In this view, welfare is at risk when the full repertoire of a species' evolved natural behaviors cannot be performed. However, some "natural" behaviors (e.g., writhing, fleeing) occur primarily in situations involving noxious or threatening stimuli. Ensuring performance of these behaviors would thus seem counterproductive. A refinement of this approach states that for good welfare, animals must be able to express evolved adaptive responses as and when needed, rather than having to express all natural behavior. However, such responses do not always successfully deal with challenges, especially in captive environments that are far removed from those in which the species evolved. Therefore, the freedom to perform these behaviors per se does not necessarily result in freedom from the threat or danger that motivates them. A fuller discussion of limitations to the freedom approach is provided by Fraser et al. (1997). In what follows, we consider welfare-related hypotheses that this approach generates, but we do not discuss it in the context of welfare assessment because measures of deviations from nature are not used to directly evaluate well-being.

The function approach can be exemplified by the following quote: "An animal is in a poor state of welfare only when physiological systems are disturbed to the point that survival or reproduction are impaired" (McGlone, 1993, p. 28). The focus on biological function is appealing in that relevant indicators such as productivity, health and disease status, body condition, and physiological and immunological state can readily be measured using tried and tested methods (see Volume 1, Chapter 5, this handbook). It is of course possible to debate the point at which disturbance of function tips over into poor welfare. This challenging question, returned to later, is also raised by a prominent function-related definition of welfare: "Welfare is the state of an individual as regards its attempts to cope with its environment" (Broom, 1986, p. 524); if measures of biological function reflect welfare state, at what point is their deviation away from a norm indicative of a failure to cope? However, a more significant problem for this approach is that measures of biological function (e.g., reproduction, body condition, health, physiological state) may all be within normal limits in animals kept in environments that provide very limited stimulation or constrain movements to a few body lengths. To many, these are welfare concerns in their own right.

This last point emphasizes that animal welfare is a human construct and that many people intuitively perceive it to be related not just to an animal's physical state but also to its mental state. A purely physically focused definition thus seems inadequate: mental experience should also be taken into account. Indeed, concern for a species' welfare is often related to perceptions of their intelligence and whether they have a mind (Davis & Cheeke, 1998); the capacity for subjective experience, including mental suffering, is seen as morally relevant (Bekoff, 2007; Brambell, 1965; Rollin, 2006), and some legislation explicitly argues that it is the sentience of protected species that underpins our moral obligations to them (European Union, 1997; Australian Government, 2008). An assumed lack of sentience may therefore be one reason why many invertebrates often are not protected by law, although whether this assumption is correct is far from clear (e.g., Sherwin, 2001).

The feelings approach reflects these perspectives. In its strongest version it argues that mental states are the determinants of animal welfare: "Neither health nor lack of stress nor fitness is necessary and/or sufficient to conclude that an animal has good welfare. Welfare is dependent on what animals feel" (Duncan, 1993, p. 12); indeed, "let us not mince words: Animal welfare involves the subjective feelings of animals" (Dawkins, 1990, p. 1). We believe that this approach most closely captures the essence of what animal welfare means to many people (cf. Davis & Cheeke, 1998); most of us are not concerned about plant welfare because we do not think that plants can suffer, even though they can be kept in unnatural ways and fail to function physically. However, the feelings approach can generate perplexing scenarios. For example, an animal unaware of its pain-free cancer may be deemed to have good welfare, even though its physical health is poor. For some this is a step too far, and several prominent animal welfare scientists propose that good animal welfare is a combination of being happy or having what one wants, as well as being physically healthy (Broom, 1991; Dawkins, 2006; Webster, 2005).

An animal's mental or affective state is thus viewed by most researchers as a key determinant of its welfare, even if it is not the only one. If we accept this to be the case, we are then faced with a challenge of how to measure these states in animals. Most philosophers and scientists agree that the direct measurement of conscious or subjective experience in other humans, let alone nonhuman animals, is not currently possible and may never be so: We cannot know the mental experiences of others from external observation of their behavior, their physiology, or even their neural state (Hyslop, 2014). This perceived inability to study subjective experience scientifically is likely to be one reason why some animal welfare scientists reject the feelings approach and opt for the pragmatism of the function approach (Fraser et al., 1997).

However, others provide philosophical arguments that animal subjectivity is accessible to observation and can be revealed through the expressive quality of behavior (Wemelsfelder, 1997). Another approach is to draw on arguments by analogy and propose that, although we cannot know for certain about the minds of other animals, we can search for similarities between their behavior and brain function and those of humans, and then use these to argue for similarities in mental experience (Bekoff, 2007; Dawkins, 2006; Griffin, 1992). This position is in line with a newfound willingness to bring mental phenomena, including consciousness, thought, and emotion, back into the realms of scientific enquiry, following the dominance of behaviorism for much of the 20th century. It is also implicit in the use of animal models in biomedical research into chronic pain or affective disorders, for example. Although comparative psychologists and behavioral biologists have generally been very wary of discussing the animal mind (e.g., Tinbergen, 1951; Wynne, 2007), neuroscientists are increasingly choosing to study archetypal mental phenomena such as emotion (LeDoux, 1996; Panksepp, 1998; Rolls, 2014; see also Volume 1, Chapter 23, this handbook).

The feelings, function, and freedom approaches to defining animal welfare all have pros and cons, and the feelings and function approaches each have proponents in contemporary animal welfare science. Our preference is for the feelings approach because we believe that it most closely captures why people are concerned about animal welfare, and hence why animal welfare science exists at all. This view of animal welfare also has the most relevance to comparative psychologists. In the following sections, we therefore use this approach to frame our discussions.

MEASUREMENT OF ANIMAL WELFARE: THE FOUNDATION OF ANIMAL WELFARE SCIENCE

Accurate, reliable measurement is absolutely critical for a valid science of animal welfare, and for application of this science to real-world concerns. During the last half century, two main methods for assessing animal welfare have emerged: the welfare indicators method and the motivation and preference method (see Mendl, 2001). Here, we provide a brief overview of these methods and their limitations. First, however, we consider the challenge for measurement generated by defining animal welfare in terms of feelings, so as to provide context for our subsequent discussion of measurement methods.

The Challenge of Measuring Animal Feelings

To implement the feelings approach to animal welfare, we need to be able to make inferences about *emotions*—the positive and negative affective states that are key determinants of wellbeing. Contemporary psychological theories recognize that emotional or affective states comprise behavioral, physiological, and subjective components (see Scherer, 2005; Paul, Harding, & Mendl, 2005). For example, an encounter with danger can trigger the urge to run away, an increased heart rate, and the subjective feeling of fear. This componential view allows us to separate the study of conscious emotion (the subjective feelings part) from other aspects of emotional states, and it raises two distinct questions: (a) In what emotional state is the animal and (b) is the animal capable of consciously experiencing that state?

As we have discussed, the latter question is difficult and perhaps impossible to answer, depending on one's philosophical stance. Nevertheless, the scientific study of consciousness, including in animals, is a growing area and studies of metacognition, blindsight, and brain activity (Boly et al., 2013; Cowey & Stoerig, 1995; Smith, Shields, & Washburn, 2003; see also Chapter 31, this volume) are providing exciting new insights. Progress in this field allows us to pursue the former question in the hope that we may one day be able to combine findings of the different research streams to answer both questions.

To answer the first question—in what emotional state is the animal—requires a definition of emotion that can be implemented in the absence of direct knowledge about animal consciousness. The defining characteristic of emotions that distinguishes them from other mental states is that they have valence: they are positive or negative. Dimensional models of emotion thus argue that emotions can be described by two or three common characteristics (dimensions)— one of which is always valence—that may represent the activity of underlying neurobehavioral systems (e.g., Russell, 2003; Watson, Wiese, Vaidya, & Tellegen, 1999). Different emotions are conceptualized as being positioned at different locations within the two- or three-dimensional space.

A definition of emotion that reflects this view is the following: "Emotions are states elicited by rewards and punishers," where "a reward is anything for which an animal will work" and "a punisher is anything that an animal will work to escape or avoid" (Rolls, 2014, p. 14). This definition, rooted in measurable behavior, allows one to assume that positive states are generated when animals are exposed to rewards or when punishers are omitted or removed, and that negative states are induced when animals are exposed to punishers or when rewards are omitted or removed (Rolls, 2014). An animal's emotional state when exposed to particular stimuli can thus be operationally defined.

In contrast to dimensional models, discrete emotion theorists argue for a limited number of basic emotions, each reflecting the activity of separate biological systems. On the basis of a cross-cultural analysis of facial expressions, Ekman (1992) identified six basic human emotions: fear, sadness, happiness, anger, disgust, and surprise. Panksepp (1998) proposed seven distinct emotional systems in animals: seeking, rage, fear, panic, play, lust, and care. Identifying which state an animal is in requires operational definitions. This is likely to be challenging if discrete emotions are characterized primarily by the distinctive qualitative feel of each emotion in humans, which is difficult to translate into an operational definition and may be without parallel in other species. Panksepp argued, however, that his emotional systems are characterized and identifiable by integrated neurobehavioral changes, such as energized investigation of the environment (seeking), vigilance, freezing and flight (fear), and nurturing, protective behavior (care). Furthermore, appraisal theories of emotion propose that specific characteristics of events (e.g., predictability, suddenness, novelty, pleasantness) map directly on the discrete human emotions that they generate (Scherer, 2005). If these mappings hold for nonhuman animals, then exposing animals to particular combinations of event characteristics should result in similar discrete emotions to those experienced by people (Désiré, Boissy, & Veissier, 2002).

We thus argue that it is possible to provide a logical and operational approach to measuring animal welfare defined in terms of feelings. In particular, the valence of an animal's emotional state—the key determinant of its welfare—is measurable, even if we cannot be certain that this state is consciously experienced. Given this, we now consider the motivation and preference and welfare indicators methods for assessing animal welfare.

The Motivation and Preference Method

The rationale for motivation and preference methods is that animals will experience negative affective states and suffer if deprived of things that they are motivated to acquire or if exposed to things that they are motivated to avoid (Dawkins, 1990). By measuring preferences, researchers can thus determine what animals want and don't want, and therefore what they should or should not be exposed to to minimize suffering and enhance welfare. The assumptions behind this method correspond closely to those of Rolls's (2014) operational definition of emotional valence. The method is thus directly applicable to the feelings approach. Advocates of the function approach may also use the method, arguing that an inability to access desired things or avoid disliked things can overtax an animal's normal biological functioning.

The first study to use this method was inspired by the Brambell (1965) committee's recommendations that the fine-gauge wire flooring of laying hens' (*Gallus gallus domesticus*) cages should be replaced by sturdier rectangular mesh to provide more comfort for the birds. Hughes and Black (1973) found that, when given the opportunity to choose, hens actually preferred to spend more time on the fine-gauge wire. Allowing the birds to choose thus revealed preferences at odds with human perceptions, emphasizing the value of this method.

Since this pioneering work, many studies have investigated preferences for various physical and social aspects of husbandry. Over time, methods have evolved to incorporate ideas from experimental psychology and the microeconomics of consumer demand to determine how hard animals will work to access or avoid a resource or environment. This provides information about how strongly an animal values a resource that cost-free choices do not. For example, Mason and colleagues (2001) gave an individual mink (*Mustela vison*) access to a series of cages containing resources akin to those they use in the wild, and whose absence in captive housing might generate negative states. These included a water bath (mink are semi-aquatic), prey-like objects, an elevated viewpoint, and an extra nest-site. Using a *closed-economy design* with mink housed permanently in the apparatus for the study's duration, Mason et al. varied the costs of accessing resources by systematically adding weights to each cage door. Motivation to visit each resource was quantified (e.g., maximum cost paid; total expenditure [total weight pushed for each resource across the study]). The water bath emerged as the most highly valued resource. This prompted discussions about whether access to swimming water should be a welfare requirement for this species, even though mink appear to thrive in captivity without this resource, as assessed by growth, reproduction, and body and coat condition.

Despite the obvious appeal of "asking the animal," and its direct relevance to the feelings definition of animal welfare, detailed scrutiny has raised important issues of implementation and interpretation (e.g., Fraser & Nicol, 2011; Houston, 1997; Kirkden & Pajor, 2006; Mason, McFarland, & Garner, 1998). For example, preferences can only be expressed relative to what is on offer, and so the addition or removal of new options may alter choices. Resources may be undervalued if the test requires them to be presented in ways that may restrict their use (e.g., limited access time, such as 15 s exposure to a conspecific); the instrumental response the animal needs to perform is not evolutionarily appropriate to the resource; or "substitutes" or the resource itself are available outside an open-economy test. On the other hand, motivation for resources may be increased by experience with them before or during the tests. For example, Phillips et al. (1996) showed that prior experience of a particular flooring type increased sows' (*Sus scrofa*) initial preference for that floor, and Warburton and Mason (2003) found that mink worked harder for toys that they could see during a test than for similar stimuli that were visually screened.

The implications of preference tests for practical welfare enhancement should thus be considered carefully. Such tests can identify stimuli that induce positive affect, without this necessarily meaning that animals without such stimuli experience negative states. Furthermore, animals may show short-term preferences for things that can have adverse longer-term effects (e.g., sugary or fatty foods). The points at which resources should be deemed essential for good welfare (i.e., their absence is likely to cause suffering), or aversive enough to warrant exclusion from an environment (i.e., their presence is likely to cause suffering), can also be debated. One solution is to suggest that resources for which animals will pay as great a maximum cost as for a clearly vital resource (e.g., food) are essential for good welfare. Finally, there may even be circumstances in which motivation to access a resource does not necessarily map on a positive affective state, when inspecting a dangerous predator or rival, for example (Mason & Burn, 2011). These would be exceptions to the definitions of rewards and punishers cited previously.

Careful consideration of these issues and appropriate experimental design allows animal welfare researchers to use motivation and preference methods to help (re)design housing and husbandry procedures to enhance welfare and to identify those stimuli which are likely to generate positive or negative affective states. If we assume that motivation to work for or avoid stimuli reflects the affective valence that they induce, that the work required is equally appropriate to each resource, and that units of resource are comparable, the method offers a potential common currency (work done/unit resource) for directly comparing the affective value of different resources and hence determining their welfare significance.

The Welfare Indicators Method

Systematic measurements of motivation and preference are time consuming and best carried out under controlled laboratory conditions. They are therefore of limited use under field conditions (e.g., farms or zoos). The *welfare indicators method* offers a potentially quicker way of assessing well-being by using a range of behavioral, physiological, and physical markers to compare animals that are treated in different ways. The rationale for linking indicators to welfare depends on how welfare is defined. Proponents of the function approach assume that the indicators reflect the integrity of an animal's biological function. Proponents of the feelings approach assume that the indicators provide information about the animal's emotional state. The degree to which these assumptions can be supported varies from indicator to indicator. In Table 35.1 we list some of the many welfare indicators that have been used, broken down into categories on the basis of the type of indicator (behavioral, physiological, physical) and, in some cases, functional grouping (e.g., health, reproduction). We also list assumptions for why these indicator categories provide useful information in the context of the function and feelings approaches.

Welfare indicators from the function perspective. Indicators of poor welfare should

TABLE 35.1

Examples of Welfare Indicators Used in Animal Welfare Research and the Assumptions That Underpin Their Use by Proponents of the Feelings and Function Approaches

Category of welfare indicator	Examples	Assumptions for function approach	Assumptions for feelings approach
Health and survival	Illness, injury, bone strength and damage, body condition, weight, growth, longevity, mortality	Diminished health and survival reflect a decrease in effective biological function	Diminished health and survival are accompanied by negative affective states
Reproduction	Number of offspring, offspring birth weight, offspring survival to weaning	Lowered reproduction indicates less effective biological function	Lowered reproduction occurs in situations associated with negative affect
Physiological measures linked to the concept of stress	Corticosterone, cortisol, epinephrine, heart rate, heart rate variability, blood pressure, temperature, markers of oxidative stress	Elevated markers of physiological stress indicate that the animal is struggling to cope or function effectively	Elevated markers of physiological stress are associated with negative affective states
Other physiological indicators	Endogenous opioids, oxytocin, serotonin, vasopressin	Changes can be linked to other stress responses	Changes reflect specific affective states or valence
Immune function indicators	Antibody response to challenge, lymphocyte proliferation, heterophil–lymphocyte ratio, cytokines	Altered immune function can threaten biological function via inflammation, infection, and autoimmune diseases	Altered immune function occurs in situations associated with negative affect
“Abnormal” or damaging behavior	Stereotypic behavior, redirected behavior, vacuum behavior, hyperaggression, cannibalism	Abnormal or damaging behaviors reflect a decrease in the ability to cope or function effectively	Abnormal or damaging behaviors occur in situations associated with negative affect
Behavioral indicators of disease, pain and other affective states	Inactivity, posture, responsiveness, “sickness behavior,” play, vocalizations, facial expressions, affiliative behavior, aggression, response to novelty, startle, exploration, neophobia, anhedonia, tonic immobility	Changes can be linked to decreases in biological functioning, such as disease, injury, starvation, etc.	Changes reflect specific affective states or valence

reflect a decrease in effective biological functioning. At any one time, however, measures of an animal’s biological processes may deviate from a notional optimum required for maximizing survival and reproductive success. This may happen for a range of reasons, including temporary adjustments allowing adaptation to new environmental challenges or alterations that anticipate change. So although it may be possible to demonstrate that, for example, animals in one type of housing exhibit different levels of some welfare indicators relative to animals in another type of housing, the point at which these changes in biological function are significant enough to become a welfare concern is a key question for the function approach. McGlone (1993) argued that this was not until survival and reproduction are impaired. In this view valid indicators of lowered reproduction and survival are the benchmark for poor welfare, and the other indicators in Table 35.1 are useful only if they provide accurate proxy measures of these changes. A similar stance was taken by Moberg (2000), who proposed that only when responses to challenge use resources that are required for other important biological activities, such as growth and reproduction, will a prepathological or pathological state that compromises welfare develop. This “cut-off” issue is avoided if indicators are used to make a relative rather than absolute evaluation of animal welfare. Thus, it may be adequate to report that the welfare indicator profile of animals in one type of housing suggests that their biological function is under more threat than those in a different housing system, and hence that the latter system should be favored.

Welfare indicators from the feelings perspective. If we accept the definition of emotion given previously, indicators that change reliably when an animal is exposed to a stimulus that it finds rewarding (will work for) or punishing (will work to avoid) can be assumed to reflect positive and negatively valenced states, respectively. Motivation and preference methods can be used to identify rewarding and punishing stimuli for use in this validation process. For example, Nicol et al. (2009) measured a large number of behavioral, physiological, and physical indicators in hens housed in three different housing systems for several weeks each. They then tested individual chicken preferences for the systems and searched for indicators that had been reliably higher or lower in the systems that the chickens preferred. In this way, they identified indicators such as body temperature, heterophil–lymphocyte ratio, and response to novelty that changed reliably when chickens were housed in more preferred environments. They could thus screen a large number of measures and suggest which might be valid indicators of positive or negative states.

The appraisal theory of emotions (e.g., Scherer, 2005) offers a related way of validating welfare indicators. If it can be assumed that stimuli with characteristics (e.g., novelty, suddenness, pleasantness) that generate specific emotions via appraisal processes in humans will also do so in other animals, then the profile of behavioral and physiological responses to these stimuli can be interpreted as indicators of those particular emotions (Désiré et al., 2002), and likewise for responses induced by drugs that generate specific emotions in people. A merit of this human-inspired approach (and others outlined later in this chapter) is that because humans are able to report felt emotions linguistically, they are arguably the best models for revealing how behavior, physiology, and felt affect relate. Using humans as models for other species in this way can thus be useful, as long as the underlying assumptions about biological homology are warranted and the dangers of naive anthropomorphism are guarded against (Burghardt, 2007; Wynne, 2007).

In reality, many studies do not yet validate indicators of affective state in these ways but use other reasons to link welfare indicators to affect: (a) they change reliably in situations that threaten or enhance animals' survival chances; and (b) they are closely correlated with reported emotions in humans. Both rationales have merits but are based on assumptions that can be challenged.

An example of a behavioral indicator used to address welfare concerns is repetitive, invariant, and apparently functionless stereotypic behavior (e.g., pacing, feather-plucking). Stereotypies are usually observed in aversive conditions (e.g., barren cages, food restriction) that thwart strong motivations, encouraging animals to persistently repeat intention, redirected or displacement activities (Mason & Latham, 2004), and changing brain function to make animals more perseverative (e.g., M. A. Jones, Mason, & Pillay, 2011). Stereotypies may indicate cumulative poor welfare: Laboratory primates exposed to many aversive experiences during their life (e.g., isolation rearing, stressful procedures) become the most stereotypic (e.g., Gottlieb, Capitanio, & McCowan, 2013).

Like all welfare indicators, however, stereotypic behavior is not perfect. Its downside is a tendency to false negatives: Not all animals faced with aversive conditions display it. Those who do not become stereotypic despite living in impoverished environments often seem just as stressed, sometimes more so, than identically housed stereotypic conspecifics (Mason & Latham, 2004). Such findings may reflect individual differences in response style with, for example, inactivity occurring instead of stereotypy in some situations (e.g., M. A. Jones et al., 2011). Moreover, chronic cold, pain, and fear typically do not cause stereotypies, despite being aversive.

Indicators designed to assess animal emotion. In addition to the welfare indicators listed in Table 35.1, animal welfare researchers have been active in developing indicators specifically intended to assess emotional states. Some of these and their rationales are summarized in Table 35.2. The first three have their origins in animal welfare science, have been studied in a variety of species, and have had a range of impacts. The *qualitative*

TABLE 35.2

Examples of Welfare Indicators Specifically Designed to Assess Animal Emotions

Welfare indicator	**Rationale for the link between the indicator and affective state**
Qualitative behavior assessment (see Wemelsfelder et al., 2001)	It is argued that subjective states such as emotion are accessible to direct observation and measurement, and that they are manifest in the way that the animal interacts with a situation—how it expresses its behavior (e.g., boldly, fearfully, aggressively) as opposed to exactly what it does. In this view, measurements of the qualitative nature of behavior, for example, by using observer-generated descriptive terms, can capture the subjective and emotional states of the animal.
Anticipatory behavior (see Spruijt et al., 2001)	It is proposed that reward sensitivity changes according to an animal's overall affective state. A negative state resulting from cumulative negative experiences leads to increased reward sensitivity, although chronic stress and negative affect can result in anhedonia and decreased reward sensitivity. Reward sensitivity can be measured as a change in anticipatory behavior during presentation of a learnt conditioned stimulus predicting an impending reward. Animals in short-term negative states are predicted to show increased anticipatory behavior.
Cognitive bias (see Harding, Paul, & Mendl, 2004)	People in negative states show heightened attention to negative stimuli, retrieve negative memories more readily, and make negative judgments about ambiguous stimuli or future events. From an evolutionary perspective, if moods provide information about the environment by integrating previous experience of rewarding and punishing events, then a negative mood should influence a cautious (pessimistic) judgment of ambiguity (avoid rather than approach a rustle in the grass). Affect-induced judgment biases can be measured by training animals to make one response (P) to a cue signaling a positive outcome and another response (N) to a cue signaling a negative outcome. Animals in a negative state are then predicted to show a pessimistic N response to an intermediate ambiguous cue.
Drug discrimination (see Carey & Fry, 1995)	Animals are trained to make one response (C) to acquire a reward when in a control state and another response (D) when under the influence of a drug thought to induce a specific emotional state (e.g., anxiolytic, anxiogenic). In a test, if response D is shown when an animal is exposed to an environment or procedure thought to have an affective or welfare impact, it can be inferred that the animal is experiencing an emotional state similar to that induced by the drug.
Drug self-administration (see Danbury, Weeks, Chambers, Waterman-Pearson, & Kestin, 2000)	Animals are allowed to choose between a food or fluid containing a drug thought to induce or alter emotional states (e.g., painkillers, anxiolytics) and a control food or fluid that does not contain the drug. It is predicted that, for example, animals experiencing pain will show a stronger preference for the drug-laced food or fluid than will animals who are free from pain.
Facial expressions and vocalizations (see Langford et al., 2010)	Facial expressions are key indicators of emotional state in humans, so there is interest in whether this is also the case in nonhuman animals. Recent studies indicate that particular changes in facial appearance—pain faces—may reliably occur in animals (e.g., mice, horses, cats) experiencing pain. Some authors suggest that these are specific signals of affective pain as opposed to nociception. Vocalizations made by animals exposed to stimuli or events that are rewarding or aversive have also been used as indicators of affective state in a number of captive species, including rats, pigs, primates, and chickens.
Emotional valence lateralization (see Leliveld, Langbein, & Puppe, 2013)	It is hypothesized that the right hemisphere dominates processing of negatively valenced information and the left hemisphere of positive information. It is predicted that stimuli inducing negative states are more likely to be attended to using the contralateral left visual or auditory fields, and that animals in a negative state are more likely to show left visual or auditory field-dominated responses to novelty or threat.

behavior assessment (QBA) method shows good interobserver reliability, has discriminated between animals treated in a variety of different ways, and has been correlated with other welfare indicators (e.g., Stockman et al., 2011). The interpretation of the resulting ratings in terms of subjective state depends on accepting the philosophical arguments put forward by Wemelsfelder (1997). Acceptance of the method as a whole, combined with its relative ease of use, is evident from the inclusion of QBA in the pioneering EU Welfare Quality on-farm welfare assessment approach.

Studies of rat (*Rattus norvegicus*) *anticipatory behavior* during a cue predicting reward suggest that it shows a biphasic relationship with affect—increasing in acute negative states and decreasing in chronic negative states (Van der Harst & Spruijt, 2007). Anticipatory behavior may vary between species (e.g., when food is anticipated, activity increases in rats and decreases in cats [*Felis catus*]; Spruijt, van den Bos, & Pijlman, 2001). Interpretation thus requires knowledge of how long an animal has been exposed to a potentially negative environment and of species-specific appetitive responses. As well as being a potential indicator of affective state, anticipation associated with signaled rewards is hypothesized to generate positive affect. If so, cueing reward delivery could be used to enhance welfare (Van der Harst & Spruijt, 2007).

The use of *judgment biases* as indicators of affective state draws on findings that people reporting positive or negative emotions reliably exhibit, respectively, optimistic or pessimistic judgments about ambiguous stimuli (Mineka, Watson, & Clark, 1998; Paul et al., 2005). Around 65 published studies have investigated whether a similar relationship between emotion and decision-making exists in animals (Gygax, 2014; Mendl, Burman, Parker, & Paul, 2009; see also Chapters 15 and 16, this volume), and evolutionarily based arguments for why mood states should influence decision making under ambiguity across species have been proposed (Mendl, Burman, & Paul, 2010; Nettle & Bateson, 2012). The majority of studies support the hypothesized link between affect and decision making, that animals in putative negative states judge ambiguous stimuli as predicting negative outcomes, although there are some null findings and contradictory results. The method therefore still needs to be refined, but it shows great promise as a new measure of affective valence that has cross-species generalizability and a theoretical rationale.

Sensitivity and specificity of welfare indicators. The ideal well-validated welfare indicator should generate few false negatives (i.e., show *sensitivity*: a low rate of failing to respond when a change in function or feelings actually occurs) and false positives (i.e., show *specificity*: a low rate of signaling a change in function or feelings when none is actually occurring). Some studies have identified commonly used welfare indicators that do not appear to be good measures of affective valence—the key determinant of animal welfare. In particular, acute changes in many stress physiology indicators such as cortisol, corticosterone, and heart rate (see Volume 1, Chapter 5, this handbook) instead seem to be good measures of emotional arousal. For example, rats exposed to a sexual encounter or social defeat show virtually identical changes in corticosterone (Buwalda, Scholte, de Boer, Coppens, & Koolhaas, 2012), even though they find the former rewarding and the latter aversive. This equates to a lack of specificity. Similarly, Nicol et al. (2009) found that corticosterone levels did not discriminate between more preferred and less preferred environments in chickens. However, if independent measurements of affective valence are available, stress physiology indicators may show us how intense or activating these states are.

Integrating different welfare indicators. Although it is widely advocated that studies should use a range of indicators to allow triangulation of conclusions about animal welfare (e.g., Broom, 1991), most use only a limited number for practical, temporal, and financial reasons. Nevertheless, combining readouts from even a small number of indicators can be a challenging task if they do not all point in what intuitively seems to be the same direction. How should one weigh the relative importance of, for example, differences in cortisol levels, antibody response to antigen challenge, time spent stereotyping, and body lesions in coming to an overall evaluation of the threat to biological function generated by different husbandry systems?

Narrative arguments for the importance of different indicators are often provided to justify conclusions in studies using multiple measures, but there is a risk that these may be open to expectation biases or other influences. Recently, there have been systematic attempts to weight the importance of different welfare indicators using mathematical algorithms formulated largely on the basis of expert opinion. These have been developed in the context of on-farm welfare assessment, where large numbers of indicators are measured (Botreau, Veissier, & Perny, 2009). They represent a way forward in tackling one of the major challenges of the welfare indicators method. However, reliance on expert opinion risks perpetuating received wisdom or resulting in algorithms that are strongly influenced by one or two measures (e.g., Heath, Browne, Mullan, & Main, 2014), and alternative ways of establishing the relative importance of different indicators are needed. The motivation and preference method may be able to avoid this indicator combination problem if a valid common currency (how hard animals work to access or avoid resources) can be established that allows different resources or environments to be directly compared. Of course, in many studies, indicators may line up in a coherent way and in these cases interpretation is more straightforward and confidence in the findings can be strong. Overall, welfare indicators provide the most powerful tools for rapid and practical welfare assessment, as long as a clear link to animal function or feelings can be established.

GENERIC CAUSES OF AND SOLUTIONS TO WELFARE PROBLEMS

Having discussed the central question of how to assess animal welfare scientifically, we now summarize some ways in which welfare problems can be caused. Rather than considering specific scenarios that generate animal welfare concerns—which can range from genetically induced issues such as difficulty breathing in brachycephalic dogs, to the densely stocked groups in which fattening pigs are often housed, to the monotonous environments of otherwise well-cared for zoo animals—we try to identify generic causes of welfare problems, particularly those with psychological or behavioral elements.

We list some of these causes, and associated examples, in Table 35.3. The categories are not mutually exclusive and the list is not exhaustive, but it does suggest general preventative actions that may be implemented to decrease the likelihood of welfare problems. The most obvious include minimizing aversive events (e.g., by using analgesics during painful procedures) and trying to ensure that animals can carry out highly motivated behaviors, sometimes referred to as *behavioral needs* (Jensen & Toates, 1993), such as foraging, urinating, and defecating away from lying areas, and escaping from aggressive conspecifics. If these are incompatible with particular housing systems, research findings can be used to challenge the ethical acceptability of such systems, suggest changes to their design, or offer practical ways for enhancing welfare within their constraints. As just one example, Carlstead et al. (1993) demonstrated that provision of camouflaged areas of cover can ameliorate the otherwise aversive impact of a barren zoo enclosure on small felids such as the leopard cat (*Felis bengalensis*).

Another practical way of minimizing the negative impact of certain situations is to enhance the predictability of aversive husbandry events by signaling their occurrence, thus training animals that nonsignaled times are safe. This has been used successfully in a number of animal welfare studies (Bassett & Buchanan-Smith, 2007). The negative impact of a situation can also be reduced by using positive reinforcement training to reward animals for participating or to desensitize them to aversive stimuli. This approach has been used in various taxa, and Laule et al. (2003) reviewed its utility in nonhuman primates where it has been used successfully to train animals to voluntarily partake in procedures such as blood sampling.

Boredom is a frequently used term in lay discussions of animal welfare. It is easy to imagine how the apparent lack of stimulation provided by many types of animal housing provides little to occupy the animal's brain for large passages of time. However, operational definitions of this state facilitating experimental studies have proved elusive, leading to claims of anthropomorphism when boredom is mentioned. Recently, Meagher and Mason (2012) proposed that, as a state induced by lack of stimulation, boredom should result in elevated interest in all stimuli, whereas a related state like apathy should result in decreased interest in or responses to stimuli and anhedonic depression should be manifest as a specific lack of responsiveness to rewarding stimuli. Using these definitions, they found that compared to mink housed with environmental enrichment stimuli, those housed in barren empty cages did indeed show evidence of boredom as opposed to apathy or depression.

Notwithstanding the debates about boredom and how to measure it, environmental enrichment

TABLE 35.3

Generic Psychological and Behavioral Causes of Animal Welfare Problems

Generic cause	Explanation	Examples
Exposure to aversive events	Cumulative experience of aversive events will, by definition, generate negative affective states and hence poor welfare.	Castration and tail-docking in lambs; pain from leg disorders in broilers and cattle; injurious behavior (e.g., aggression, tail-biting, feather-pecking) in groups of pigs and chickens; punishment-based training regimes for dogs or horses; chronic heat or cold
Memory of aversive events	Cues associated with previous aversive events may trigger negative affective states even in the absence of the original stimuli.	Odor of husbandry procedures (e.g., smell of dis-budding process); humans associated with veterinary inspection and routine procedures (e.g., restraint, weighing, vaccination)
Thwarting of specific, highly motivated behavior, and resulting lack of reward	Thwarting of highly motivated behavior may lead to a negative frustration-like state, the development of abnormal behaviors, failure to achieve goals or "behavioral needs," and a lack of reward.	Food or foraging restriction in sows and broiler breeders; restricted movement in stall-housed sows; confinement in farm, lab, and zoo animals; restricted mating opportunities; inability to escape aggression; restricted ranging in wild carnivores; isolation of social species (e.g., rats, primates, horses)
Lack of general stimulation or challenge	Animals are "designed" through evolution to gather information and respond to challenges. A lack of stimulation may lead to a "limbo" or boredom state.	Relatively barren social and physical environments of many farmed (e.g., battery chickens, pigs, mink) and laboratory animals (e.g., caged rodents and primates)
Lack of predictability or controllability	Lack of predictability and controllability, particularly of punishers, are well known to cause stress responses and hence may influence affect and welfare. In certain cases, overpredictability of rewards can generate anticipatory frustration and aggression.	Unpredictable rough or gentle handling by stockpersons; unpredictability of frequent aversive events such as blood sampling or handling in lab animals; lengthy predictive cues for highly rewarding events (e.g., noise of approaching food trolley or dispenser in pigs and mink)
Mismatch between captivity and the behavior and ecology of species in the wild: identifying species-specific problems	Wild animals are adapted to behavioral and ecological niches that predispose specific behaviors or requirements which, if not met, lead to welfare problems.	Confinement of polar bears and other species that range widely; provision of inappropriate diet or foodstuffs for ungulates

has been used to tackle this perceived problem, among others, for many years. Studies have shown that additions to housing conditions can result in changes which appear beneficial for welfare (Mason & Burn, 2011; Young, 2003). Recently, there has also been increasing interest in the idea that exposing animals to learning and memory tasks offers a form of *cognitive enrichment* (Meehan & Mench, 2007) with animal welfare benefits. For example, pigs required to learn that individual-specific sound cues signal food availability at a feeder, and then to work for this food by pushing a button, showed welfare benefits as indicated by reduced fear-like behavior in an open-field test, and reduced sympathetic activity and agonistic behavior (Zebunke, Puppe, & Langbein, 2013). It is also possible that prediction and anticipation of the food reward contributed to these findings (cf. Van der Harst & Spruijt, 2007).

Another cognition-related effect on welfare is the inadvertent triggering of memories of previous aversive experiences. The potential for episodic-like memories in animals has been the subject of much recent study (Clayton, Bussey, & Dickinson, 2003; Clayton & Dickinson, 1998) and there is evidence that a variety of species, including primates, rodents, and pigs, are able to remember what happened, where, and when (www memory)—the basic characteristics of an episodic memory (Clayton & Dickinson, 1998; see also Chapter 11, this volume). Although it is not known whether the conscious experience of a previous event that characterizes human episodic memory (*autonoetic consciousness*; Tulving, 1985) occurs in other species, if www memory is accompanied by such experiences in animals, the potential for evoking lucid memories of previous aversive events could be a major cause of poor welfare from the feelings perspective (Mendl, Burman, Laughlin, & Paul, 2001). In any case, retrieval of aversive memories may trigger escape behavior and physiological states which themselves can be damaging. The potential impact of www memory, and also future planning, on animal welfare is considered by Mendl and Paul (2008), and it would seem prudent to avoid exposing animals to cues associated with aversive events. The ability of animals to spontaneously recall such events in the absence of cues is not well understood, although there have been attempts to start measuring this in animals (Basile & Hampton, 2011).

Finally, a knowledge of the species' behavior and ecology in the wild can be valuable in predicting aspects of captivity that it may struggle to deal with and hence may lead to welfare problems. This is an example of how the freedom approach can offer important welfare-relevant hypotheses, which is particularly relevant for captive wild animals in zoos where the issue of domestication does not muddy our understanding of what the species' natural environment is (see Volume 1, Chapter 16, this handbook). As one example, Clubb and Mason (2003; see also Mueller et al., 2011) used a comparative approach to show that wide-ranging carnivores are more predisposed to develop pacing stereotypies and to have higher infant mortality in zoos than species with smaller ranges. Understanding these relationships can allow prediction of particular problems for particular species, and hence pre-emptive management to avoid these (Mason, 2010).

CONCLUSIONS AND FUTURE CHALLENGES

In this brief overview we have discussed the complexities of scientifically studying animal welfare and the approaches being taken by animal welfare scientists to tackle these. We focused on broad conceptual issues and those most relevant to comparative psychologists. Here, we conclude by briefly considering a selection of future challenges.

Development of more accurate welfare indicators remains a critical goal for the scientific study of animal welfare. This will involve refining the ways that existing measures are used as well as developing new ones. Our feelings-based view is that these measures should be validated using stimuli or environments that animals will work for (are rewarding and hence induce a positive affective state) or work to avoid (are punishing and hence induce a negative state). Reference to human findings is also likely to remain important, for example, in the operationalization of states such as boredom, depression, or happiness. Measures should be as sensitive and specific as possible, minimizing false negatives and positives, and this requires validating them against a range of rewarding and punishing stimuli as well as stimuli that have little affective value (but are perhaps highly arousing, general activation being a major confound for many measures). Increasing interest in the notion that we should not simply minimize suffering but also increase positive states to generate "a life worth living" (Yeates, 2011, p. 397) will also require animal welfare scientists to address the question of whether and how positive states can be identified. The search for indicators of *positive welfare* has already begun (Boissy et al., 2007), candidate measures such as play behavior are being investigated (Held & Spinka, 2011; see also Volume 1, Chapter 34, this handbook), and methods for inducing positive affect are being proposed (Van der Harst & Spruijt, 2007; see also Volume 1, Chapter 23, this handbook).

Indicators ideally should be quick and simple to implement so as to facilitate their use in laboratory and field conditions. New technologies may help achieve this. For example, thermal imaging (e.g., Edgar, Lowe, Paul, & Nicol, 2011), accelerometry (e.g., S. Jones et al. 2014), and computer vision techniques (e.g., Dawkins, Cain, & Roberts, 2012) are already making important contributions to animal welfare assessment. In addition to developing better welfare indicators, the issue of how to integrate these to provide an overall welfare judgment remains a major challenge—at least when indicators do not agree—and new approaches are required that do not rely solely on expert opinion. Cross-validating welfare indicators against motivation and preference methods is one promising way forward (Nicol et al., 2009).

Another goal for animal welfare scientists is to better understand why individuals can vary so much in how they respond to environmental conditions (Koolhaas et al., 1999). As mentioned earlier, some animals may react to barren conditions by developing stereotypies, whereas others become very inactive. Here, response style should not be confused with differences in welfare. However, if a range of welfare measures detect clear and consistent individual differences, this may reflect real variation in the ability to adapt to the same environment. With the prospect of more intensive farming practices on the horizon because of concerns about future global food security and supply (Garnett et al., 2013; Walker et al., 2014), better knowledge is needed about what makes individuals "resilient" in the face of pressures, including high stocking densities, demand for more rapid growth, and increasing disease prevalence. The roles of genetic, experiential, and epigenetic factors in influencing coping abilities or vulnerability are important topics for animal welfare scientists, and improved understanding will allow us to identify individuals who are better able to cope with specific challenges and disentangle the factors that differentiate resilient from less-resilient individuals (Karatsoreos & McEwen, 2011).

A challenge of direct relevance to comparative psychologists is to understand how animal welfare affects the results of animal studies. Anxiety and fear-like states can clearly interfere with performance in behavioral tests, and it is well established that physiological stress has a variety of influences on cognitive functions, including attention, learning, and memory (McEwen & Sapolsky, 1995; Mendl, 1999; see also Volume 1, Chapter 19, this handbook). Links between stress or depression-like states and immune function, cardiovascular health, and gastrointestinal function (Sapolsky, 2004) suggest that the potential for animal welfare to have impacts on the outcome of biological research is widespread.

Furthermore, a body of research indicates that standard laboratory rodent housing may affect brain development, leading to abnormal and anxiety-like behavior that is likely to influence research findings (see Volume 1, Chapters 21 and 22, this handbook). More complex caging environments can ameliorate these effects (Würbel, 2001), and animal welfare researchers have been instrumental in arguing that, rather than disrupting standardization and reproducibility of experimental results, cage enrichment may actually increase external validity of findings without affecting variability of data, and hence such concerns should not be a barrier to their uptake (Wolfer et al., 2004). Animal welfare science can thus play an important role in helping to improve the quality of animal research.

A deeper understanding of the mental experiences of other animals remains a major goal for those favoring the feelings definition of animal welfare. Terms such as *emotion* and *suffering* will inevitably draw the accusation of a lack of objectivity (e.g., Wynne, 2007), but if clear arguments can be used to operationally define such terms, as we have tried to do here for emotion, this should help us avoid the trap of naive anthropomorphism (Burghardt, 2007). We also hope that the scientific attention that consciousness is now receiving, including in animals, will lead to breakthroughs that have a major impact on our understanding of animal mind.

Even when welfare is accurately measured, problems detected, and answers offered, a completely different type of challenge is to then effectively implement the solutions. This area of animal welfare research involves consideration of human psychology, the social science of change management, economic modeling, politics, and legislation. Recent studies show some success in using research findings to change farmer practices with the aim of improving welfare (e.g., Main et al., 2012). By achieving this goal, animal welfare research can aspire to be one of a limited number of disciplines that truly spans from underpinning fundamental science, through applied research, to translation and implementation of findings in the "real world."

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Index