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When Emotion and Time meet from Human and Rodent Perspectives: A central role for the Amygdala?

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Abstract

Initiated by a long stay of Valérie Doyère in the laboratory of Joseph LeDoux, a Franco-American collaborative group was formed around the topic of emotion and time perception in a comparative perspective between humans and non-human animals. Here, we discuss results from our studies on the mechanisms underlying time distortion under two conditions, timing of a threatening stimulus and timing of a neutral stimulus in the context of fear, with insights from neurodevelopment. Although the type of temporal distortion depends on the experimental situations, in both humans and rodents a high-arousal emotion automatically triggers acceleration of an ‘internal clock’ system, an effect that may rely on the early maturing amygdala. Our studies, particularly in humans, also point to the role of attention and self-awareness in regulating the effect of fear on timing, relying on the prefrontal cortex, a late maturing structure. Thus, in line with LeDoux, while the amygdala may process all characteristics of events (including time) necessary to quickly trigger appropriate survival behaviors, some type of time distortions may rely on higher-order processing, some specific to humans. The extent of the network underlying threat-related time distortions remains to be explored, with species comparisons being a promising means of investigation.

Keywords: Fear, Duration, Amygdala, Prefrontal cortex, Neurodevelopment

Joseph LeDoux (2022) stated: “as soon as there was life, there was danger and survival behaviors”. The defensive survival function is thus innate and shared by all animals, including humans. In the numerous neuroscience studies that LeDoux has conducted, he has accumulated data demonstrating the primordial and key role of the amygdala in the defensive survival circuit. Its role is to detect threat (dangerous or non-dangerous stimulus), and, in response, to initiate defensive survival behaviors. However, “as soon as there [is] life”, all animals are also immersed in a temporal world characterized by a continuous flow of successive events separated by temporal intervals. The capacity for timing is therefore another fundamental and innate function allowing us to detect and encode *when* a given event occurs, enabling us to prepare ourselves to act accordingly and in time at the next occurrence. Initiated by a long stay of Valérie Doyère from CNRS at Joseph LeDoux’s lab at NYU, a Franco-American collaborative group was formed around the topic of “Emotion & Time”, with experts in fear/threat conditioning in rodents, or in timing research in humans and animals. Their experimental work highlighted a key role of the amygdala in time encoding processes in associative learning. The amygdala in effect has two overlapping roles, one to encode and anticipate which event will come (threat properties), and the other to expect when it will come (temporal properties). The idea is that the amygdala is involved in processing all characteristics of events (e.g., degree of threat, temporal and spatial features) necessary to trigger appropriate survival behaviors. But the perception of elapsing time is also modified by emotional states that produce temporal distortions, and the amygdala, as an emotion processing structure (Phelps and LeDoux, 2005), may also be at play. In the tradition of William James’ theory on emotion, LeDoux distinguished between the defensive survival system and emotion of fear. Paying attention to what we feel, i.e., awareness of changes in the autonomic and sensorimotor nervous systems helps us understand that we are afraid, that is, to name what we feel (emotion of fear). In this view, the amygdala is only a part of a larger neural network underlying mechanisms of

emotion. In this manuscript, we will discuss selected studies showing the role of amygdala in time distortions produced by threat cues, and the extent to which an amygdala-prefrontal cortex network is involved in timing an emotional cue and the modulatory effects of emotion on time perception through its higher cognitive functions (attention, executive functions).

Timing of a threatening cue

While mechanisms underlying reactions to threats and/or learning and remembering about them have been, and still are, the focus of a wide range of studies, the question regarding the timing of a threatening cue is often overlooked, despite its central role in forming associations that underlie adaptive behavior (e.g., Balsam and Gallistel 2009; De Corte et al. 2018). In animals such as rodents, this lacuna might have been due to the notoriously imprecise temporal characteristics of defensive responses such as freezing. However, there are numerous neural data indicating the brain ‘knows’ about time. Moreover, when questioning the organism using indirect methods, it is clear that what Pavlov (1927) had reported on time in an appetitive situation is also true for aversive stimuli, with learning of the temporal interval between the conditioned stimulus (CS) and the aversive unconditioned stimulus (US) occurring rapidly, even after a single pairing (for review, see Diaz-Mataix et al. 2014). Moreover, following the renewed focus in fear/threat memory reconsolidation prompted by Glenn Schafe and Karim Nader at LeDoux’s lab in 2000, we demonstrated that the CS-US interval is a key element in triggering reconsolidation, and that the process involves the basolateral amygdala (not the central amygdala) (Diaz-Mataix et al. 2013).

It is one thing to acknowledge the encoding of the CS-US interval and its importance in learning and updating associative memory, and another to evaluate the extent to which the interval duration is perceived differently due to the aversiveness of the threatening cue. The timing of a threatening cue can be investigated in two ways: (1) through the acquired temporal

expectancy in anticipation of an adverse event that may occur (as in Pavlovian conditioning); (2) through time estimation of a threatening cue which, in this case, does not necessarily predict the arrival of an event at a specific time. Animal research has been mainly concerned with the first, whereas the second has been used more in humans, as it is easier to assess it in them than in animals.

The question of a potential distortion of duration estimation in case of threatening cues has been systematically studied in humans by Sylvie Droit-Volet. In her original study, Droit-Volet et al (2004) have used the temporal bisection task that was initially developed in animals. In that study, participants were initially trained to associate a response (key press on specific letters on a keyboard) with a short (400 ms) and a long (1600 ms) standard duration presented in the form of a pink oval shown in the center of a computer screen (Figure 1A). Then, in a testing phase, they were presented with comparison durations of either the same duration as the standard durations, or an intermediate duration (600, 800, 1000, 1200, 1400 ms). They were asked to judge whether the comparison duration was more similar to the short or the long standard duration. However, in this testing phase, the pink oval was replaced by facial expressions of anger, happiness, sadness or neutral expressions. The psychophysical function remained orderly in all emotional conditions, with the proportion of « long » responses increasing with the length of the comparison durations. In addition, the emotion of fear did not lead to any violation of the main characteristic of time judgment found in most psychophysical studies: the coefficient of variation of estimates (standard deviation/mean) remains constant when stimulus durations vary (Wearden, 2016). In other words, the precision of time judgment is proportional to the duration judged, thus following the scalar property of variance consistent with Weber's Law. These first results in humans suggested that the perception of threatening stimuli does not disrupt time judgment. In other words, our fundamental sense of time is not lost under the influence of fear. However, although the stimulus durations were identical for all

facial expressions, humans' psychophysical function in the bisection test was significantly shifted toward the left for the angry faces, compared to the other faces (Figure 1A). The fact that the participants responded "long" more often (lengthening effect) means that the stimulus duration was judged to be longer than it actually was, consistent with an overestimation of time. The leftward shift of the psychophysical function for angry faces has been found when the face and/or gaze is oriented toward the observer, i.e., when the other represents a direct threat (Doi and Shinohara 2009; Kliegl et al. 2015). The perception of a direct threat thus produces a subjective extension of time (time-lengthening effect).

Although valence, stimulus type and temporal paradigm may also play a significant role as suggested by a recent meta-analysis (Cui et al, 2023), the lengthening effect of time when participants perceive threatening stimuli has been replicated in several studies in humans using similar temporal bisection tasks or other tasks (temporal reproduction, verbal estimation) and with a wide variety of other threatening stimuli (e.g., pictures, sounds, emotional bodily posture), sometimes in addition with physiological indices (e.g., Noulhiane et al. 2007; Grommet et al. 2011; Mella et al. 2011; Van Volkinburg and Balsam 2014; Droit-Volet and Gil 2016; Ogden et al. 2019).

The animal research is far less rich in data at the behavioral level, related in part to the reduced number of laboratory situations that can be used in animals, but gives greater access to the neural networks and mechanisms involved (Tallot and Doyère 2020). However, the behavioral studies in animals have yielded different effects depending on the paradigm used. In a bisection task close to the one used in humans, in which a given lever press (left or right) earned a food reward following a 2- or 8-s standard duration, Kamada and Hata (2018, 2019) assessed how rats judged the duration of a fear-evoking cue (conditioned stimulus, CS+) due to its previous pairing with a foot-shock, in comparison with their duration judgment of a cue that had been explicitly trained as safe (i.e., CS+ vs. CS- differential fear conditioning task). As in

humans, they found time distortions in rats, but in the opposite direction. The rats underestimated the duration of a CS+ compared to the duration of a CS-, and this effect was reduced by pharmacological inactivation of the basolateral amygdala. Other studies in rats have used a peak-interval-like Pavlovian conditioning task (Meck and MacDonald 2007; Boulanger-Bertolus et al. 2015; Saleille et al. 2022). In Saleille et al. (2022), a cue (tone) of a given duration (60s) (CS) was associated with an unconditioned stimulus (US) delivered 20s after the CS onset, which was aversive (shock) in some sessions and appetitive (chocolate pellet) in other sessions. In addition, probe trials were given, where only the CS was presented (peak interval). In these probe trials, the rats began responding in anticipation of the reward and stopped responding once the US-expected time had passed. The response rate plotted across the probe trials followed a normal distribution with a peak (peak time) centered near the target duration (here 20s). In this peak-interval-like Pavlovian conditioning task, the rats' temporal expectancy of the US arrival peaked earlier for the CS predicting an aversive US, compared to a CS predicting an appetitive US (Figure 1B). In fact, rats expected the arrival of the US earlier than its due time (i.e., overestimation of duration) when the CS was threatening, and at the correct time in case of the rewarding US. Importantly, the effect was scalar (constant coefficient of variation, Weber's law). These results in this specific condition are therefore in accordance with the lengthening effect reported above in humans.

Using both subjective and physiological indices, numerous studies have argued that the time-lengthening effect observed when facing threatening stimuli is due to an increase in the level of arousal (e.g., Mella et al. 2011; Gil and Droit-Volet 2012). It is generally assumed that increasing the level of arousal in the presence of a threat speeds up the system used for measuring time ('internal clock'). If our internal clock tells us that the elapsed time is longer under threat, we act sooner, thus ensuring a proper behavioral adaptation to a dangerous situation. The perception of an angry face activates the amygdala in humans (i.e., Phelps 2006).

Electrophysiological recordings in behaving rats also revealed an increase in coherence of neural oscillatory activity within a specific 3-6 Hz frequency range between the basolateral amygdala (BLA) and the dorsomedial striatum to which the BLA projects, with a temporal dynamic aligned with the timed behavioral expectancy of US arrival, in an aversive task like in Figure 1B (Dallérac et al. 2017). A more recent study highlighted a larger amygdala-connected circuit in the temporal expectancy of an aversive US, involving the medial prefrontal cortex which projects to the medial striatum (Tallot et al. 2020). These amygdala-connected networks may underlie behaviors in the presence of dangerous stimuli that are well programmed in time in order to avoid their harmful consequences. Indeed, animals must anticipate predators' behaviors, they must act at the right time, and escape as quickly as possible when necessary. Therefore, estimating time and accelerating time when action is urgent for survival are fundamental in threatening situations.

Effect of fear/threat on timing a neutral cue

Emotion can also have an impact on perception of duration of events that are not *a priori* threatening by themselves. These situations are more in line with what we, humans, experience when we feel that time flies or drags depending on our mood of the moment. This phenomenon has, however, not been extensively studied experimentally. In humans, Fayolle et al. (2015) tested the effect of fear on timing of a neutral stimulus (blue circle) in a temporal bisection task, and recorded physiological indices of the increase in the individual's level of arousal (electrodermal activity). In their experiment, participants were instructed that a given signal predicts the arrival of electric shocks during the next stimulus to-be-timed (shock trial) (which was effectively the case, with a random time of arrival of shock during that stimulus), and another signal predicts no shock (no-shock trial). When testing with different ranges of standard durations (0.2/0.8 s, 0.4/1.6 s, 1.2/4.8 s, 2/8 s), they observed a leftward shift of the bisection

function for the trials with the emotion-triggering signal compared to those without. In addition, the results showed a clear increase in the magnitude of the time distortion with the range of the duration to be estimated, i.e., a multiplicative effect (emotion x duration) consistent with the hypothesis of an acceleration of an ‘internal clock’ system under the effect of increased level of arousal in fear condition. Similar effects were reported in a study using the same experimental design in a temporal reproduction task (Zhao and Zeng 2022). To what extent the observed effect may partially be due to some aversiveness acquired by the initial neutral timing cue because of its pairing with shocks is a question in this paradigm. However, a previous bisection study (Droit-Volet et al. 2011) showed similar effects when participants had been viewing a fear-inducing movie prior to testing with neutral cues. Thus, a fear-evoking manipulation also produces a lengthening of subjective time in humans.

In rats, various effects have been reported on the effect of fear on timing of a neutral cue. In one paradigm, after the animal had been trained in an instrumental peak interval task, i.e. learning to press a lever to earn a reward after a fixed interval (e.g. 30s) after the onset of a to-be-timed cue, it received in another cage CS-US pairings, with the CS predicting the arrival of a foot-shock (US) at a given time after its onset. The effect of the ‘fear-CS’ on timing was assessed by presenting the CS at specific moments while the animal was performing the instrumental peak interval task (thus timing the interval to the reward availability), and comparing trials with and without the presentation of the ‘fear-CS’. In such a paradigm, Brown et al. (2007) reported that a 6-s ‘fear-CS’ when presented 3s after the onset of a timing cue shifted the temporal curve to the right (see also Meck and MacDonald 2007; Matthews et al 2012, for other temporal parameters). These right shifts were also observed with appetitive distractors (Buhusi et al. 2022), and both BLA and the prefrontal cortex have been implicated in these effects (Meck and MacDonald 2007; Matthews et al. 2012; Buhusi et al. 2022). In Brown et al.’s study, a shift was also obtained if the 6-s ‘fear-CS’ was presented 9s before the

onset of the timing cue, suggesting a long-lasting impact, that is not accounted for by an immediate distracting effect on timing. However, when tested in a temporal bisection task, a ‘fear-CS’ presented immediately before the to-be-timed cue (Faure et al. 2013) or unpredictable foot-shocks delivered throughout the bisection session (Meck 1983; Garces et al. 2018) did not produce a shift of the psychometric curve, but instead a decrease in its slope, suggesting a diminished precision or more variability in time estimation. Interestingly, lesion of the central amygdala (CeA) or its dysfunction in a Huntington rat model (with dysfunctional CeA, but intact BLA) mitigated these effects (Faure et al. 2013; Garces et al. 2018).

To what extent are humans special?

In summary, distortion effects on timing in humans are “robust” for the high-arousal emotion of fear, with elapsed time being generally judged to last longer, interpreted as reflecting a speeding up of an ‘internal clock’ system (Droit-Volet and Meck 2007; Droit-Volet and Gil 2009; Droit-Volet et al. 2013; Lake et al. 2016; Thönes et al. 2018). In rodents, the effects are less consistent and seem at first sight to differ in part from the ones observed in humans, with durations judged longer (when expecting a shock at a given time), or shorter (when distracted from timing another event), or unchanged but with more variability in the judgment. This suggests a combination of ‘clock rate/speed’ and attentional mechanisms depending on experimental situations, with a faster clock producing leftward shifts (i.e., subjective lengthening) and a diverted attention opposite rightward shifts (i.e., subjective shortening).

Fundamental processes regarding the perception of time and memory of time are, however, common to both species, and both are subject to time distortion in high-arousal emotional conditions. One among the various potential reasons for the discrepancy between humans and animals in the results reported above could come from the fact that assessments in rodents require many more testing trials, and any effect on ‘clock speed’ may disappear as the

animal is exposed to the ‘distorted time’ and incorporates it as a new learned duration. Another reason might be that the time course of some of the emotional effects are short-lived and, as a consequence, other processes (e.g., attention or decision processes) could reduce this effect and have an impact over a longer time scale.

Another potential reason is that the studied ‘emotional state’ and the underlying processes that is supposed to be similar between humans and animals is in fact partly different. LeDoux considers the defensive survival circuit to be only one part of the emotional system of fear. In humans, he proposes, the emotion of fear appears when humans consciously access this experience which allows them to give a verbal report about their experience, i.e., to say that they feel the emotion of fear. According to LeDoux (2020), the prefrontal cortex re-represents the non-conscious responses in order to transfer it into a conscious experience. He thus differentiated the unconscious/implicit process from the conscious/explicit process. The amygdala is thought to be an implicit processor that controls fearful/defensive behaviors non-consciously, while cortical circuits produce the explicit conscious experience of fear (LeDoux, 1996), directly derived from automatic emotional responses. Humans also construct knowledge in memory from their experiences of fear in different situations, a kind of thought schema in semantic memory (i.e., general knowledge structure). These memory-based schemas involve a large neural network including the parietal and the prefrontal cortex (Anderson, 1984; Binder and Desai, 2011). The role of schemas in allocating attention and encoding processes is now well known (e.g., Anderson, 1984). These thought schemas also contribute to the appraisal of future threatening situations and associated responses, give them a cognitive meaning, which participates in regulating the physiological and behavioral survival responses through top-down processes such as higher-order processes (decision-making, voluntary allocation of attention/controlled attention). In this line, Droit-Volet et al. (2015) showed that the magnitude of time distortions did also depend on explicit knowledge about the effect of emotion on time

judgment. In the temporal bisection task with the angry and neutral faces, when participants were given the false information that angry faces cause a subjective shortening of time, it indeed significantly reduced the magnitude of the lengthening effect observed for angry faces, without eliminating it, compared with that obtained in participants who received true information (emotion causes a lengthening of time) or no information at all. Yuan et al. (2020) also found that deliberately suppressing expressions of fearful emotions by training participants to remain calm did not eliminate time overestimation in threatening conditions either. Therefore, explicit knowledge does not have the power to produce specific time distortions and eliminate the distortion effect due to the automatic increase in arousal, but does act by regulating (reducing) the automatic emotional effect on time judgment.

In humans, the prefrontal cortex is also involved in the ability to introspect on the self, a capacity which varies between individuals (Fleming et al. 2010), and the self-consciousness may influence time perception (Mioni et al. 2023). Lamotte et al. (2012) assessed participants' consciousness as being more or less often subject to time distortions in daily life using a metacognitive questionnaire about time. They found that the more participants were aware of being subject to time distortion, the smaller the temporal distortion observed in a given situation.

Interestingly, self-conscious emotions, also known as secondary emotions such as guilt or shame (Tracy et al. 2007), produce an opposite effect on time judgment than that found for the high-arousal primary emotions (fear). Using temporal bisection tasks similar to those used with threatening stimuli, but with facial expressions of shame and neutrality, Gil and Droit-Volet (2011) did not observe a leftward shift in psychophysical functions as for the emotion of fear, but a rightward shift for the images of shameful faces compared with those of neutral faces, the participants responding more often "short" for the former than for the latter. This suggests that the duration of shameful faces is subjectively underestimated compared to their

actual duration. Underestimation of time is often attributed to attentional mechanisms. Indeed, when attention is diverted from time processing, the stimulus duration is judged to be shorter, as shown in numerous studies using dual tasks or attentional distractors (Zakay and Block 1996). Consequently, the temporal shortening effect observed in case of secondary emotions has been explained by the attention captured by the self-reflected awareness to the detriment of time processing, probably related to the evaluation of the origin of the shame, i.e., the fault that violated the moral norm.

Sarigiannidis et al. (2020) also showed that human participants' level of anxiety significantly modulated the effect of fear on time perception, even producing temporal underestimation instead of overestimation. This suggests that there are variations in time judgments under threatening conditions with inter-individual differences in subjective experiences of fear linked for example to personality traits or disorders (e.g., generalized anxiety disorder), and that the direction of the effects may be opposite in humans depending on the situation, even with primary emotions such as fear. It thus raises the question of whether the various effects reported in rodents may be linked to different levels of anxiety or stress induced by each specific experimental situation. It may also be related to the extent with which it implicates separate nuclei of the amygdala (BLA, CeA), and their specific connectivity with other brain areas that have been implicated in timing, in particular the dopaminergic system (Buhusi and Meck 2005; Doyère and El Massioui 2016; see figure 1C), which may modulate timed actions. In sum, there is a modulation of time judgment in threatening situations that could be caused by changes in arousal-associated 'clock rate', in decision-making processes and/or attention mechanisms. The varying degrees to which these different processes are involved in the different specific emotional situations studied may explain the differences in time distorting effects between humans and animals. However, whatever the case, humans and

rodents demonstrate time distortion in emotional situations, suggesting, at least in part, similar functioning and underlying mechanisms.

Neurodevelopmental clues

A large amygdala-connected network encompassing the prefrontal cortex may thus underlie timing of emotional cues as well as the distortion of timing by emotion. Interestingly, maturation of the brain areas of the network is asynchronous, with the amygdala functionally mature early and the prefrontal cortex the latest (Tottenham and Gabard-Durnam 2017). The prefrontal cortex is the latest brain region to reach full maturity in humans and rodents, with maturation continuing between adolescence and young adulthood (Sowell et al. 1999; Kolk and Rakic 2022). The development of the prefrontal cortex is correlated with the development of higher executive functions and the control (regulation, inhibition) of emotional and instinctual behaviors (Fuster 2002). In the case of emotions, the developmental trajectories are different for the basic emotions (fear, anger) and for the self-conscious emotions (shame, guilt). Indeed, while the expression of fear emotion is observed very early in infancy, in the first months of life (Izard et al. 2010), the self-conscious emotions are acquired gradually and do not emerge until 18-24 months. They also evolve during childhood, along with the cognitive abilities that enable children to learn, evaluate and understand the meaning of social situations, and to manage their relationships with other people who may express different emotions to the child (Lazarus 1997; Tracy et al. 2007). The development of the self-conscious emotion thus requires the development of higher cognitive abilities, which depend on the maturation of the prefrontal cortex. We might thus expect the effects of emotion on timing to differ depending on the developmental stage, the type of emotion, and the emotional context.

Consistent with the delayed development of an understanding of shame in other people, the shortening effect produced in adults when judging the duration of an adult face expressing

shame was not observed in young children aged 5 years (Gil and Droit-Volet 2011). However, children of the same age, or even younger (3 years old), showed a significant lengthening effect for angry faces to the same extent as in adults (Gil et al. 2007). Thus, time distortions in some threatening situations may be innate (or at least early) and automatic, as is also implicit time processing in humans (Droit-Volet 2013; Droit-Volet and Coull 2016). In rodents, temporal expectancy of an aversive event (i.e., implicit timing) also develops early, well before the full maturation of the prefrontal cortex, and even before the striatum has reached full adult-like functionality (Boulanger-Bertolus et al. 2014; Tallot et al. 2016, 2017). Thus, some fundamental mechanisms of time perception and its distortion likely rely on neural networks, including the amygdala, that are functional enough at an early age. The fact that projections from the amygdala to the prefrontal cortex may mature earlier than the reverse ones, and that other early-maturing brain areas may have some timing abilities (Tallot and Doyère 2020), may play a significant role in the early developmental emergence of reactions behaviors in situations of punctate threats, before the development of the ability to regulate these behaviors.

In conclusion, “all animals” (humans and rats) show distortion of time under the effect of emotions. The type of temporal distortion depends on the emotions and emotional situations tested, which differ between animals and humans. Nevertheless, in both species, the temporal effects are similar, and early in development in the case of the primary emotion of fear, which is a physiologically salient part of a defensive process for survival. The amygdala, which matures very early, contributes to this distortion of time in threat conditions. However, interval timing involves large neural networks beyond the amygdala, which was the structure the most studied by LeDoux’s team. We have mentioned the prefrontal cortex and its role, but other structures are likely involved (e.g., insula, striatum, Supplementary Motor Area, parietal cortex; see for reviews Buhusi and Meck 2005; Coull et al 2011; Merchant et al 2013). In addition to, or with, the amygdala, the cerebellum may also play a special role in time distortion by emotion,

given that it is involved in processing emotion and in fear conditioning (for recent reviews, see Hwang et al. 2022; Pierce et al. 2023), as well as in timing (Andersen and Dalal 2024), and that its deep nuclei connect to the BLA via the thalamus (Jung et al. 2022). Clearly, how extensive is the network responsible for time distortions under threat and its regulation remains to be explored, with comparison between species being a promising means of investigation. As timing is an integral part of defensive survival behavior, how minimal the functional maturation of that network needs to be to support temporally adaptive behavior under threat remains a challenging question.

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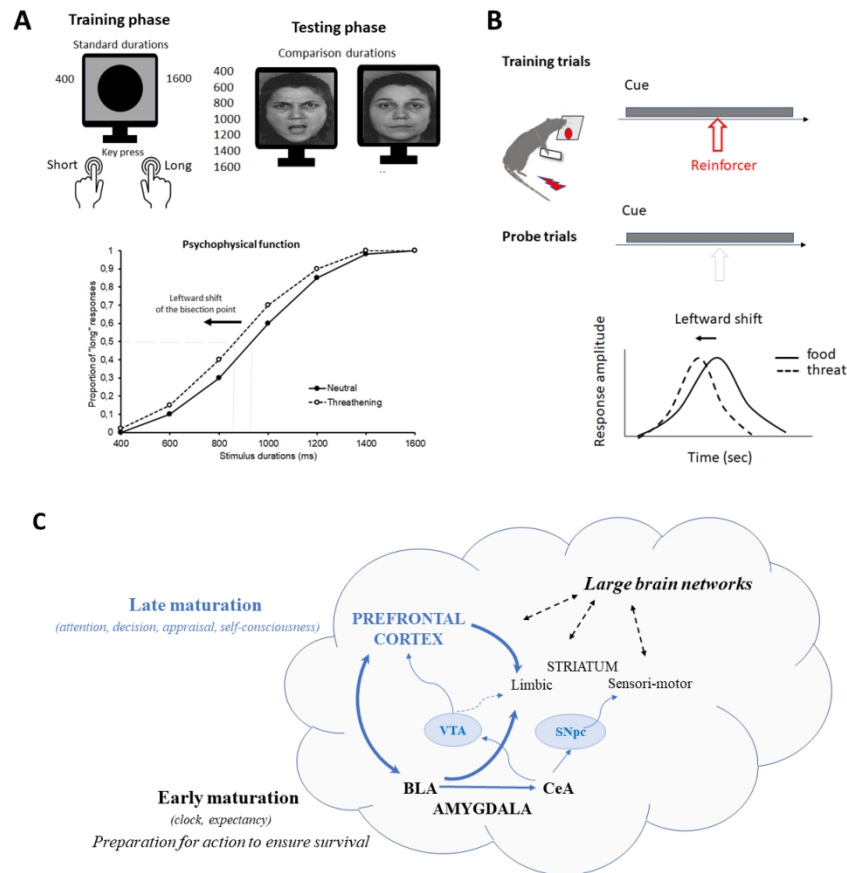
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Caption to figure:

A. Schematic of temporal bisection task in humans, with the example of a leftward shift of the psychophysical function when the participant judges the duration of a threatening cue, such as an angry face (i.e., overestimation of time), relative to when judging the duration of a neutral face. **B.** Schematic of a peak interval like Pavlovian task in rats, in which a cue predicts the arrival of a positive (food) or negative (foot-shock) reinforcer at a specific time after the cue onset. During probe trials, when the reinforcer is omitted, the peak of the averaged response amplitude is shifted to the left when the animal is expecting a foot-shock, as compared to when it expects a food pellet. **C.** Summarizing maturation of emotion (fear) and interactions with time judgement, some of which being common to humans and animals, other of which, likely specific to humans, are heavily dependent on the prefrontal cortex. Schematic representation of amygdala-connected neural networks, with a special focus on the basolateral (BLA) and central (CeA) parts involved in fear-modulated temporal expectancy and emotion-related time distortions, and their differential developmental maturation, with early maturation of the amygdala and later maturation of the prefrontal cortex. We propose that whereas the BLA connection on the prefronto-striatal network would be involved in scalar temporal expectancy, the CeA would likely affect emotion-based temporal distortion (attention, decision) via its connections with the dopaminergic system (Ventral Tegmental Area, VTA, and Substantia Nigra pars compacta, SNpc). Note that connectivity from dopaminergic centers to the amygdala are not represented. Modulation of time judgment by emotion likely involves also larger brain networks, depending on the emotional situations, not represented here, such as insula, supplementary motor area, hippocampus, and parietal cortex.



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