

Cognitive-emotional interactions

How emotions colour our perception of time

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Our sense of time is altered by our emotions to such an extent that time seems to fly when we are having fun and drags when we are bored. Recent studies using standardized emotional material provide a unique opportunity for understanding the neurocognitive mechanisms that underlie the effects of emotion on timing and time perception in the milliseconds-to-hours range. We outline how these new findings can be explained within the framework of internal-clock models and describe how emotional arousal and valence interact to produce both increases and decreases in attentional time sharing and clock speed. The study of time and emotion is at a crossroads, and we outline possible examples for future directions.

Introduction

Time and emotion are inextricably linked by the rhythm and tempo of a myriad of external and internal events, which comprise music, film, dance, sports, courtship, social conflict and everyday activities. Although many studies have shown that humans, like other animals, are able to measure the passage of time accurately in the milliseconds-to-hours range, how our sense of time is altered

Glossary

Circadian timing: time is measured by biological oscillations or cycles that can range from milliseconds to years. Circadian rhythms are defined by oscillations that last approximately a day (i.e. 24 h) due to the internalization of the Earth's light-dark cycle by molecular mechanisms expressed in a variety of tissues. Circadian rhythms are a fundamental property of all higher forms of life and, in mammals, are regulated by a master clock in the suprachiasmatic nucleus. Although dependent upon light entrainment, the circadian clock is quite robust and can free run at high precision for several months without external correction [1,2,16].

Embodied emotions: refer to the fact that perceiving another person's emotional expressions and thinking about emotion automatically produce 'perceptual, somatovisceral, and motoric re-experiencing (collectively referred to as "embodiment") of the relevant emotion in one's self' (Ref. [54], pp. 1002).

Emotion: a response of the whole organism, involving (i) physiological arousal, (ii) expressive behaviors and (iii) conscious experience. Emotion might occur before cognition as the pathways from eyes, ears and nose bypass the cortex and go, by way of the

thalamus, directly to the amygdala. Emotional intensity refers to the strength of an emotional stimulus, whereas emotional valence refers to whether the stimulus is positive or negative. Functional neuroimaging and lesion-based experiments have demonstrated the crucial role of the amygdala in recognition of certain emotions signaled by sensory stimuli (notably fear and anger in facial expressions or cues predicting electric shock) that might be independent of the intensity of the stimulus [7,20]. One proposal is that fear and/or anger biases attention towards threat-related stimuli by enhancing the output from an amygdala-centered 'pre-attentive threat evaluation mechanism' [48].

Expressed emotions: refer to the emotional responses to directly experienced emotional stimuli. In recent theories of embodied cognition, perceiving a threatening object/event (e.g. a snake) produces fear-related emotional states and remembering this object/event activates the originally experienced emotional states [54-56].

Horizontal shifts: in timing functions occur when the entire sigmoidal-shaped (bisection procedure) or Gaussian-shaped (peak-interval procedure) function relating the probability of a response to signal duration is shifted to the left (increase in clock speed) or to the right (decrease in clock speed) relative to control conditions. These horizontal shifts lead to changes in the point of subjective equality (PSE) for the bisection procedure and changes in peak time for the peak-interval procedure. In contrast, vertical shifts in timing functions occur when the functions are flattened and shifted either up or down while maintaining the same PSE or peak time values [17,26].

Interval timing: usually defined at the discrimination of durations in the seconds-to-minutes range, but can be extended to both shorter (e.g. milliseconds) and longer (e.g. hours) ranges. Interval timing is less precise than circadian timing, but has an advantage in increased flexibility in that it can run, stop/pause and reset on command [1,2,16]. Although the suprachiasmatic nucleus appears unnecessary for interval timing, time of day effects have been observed for the timing of auditory and visual signals in the seconds-to-minutes range [1,21]. To date, five main types of cognitive and affective factors have been identified that influence interval timing: attention, modality, arousal, affective valence and linguistic factors [8-15,18-26].

Prospective timing: refers to situations in which the participant is aware ahead of time that the duration of an event will be relevant to guiding behavior, whereas **retrospective timing** occurs in situations where the participant is unaware of the importance of the duration of an event before its occurrence and must reconstruct the temporal sequence and durations of events based upon memory. Most research conducted on timing and time perception involves prospective timing and includes the study of a specialized timing module or internal clock [1,2].

Scalar property/Weber's law: one of the hallmark signatures of interval timing that describes the linear relationship between target durations and the standard deviation of duration judgments, indicating that variability in timing behavior grows proportional to the mean of the interval being estimated. In this sense, duration discrimination is relative rather than absolute, that is time perception is like a rubber band in that it can be stretched to produce time-scale invariance across different durations [1,2].

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by our emotions is not well understood [1–3]. As far back as 1890, William James wrote: ‘our feeling of time harmonizes with different mental moods’ and inquired as ‘to what cerebral process is the sense of time due?’ [4]. More recently, Paul Fraisse has argued that timing and time perception not only involve cognition but are also intimately connected to our emotional life [5]. However, whereas the investigation of emotion-related topics is growing rapidly [6,7], analysis of the complex interplay between emotion and interval timing remains relatively rare [8]. Furthermore, the pioneering studies on time and emotion have frequently used nonstandardized emotional stimuli, which make their findings inconsistent and difficult to interpret [9–15]. However, several recent studies have used standardized emotional material, which has allowed us to gain a better understanding of the psychological mechanisms underlying time distortions in response to emotion. This article discusses the results of these new studies and integrates them with internal-clock models of interval timing (Box 1).

Explanations of time distortions within the context of internal-clock models

Inspection of internal-clock models (Box 1) suggests that variations in our feeling of prospective time are caused by different mechanisms – attentional time sharing, clock speed and memory distortion – occurring at different levels of the processing of temporal information. It has been proposed that these different mechanisms result in distinct patterns of timing behavior [1,2,16,17].

There is now ample evidence to indicate that when non-temporal and/or emotional events capture attention, processing resources can be diverted away from the timer. This causes the subjective experience of time to be shorter than it really is [18–20]. This shortening effect can be explained by a loss of pacemaker pulses due to the effects of attention on the switch. Re-direction of attention can increase the latency of switch closure and inattention can cause the switch to fluctuate between the closed and the opened states [21–23].

Conversely, the subjective experience of time is lengthened (durations seem longer than normal) by increases in

Box 1. Internal-clock models of interval timing

As illustrated in Figure 1, cognitive psychologists have used an information-processing (IP) framework involving clock, memory and decision stages to study the ability of humans and other animals to time events prospectively in the milliseconds-to-hours range [34]. According to these models, the raw material for time representation comes from a clock stage consisting of a pacemaker that emits pulses at a given rate, a switch controlling how the pulses are gated and an accumulator in which the number of pulses is stored during the event(s) being timed. At the onset of the event to be timed, the switch closes, thus allowing the pulses generated by the pacemaker to enter the accumulator. At the offset of this event, the switch opens and stops the pulse transfer. The accumulator thus achieves a monotonic integration of the pulses with the duration: the longer the stimulus duration, the more pulses are accumulated, and the longer the duration is judged to be. According to these information-processing models, temporal judgments also depend on memory and decision stages. The current duration measured by the accumulator is compared, using comparison rules, with a sample drawn from a distribution of duration values stored in reference memory to determine whether to respond.

Although IP models have become highly influential within the field of interval timing, researchers are becoming increasingly aware that these accounts lack sufficient neurological specification to isolate interval-timing processes from other cognitive functions, such as attention, memory and decision making [60]. Consequently, a variety of neurobiological frameworks for studying timing in the seconds-to-hours range have been developed to complement these IP models. The most prominent of these models, referred to as the striatal beat-frequency (SBF) model [1,60–62], has been applied to several properties of interval timing, including the effects of arousal/emotion on clock speed. In the SBF model as illustrated in Figure 2, the oscillatory activity of a subset of cortical neurons is synchronized with the onset and offset of a relevant stimulus. When this stimulus is timed, spiny neurons in the striatum serve as coincident detectors of specific patterns of oscillatory input from the cortex. In this way, the striatum is able to ‘read’ the temporal code provided by oscillating neurons in the cortex, and its synaptic connections are strengthened or weakened depending upon the occurrence of feedback and resulting dopaminergic input from the substantia nigra. Clock speed is altered in this system by the dopaminergic modulation of the cortical oscillation frequencies that are being input to the striatum. Although a growing body of evidence points towards the selective involvement of cortico-striatal circuits in timing and time perception [50,63,64], there remains considerable debate about how these circuits encode and decode time [58,65–68].

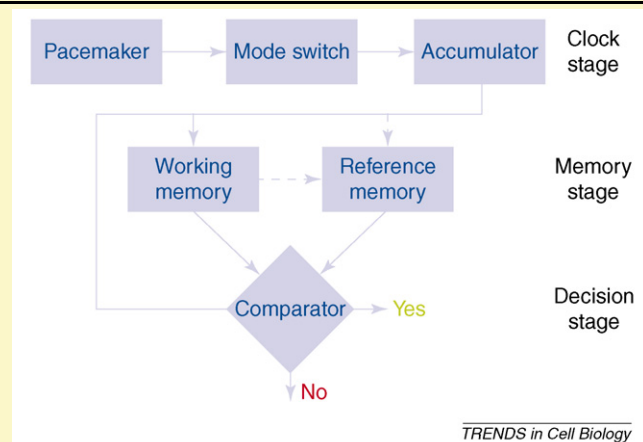


Figure 1. The information-processing model. Adapted, with permission, from Ref. [34].

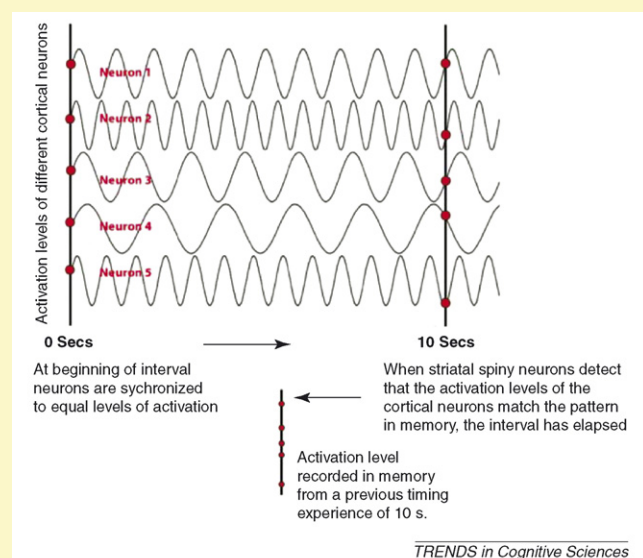


Figure 2. The striatal beat-frequency model. Adapted, with permission, from Ref. [62].

arousal. According to the internal-clock models, increased arousal accelerates the pacemaker, thus causing more pulses to accumulate within the same physical unit of time. This sensitivity of clock speed to arousal has been documented in studies that have presented a repetitive series of auditory clicks or visual flickers designed to increase arousal before the timed event (for example, see Ref. [24]), altered body temperature to manipulate arousal through metabolic processes [25], or administered drugs that modulate arousal by altering the effective levels of dopamine (DA) in the brain [26]. For example, the administration of psychostimulants, such as cocaine and methamphetamine, increases arousal and produces an overestimation of durations, which is characteristic of an increase in clock speed, whereas the administration of antipsychotics, such as haloperidol and pimozide, decreases arousal and produces an underestimation of durations, as if the internal clock was running slower [1,17].

Other aspects of the internal-clock model can also be distinguished by their pharmacological profiles. For example, whereas DA primarily affects clock speed, cholinergic drugs have their primary effects on memory for time [17]. The release of noradrenaline, which affects attentional processes, appears to impact time perception by modifying the latency to close or open the switch [27]. The latency to begin timing (primarily mediated by noradrenaline) versus the speed of the clock once timing has begun (primarily DA-mediated) can also be differentiated behaviorally, provided that several durations are used in the same experiment [28,29]. The clock-speed effect is proportional to the durations being timed, that is increasing the rate of pulse accumulation leads to larger and larger overestimations as the target duration of the interval being timed increases. By contrast, effects on the latency to initiate and/or terminate the timing process involve the closure or opening of the switch that allows pulses to be transferred to the accumulator. This would be expected to produce an absolute effect on the horizontal placement of psychophysical functions regardless of the duration being timed, that is decreasing the latency to start the clock will shift all timing functions to the left by an absolute (e.g. 800 ms) rather than a proportional (e.g. 20%) amount of time.

Clock-speed effects can also be distinguished from modifications of the memory-translation constant related to effects on encoding and memory content [1]. Arousal effects on clock speed appear to be immediate, but relatively transient in the face of feedback, because the participants are able to recalibrate their timing functions with continued training under conditions in which clock speed is modified. By contrast, distortions in the content of temporal memory emerge gradually as new clock readings are translated and encoded into memory. This memory 'corruption' appears to be relatively permanent even in the face of corrective feedback due to the multiplicative distortion during translation [17,30].

To summarize, the direction, magnitude, speed of emergence and robustness of temporal distortions vary as a function of which specific mechanisms (e.g. attention, clock or memory) are affected. The main question is to determine which of these mechanisms (if any) are involved in the

effect of emotion on time perception as a function of the emotional stimuli used.

The effect of emotional stimuli (sounds and pictures) rated for valence and arousal on timing and time perception

As mentioned earlier, a consistent picture of the effects of emotion on time perception has been difficult to discern, in part because most early studies used idiosyncratic emotional stimuli, causing problems for interpretation and generalization. Recently, several studies have examined this issue using standardized stimulus sets, such as the International Affective Digital Sounds system (IADS) [31] and the International Affective Picture System (IAPS) [32]. We focus on these studies here, with particular attention to the effects of valence (unpleasant/pleasant) and arousal (low/high).

Using the IADS, Noulhiane *et al.* [33] recently found that emotional sounds were judged longer than neutral sounds, regardless of arousal, for durations up to 4 s. Noulhiane *et al.* interpreted these intriguing data within the context of scalar timing theory [34] and proposed that emotion-induced activation temporarily increases the speed of an internal clock (thereby leading to longer perceived durations) until clock speed returns to baseline after 3-4 s. This study is among the first to report that the effects of emotion on time perception may be relatively short-lived and are maximal for sound durations around 2 s. Of particular interest is their report that negative sounds were judged to be longer than positive ones, suggesting that negative stimuli produce a greater increase in arousal. In addition, their finding that high-arousing stimuli were perceived to be shorter than low-arousing stimuli is consistent with models of interval timing that use attention to modify the allocation of processing resources to temporal versus non-temporal factors [18,19].

Angrilli *et al.* [35] used the IAPS stimuli to investigate the effects of valence and arousal on time perception and used converging measures of attention and physiological arousal to validate the source of these effects. The pattern of results found with the IAPS appeared complex: there was no main effect of arousal or valence, but there was a significant interaction between these two dimensions. In the high-arousal condition, the duration of negative pictures (baby with eye tumor, smashed head) was overestimated, whereas that of positive pictures (erotic scenes) was underestimated. In the low-arousal condition, negative pictures (dead cow, rat in the dirt) were underestimated and positive pictures (pet dogs, happy baby) were overestimated. This opposite effect of valence as a function of the arousal level suggests that two different mechanisms are triggered by arousal levels: a controlled-attention mechanism for low arousal and an automatic mechanism related to motivational-survival systems for high arousal.

In the case of low arousal, as ascertained by heart rate, negative pictures elicited a stronger orienting reaction than did positive pictures; more attention was paid to negative than to positive pictures and the former was judged as being shorter. In addition, skin conductance measures that are strongly correlated with changes in emotion increased with the level of arousal. At the same level of high arousal, it has

been proposed that emotions are organized around two motivational systems: one defensive and one appetitive. As stated by Bradley [36], the defensive system is primarily activated in threatening contexts, and a basic behavioral repertoire is built on withdrawal, escape and attack. Conversely, the appetitive system is activated in contexts, including sustenance, procreation and nurturing, with a basic behavioral repertoire of ingestion, copulation and care giving. Consequently, high-arousal/unpleasant conditions, which require defensive motor behaviors, involve the ability to produce a rapid reaction (attack, escape). This causes autonomic nervous system activity (e.g. blood pressure increases, pupils dilate, muscles contract) that would be associated with a speeding up of the clock. Indeed, when the passage of time is experienced as passing faster, the readiness for action is more rapid. This might explain why Angrilli *et al.* [35] found a temporal overestimation of high-arousal/unpleasant pictures for the 2 s duration, but not for the longer durations. As suggested by Angrilli and colleagues, attention-related mechanisms presumably prevail at longer durations because of the expected diminution of the autonomic response within a few seconds of the stimulus presentation.

Taken together, the findings of Angrilli *et al.* [35] and Noulhiane *et al.* [33] emphasize the importance in time studies of investigating the temporal dynamic of emotions, because the effects of emotion might change in a systematic fashion with the passage of time. These data also suggest that negative images in the high arousal condition activate the defensive system. Consequently, in comparison to

positive images, the internal clock will run relatively faster under high arousal conditions for negative images and lead to their overestimation. By contrast, negative pictures in the low arousal condition will be underestimated because the capture of attention by those pictures means that less attention will be allocated to the timing system and, therefore, fewer pulses accumulated. In other words, under low arousal conditions, the capture of attention by the features that define the emotional valence of the stimulus diverts processing resources away from the timing system itself [18,19].

Time perception thus appears to be a sensitive index of the basic function of emotions. However, a description of emotional space involving only two major dimensions (valence and arousal) is insufficient to account for the different adaptive functions of emotions [37], and their consequences for temporal processing. For example, given the same high-arousal level, is the magnitude of time distortion similar for pictures that elicit fear to that for pictures that elicit disgust? Consistent with theories suggesting a close relationship between emotion and action readiness [38,39], recent studies conducted by Droit-Volet and her colleagues ([40–44] and (S. Gil and S.D.-V., unpublished)) on the processing of emotional facial expression suggest that the urgency of action for incoming events is one of the crucial factors affecting our perception of time.

Time and facial expression

Faces are often used in studies on emotions, because perceiving other people's emotional states is essential for

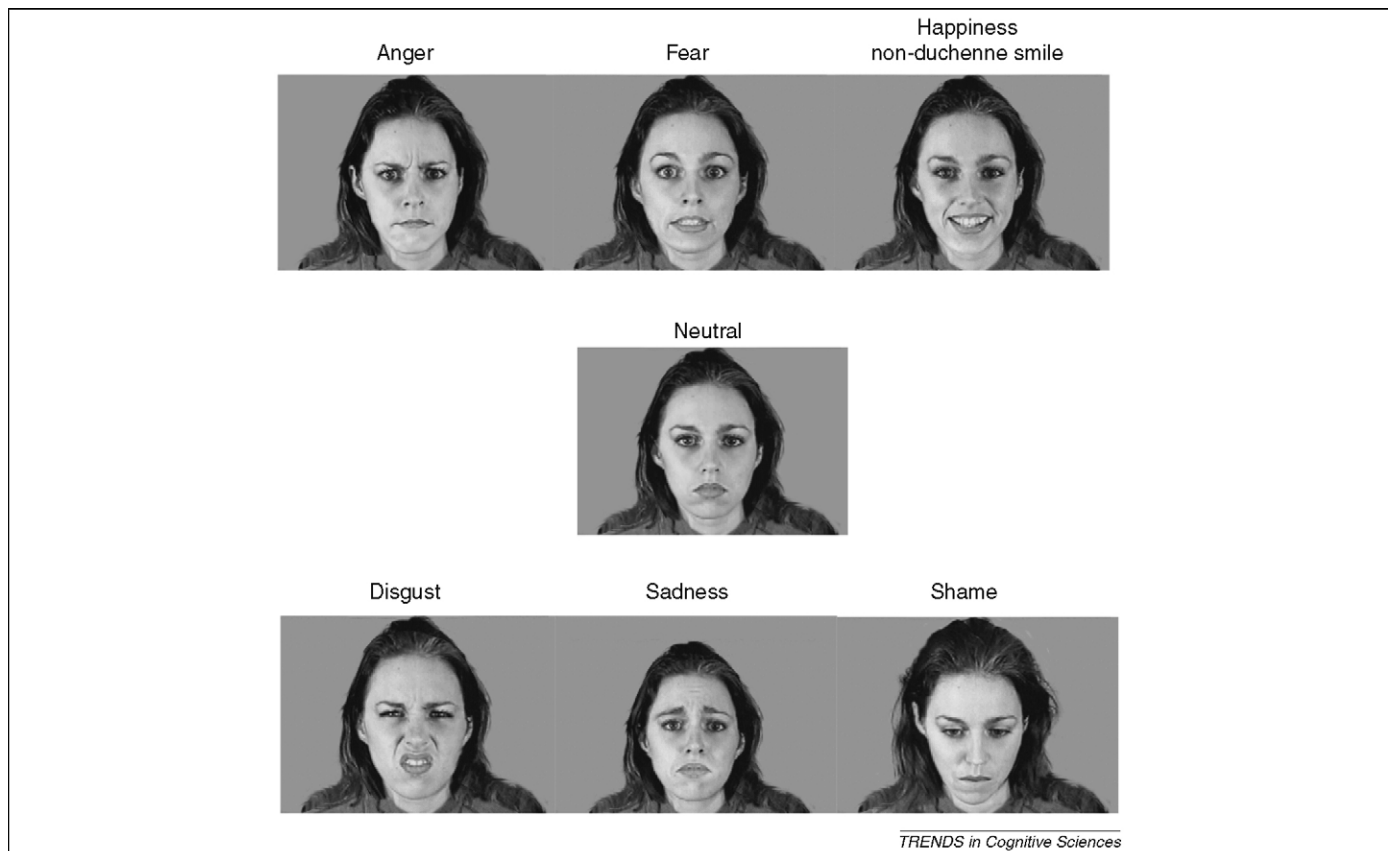


Figure 1. An example of one of the female faces with the neutral expression (center) and the six emotions tested (upper and lower rows). Adapted, with permission, from (S. Gil and S.D.-V., unpublished).

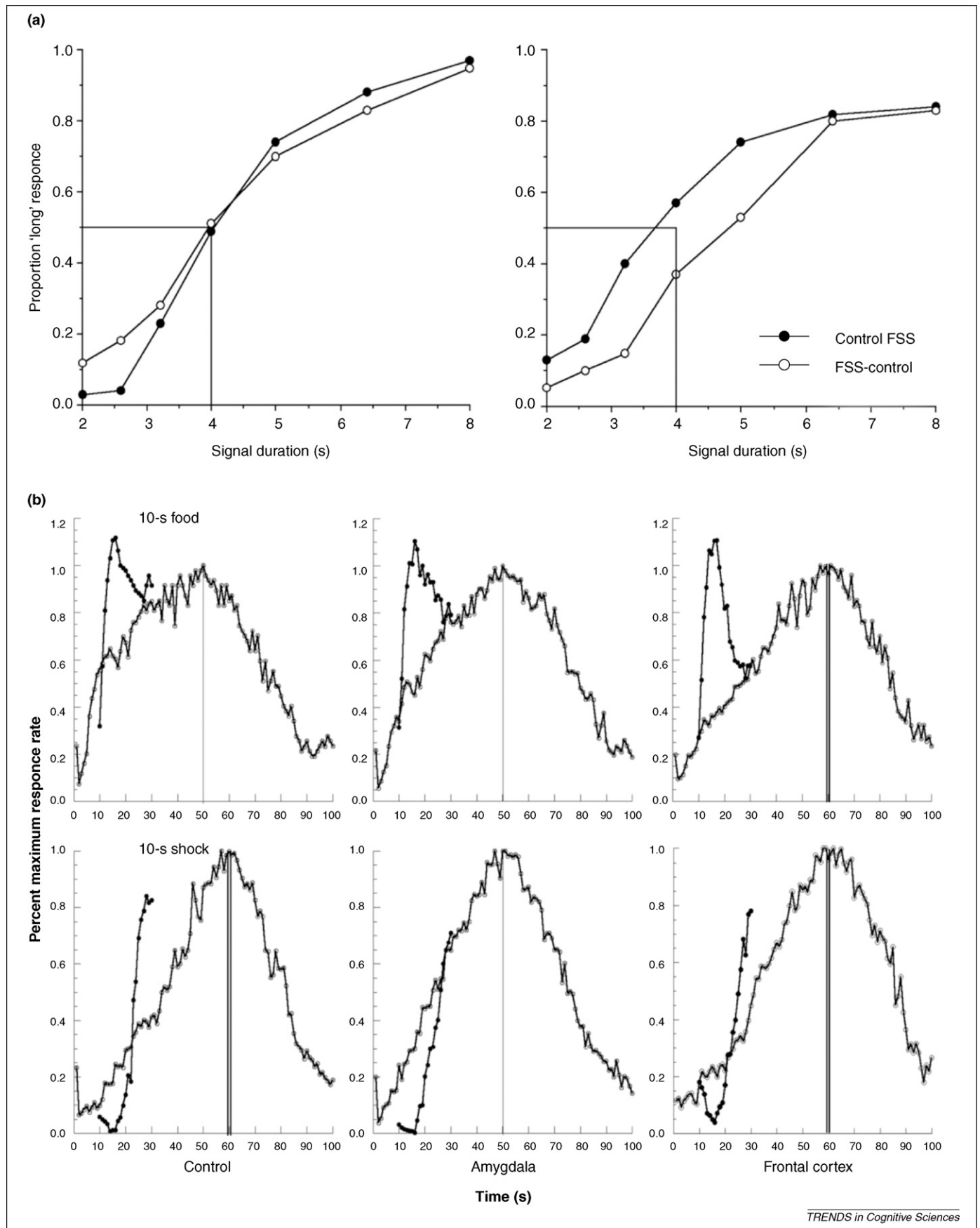


Figure 2. (a) Median proportion 'long' response as a function of signal duration during seven-signal duration bisection training (left panel) and testing (right panel). Open circles indicate rats trained under continuous footshock stress (FSS) and tested without the stressor (control); closed circles indicate rats trained without the stressor and tested under continuous FSS. Adapted, with permission, from Ref. [26]. (b) The role of the amygdala in the ability to divide attention between two signals and time them simultaneously was investigated under both appetitive and aversive conditions using peak-interval procedures. Failure to divide attention results in the sequential

the determination of appropriate behavior in social interactions [45]. Droit-Volet *et al.* [40] investigated how the perception of facial expressions of emotion affects our experience of time by using the duration bisection task [46,47]. In this task, participants were trained to discriminate between two standard durations, that is a short (400 ms) and a long duration (1600 ms), presented in the form of a pink oval. They were then required to classify comparison durations (equal to the standards or of intermediate value) as being more similar to the short or to the long standard durations. These comparison durations were presented in the form of faces with three different emotions (anger, happiness or sadness) and a neutral-baseline expression (as shown in Figure 1). The results showed a significant leftward horizontal shift of the bisection function for angry faces compared with the neutral faces; indicating that the presentation duration of angry faces was judged to be longer than for neutral faces. By contrast, sensitivity to time (the consistency with which participants judged a particular intermediate duration as either 'short' or 'long') did not change with the facial expression. Thus, viewing angry faces distorts time perception, such that event durations are judged to be longer than normal. These findings are consistent with those previously reported by Schiff and Thayer [10; these results showed that a period of time spent in an eye-contact task was judged longer with an angry than with a friendly partner. Further analyses of the data indicated that this effect was multiplicative (i.e. overestimations were greater for longer durations), indicating that the lengthening of time estimates resulted from an arousal-related acceleration of clock speed. Furthermore, this temporal bias with angry faces occurs at an early age (3 years), and does not change across different stages of development [42], which suggests that it reflects a basic phenomenon of adaptation in social interactions.

Seeing an angry face might present a threatening situation because the partner could become aggressive. In other threatening situations, it has been systematically shown that humans and other animals tend to overestimate the duration of events. For example, rats show a similar horizontal shift to the left in bisection functions when electric footshocks are administered during a test phase [26]. This effect appears to be due to increased arousal, because methamphetamine produces similar results (Figure 2a – left-hand panel). By contrast, another group of rats trained to time under the stressful footshock condition exhibited a shift to the right in their timing functions when the footshock was discontinued during test sessions; this is a similar result to that observed after haloperidol injections or the withdrawal of methamphetamine [26] (Figure 2a – right-hand panel). In human

adults, Langer *et al.* [13] have also shown that blindfolded participants overestimated time more when moving on a platform towards a drop (danger) than when moving away from it (safety). Furthermore, the imminence of the danger increased their temporal overestimation, which was greater when they stopped at 15 rather than 20 feet from the drop. In the same manner, Watts and Sharrock [14] reported that a 45 s period spent watching a spider is judged longer by arachnophobic participants than by other non-arachnophobic individuals.

In summary, there is a growing body of evidence indicating that in threatening situations, for example when confronted with angry faces or electric footshock, there is an increase in arousal that leads to acceleration in clock speed and, in some cases, increased attention to the duration dimension of those stimuli associated with the fear-provoking event (i.e. more attention is directed toward timing the specific events associated with the fear eliciting stimulus, and less attention is directed toward the timing of other neutral or appetitive events occurring within the same context). Impairments in simultaneous temporal processing resulting from selective attention to the fear-provoking stimulus can be abolished by inactivation of the amygdala, as demonstrated by Meck and MacDonald [20] and illustrated in Figure 2b. The similar patterns of temporal bias obtained in different threatening contexts in both rats and humans at different ontogenetic stages suggest that these responses to fear-eliciting stimuli reflect an automatic, unconscious program of responses to danger, as described by evolutionary theories of anxiety and emotion [48].

Although arousal is clearly a very important factor in the effects of emotion on time perception, it is not the only factor. Droit-Volet and colleagues [40] found that angry faces produced the most temporal bias, and fearful faces were a close second (S. Gil and S.D.-V., unpublished) (Figure 3), followed by happy and then sad faces. These results are consistent with the idea that anger tends to be especially arousing. However, for other facial expressions, such as disgust or shame, the temporal pattern was different. Gil and Droit-Volet (unpublished) observed no change in bisection functions for disgust, and a shift to the right for shame, which indicates a temporal underestimation. This result is expected because shame, which is a social-moral emotion, captures attention by a reflexive activity of self-awareness that directs attention away from the stimulus to be timed [49]. The redirection of attention would lead to a loss of pulse accumulation and lower clock readings [19]. To summarize, for the short durations tested, these results suggest that the internal clock speeds up when the emotion perceived in the other individual involves readiness for

processing of the signals and the suspension of timing for one of the signals, while the other signal is selectively attended to. The effects of amygdala or frontal cortex lesions were compared in rats trained to time both a 50 s visual signal paired with food and an embedded 10 s auditory signal that was paired with either food (top row) or footshock (bottom row). Columns (left to right) represent groups of rats with control surgeries, radiofrequency lesions of the amygdala, or aspiration lesions of the frontal cortex, respectively. The 10 s auditory signals (filled circles) were randomly embedded within the 50 s visual signals (open circles) and are plotted at their average time of occurrence. Single vertical lines indicate when the peak time was at the programmed time of reinforcement for the visual signal (e.g. 50 s) and double vertical lines indicate when the peak time was shifted to the right by 10 s (e.g. 60 s) due to the effect of selective attention. When both signals were paired with food, control and amygdala-lesioned rats were able to divide attention and time both signals simultaneously, whereas when the embedded auditory signal was paired with footshock, control rats were impaired in their ability to divide attention and were able to time only one signal at a time. By contrast, inactivation of the amygdala blocked this fear-related impairment and allowed rats to time both signals simultaneously, whereas rats with frontal cortex lesions demonstrated sequential processing under all conditions. These results support the proposal that the frontal cortex exerts primary control over the allocation of attentional resources but that, under stressful conditions, the amygdala is crucial for the emergence of fear-evoked increments in selective attention leading to deficits in simultaneous temporal processing. Adapted, with permission, from Ref. [20].

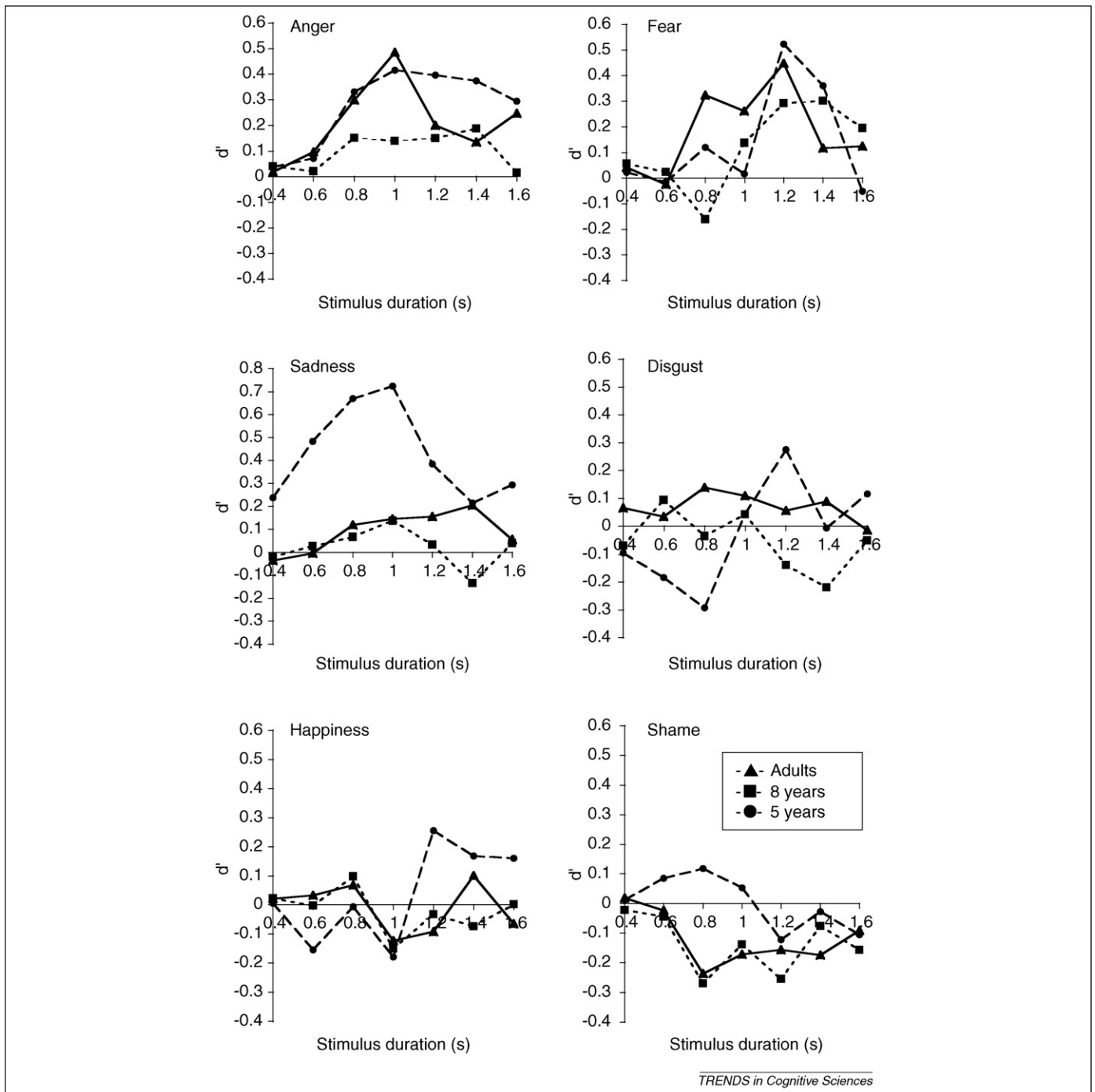


Figure 3. The effect of emotional faces on time perception in children and adults. In a duration bisection task, the participants had to categorize as 'short' or 'long' the presentation durations (between 400 and 1600 ms) of faces expressing a specific emotion or neutrality. The panels show the results found by Gil and Droit-Volet (unpublished) with children aged 5 and 8 years old, as well as with adults, when the participants were presented with faces expressing neutrality and a specific emotion in the same session: anger, fear, sadness, disgust, happiness (non-Duchenne smile) or shame. d' is the difference between the proportion of 'long' responses for an emotional facial expression and that for the neutral expression. A d' greater than zero indicates that the emotional expression is overestimated compared with the neutral expression, and a d' shorter than zero indicates that the emotional expression is underestimated compared with the neutral expression. The results are consistent with those found by Droit-Volet *et al.* [40]. They showed that anger and fear produced an overestimation of time with a magnitude that did not vary with age, except for the angry faces that were relatively less overestimated in the 8-year-olds. To a lesser extent, the facial expression of sadness also produced an overestimation of time, although the 5-year-olds overreacted to sadness compared with the older participants. The happy faces also produced an overestimation of time, but only with the Duchenne smile (shown in Figure 4), and not with the non-Duchenne smile. By contrast, the disgusted faces did not produce any time distortions. Contrary to the other facial emotions, shame produced an underestimation of time, except in the youngest children. Further analyses revealed that the temporal overestimation was linked to the emotional expressions that increased the level of arousal, thus in turn increasing the rate of the pacemaker of an internal clock. By contrast, the temporal underestimation was linked to the attention-related processes, the emotional stimulus attracting attention away from the processing of temporal information. Adapted, with permission, from Ref. [40] and (S. Gil and S.D.-V., unpublished).

action, and does so to a greater extent in the case of urgent action (angry faces). It is thus reasonable to suppose that the urgency to produce an immediate action (avoidance/withdrawal) is higher in the presence of an angry individ-

ual than of a disgusted individual. Recent studies have shown that dopaminergic function in the basal ganglia plays an important role in the efficiency of timing and motor output [50] as well as in the processing of anger [51].

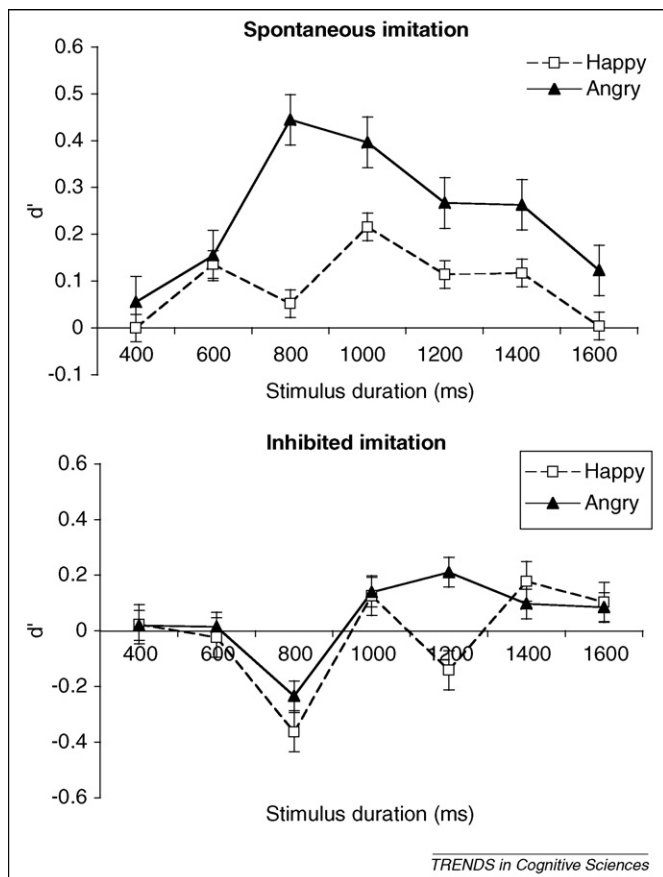


Figure 4. The effect of emotional faces on time perception in adults. In this duration bisection task, the participants had to categorize as more similar to a 'short' or a 'long' standard duration, the presentation duration (between 400 and 1600 ms) of faces with two different emotional expressions (anger and happiness) and a neutral-baseline expression. The figures show the d' -score plotted against the stimulus durations. The d' is the difference between the proportion of 'long' responses (stimulus duration judged as more similar to the 'long' than to the 'short' standard) for an emotional facial expression and that for the neutral expression. A d' greater than zero indicates that the emotional expression is overestimated compared with the neutral expression, and a d' shorter than zero indicates that the emotional expression is underestimated compared with the neutral expression. The results showed that, in the spontaneous imitation condition (upper panel), the presentation duration of angry and happy faces was significantly overestimated, and that this overestimation was greater for anger than for happiness. In the inhibited imitation condition (lower panel), the d' was close to zero indicating no time distortion. Adapted, with permission, from Ref. [41].

This finding suggests a common arousal-based mechanism for reaction time, probably related to the general role of DA on the rapid access of relevant incoming events to timing and motor control centers [48,52].

Time and embodied emotion

How can the perception of an emotion, such as anger, expressed by another individual accelerate our internal clock? The expression of an emotion might elicit a different emotion in an observer. For example, an expression of anger is more likely to elicit fear than anger in the observer [53]. Consequently, it might be fear, not simply the perception of anger, that increases clock speed. However, various lines of evidence indicate that there is a close connection between the neural substrates of emotion perception and emotional experience; the neural system that is activated in the observer of an emotion is just as if they were actually experiencing this emotion themselves (for a review, see Ref. [54]). For the motor simulation version of the embodi-

ment theory of emotions, the perceptual systems relay information to neurocognitive mechanisms underlying emotional experience via an unconscious motor simulation of viewed expressions [54–56]. It has been shown that individuals automatically imitate perceived facial expressions and that this voluntary adoption of emotional facial expressions produces autonomic changes that are correlated with the emotional states [57]. In an elegant demonstration of the effect of embodied emotion on time perception, Effron *et al.* [41] found that the overestimation of the duration of presentation of angry faces was not observed when the imitation of facial expression was inhibited by a pen held between the participants' lips (as illustrated in Figure 4). In a similar study, Mondillon *et al.* [43] determined an empathy quotient and found a reduced temporal overestimation for angry faces in the low empathy compared with the high empathy participants. On the basis of these results on time perception, we might assume that it is because we feel in our own body the anger of another, by an imitation process, that we also become angry and/or aroused. The nature of the social relationship with other individuals (mother–child, boss–employee) that motivates us to imitate them might thus modulate the effects of facial expressions on timing and time perception. Mondillon *et al.* [43] also found an 'in-group' advantage with a temporal bias occurring when Caucasian participants were presented with Caucasian, but not with Chinese, facial expressions. It remains to be determined whether this social factor regulates emotion–time relationships as a selective filter or as an inhibitory mechanism of imitation. Whatever the case, these results point to a

Box 2. Outstanding questions

- How the effects of emotion on timing and time perception evolve over the course of the duration of an event remains to be determined. Current evidence suggests that the changes in clock speed after the presentation of a static emotional stimulus (e.g. a photograph) diminish within a few seconds, but the effects of more dynamic stimuli (e.g. a video) are uncertain as is the occurrence of rebound effects, that is a shift of clock speed in the opposite direction from the initial effect when the emotional stimulus is removed.
- Determination of the variation in emotional effects on interval timing as a function of the nature of the stimulus events (e.g. photographs or faces versus simple lights or sounds) will help to address the issue of how attentional time sharing is influenced by the nature of the stimulus – including social aspects, arousal and valence.
- The study of emotion and retrospective time perception, especially with regard to autobiographical memories, is an extremely fruitful avenue for future research that might challenge the types of internal-clock models reviewed in the current article because of the need to recreate these emotions and events from memory. Variation in current emotions might also alter the perception of past events, including their durations.
- The role of time in the regulation of social behavior and cognition as a function of normal aging or/and different pathologies might help to explain differences in the emotional reaction to increases or decreases in clock speed as well as the stimulus features controlling attentional time sharing and/or clock speed.
- How time perception can affect emotional satisfaction is an area that is particularly ripe for investigation. For example, the perception of time going faster might make one happier with the performance of a web browser, and various aspects of the browser (e.g. colour, layout and dynamics of graphical content) are likely to influence attentional timing sharing and/or clock speed [69].

previously unrecognized role for time in the regulation of behavior in social interactions.

Concluding remarks

Our review of the literature on the effect of emotions on timing and time perception reveals that our feeling for time is fundamentally inseparable from our subjective experience of the environment. Time can be distorted to appear shorter or longer than it really is. For example, it seems to fly when we are with our lover and drag when our partner is terribly boring. Consequently, the direction of temporal distortions as well as their magnitude might be important clues helping us to gain a better understanding of the role of emotions. Because variations in emotional arousal and valence provide a means for isolating timing circuits not derivative of other cognitive processes (e.g. memory and decision making) the examination of the relationships between time and emotion provides a promising avenue of research for both experts and non-experts in the field of time psychology [1,58,59] (See Box 2 for examples of future directions).

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