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Opinion

Language Evolution: A Changing Perspective

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From ancient times, religion and philosophy have regarded language as a faculty bestowed uniquely and suddenly on our own species, primarily as a mode of thought with communication as a byproduct. This view persists among some scientists and linguists and is counter to the theory of evolution, which implies that the evolution of complex structures is incremental. I argue here that language derives from mental processes with gradual evolutionary trajectories, including the generative capacities to travel mentally in time and space and into the minds of others. What may be distinctive in humans is the means to communicate these mental experiences along with knowledge gained from them.

Trends

From the Bible to Chomsky, language has been commonly viewed as representing a profound change in thought, appearing suddenly and uniquely in humans, with communicative language as a byproduct.

Modern research increasingly suggests mental continuity, more consistent with evolutionary theory, with nonhuman animals showing evidence for mental functions such as mental time travel and theory of mind that are critical to communicative language.

Language can then be viewed as a device for sharing thoughts and experiences rather than as a vehicle for those mental contents themselves.

Nonhuman animals such as great apes and dogs are more capable of understanding human-like language than of producing it, so communicative language in humans depended on adapting output systems to be flexible enough to convey the generativity of thought.

Such a system may have originated in bodily gesture before incorporating vocal signals that eventually provided us with speech.

Is Language Uniquely Human?

According to the Old Testament, language was a gift to Adam and was for a time the common language of all humans. When people built the Tower of Babel so that they might reach closer to Heaven, the Lord thought them disrespectful and dispersed them, and confounded their languages so they could no longer communicate. Echoing this story Noam Chomsky has argued that language was bestowed on some individual, whom he whimsically names Prometheus, within the past 100 000 years, well after *Homo sapie*ns is thought to have emerged as a distinct species [1]. Languages subsequently proliferated into the 6000 or so languages of the world, the vast majority mutually incomprehensible.

The notion that language emerged in humans well after our species itself evolved receives some support from archaeology, based on an apparent explosion of artistic and technological innovation within the past hundred millennia followed by dispersal from Africa in which *H. sapiens* eventually replaced other large-brained hominins such as the Neanderthals and Denisovans. Human artifacts from this period included cave art, musical instruments, sculpture, bodily embellishments, and notations for record keeping and ended an apparent stasis in tool manufacture toward more innovative and varied forms. This surge of activity has been variously labeled the 'human revolution' [2], the 'great leap forward' [3], and the last of seven 'major transitions in evolution' [4] that began with the emergence of replicating molecules. The paleoanthropologist Ian Tattersall writes 'The entirely novel competitive entity represented by behaviorally modern *Homo sapiens* appeared on the planet far too rapidly to be accounted for by the slow workings of natural selection at the individual level' [5].

The Evolutionary Challenge

Such views are antithetical to the theory of evolution. Charles Darwin himself wrote 'If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down. But I can find no such case' [6].

Could language be the case that Darwin feared? Chomsky has often characterized language as 'an organ of the body' and 'on a par with the digestive and immune systems' [7]. Language is

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also undeniably complex, given that its rules of operation are still not well understood after some 60 years of Chomskian linguistics. The emergence of an organ as complex as language in a single step seems clearly counter to Darwinian theory.

Evolutionary theory, however, has itself undergone changes, with the **Modern Synthesis** (see Glossary) and the later **Extended Evolutionary Synthesis** incorporating ideas from genetics, embryology, and population thinking, raising the possibility of more rapid change than that implied by the selection of random mutations [8]. However, it remains problematic whether this can drastically alter the Darwinian scenario, let alone explain the emergence of language in a single step. Pinker and Bloom discuss a number of neo-Darwinian possibilities including the view that language is a '**spandrel**' – a byproduct of the brain's evolved capacity for computation [9] – but conclude that 'there is every reason to believe that language has been shaped by natural selection as it is understood within the orthodox "synthetic" or "neo-Darwinian" theory of evolution' [10]. Gould and Eldredge wrote of '**punctuated evolution**', implying that evolution can proceed in spurts, but they were clear that it is 'not about ecological catastrophe or sudden genetic change' [11]. Chomsky himself [1] appealed to **evo–devo**, whereby complex changes can occur through mutations in regulatory genes that orchestrate the timing of development rather than through the emergence of new genes. Such mutations, however, do not add complexity, suggesting they cannot explain the sudden emergence of a system as complex as grammar [12].

Another prediction of the synthesis is that evolutionary change can be hastened through '**niche construction**', whereby organisms modify their own environments, biasing the process of selection [8]. This might have influenced and perhaps accelerated evolutionary change during the Pleistocene, which saw the emergence of what has been termed the 'cognitive niche' [13], but this would imply a gestation period of some 2 million years rather than a sudden change within the past 100 000 years. Some have also contested the archeological evidence for the 'human revolution', suggesting either that the changes were continuous and date back to precursors of *H. sapiens* [14] or that the impression of change was more a question of sporadic regional variation than of discontinuity through time [15].

Language and Thought

A common theme among those who argue for the sudden emergence of language is that it signaled a change in the manner of thought itself. Thus, Tattersall writes that from about 100 000 years ago 'we start finding plausible indications that members of the new species were starting to think symbolically' [5]. Chomsky writes of 'internal language' (I-language) as the fundamental basis of human symbolic thought with communication merely a byproduct [1,7]. It is, then, through a secondary process of 'externalization' that the diverse languages, spoken and signed, are formed. I-language is considered common to all humans, underlying what Chomsky calls 'universal grammar' – a term that goes back to 17th-century scholars who sought to identify aspects of language common to all languages [16]. There have been many attempts to specify such a grammar, once satirized by James D. McCawley in his book *Thirty Million Theories of Grammar* [17], but Chomsky's most recent and most economical account is the Minimalist Program [18]. The main ingredient is 'unbounded Merge', whereby elements are merged recursively to generate a potential infinity of structures.

The burden of explaining language evolution is lessened, however, if language is regarded as communication, not thought. In this case thought can be considered to have precursors in nonhuman animals (e.g., [16,19]) rather than to have appeared in a single step in *H. sapiens*. Language can then be considered primarily as a device for sharing our thoughts and experiences – more a tool than a fundamental cognitive shift [20,21]. In moving the emphasis to language as communication rather than thought, this more commonsense view, in the words of

Glossary

Evo–devo: derived from evolutionary developmental biology and incorporates the idea that regulatory genes, highly conserved across species, can influence embryonic development through varying the timing and expression of other genes. For example, although different species have dissimilar limbs, such as legs, flippers, or wings, their development is controlled by very similar genes, with the differences due to the way their expression is regulated.
Extended Evolutionary Synthesis: extensions of the Modern Synthesis, dating from the mid-20 century, incorporating further developments in genetics, biology, and population thinking; includes aspects such as evo–devo, punctuated evolution, spandrels, and niche construction.
Modern Synthesis: early 20-century integration of Darwinian evolutionary theory with Mendelian inheritance and population-level ideas.
Niche construction: process by which organisms construct their own environment, which can then alter the selection of traits that are adaptive. For example, traits adapted for survival in a hunter–gatherer society may differ from those adaptive in city life.
Punctuated evolution: the idea that new species evolve relatively rapidly followed by a period of stasis with little genetic change.
Spandrel: an architectural term referring to the triangular space between an arch, a pillar, and a ceiling that is sometimes appropriated by artists for added decoration. The term is borrowed in biology to refer to a byproduct of a feature that evolved for different reasons. A simple example is the use of the nose to hold spectacles. The brain has been claimed to provide a rich source of spandrels, with activities such as music or chess perhaps being byproducts of a computational faculty selected for other adaptive functions.

Dor, 'turns the Chomsky proposal on its head' [21]. The 'great leap forward', if indeed a reality, can then be attributed to an enhanced capacity to share knowledge and experience rather than the thoughts themselves.

This is not to say that thought is independent of language. Indeed, many if not most of our thoughts and knowledge are derived from what other people tell us. However, thoughts themselves, whether derived from personal experience or from communication with others, are not the same as the language in which they are expressed. We often cannot find words for particular thoughts we have or for individuals we can envisage although their names escape us. Thought cannot be tied to any specific language, and when we translate from one language to another the thought remains – at least ideally – despite being expressed in different words [22]. Even in retelling stories within the same language, we typically do not use the same words or expressions. As a source of knowledge, however, language creates a ratchet effect so that knowledge can build over time and spread among individuals, allowing specializations to develop [4]. In these ways language may have been influential in a human revolution, but through its power of communication rather than from a change in the innate structure of thought itself.

If expressive language is designed for the communication of thought, its properties must be at least partly shaped by the way in which thought itself is structured. In this respect the account to be given here is in accord with Chomsky's. The difference lies in the suggestion here that the nature and structure of thought have a long and gradual evolutionary history.

Several authors have speculated about possible precursors of language, including the manufacture and use of tools [23,24], navigation [25,26], reciprocal altruism [27], and social understanding [28]. Here I focus on two mental capacities that seem especially critical to the recursive, generative nature of language itself and that may ultimately obviate the need for any special mechanism unique to language, or indeed to our own species.

Mental Time Travel

'Displacement' is a design feature of language enabling reference to events at other places and other times, past or future [29], and is increasingly recognized as critical to its evolution (e.g., [30,31]). This in turn must depend on the ability to imagine such events, such as what you did yesterday or plan to do tomorrow. Although some, including myself, have claimed that mental time travel itself is uniquely human [32,33], the evidence increasingly suggests that it may have a long evolutionary pedigree, with behavioral evidence from species as disparate as scrub jays [34], rats [35], and chimpanzees [36,37]. Behavioral evidence, however, can be ambiguous or flawed [38], and my own shift to an acceptance of evolutionary continuity was prompted mainly by evidence from neuroscience [39].

It is well established that the hippocampus in humans is activated when people consciously remember past episodes or imagine future ones [40,41] or even imagine purely fictitious ones [42]. In the rat, 'place cells' in the hippocampus record where the animal is located in a spatial environment [43] and sometimes trace out trajectories even when the animal has been removed. The trajectories are sometimes 'replays' of trajectories previously taken, sometimes the reverse of those trajectories [44], and sometimes trajectories the animal did not take [45], some of which may be anticipations of future trajectories [46]. Reviewing this evidence, Moser, Rowland, and Moser write that 'the replay phenomenon may support "mental time travel" . . . through the spatial map, both forward and backward in time' [47]. Mental travels through known spatial locations may be a common capacity of animals that move about physically in space and need to know whether they are, where they have been, and where they might go next.

In humans the hippocampus seems to be involved in language itself [48,49]. Even in the rat, however, hippocampal activity has some language-like properties. It is influenced by activity in the neighboring entorhinal cortex in a modular fashion, adjusting for parameters like spatial scale, direction of the head, and proximity to borders. Different combinations of modules can result in thousands of combinations, comparable to 'that of an alphabet in which all words of a language can be generated by combining only 30 letters or less' [47]. In short, spatial imagination, like language, is generative. I can imagine myself in different locations, such as my office, in many different ways and at different spatial scales. I can zoom out from the office to its location in the house, the location of the house in the city, the city in the country, and so on. Even in the rat, the spatial scale zooms out as recording shifts from the rearward to the forward end of the hippocampus [50] and this arrangement is mirrored in human hippocampal activity as people process narratives linked to videos, with increasingly forward activation as the focus shifts from detail to more global understanding [51].

Generative grammar itself, then, may depend on the generative nature of spatiotemporal imagination rather than on any property unique to language itself. The zooming property implies recursion, in which spatial maps are nested in maps at larger scales. It has even been proposed that Chomsky's Minimalist Program and the concept of Merge can be applied to simple sensorimotor actions such as grasping and manipulating an object [52]. We are profoundly spatial creatures and even our non-spatial thoughts, such as reasoning and logic, may be grounded in spatial metaphor rather than abstract symbols [53]. The concept of universal grammar has been doubted [54,55], but if it can be said to exist its universality may reside in the common experience of the spatiotemporal world rather than in the innate structure of language.

Theory of Mind

We travel mentally not only in time and space but also into the minds of others. The capacity to understand what others feel, think, or believe is known as theory of mind and underlies the human obsession with storytelling, whether in the form of novels, plays, movies, TV soaps, gossip, or, in earlier times – and among present-day African tribes – stories told around the campfire at night [56]. It has been suggested that storytelling drove the evolution of language itself [57].

Theory of mind is required for language in a capacity other than storytelling. Language is not merely a matter of words; it requires that the speaker and listener (or signer) know what is in each other's mind and that each knows that the other knows this – requiring metacognition [58,59]. In this sense language is underdetermined [60]. Even individual words may carry multiple meanings depending on context. An extreme example is the English word 'set', which, according to the Chambers Dictionary, has 105 different meanings.

Whether nonhuman species possess theory of mind has been much disputed since Premack and Woodruff in 1978 asked 'Does the chimpanzee have a theory of mind?' [61] Thirty years later there was still disagreement; in one view, the answer was negative and the very idea that chimpanzees might have theory of mind was deemed 'Darwin's mistake' [62], while others found evidence that chimpanzees could be shown to understanding the goals, intentions, perceptions, and knowledge of others but not their beliefs or desires [63]. A more recent study, however, showed that great apes look in anticipation of where a human agent will falsely believe an object has been hidden [64] – they seem to pass the false-belief test, often regarded as the gold-standard test of theory of mind [65]. This study joins a chorus of studies gradually showing greater mental continuity between humans and other species than is commonly assumed. Even rhesus monkeys may be capable of spontaneous metacognition [66].

A neural network for mental orientation in 'space, time, and person' is now fairly well established in humans and includes widespread regions in the frontal, parietal, and temporal cortices [67]. This network overlaps extensively with what has been termed the 'default mode network', which is active in 'mind wandering' – spontaneous internal activity unrelated to the concerns of the moment [68]. Homologous networks have been identified in monkeys [69] and rats [70], again suggesting evolutionary continuity. Of course, internal thinking may be less complex in rats and monkeys than in humans, but we should bear in mind Darwin's edict: 'The difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind' [71].

In summary, comparative research is increasingly drawn to the conclusion that some nonhuman animals are capable of more 'advanced' cognition than hitherto realized, suggesting evolutionary continuity rather than a sudden shift in cognition that somehow made humans special. Mental excursions in time and space and into the minds of others may be more comprehensive and sophisticated in humans than in other species in part because of communicative language itself, which feeds our mental travels through storytelling and our minds through the exchange of knowledge. Their origins, however, may go well back in our evolutionary history.

The Communicative Aspect

According to a shifting tide of opinion, it is in our ability to communicate our thoughts, rather than our thoughts themselves, that we differ most profoundly from other species and it is our

Box 1. The Gestural Theory of Language Origins

Among primates only humans appear capable of vocal learning [77] and therefore of speech. Language, however, is not restricted to speech; sign languages have all the hallmarks of true language [78]. This raises the possibility that language originated, not from vocal calls, but from manual gestures. This idea goes back to the 18th century [79–81] and has been increasingly endorsed over the past few decades (e.g., [82–90]).

Captive great apes have never developed anything resembling speech but have learned to use manual gestures [72,91] in ways that have language-like features; great apes in the wild also communicate bodily in ways that are more language-like than their vocalizations [92]. People, too, gesture manually while speaking [93,94], and like speech, gesture involves the hippocampus [95]. Some have supposed that visible gesture and vocal language have always been equal partners [96,97] (but see [98] for a contrary view).

Gestural communication may derive from the primate 'mirror system', a brain circuit active during both the production and the perception of intentional movements, suggesting a natural basis for communication [85]. In macaques the system responds to actions perceived acoustically as well as visually but not to animal calls, implying that the incorporation of vocal action evolved relatively late [99]. Brain imaging of a homologous system in humans suggests that it expanded to encompass the language circuit [100].

Bodily actions provide a natural basis for relaying events in our predominantly spatial world, especially through hand and arm movements as exemplified in sign languages. During the Pleistocene, with the emergence of the genus *Homo*, brain size increased and the hands were increasingly freed by the shift to obligate bipedalism, allowing communication through gesture and mime [101]. In the interests of efficiency, mimed gestures were probably simplified and conventionalized over time, losing their iconic quality [102]. Tomasello writes that human language might have 'evolved quite a long way in the service of gestural communication alone, and the vocal capacity is actually a very recent overlay' [89].

To some, a transition from the visible to the acoustic mode seems too extreme to be credible (e.g., [103,104]). Speech, however, is itself a system of gestures of the tongue, lips, and larynx [105]. Movements of the hand and mouth are linked neurally, phylogenetically, developmentally, and behaviorally [106–109], suggesting that mouth gestures might plausibly have blended into manual ones [110], and the visible movements of speech remain verbally informative [111], although adding vocalization makes the gestural content more accessible as audible speech. The acoustic code, however, is more arbitrary and is sustained largely through culture, although it does carry non-arbitrary associations [112,113].

The transition might be an early example of miniaturization – tucking the burden of communication into the mouth and freeing the hands and arms for activities such as carrying or making and using tools. It was perhaps this switch, and not language itself, that produced the 'human revolution' [114], but it did not stop there. Subsequent shifts, from writing to the Internet, have profoundly shaped and widened human culture.

capacity to communicate that gives an inflated view of human cognition. The difference has more to do with production than with understanding. Great apes [72] and even dogs [73,74] can understand and respond to spoken requests involving sequential processing and substantial word vocabularies, which implies a degree of symbolic understanding but a lack of the means to produce anything approaching human productive language. Great apes, at least, may come closer through bodily movement and gesture than through vocalization (Box 1).

The pressure to develop output systems flexible enough to communicate our thoughts and experiences probably grew during the Pleistocene when our hominin forebears were increasingly forced from a forested environment to more open territory with dangerous predators, and survival depended on cooperation and social interaction – the aforementioned 'cognitive niche' [13]. The initial impetus may have come from the sharing of episodic events, whether remembered, planned, or fictitious but perhaps also increasingly including information about territory, danger, food sources, tool making, and the habits and abilities of individuals. Its course of evolution is probably best indexed by the threefold increase in brain size that began some 2 million years ago and is probably attributable to the emergence of grammatical language [75] and the vast increase in knowledge that it afforded. The increase in brain size was incremental through this period, again suggesting gradual evolution rather than the sudden appearance of a prodigious Prometheus within the past 100 000 years.

Concluding Remarks: Is Rapprochement Possible?

There are some signs that the longstanding divide over language evolution may be softening. Through progressive modifications, Chomsky's theory of syntax has become simpler. This is suggested in the title of the current Minimalist Program, whose primary ingredient is Merge, recently described as the 'simplest case', requiring a 'slight mutation' producing a 'slight rewiring of the brain' [7]. These descriptions now seem at odds with earlier notions of language as a bodily organ producing a major transition in evolution and are perhaps an attempt to bring the evolution of language within the bounds of evolutionary credibility.

At the same time, Minimalist theory seems to place a greater burden on externalization to explain how a concept as apparently simple as Merge can account for the complex and varied grammars among the 6000 or so languages, spoken or signed, in the world. A recent article points out that the parsing of a sentence cannot be based simply on the string of words or signs but must depend on an internal device to impose hierarchical structure; in its simplest form, that device is Merge, applied recursively. The question then is whether this internal structuring is 'uniquely human (species-specific) and uniquely linguistic (domain-specific)' [76] or whether it depends on the way that experience and knowledge have been incrementally structured over millions of years of evolution (see Outstanding Questions).

Outstanding Questions

Can we identify aspects of thought that are present only in humans and that have no counterparts in nonhuman animals?

If so, can we find evidence that such aspects evolved suddenly within the time span of *Homo sapiens* or is it more plausible to suppose that they evolved more gradually, such as during the Pleistocene?

Can we find anatomical, genetic, or fossil evidence that bears on the origins of speech as distinct from language itself?

Or does the evidence further support the origins of expressive language in manual gestures rather than vocal calls?

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References

1. Chomsky, N. (2010) Some simple evo devo theses: how true might they be for language? In *The Evolution of Human Language* (Larson, R.K., ed.), pp. 45–62, Cambridge University Press
2. Mellars, P. and Stringer, C., eds (1989) *The Human Revolution: Behavioral and Biological Perspectives on the Origins of Modern Humans*, Princeton University Press
3. Szathmáry, E. (2015) Toward major evolutionary transitions theory 2.0. *Proc. Natl Acad. Sci. U. S. A.* 102, 10104–10111
4. Diamond, J. (1992) *The Third Chimpanzee: The Evolution and Future of the Human Animal,* HarperCollins
5. Tattersall, I. (2016) A tentative framework for the acquisition of language and modern human cognition. *J. Anthropol. Sci.* 94, 157–166
6. Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection,* John Murray
7. Chomsky, N. (2015) Some core contested concepts. *J. Psycholing. Res.* 44, 99–104
8. Laland, K.N. *et al.* (2015) The extended evolutionary synthesis: its structure, assumptions and predictions. *Proc. Biol. Sci.* 282, 20151019

9. Gould, S.J. and Lewontin, R.C. (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. Biol. Sci.* 205, 281–288
10. Pinker, S. and Bloom, P. (1990) Natural language and natural selection. *Behav. Brain Sci.* 13, 707–784
11. Gould, S.J. and Eldredge, N. (1977) Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology* 3, 115–151
12. Christiansen, M.H. and Chater, N. (2008) Language as shaped by the brain. *Behav. Brain Sci.* 31, 489–558
13. Pinker, S. (2010) The cognitive niche: coevolution of intelligence, sociality, and language. *Proc. Natl Acad. Sci. U. S. A.* 107, 8993–8999
14. McBrearty, S. and Brooks, A.S. (2000) The revolution that wasn't: a new interpretation of the origin of modern human behavior. *J. Hum. Evol.* 39, 453–563
15. Shea, J.J. (2011) *Homo sapiens* is as *Homo sapiens* was. *Curr. Anthropol.* 52, 1–35
16. Fitch, W.T. (2010) *The Evolution of Language,* Cambridge University Press
17. McCawley, J.D. (1982) *Thirty Million Theories of Grammar,* University of Chicago Press
18. Chomsky, N. (1995) *The Minimalist Program,* MIT Press
19. Hurford, J.R. (2007) *The Origins of Meaning,* Oxford University Press
20. Everett, D.L. (2012) *Language: The Cultural Tool,* Pantheon
21. Dor, D. (2015) *The Structure of Imagination: Language as a Social Communication Technology,* Oxford University Press
22. Jackendoff, R. (2011) What is the human language faculty? Two views. *Language* 87, 586–624
23. Steedman, M. (2014) On dendrophilia: Comment on "Toward a computational framework for cognitive biology: unifying approaches from cognitive neuroscience and comparative cognition" by W. Tecumseh Fitch. *Phys. Life Rev.* 11, 382–388
24. Stout, D. and Chaminade, T. (2012) Stone tools, language and the brain in human evolution. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 367, 75–87
25. Hauser, M.D. *et al.* (2010) The faculty of language: what is it, who has it, and how did it evolve? *Science* 298, 1569–1579
26. Berwick, R.C. and Chomsky, N. (2016) *Why Only Us: Language and Evolution,* MIT Press
27. Bickerton, D. (1995) *Language and Human Behavior,* University of Washington Press
28. Seyfarth, R.M. and Cheney, D.L. (2014) The evolution of language from social cognition. *Curr. Opinion Neurobiol.* 28, 5–9
29. Hockett, C.F. (1960) The origins of speech. *Sci. Am.* 203, 88–96
30. Bickerton, D. (2014) *More than Nature Needs: Language, Mind and Evolution,* Harvard University Press
31. Gärdenfors, P. and Osvath, M. *et al.* (2010) Prospection as a cognitive precursor to symbolic communication. In *The Evolution of Human Language* (Larson, R.K., ed.), pp. 103–114, Cambridge University Press
32. Tulving, E.R. (2002) Episodic memory: from mind to brain. *Annu. Rev. Psychol.* 53, 1–25
33. Suddendorf, T. and Corballis, M.C. (2007) The evolution of foresight: what is mental time travel, and is it unique to humans? *Behav. Brain Sci.* 30, 299–351
34. Clayton, N.S. *et al.* (2003) Can animals recall the past and plan for the future? *Trends Cogn. Sci.* 4, 685–691
35. Wilson, A.G. *et al.* (2013) Event-based prospective memory in the rat. *Curr. Biol.* 23, 1089–1093
36. Janmaat, K.R.L. *et al.* (2014) Wild chimpanzees plan their breakfast time, type, and location. *Proc. Natl Acad. Sci. U. S. A.* 111, 16343–16348
37. Osvath, M. and Karvonen, E. (2012) Spontaneous innovation for future deception in a male chimpanzee. *PLoS One* 7, e36782
38. Suddendorf, T. and Corballis, M.C. (2010) Behavioural evidence for mental time travel in nonhuman animals. *Behav. Brain Res.* 215, 292–298
39. Corballis, M.C. (2013) Mental time travel: a case for evolutionary continuity. *Trends Cogn. Sci.* 17, 5–6
40. Addis, D.R. *et al.* (2007) Remembering the past and imagining the future: common and distinct neural substrates during event construction and elaboration. *Neuropsychologia* 45, 1363–1377
41. Buckner, R.L. (2010) The role of the hippocampus in prediction and imagination. *Annu. Rev. Psychol.* 61, 27–48
42. Hassabis, D. *et al.* (2007) Using imagination to understand the neural basis of episodic memory. *J. Neurosci.* 27, 14365–14374
43. O'Keefe, J. and Nadel, N. (1978) *The Hippocampus as a Cognitive Map,* Clarendon Press
44. Foster, D.J. and Wilson, M.A. (2006) Reverse replay of behavioural sequences in hippocampal place cells during the awake state. *Nature* 440, 680–683
45. Gupta, A.S. *et al.* (2010) Hippocampal replay is not a simple function of experience. *Neuron* 65, 695–705
46. Pfeiffer, B.E. and Foster, D.J. (2013) Hippocampal place-cell sequences depict future paths to remembered goals. *Nature* 497, 74–79
47. Moser, M.B. *et al.* (2015) Place cells, grid cells, and memory. *Cold Spring Harb. Perspect. Biol.* 7, a021808
48. Covington, N.V. and Duff, M.C. (2016) Expanding the language network: contributions from the hippocampus. *Trends Cogn. Sci.* 20, 869–870
49. Duff, M.C. and Brown-Schmidt, S. (2012) The hippocampus and the flexible use and processing of language. *Front. Hum. Neurosci.* 6, 69
50. Strange, B.A. *et al.* (2014) Functional organization of the hippocampal longitudinal axis. *Nat. Rev. Neurosci.* 15, 655–669
51. Collin, S.H.P. *et al.* (2015) Memory hierarchies map onto the hippocampal long axis in humans. *Nat. Neurosci.* 18, 1562–1564
52. Knott, A. (2012) *Sensorimotor Cognition and Natural language Syntax,* MIT Press
53. Lakoff, G. (2014) Mapping the brain's metaphor circuitry: metaphorical thought in everyday reason. *Front. Hum. Neurosci.* 9, 958
54. Evans, N. and Levinson, S.C. (2009) The myth of language universals: language diversity and its importance for cognitive science. *Behav. Brain Sci.* 32, 429–492
55. Tomasello, M. (2009) Universal grammar is dead. *Behav. Brain Sci.* 32, 470
56. Wiessner, P.W. (2014) Embers of society: firelight talk among the Ju/'huansi Bushmen. *Proc. Natl Acad. Sci. U. S. A.* 111, 14027–14035
57. Harari, Y.N. (2014) *Sapiens: A Brief History of Humankind,* Harvill Secker
58. Grice, H.P. (1989) *Studies in the Ways of Words,* Cambridge University Press
59. Sperber, D. and Wilson, D. (2002) Pragmatics, modularity and mind-reading. *Mind Lang.* 17, 3–23
60. Scott-Phillips, T. (2015) *Speaking Our Minds: Why Human Communication is Different, and How Language Evolved to Make it Special,* Palgrave Macmillan
61. Premack, D. and Woodruff, G. (1978) Does the chimpanzee have a theory of mind? *Behav. Brain Sci.* 4, 515–526
62. Penn, D.C. *et al.* (2008) Darwin's mistake: explaining the discontinuity between human and nonhuman minds. *Behav. Brain Sci.* 31, 108–178
63. Call, J. and Tomasello, M. (2008) Does the chimpanzee have a theory of mind? 30 years later. *Trends Cogn. Sci.* 12, 187–192
64. Krupenye, C. *et al.* (2016) Great apes anticipate that other individuals will act according to false beliefs. *Science* 354, 110–116
65. Wimmer, H. and Perner, J. (1983) Beliefs about beliefs: representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition* 13, 103–128
66. Rosati, A.G. and Santos, L.R. (2016) Spontaneous metacognition in rhesus monkeys. *Psychol. Sci.* 27, 1181–1191

67. Peer, M. *et al.* (2015) Brain system for mental orientation in space, time, and person. *Proc. Natl Acad. Sci. U. S. A.* 112, 11072–11077
68. Buckner, R.L. *et al.* (2008) The brain's default network: anatomy, function, and relevance to disease. *Ann. N. Y. Acad. Sci.* 1124, 1–38
69. Vincent, J.L. *et al.* (2007) Intrinsic functional architecture in the anaesthetized monkey brain. *Nature* 447, 83–86
70. Lu, H. *et al.* (2012) Rat brains also have a default mode network. *Proc. Natl Acad. Sci. U. S. A.* 109, 3979–3984
71. Darwin, C. (1871) *The Descent of Man and Selection in Relation to Sex.* (2nd edn), Appleton
72. Savage-Rumbaugh, S. *et al.* (1998) *Apes, Language and the Human Mind,* Oxford University Press
73. Kaminski, J. *et al.* (2004) Word learning in the domestic dog: evidence for 'fast mapping'. *Science* 304, 1682–1683
74. Pilley, J.W. and Reid, A.K. (2011) Border collie comprehends object names as verbal referents. *Behav. Proc.* 86, 184–195
75. Falk, D. (2016) Evolution of brain and culture: the neurological and cognitive journey from Australopithecus to Albert Einstein. *J. Anthropol. Sci.* 94, 99–111
76. Everaert, M.B.H. *et al.* (2015) Structures, not strings: linguistics as part of the cognitive sciences. *Trends Cogn. Sci.* 19, 729–743
77. Pfenning, A.R. *et al.* (2014) Convergent transcriptional specializations in the brains of humans and song-learning birds. *Science* 346, 1256846
78. Emmorey, K. (2002) *Language, Cognition, and Brain: Insights from Sign Language Research,* Erlbaum
79. de Condillac, E.B. (1971) *An Essay on the Origin of Human Knowledge: Being a Supplement to Mr. Locke's Essay on the Human Understanding, A Facsimile Reproduction of the 1756 Translation by T. Nugent of Condillac's 1747 Essay,* Scholars' Facsimiles and Reprints
80. Rousseau, J.-J. (1782) *Essai sur l'Origine des Langues.* Geneva
81. Vico, G. (1744/1953) La Scienza Nova, Laterza
82. Hewes, G.W. (1973) Primate communication and the gestural origins of language. *Curr. Anthropol.* 14, 5–24
83. Kimura, D. and Archibald, Y. (1974) Motor functions of the left hemisphere. *Brain* 97, 337–350
84. Armstrong, D.F. *et al.* (1995) *Gesture and the Nature of Language,* Cambridge University Press
85. Rizzolatti, G. and Arbib, M.A. (1998) Language within our grasp. *Trends Neurosci.* 21, 188–194
86. Corballis, M.C. (2002) *From Hand to Mouth: The Origins of Language,* Princeton University Press
87. Rizzolatti, G. and Sinigaglia, C. (2006) *Mirrors in the Brain: How Our Minds Share Actions and Emotions,* Oxford University Press
88. Pollick, A.S. and de Waal, F.B.M. (2007) Ape gestures and language evolution. *Proc. Natl Acad. Sci. U. S. A.* 104, 81–89
89. Tomasello, M. (2008) *The Origins of Human Communication,* MIT Press
90. Arbib, M.A. (2012) *How the Brain Got Language: The Mirror System Hypothesis,* Oxford University Press
91. Gardner, R.A. and Gardner, B.T. (1969) Teaching sign language to a chimpanzee. *Science* 165, 664–672
92. Hobaiter, C. and Byrne, R.W. (2011) Serial gesturing by wild chimpanzees: its nature and function for communication. *Anim. Cogn.* 14, 827–838
93. Kimura, D. (1973) Manual activity during speaking.1. Right-handers. *Neuropsychologia* 11, 45–50
94. Goldin-Meadow, S. and Brentari, D. (2015) Gesture, sign and language: the coming of age of sign language and gesture studies. *Behav. Brain Sci.* Published online October 5, 2015. http://dx.doi.org/10.1017/S0140525X15001247
95. Hilverman, C. *et al.* (2016) Hippocampal declarative memory supports gesture production: evidence from amnesia. *Cortex* 85, 25–36
96. Kendon, A. (2011) Vocalisation, speech, gesture, and the language origins debate. *Gesture* 13, 349–370
97. McNeill, D. (2012) *How Language Began: Gesture and Speech in Human Evolution,* Cambridge University Press
98. Corballis, M.C. (2014) The word according to Adam: The role of gesture in language evolution. In *From Gesture in Conversation to Visible Action as utterance: Essays in Honor of Adam Kendon* (Seyfeddinifur, M. and Gullberg, M., eds), pp. 177–197, John Benjamins
99. Kohler, E. *et al.* (2002) Hearing sounds, understanding actions: action representation in mirror neurons. *Science* 297, 846–848
100. Haberling, I.S. *et al.* (2016) Language, gesture, and handedness: evidence for independent lateralized networks. *Cortex* 82, 72–85
101. Donald, M. (1991) *Origins of the Modern Mind,* Harvard University Press
102. Burling, R. (2005) *The Talking Ape,* Oxford University Press
103. MacNeilage, P.F. (2008) *The Origin of Speech,* Oxford University Press
104. Burling, R. (1999) Motivation, conventionalization, and arbitrariness in the origin of language. In *The Origins of Language: What Human Primates can Tell Us* (King, B.J., ed.), pp. 307–350, School of American Research Press
105. Studdert-Kennedy, M. (2005) How did language go discrete? In *Language Origins: Perspectives on Evolution* (Tallerman, M., ed.), pp. 48–67, Oxford University Press
106. Bass, A.H. and Chagnaud, B.P. (2012) Shared developmental and evolutionary origins for neural basis of vocal–acoustic and pectoral–gestural signaling. *Proc. Natl Acad. Sci. U. S. A.* 109, 10677–10684
107. Gentilucci, M. *et al.* (2001) Grasp with hand and mouth: a kinematic study on healthy subjects. *J. Neurophysiol.* 86, 1685–1699
108. McNeill, D. (1985) So you think gestures are nonverbal? *Psychol. Rev.* 92, 350–371
109. Petrides, M. and Pandya, D.N. (2009) Distinct parietal and temporal pathways to the homologue of Broca's area in the monkey. *PLoS One* 7, e1000170
110. Corballis, M.C. (2012) How language evolved from manual gestures. *Gesture* 12, 200–226
111. McGurk, H. and MacDonald, J. (1976) Hearing lips and seeing voices. *Nature* 264, 746–748
112. Ramachandran, V.S. and Hubbard, E.M. (2001) Synaesthesia – a window into perception, thought and language. *J. Conscious. Stud.* 8, 3–34
113. Blasia, D.E. *et al.* (2016) Sound–meaning association biases evidenced across thousands of languages. *Proc. Natl Acad. Sci. U. S. A.* 103, 10818–10923
114. Corballis, M.C. (2004) The origins of modernity: was autonomous speech the critical factor? *Psychol. Rev.* 111, 543–552