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Author manuscript

*Neurosci Biobehav Rev.* Author manuscript; available in PMC 2017 May 01.

Published in final edited form as:

*Neurosci Biobehav Rev.* 2016 May ; 64: 403–420. doi:10.1016/j.neubiorev.2016.03.003.

## Emotional Modulation of Interval Timing and Time Perception

Jessica I. Lake<sup>1,2,3</sup>, Kevin S. LaBar<sup>2,3</sup>, and Warren H. Meck<sup>2</sup>

<sup>1</sup>Department of Psychology, University of California, Los Angeles, Los Angeles, CA, USA

<sup>2</sup>Department of Psychology and Neuroscience, Duke University, Durham, NC, USA

<sup>3</sup>Center for Cognitive Neuroscience, Duke University, Durham, NC, USA

### Abstract

Like other senses, our perception of time is not veridical, but rather, is modulated by changes in environmental context. Anecdotal experiences suggest that emotions can be powerful modulators of time perception; nevertheless, the functional and neural mechanisms underlying emotion-induced temporal distortions remain unclear. Widely accepted pacemaker-accumulator models of time perception suggest that changes in arousal and attention have unique influences on temporal judgments and contribute to emotional distortions of time perception. However, such models conflict with current views of arousal and attention suggesting that current models of time perception do not adequately explain the variability in emotion-induced temporal distortions. Instead, findings provide support for a new perspective of emotion-induced temporal distortions that emphasizes both the unique and interactive influences of arousal and attention on time perception over time. Using this framework, we discuss plausible functional and neural mechanisms of emotion-induced temporal distortions and how these temporal distortions may have important implications for our understanding of how emotions modulate our perceptual experiences in service of adaptive responding to biologically relevant stimuli.

### Keywords

interval timing; temporal processing; amygdala; striatum; medium spiny neurons; striatal beat-frequency model; fear conditioning; threat; orienting; arousal; attention

## 1. Introduction

The ability to accurately perceive time is critical for adaptively navigating through our everyday lives. We utilize timing processes to gauge whether we have enough time to cross the street before an approaching car arrives at the intersection, to maintain a regular rate of conversation flow when speaking with a friend, and when we determine a website is not loading properly and click “refresh” e.g., (5, 27, 168). Given the ubiquity of actions and decisions that rely on timing processes, it is noteworthy that our perception of time is often distorted rather than perceived veridically. The cognitive processes that support time

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Please address all correspondence to: Dr. Warren H. Meck, Department of Psychology and Neuroscience, Genome Science Research Building II – Rm. 3010, 572 Research Drive – P.O. Box 91050, Duke University, Durham, North Carolina 27008 USA, meck@psych.duke.edu.

perception appear to be flexibly modulated by components of our ongoing experiences. Such temporal distortions may allow us to adaptively respond to stimuli in our environment (e.g., 114, 140, 168, 175).

Perhaps the strongest and most salient manipulations of time perception come from experiences of emotion. Common expressions such as “time flies when you’re having fun” or “time seemed to move in slow motion” illustrate the pervasiveness of emotional distortions in our perception of time. In line with anecdotal experiences, early human studies suggested that emotionally arousing experiences led to the overestimation of temporal durations- participants believed that more time had passed during an emotional event than actually had (e.g., 113, 134, 234, but see 76). For example, when asked to estimate an interval of time while moving towards a precipice, participants overestimated how much time had passed relative to when they were moving away from the precipice towards safety (134). Despite fairly consistent reports of temporal overestimation in response to emotional events, these studies suffered from methodological limitations. For example, appropriate comparisons between emotional and non-emotional control conditions were not performed. Instead, temporal estimates were either compared to physical durations of time (113, 134), or to estimates of empty temporal intervals (234), rather than to estimates of a neutral stimulus. Without a neutral baseline condition, it is difficult to conclude that the overestimation biases observed were specifically due to the emotional content of the stimuli rather than to other properties of the emotional event. These studies also only used a single emotion-related stimulus, relied on a limited number of trials, and did not compare temporal estimates across multiple durations or levels of arousal. These issues limit a comprehensive understanding of the relationship between emotion and time perception, as well as the underlying mechanisms that support it.

Only recently has empirical research begun to consider the mechanisms underlying emotional distortions in the subjective experience of time more systematically. Researchers have improved upon earlier study limitations by utilizing standardized tasks that allow for distortions to be compared across multiple durations and standardized emotional stimuli that allow for more mechanistic interpretations of resultant temporal distortions. Such studies have frequently interpreted findings within the context of pacemaker-accumulator (PA) models of time perception (94, 241, 245). However, a review of the existing literature suggests that such interpretations have been limited by a variety of factors.

We begin by reviewing the basic tenets of PA models and describe the mechanisms of temporal distortions within this model framework that are most relevant to the study of emotional distortions of time perception. Next, we will argue that using PA models to interpret the extant literature on emotional effects on time perception is limiting due to different interpretations of such models and different operational definitions of arousal and attention as plausible temporal distortion mechanisms across timing and affective/cognitive science fields. After a review of the current literature, we propose a new model of emotional influences on time perception that may provide a better framework for understanding underlying mechanisms. We will consider how these proposed mechanisms might be neurally instantiated based on the neurobiologically inspired striatal beat frequency (SBF) model of interval timing in conjunction with existing time perception and affective/cognitive

neuroscientific evidence. Finally, we address possible implications of the described effects of emotion on time perception and suggest avenues for further exploration of such interactions.

## 2. Pacemaker-Accumulator models of timing: Arousal, attention, and working memory

Pacemaker-accumulator (PA) models of time perception (Fig. 1 – 94, 241, 270) posit that there are three main levels in making a temporally based judgment involving clock, memory, and decision-making stages. During the clock stage, a pacemaker emits pulses that are subsequently collected by an accumulator. The number of pulses collected by the accumulator represents the duration of time that has elapsed during the timing of a particular interval. A switch controls the transfer of pulses from the pacemaker to the accumulator (138). When the switch closes, pulses pass into the accumulator; pulses are blocked when the switch is open. In the memory stage, the duration of the interval being timed (represented by the number of pulses collected in the accumulator) can be transferred from working memory to long-term memory. Lastly, in the decision-making stage, the temporal interval being timed is compared to duration representations stored in long-term memory to determine if the current interval is of an equivalent duration. If, for example, an individual is required to perform an action after a specific time interval has elapsed, that individual will compare the current interval being timed with previous representations of this interval stored in memory and will effect the appropriate behavior when these two representations are judged to be equivalent. Scalar timing theory states that the variability in temporal estimates is proportional to the duration of the interval, such that estimates of longer intervals are more variable than those of shorter durations (e.g., 36, 92, 94).

According to pacemaker-accumulator models, the subjective experience of time can be differentially modulated depending on what stage in the model the distorting influence affects. The current discussion will focus on the functionality of the pacemaker, the switch that connects the pacemaker to the accumulator, and the working memory filter. These mechanisms are most relevant for prospective timing tasks, which explicitly instruct participants that they will be making temporal judgments and do not require mnemonic reconstruction of temporal durations. Such prospective timing tasks will form the focus of the current review.

Within the time perception literature, arousal is conceptualized as any manipulation that changes the rate of the pacemaker, with an increase in pacemaker rate or internal clock speed equivalent to an increase in arousal. This increase in pacemaker rate results in a greater number of pulses being emitted and sent to the accumulator during the timing of a specific event. The comparison of an interval timed with a faster pacemaker (i.e., higher arousal) to the representation of this interval stored in long-term memory, would result in the interval being judged as longer, as more pulses have collected in the accumulator over the same period of physical time. Increasing arousal is considered by many timing researchers to be equivalent to increasing the pacemaker rate. Importantly, influencing the pacemaker rate

causes shifts in perceived duration that are proportional to the interval duration being timed (92, 94).

Behavioral and pharmacological manipulations in humans and non-human animals have produced changes in pacemaker rate or clock speed that have been labeled as arousal effects, based on an operational definition of arousal as an increase in pacemaker rate/clock speed. In non-human animal models, administration of dopaminergic drugs produces effects consistent with changes in pacemaker rate, demonstrating proportional shifts in timing functions (171, 174). Cocaine and methamphetamine, psychostimulants that increase the effective level of dopamine in the synapse, also increase clock speed, resulting in overestimations of duration (e.g., 34, 153, 154, 157, 156, 171, 174, 254), whereas haloperidol administration, which decreases the effective level of dopamine in the synapse, decreases clock speed, resulting in underestimations of duration in rats (152, 171–174). Human studies have also shown changes in timing performance after dopaminergic manipulations, consistent with changes in the speed of an internal clock that have been attributed to arousal (e.g., 10, 44, 131, 148, 212–214). Increases in body temperature also result in proportional increases in temporal durations, whereas decreases in temperature result in underestimation of duration (251). Lastly, visual flickers or auditory clicks preceding temporal judgments have been shown to increase the rate of the pacemaker (e.g., 73, 209 – but see 215). While these findings have been interpreted as evidence of arousal-related distortions of time, using the operational definition of arousal as any effect which speeds the rate of an internal clock (69), their relationship to the construct of arousal as defined within the fields of affective and cognitive science is unclear. This issue will be addressed later in this review.

Attention is defined within the time perception literature as the allocation of processing resources to timing versus other processes, and is generally conceptualized as controlling the functionality of a gate or switch (see 138 and 268 for a discussion of the differences between the gating and switching of pulses as related to attention) that regulates the flow of pulses into the accumulator by the switch (for example) by alternating between an open and a closed state (e.g., 28, 88, 172, 268). Switch-related effects on time perception can result in either additive or proportional distortions across durations, depending on the nature of the change in switch activity. The latency with which the switch closes, allowing pulses to pass through to the accumulator to start the timing process, as well as the latency with which the switch opens to stop the accumulation process, can be modulated. Start/stop latency effects are independent of stimulus duration, resulting in distortions of temporal estimates that are additive, rather than proportional, across stimulus durations (138, 180, 208). In other words, timing functions are shifted by a relatively fixed value regardless of the stimulus duration being timed. It should be noted that while differences in start/stop latencies bias temporal estimates, these differences are typically not thought to affect temporal sensitivity (93).

If attention resources are divided throughout the timing of a stimulus, the switch is said to ‘flicker’ between an open and a closed state (70, 83, 145, 147, 149, 206, 207). Flickering of the mode switch results in temporal distortions that, like changes in pacemaker rate, are proportional to the duration of the stimulus being timed. A general assumption of pacemaker-accumulator models is that full attention is dedicated to timing under normal

conditions and, thus, attention can only be distracted from timing, decreasing the perceived duration of temporal estimates. This assumption is likely due to the fact that these models were originally based on behavioral neuroscience research using animal subjects typically rewarded for timing performance. High levels of motivation resulted in high behavioral performance and thus increases in attention were unlikely to be observed.

Many studies provide evidence of temporal distortions resembling those predicted by attention models of time perception within the tradition of PA models (e.g., 26, 28, 270). In rats, the presentation of a warning signal in a different modality from the stimulus to be timed led to underestimations of duration (172). This warning signal is thought to prepare the animal for timing the signal but, when the signal is in a different modality, the need to reorient attention increases the latency of switch closure. Pharmacological interventions provide further evidence for the operation of a switch latency effect. When clonidine was administered to rats trained on a peak procedure task in which they were required to press a lever after a learned temporal interval had elapsed, the rats responded later than the duration of the trained interval (208). The magnitude of this effect across different interval durations suggested an additive rather than a proportional temporal shift, supporting a switch latency mechanism over a pacemaker interpretation. As clonidine inhibits the release of norepinephrine, this attention effect is consistent with the proposed role of this neurotransmitter in attention processes (e.g., 9, 216). Evidence supporting a flickering switch mechanism of temporal distortion comes from studies demonstrating that dividing attention between a temporal and non-temporal task decreases temporal estimates, with the amount of attention dedicated to timing versus the non-temporal task influencing temporal estimates (45).

More recent instantiations of PA models of time perception support an influence of resource-sharing on time perception but suggest that resource-sharing processes modulate the working memory stage instead of the accumulation stage. Such resource-sharing models of working memory and attention suggest that the degree to which working memory/attention resources are devoted to other processes predicts the rate of working memory decay for an interval being timed (e.g., 28, 83, 84, 150). This working memory decay is proportional to the contrast between the event being timed and the other processes to which resources are allocated. The main difference between this working memory decay effect and the “flickering switch” attention effect is that the working memory decay account suggests that the duration of a stimulus is accurately perceived but distortions result from a “leaky” working memory filter, whereas the flickering switch account suggests that attention distraction shortens the perceived duration of a stimulus. Nevertheless, researchers have argued that working memory and attention are subserved by the same underlying processes directed either towards internal representations or external representations, respectively (11, 35, 91, 123). Based on such theories, the influence of resource-sharing on time perception likely involves the same underlying processes whether they act on the switch or working memory stage. Given that the working memory effects most relevant to the current discussion are quantitatively indistinguishable from flickering switch attention effects, it will be beyond the scope of this manuscript to attempt to dissociate resource-sharing effects at these different phases.

### 3. Complications with using pacemaker-accumulator models as a framework for emotional timing

The emotional timing literature has largely relied on PA models as a framework within which to interpret temporal distortions, attributing such distortions mainly to arousal or attention mechanisms. However, two main issues have limited interpretations based on this framework. Firstly, the implementation of PA models has varied across studies, with different interpretations of what constitutes a pacemaker or switch-like effect. Secondly, different operational definitions of and proposed relationships between arousal and attention in timing and affective science literatures have resulted in conflicting interpretations of how these two constructs relate to pacemaker and switch-like mechanisms, limiting the usefulness of these constructs as implemented in emotional timing studies. These issues are discussed in detail below.

#### 3.1. Problems with interpretations of pacemaker-like and switch-like mechanisms

Problems with interpretations of emotional distortions of time perception within the PA model framework have been partially driven by different interpretations of what does and does not constitute “pacemaker-like” or “switch-like” activity. Two main criteria have been used to support a pacemaker-like mechanism. Firstly, based on the implicit assumption of PA models that full attention is dedicated to timing under normal conditions, some emotional timing studies have adopted the view that pacemaker effects are reflected by the overestimation of temporal durations whereas switch-like effects are exclusively reflected by the underestimation of temporal durations (65, 74, 99, 238).

A second interpretation of pacemaker-like effects has focused on the scalar property of the pacemaker, whereby temporal distortions are interpreted as pacemaker-like effects if temporal estimates proportionally increase across durations (64, 65, 67, 71, 95, 96, 98, 102). Nevertheless, differences in the temporal tasks employed have influenced interpretations in favor of or against a pacemaker-like mechanism. For example, in Droit-Volet et al. (65), a pacemaker mechanism was supported using a temporal bisection procedure because the magnitudes of observed overestimation effects for emotional stimuli increased with increasing durations, whereas results which did not show an increased magnitude of overestimation across durations in the bisection procedure have been interpreted as a switch latency or attention effect (97, 102). However, considering the constraints associated with this procedure is important when testing for pacemaker-like effects across durations (130). In the temporal bisection procedure, participants are trained on two anchor durations—one long and one short—and then tested on a series of durations, typically within the range of the anchor durations, and asked to judge whether the comparison stimulus is closer to the short or to the long anchor duration. Using this procedure typically results in timing functions with floor and ceiling effects around the anchor durations, as such discriminations are often simple discriminations to make. As such, assessing whether shifts in timing functions across comparison durations are proportional or additive within a single duration range is difficult, since these additional constraints on judgments likely bias responses. Thus, when using the bisection procedure, the validity of labeling an interaction between emotion and duration as a pacemaker-like effect (65) or of suggesting that the lack of such an

interaction is evidence against a pacemaker mechanism (97, 102) is questionable when the magnitude of estimates are assessed within a single temporal range. See Kliegl et al. (124) for a novel use of the temporal bisection procedure in conjunction with evaluative conditioning in order to avoid sensory confounds by having the same stimulus serve as both the neural and the emotional signal depending on prior conditioning.

An alternative strategy when using a temporal bisection procedure that has been implemented is the comparison of temporal distortion magnitudes at the point of subjective equality (PSE) across multiple duration ranges to assess if temporal distortions conform to the scalar property and are thus pacemaker-like (e.g., 69, 102, 130, 187). Some emotional timing studies have interpreted findings as support for a pacemaker-like mechanism when the magnitude of PSEs increases as the durations within the duration ranges increase (71, 67). Other studies have not shown increases in the magnitude of PSEs across duration ranges (64, 99, 102, 229) and have interpreted the lack of proportional effects across duration ranges as evidence against a pacemaker-like mechanism in some cases (64, 102, 229), but as evidence that a pacemaker-like effect was short-lived in other studies (99).

Other emotional timing studies have used temporal reproduction or estimation procedures and have explored proportional increases in temporal estimates across durations to test for pacemaker-like effects. These studies have frequently reported decreases in relative (compared to a neutral condition) or absolute (compared to physical duration elapsed) temporal overestimation of emotional stimuli across increasing temporal durations (7, 14, 196), which is inconsistent with a strictly pacemaker-like mechanism. However, studies using such methods have sometimes reported that shorter durations were overestimated whereas longer durations were underestimated in duration (132, 233), regardless of their emotional content. Such a pattern of responses is consistent with Vierordt's law, which suggests that perceptions or judgments of duration are biased towards the mean of the temporal distribution (106). It is unclear if the emotional content of a stimulus interacts with regression to the mean effects to influence temporal estimates/reproductions or if regression to the mean effects on time perception may obscure pacemaker-like influences of emotion on temporal estimates/reproductions.

In addition to differing interpretations of what constitutes a pacemaker effect, studies have also relied on different definitions of switch-like effects within the context of PA models. The operation of a switch-like mechanism has sometimes been supported if temporal durations were underestimated for emotional relative to neutral stimuli (238). Other studies have allowed for a bidirectional influence of switch latency on time perception. In such cases, switch-like effects have been defined as additive (rather than proportional) changes in temporal estimates for emotional stimuli across durations or duration ranges, regardless of whether or not the emotional effect increased or decreased temporal estimates (102, 137, 229). Nevertheless, as previously mentioned, some PA models allow for the flickering rate of the switch (or a gating mechanism) to vary or for resource-sharing between temporal and non-temporal factors, which can both result in proportional effects across interval durations (28, 138, 145, 270). The possibility of proportional switch-like effects have been largely ignored in much of the emotional timing literature (but see 145, 167).

From this brief overview, it is clear that dissociating pacemaker and switch-like mechanisms of distortion within the emotional timing literature has been complicated by different interpretations of PA models. Incorporating all current views of the plausible influences of the pacemaker and switch mechanisms on temporal distortions suggests that dissociating their influences is difficult to accomplish quantitatively, as 1) both are capable of increasing or decreasing temporal estimates and 2) manipulations of either mechanism can result in proportional effects. An essential problem is that mechanistic conclusions about emotional influences on time perception have been almost exclusively based on the nature of resulting temporal distortions. A more fruitful approach might be to explicitly manipulate or measure arousal or attention to more clearly demonstrate that the proposed mechanism was responsible for the observed effects. Nevertheless, further analysis of emotional timing studies suggests that manipulation/measurement of arousal and attention has been complicated by the differing definitions of arousal and attention within and across the fields of time perception and affective science.

### **3.2. Arousal and attention constructs within affective/cognitive science literatures**

In emotional timing studies, attention and arousal are often treated as if they are unitary constructs with singular and distinct effects on time perception and have direct correspondences across time perception and affective/cognitive science fields. Nevertheless, an analysis of arousal and attention within the affective/cognitive science domain paints a picture of multifaceted constructs with complicated interactions.

Many different processes are associated with arousal within an affective science perspective (111). Arousal is characterized by both central and peripheral effects on the nervous system (136). The activity and release of modulatory neurotransmitters in the brain associated with increased arousal have widespread effects on cognition and behavior (135). For example, arousal-related norepinephrine and acetylcholine release are thought to modulate memory and attention processes (115, 121), as well as increase vigilant behaviors (52). Under high arousal states, the hypothalamic-pituitary-adrenal (HPA) axis releases the hormone cortisol into circulation (136). Arousal also causes changes in autonomic activity, shifting away from homeostasis with the activation of the sympathetic nervous system, which is associated with changes in heart rate, pupil dilation, and skin conductance responses (SCRs). A cognitive component of arousal is reflected by subjective ratings of arousal, which likely reflect appraisal-like assessments of affect intensity and biological relevance that result in changes in attention (196).

Different arousal-related responses have unique time courses. Central release of neuromodulators occurs rapidly, whereas peak changes in HPA axis release of cortisol occurs minutes after the emotionally arousing event. Physiological changes are relatively fast-acting, with differential autonomic responses evident within up to a few seconds from the onset of an emotional event. The relationship between emotion-related changes in physiological and subjective arousal has been debated within the field of affective science. While positive correlations between physiological arousal and subjective arousal processes are common (e.g., 219), studies have also shown that these processes can be separately

modulated (57, 104, 230), suggesting that they may reflect unique components of the response to an emotionally arousing event.

The construct of attention is similarly multi-faceted. Attention orienting is generally divided into exogenous and endogenous component processes (42). Exogenous attention is stimulus-driven, reflexively captured by salient stimuli, and controlled by a right-lateralized ventral frontoparietal network, whereas endogenous attention is goal-directed, serving internally generated objectives or expectations and controlled by a more dorsal frontoparietal network (42, 235, 263). Endogenous attention is thought to be relatively slower acting than exogenous attention (236). After attentional orienting, cognitive processes are necessary to either shift attention away from a stimulus (249) or to maintain attention to it (115). Cognitive processes underlying sustained attention are necessarily recruited more heavily as a temporal interval elapses (43).

Theories of emotional arousal and attention within the cognitive/affective science tradition further suggest that these constructs frequently interact, such that emotional arousal can influence attention and vice-versa. The nature of these interactions is modulated by a variety of factors, including the valence, biological relevance of the task/emotional stimuli, the time course of the task/emotional event, and individual difference factors. Theories of emotional arousal effects on attention have generally supported the idea that negatively valenced, emotionally arousing stimuli narrow attention such that attention is preferentially oriented towards and/or captured by threat relevant stimuli at the expense of neutral or threat-irrelevant stimuli (121, 163, 166). For example, threatening stimuli serving as targets in an array of distractors are more successful in capturing attention in a visual search paradigm than threat-irrelevant stimuli as evidenced by faster response times (199). At the same time, threatening stimuli that invalidly cue target locations reduce target detection speeds relative to neutral cues for subsequently presented targets, thought to reflect the holding of attention by the negatively arousing stimulus (190). Such studies support the capture and holding of attention by negatively arousing stimuli at the expense of neutral stimuli, regardless of their task relevance. These studies also highlight the importance of the relationship between the emotional stimulus and the task in predicting performance. If attention to a negatively arousing stimulus is necessary for better performance, an enhancement of performance often results, whereas if attention to a negatively arousing stimulus distracts from the ability to perform a task, emotion can impair performance.

The influence of positively valenced arousing stimuli on attention has been somewhat less straightforward. A large body of research has suggested that, in contrast to negatively valenced emotional stimuli, positively valenced emotional stimuli broaden the scope of attention (85). Nevertheless, such differences may have been driven by differences in physiological arousal changes elicited by negative and positive stimuli. For example, in a study using baby faces, considered highly arousing positive stimuli, an increase in attention orienting towards these faces was observed, similar to effects observed with threat cues (24). Another explanation for the differences observed for studies of positive emotion could be the biological relevance of the emotional stimuli utilized (247). When high approach-motivated positive affect was induced (which was likely accompanied by enhanced arousal), a

narrowing of attention was observed similar to that observed with negatively valenced, arousing stimuli (86).

Attention cuing studies reflect rather fast-acting interactions between arousal and attention within the millisecond duration range, but arousal and attention processes also interact at longer latencies during sustained attention (43, 115). Top-down attentional control processes have been shown to modulate physiological arousal (198). At the same time, the volitional modulation of physiological arousal improves sustained attention performance (197), supporting the role of arousal in modulating attention after initial orienting responses. Emotional arousal effects on sustained attention and/or working memory maintenance are also dependent on the task design, such that arousal may enhance attention maintenance when the arousing stimulus is task-relevant, whereas the maintenance of attention to a neutral stimulus is impaired by a negatively arousing distractor (61).

The temporal dimensions of a task additionally influence the impact of an emotionally arousing event on attention. For example, in the attention blink paradigm, an emotionally arousing stimulus impaired the ability to detect a task-relevant target at a 200 ms lag but not at an 800 ms lag (232). In line with such findings, short (50–500 ms) temporal lags after the presentation of an emotional distractor have impaired accuracy in responding to neutral targets, whereas longer lags (800–1000 ms) have improved accuracy (e.g., 17, 38). Such findings suggest that different underlying mechanisms or processes associated with arousing stimuli may differentially direct attention at distinct time points after the onset/offset of an emotional stimulus (192).

Finally, individual differences have been shown to modulate emotional effects on attention. Attention biases towards threat are frequently enhanced in individuals with clinical and non-clinical anxiety (for reviews see 15, 39, 211). In addition, personality factors have been shown to modulate emotional biases of attention. For example, extraversion was associated with the holding of attention by a location paired with reward, whereas introversion was associated with the holding of attention by a location paired with punishment (53). It has been suggested that these biases reflect self-relevance or familiarity (40). Individual differences in emotional recovery or self-regulation may modulate the influence of emotionally arousing stimuli on attention at different time points (192). Age has been associated with differential biases for positive versus negative stimuli, with older adults showing a greater bias towards positive stimuli than younger adults (164, 165). Altogether, this evidence supports an interactive relationship between emotional arousal and attention and its modulation by a variety of factors, namely valence, biological/task relevance of the emotionally arousing stimulus, temporal dynamics, and individual differences.

### **3.3. Arousal and attention constructs within emotional timing studies and their relationship to pacemaker and switch-like mechanisms**

Based on the multi-faceted nature of arousal and attention, it is not surprising that interpretations in favor of such mechanisms have varied across studies of emotional timing. Unlike theories of arousal and attention from an affective/cognitive perspective, some emotional timing studies have suggested that these constructs are mutually exclusive, with temporal distortions resulting from either arousal or attention processes. Others have argued

that these effects are independent but interrelated. Across studies, the roles of arousal and attention and how they correspond to pacemaker and switch mechanisms have differed.

Most researchers have advocated for a role of arousal in modulating emotion-driven temporal distortions. However, the evidence used to support this idea is varied. Based on interpretations of time perception models, some researchers have assumed that the influence of arousal is directly supported by demonstrating the operation of a pacemaker-like mechanism. In other words, support for a pacemaker effect is used to support the mechanistic influence of arousal (e.g., 65, 66, 71, 98, 103, 260). Complications resulting from such interpretations are multifold. Primarily, complications stem from different interpretations of what constitutes a pacemaker effect as discussed above. Different interpretations of pacemaker effects have led to the use of different criteria to support the role of arousal in emotion-driven temporal distortions. A direct correspondence between the pacemaker and arousal has often been assumed such that researchers have not explicitly demonstrated that changes in arousal correspond to changes in time perception. Interpretations in favor of or against the role of arousal have sometimes been based exclusively on a demonstration that the presentation of an emotional stimulus increases or decreases temporal estimates (78, 97). Many studies have not included a direct manipulation of arousal separate from other components of the emotional stimulus (e.g., valence and/or perceptual features). The importance of such a demonstration is emphasized by a recent study which found that picture complexity in emotional pictures, rather than emotional arousal, accounted for overestimation effects (82). Almost all studies of emotional influences on time perception using emotional pictures or sounds have not reported controlling for basic perceptual features (e.g., 7, 98, 102, 103, 145, 196, 231).

Other emotional timing studies have supported the contribution of arousal to emotion-induced temporal distortions not based on PA model predictions, but on subjective ratings of arousal (e.g., 7, 25, 71, 67, 98, 102, 145, 184, 196, 229, 231) and/or physiological arousal measures (e.g., 7, 71, 184) in response to emotional stimuli. As mentioned in the previous section, subjective arousal and physiological arousal are frequently correlated but do not always predict the same relationship with other variables of interest. Subjective arousal may also reflect attentional processes (196). Thus, concluding that arousal contributes to temporal distortions may reflect different underlying mechanisms depending on the component measure of arousal assessed (185).

Studies relying on different types of emotional stimuli have also had different interpretations of how distortions relate to arousal processes. Research using emotional faces have suggested that emotional arousal increases temporal overestimation, as evidenced by greater overestimation with more arousing emotional expressions, such as fear and anger (e.g., 14, 58, 65, 74, 78, 98, 99, 239, 266, 267). On the other hand, other studies, mainly using emotional pictures and sounds rated as high versus low in arousal, have suggested that arousal levels may determine the underlying mechanism that drives temporal distortion (e.g., 7, 25, 196). For example, Angrilli et al. (7) proposed the often cited idea that at low levels of arousal an attention mechanism is recruited, whereas high levels of arousal rely on an emotion-driven mechanism. These studies have provided varying interpretations of how such arousal effects might correspond to the mechanisms outlined by PA models.

Interpretations of what constitutes an arousal effect have been based on the proposed time course of arousal. For example, based on evidence that physiological arousal responses, such as SCRs, peak a few seconds after stimulus onset, some timing researchers have suggested that arousal mechanisms should have longer latency effects on time perception, and, thus, distortions occurring for shorter temporal durations could not be driven by arousal (e.g., 145, 222). Alternatively, based on the idea that emotional arousal is ephemeral, others have suggested that emotional arousal effects are supported by temporal distortions that occur for shorter durations but not for longer durations (e.g., 7, 14, 196). These conflicting interpretations are the result of differing definitions of arousal and the subcomponents of arousal being considered.

Similarly, interpretations of what constitutes an attention effect have varied across studies. Some researchers have suggested that an attention effect is reflected by an underestimation of temporal distortions resulting from the presentation of an emotional stimulus (e.g., 97, 238). Others have equated an attention effect to a switch latency effect, such that additive changes (regardless of the direction of change) in temporal distortions are thought to reflect attention processes (e.g., 102, 137, 229). Similarly, it has been proposed that attention effects could be driven by changes in both pacemaker rate and switch latency effects (132, 243). Attention has been supported as the mechanism underlying resource-sharing between emotional processes and timing (e.g., 77, 167, 181). All of these interpretations are in addition to the attentional mechanisms that putatively support low-arousal emotional stimuli (7), as well as temporal distortions occurring at short (145, 222) or long durations (7, 14, 196), as discussed above.

In addition to illustrating the multiple operational definitions of arousal and attention, these studies highlight that, in contrast to theories from affective/cognitive science, emotional timing studies have largely assumed that arousal and attention are independent and unrelated processes. Nevertheless, a few studies have provided evidence that arousal and attention processes may interact to influence time perception. For example, Mella et al. (184) found that having participants attend to the duration of a stimulus, rather than the emotionality of a stimulus, decreased physiological arousal and temporal estimates, providing a demonstration of how top-down attention processes might modulate time perception via changes in arousal. On the other hand, by having participants time the duration of a neutral stimulus presented after an emotional distractor, rather than time an emotional stimulus, Lui et al. (145) demonstrated that emotionally arousing stimuli can capture and hold attention resources, such that less attention is devoted to timing. Other emotional timing researchers have also supported the idea that arousal and attention processes are independent but interrelated (62, 95, 96, 225), though they do not specify how these processes might interact to influence time perception.

This review of how arousal and attention constructs are conceptualized in emotional timing studies demonstrates how these terms have been conflated across time perception and affective/cognitive science without a clear demonstration of how these constructs relate to underlying mechanisms. PA models of time perception do not currently allow for more detailed predictions of emotional effects on time perception that reflect the potential influence of different arousal or attention components. Thus, important distinctions have

been lost in studies of emotional influences on time perception by defining effects as being driven exclusively by arousal or attention. Surprisingly, despite favoring arousal or attention interpretations, few studies of emotional influences on time perception have actually collected online measures of arousal or attention, and even fewer have attempted to verify that variations in these measures indeed influence temporal estimates. This assessment demonstrates that more standardized operational definitions are necessary to determine the degree to which the different processes associated with emotional arousal and attention influence emotion-induced temporal distortions. To this end, we recommend that measures of arousal and attention should be collected, and it should be demonstrated that these factors predict changes in emotion-induced temporal distortions. At the same time, constructs of interest should be explicitly manipulated independently of other potential explanatory variables to the extent possible.

### 3.4. A consideration of other proposed modulatory factors

The conflicting conclusions reviewed thus far across emotional timing studies, and the differences outlined between PA models and theories of emotion and attention, suggest that PA models and the mechanisms of emotion-driven distortion that they promote may not adequately explain the variations observed within the emotional timing literature. Despite favoring arousal and attentional mechanisms of temporal distortions, researchers have also suggested emotion-driven temporal distortions may not be exclusively driven by such mechanisms (66, 68), as other factors have been found to modulate temporal distortions, specifically valence, biological relevance, and individual differences. While some researchers have previously suggested that such factors do not fit within a pacemaker-accumulator framework and have proposed that these factors represent the operation of additional mechanisms, we believe these factors are not inconsistent with a model of emotion-driven distortions of time perception that would allow for effects to be driven by physiological arousal and attention processes and their interaction. A better understanding of the modulatory role of these additional factors may help clarify the nature of emotion-induced temporal distortion mechanisms.

**3.4.1. Valence**—Multiple studies have reported differential effects of positively and negatively valenced emotions on time perception. Most of these studies, however, have reported that highly arousing positive stimuli are underestimated compared to highly arousing negative stimuli (e.g., 7, 25, 66, 188, 196, 231, 260). Nevertheless, differences in physiological arousal responses to positive and negative stimuli are sometimes found despite stimuli being rated as equally arousing (e.g., 48, 205), suggesting that differences between positive and negative emotional stimuli may actually reflect differences in physiological arousal. At the same time, it has been suggested that when emotional valence is assessed on a bipolar scale for positive and negative emotions, ratings may not accurately reflect the psychological difference in intensity between positive and negative stimuli (170). This critique is particularly relevant, given that most emotional timing studies using emotional pictures and sounds have relied on ratings of positive and negative stimuli from the International Affective Picture System (133) and the International Affective Digitalized Sounds System (18), which both use bipolar scales of valence and arousal. Alternatively,

differences in the biological relevance of negatively and positively valenced stimuli may differentially influence attention during the timing task.

**3.4.2. Biological relevance**—The influence of biological relevance in modulating attention is also likely to underlie differing effects of specific emotions with equivalent arousal levels on time perception. For example, Tipples (237) found that angry faces were overestimated in duration compared to fear faces with comparable levels of reported subjective arousal. The author suggests that angry faces might serve as signals of direct threat that preferentially activate fear-related avoidance mechanisms. Studies have also shown that despite eliciting high levels of arousal, disgust faces and disgust images have not increased temporal overestimation to the same extent as other comparably arousing negative stimuli (69, 100, 103, 229, but see 98). While disgust is a biologically relevant and adaptive emotion, it serves a biological function distinct from other negative emotions (33) and thus may elicit a unique influence on temporal distortion. A role for disgust in differentially modulating attention has been proposed (98, 100). Together, these findings suggest that the biological relevance of a specific emotion and the action tendencies that a specific emotion activates may be critical in determining the effect that different, equally arousing emotions have on time perception, potentially mediated by their modulation of attention.

The importance of the biological relevance of emotional stimuli in uniquely distorting time perception is also suggested by the role of self-relevant factors in modulating temporal distortions. Eye gaze, for example, has been shown to modulate the influence of angry facial expressions on time perception (58). Specifically, angry faces with direct gazes were overestimated compared to angry faces with averted gazes. As direct gaze is associated with a more direct indication of threat to one's person, these findings support enhanced attention or arousal in response to biologically relevant signals of threat.

Perceptual dynamics can serve as biologically relevant signals of approaching and receding objects and have been shown to engage defensive mechanisms (12, 221). Increases in the size of an object, indicative of approach, may be perceived as threatening and activate avoidance-related systems. The importance of looming objects as signals of threat is underlined by time-to-contact studies. Such studies present looming objects and require participants to press a button when they believed the object will “collide” with them, explicitly requiring a self-relevant focus. Looming objects on a collision course with an individual have been associated with faster time-to-contact responses than objects that would miss the individual (101). Furthermore, looming threats appear to move faster in approach than non-threatening objects, suggesting the importance of evaluating the threat to one's person in driving the distortions (e.g., 19, 20, 244). The underestimation of time-to-contact estimates has been shown to positively correlate with fear ratings (244). At the same time, spider and snake phobics underestimated time-to-contact estimates compared to a control group (20). Together these findings support the importance of the self-relevant nature of looming stimuli on time-to-contact estimates. While such studies do not explicitly measure time perception, it has been proposed that these effects may be driven by distortions in time perception (19, 20). This proposal is supported by evidence that looming objects are overestimated in duration compared to receding subjects (243, 246, 258).

Additional evidence for differential effects of approach and avoidance signals on time perception has been demonstrated in the auditory domain. The pitch of an approaching object is perceived as increasing while it approaches and as decreasing while it recedes (194), suggesting that pitch may also serve as a signal of approach/recession. When auditory sequences were presented with flanker tones that increased and decreased in pitch, empty intervals flanked by higher pitches were underestimated compared to empty intervals flanked by lower pitches (130). In this case, underestimation may reflect a perceived increase in the speed of an auditory object. Such an underestimation effect is adaptive during the approach of an object, as it could result in the enactment of a behavioral response earlier in time to mobilize an avoidance response. While self-relevant processing has been proposed as a unique mechanism underlying distortions in time perception (46, 222, 257, 258), it seems more parsimonious that such stimuli may modulate time perception via changes in arousal and attention.

**3.4.3. Individual differences**—Few studies of emotion-driven distortions of time perception have assessed the role of individual differences in modulating the magnitude and/or direction of temporal distortions. Positivity biases in temporal distortions have been observed for older adults (195), suggesting that changes in temporal distortions over the lifespan mirror changes in emotional development and emotional biases reported in the affective science literature. This positivity effect is likely mediated by different emotional influences on attention across the adult lifespan (164).

Consistent with the roles of fear and anxiety in modulating attention to threat, fearfulness, anxiety and nervousness have all been shown to predict greater overestimations of emotional distortions of time perception (e.g., 14, 25, 67, 239). Similarly, greater temporal overestimation has been observed for spider phobics (251), with the magnitude of this effect correlated with individual differences in the degree of self-reported fear (25). Such individual differences are consistent with enhanced attention biases towards threat in anxious and fearful individuals (e.g., 6, 15, 39).

The consideration of individual difference measures may be useful in studying emotional influences on time perception for a variety of reasons. The assessment of individual differences allows for a more ecologically valid assessment of emotional distortions of time perception. Utilization of individual difference measures may also help in the exploration of emotion-driven influences on time perception by allowing researchers to assess the contribution of certain mechanisms that may not be reflected in analyses of main effects. Thus, individual difference measures may provide a means to probe the contribution of certain mechanisms without requiring within-subjects manipulations.

#### 4. A new approach to studying emotion-driven temporal distortions

This review of emotional influences on time perception suggests that arousal and attention may both contribute to temporal distortions, but that these constructs do not necessarily map directly onto pacemaker and/or switch mechanisms. The utility of PA models has been their ability to make quantitative predictions for different modulations of timing performance. Nevertheless, such models as currently described do not appear to adequately predict the

roles of arousal and attention in modulating emotional effects on time perception. The existing literature on emotional distortions of time perception suggests that the reliance on such models has complicated interpretations due to attempts to define emotional effects by the mechanisms outlined by these PA models, and different interpretations of how these mechanisms relate to the constructs of arousal and attention. As PA models have also been criticized for their neurobiological implausibility (159, 245), the utility in adhering to such models for understanding underlying emotion-driven temporal distortions is unclear. We propose here a new theoretical approach (Fig. 2) which may be useful in advancing our understanding of the underlying processes associated with emotional distortions of time perception by more clearly demonstrating the complex relationship between arousal and attention underlying such distortions.

A critical component of this new model is the consideration of the time elapsed since the onset of the emotional event. We propose that an initial influence of emotional stimuli on time perception may be driven by the influence of salient stimuli on attention orienting. Such a mechanism is supported by evidence of a fast-acting and transient influence of attention cuing in driving temporal overestimations (75, 226, 264). As orienting responses can be modulated by emotion (23, 126), emotional arousal might modulate the magnitude of this initial influence on time perception, though emotional timing studies using temporal durations on this time scale (~50–150 ms) have been limited (231). Next, we propose a transient physiological arousal-driven increase in overestimation biases for durations up to a few seconds after an emotional stimulus onset. This physiological arousal effect is supported by the relatively short-lived nature of temporal overestimation effects that have typically been reported in emotional timing studies within a temporal range of 200 ms up to a few seconds (e.g., 7, 14, 65, 78, 196, 239). After a few seconds, physiological arousal effects may not be as clear, given the ephemeral increase in physiological arousal associated with brief emotional events that returns to baseline after a few seconds have elapsed. More dynamic or intense emotionally arousing events may extend the duration of physiological arousal effects (67).

During the time period in which time perception may be susceptible to changes in physiological arousal, temporal judgments may become increasingly influenced by the interaction of physiological arousal processes with more cognitively-driven processes involved in directing resource-sharing of sustained attention/working memory resources between emotional and timing processes. It has been suggested that arousal effects may be stronger than attention effects on time perception (225). We propose that this relationship may depend on the duration from emotional stimulus onset, such that physiological effects may be stronger initially, with attentional control processes becoming increasingly engaged as time elapses (43). The necessity of such controlled cognitive processes is highlighted by their role in both emotion appraisal/regulation (198) and in timing multi-second durations (144). The role of these processes in both emotional processing and timing suggests that both the duration from emotional stimulus onset and the duration of the stimulus to be timed may modulate the sharing of attention/working memory-related resources.

Importantly, the proposed model emphasizes that attention is not a unitary construct by demonstrating that the influence of orienting and resource-sharing processes on time

perception depends on contextual factors that contribute to the perceived emotional relevance of the stimulus to be timed (i.e., is the stimulus being timed emotional or relevant in predicting an emotional outcome or is it neutral in content?). If the stimulus to be timed is emotion-relevant, more attention is predicted to be devoted to processing its duration, resulting in a relative overestimation of its duration, whereas if it is not emotion-relevant but presented within the context of an emotional stimulus, less attention may be devoted to processing its duration, resulting in the relative underestimation of its duration.

While the resource-sharing component in the current model is driven by the nature of attention deployment, given the interactive relationship between arousal and attention, this attention deployment may not be independent of physiological arousal. For example, the degree to which a threatening stimulus increases physiological arousal may predict the degree to which cognitive resources must be engaged to down-regulate the emotional response. While the distinctions between the attentional orienting, physiological arousal, and cognitively-driven attentional phase of the proposed model are supported by evidence in the existing literature, these hypotheses remain to be explicitly tested.

In addition to this new theoretical model, we propose complementary guidelines for the study of emotional influences on time perception. A greater emphasis should be placed on using more clearly operationalized terms. Many of the limitations in interpreting effects of emotion on time perception have been the result of poorly defined constructs or conflicting definitions of constructs across studies. Researchers investigating emotional effects on time perception should be aware of differences in definitions of terms like ‘arousal’ and ‘attention’ within and between timing and affective/cognitive fields and should be careful not to conflate these terms in making predictions or interpreting findings.

We further recommend that researchers explicitly manipulate factors of interest and/or correlate factors of interest with resulting temporal distortions. For example, in attempting to dissociate between different proposed mechanisms of distortion, such as arousal or attention, it would be important to manipulate one factor independently from the other, such that different hypotheses can be made for the potential mechanisms of action. At the same time, while dimensions such as arousal and valence have been varied within emotional timing experiments, studies have rarely attempted to correlate levels of such dimensions with resulting distortions. Without demonstrating such a relationship between temporal estimates and measures of these emotional dimensions, it is difficult to conclude that such dimensions, rather than other differences between presented stimuli, are driving temporal distortions. Such correlations between proposed mechanisms of distortion and time perception are possible to assess within subjects, but examining individual differences between subjects may be a particularly fruitful approach in understanding the role a particular variable plays in driving emotional effects on time perception.

Finally, we propose that a better understanding of how emotions influence time perception will come from grounding hypotheses in affective and cognitive science. This approach will be important in bridging the gap between the timing and affective/cognitive science literatures to better determine how arousal and attention contribution to emotional distortions of time perception. The available literature suggests it will be important to

consider how additional factors, including valence, biological relevance, and individual differences modulate the relationship between arousal and attention in influencing time perception.

## 5. Putative neural mechanisms

In addition to advocating for exploration of the validity of our proposed theoretical model, we believe considering plausible neural mechanisms of temporal distortions that are consistent with this model will be important in constraining further studies of emotional distortion of time perception and advancing this burgeoning area of research. Few studies have directly investigated how emotional stimuli interact with neural timing systems to modulate temporal distortions (e.g., 56, 77, 89, 167, 181, 233, 240). A neurobiologically inspired model of time perception, namely the SBF model (4, 158, 159), in conjunction with known mechanisms by which affective stimuli modulate neural activity, may provide an important starting point for assessing how emotional stimuli modulate the inputs and/or outputs of neural timing systems. In this section, we will briefly review the SBF model and outline potential neural mechanisms of distortion within this model framework that would be consistent with the model of emotional distortions in time perception we have proposed.

### 5.1. Striatal Beat Frequency model

The SBF model of time perception accounts well for much of the pharmacological, neurophysiological, and psychological data on timing (e.g., 4, 146, 158, 259, 160–162, 200–203). The SBF model proposes that time perception is largely subserved by connections between the striatum, cortex, and thalamus, with the dorsal striatum being specifically crucial for proper timing abilities (49, 174, 177–179, 183). According to this model, the start signal to time a stimulus is marked by the phasic release of dopamine from dopaminergic midbrain projections to the cortex and dorsal striatum. This neurotransmitter release causes oscillatory cortical neurons to synchronize their firing and resets activity in the dorsal striatum. Thousands of these oscillating cortical neurons converge on individual medium spiny neurons (MSNs) in the striatum. As ensembles of cortical glutamatergic pyramidal neurons oscillate with varying intrinsic frequencies, their oscillations fall out of phase after the initial synchronizing action of dopamine. The different cortical oscillation frequencies result in input activation patterns to striatal neurons that vary with the time elapsed from the cortical synchronization event. Each MSN in the striatum is thought to integrate these oscillatory cortical inputs and respond to select patterns of cortical neuronal firing, based on previous reinforcement through long-term potentiation (LTP). In the striatum, cortical firing results in long-term depression, unless there is a concurrent release of dopamine in which case LTP may occur. This dopaminergic input, originating from the dorsal midbrain, and the LTP it induces along this pathway, may strengthen connections with cortical inputs active at the time of reinforcement. In this way, striatal neurons may become specialized in responding to specific temporal intervals, as the threshold for firing is reduced when the correct cortical inputs are present. Prior to learning, the delivery of an unexpected reinforcer causes a phasic surge of dopamine release in the striatum that may represent the dopaminergic input necessary for LTP (189). Striatal output influences activity of the thalamus via a direct and an indirect pathway, which have opposing effects on thalamic

activity. In turn, the thalamus has excitatory projections to the cortex, which then project back to the striatum, completing the cortico-thalamic-striatal loop (4). The direct and indirect pathways are suggested to play a role in the start, stop, and resetting of the timing process (159), though further research is necessary to elaborate the proposed roles of these pathways.

One of the major components of the SBF model of timing (4, 158, 159) is that integration and storage of various time intervals are proposed to occur through weighting of cortico-striatal synapses – although this proposal hasn't as yet been experimentally verified. Moreover, the SBF model is largely based on research with non-human animals, and does not specify the specific regions of the human cortex that may support interval timing in the seconds-to-minutes range. Various lines of evidence have implicated regions of the lateral frontal cortex in this function (e.g., 44, 141, 144, 151, 253), specifically emphasizing the role of the dorsolateral prefrontal cortex (dlPFC), pre-supplementary motor cortex (pre-SMA), and right inferior frontal cortex (IFC) (though parts of the parietal and temporal cortices have also been implicated (44)). The importance of the dlPFC in time perception (141, 144) is supported by its role in working memory and attention (e.g., 47, 127, 153, 193), as the processes underlying these functions appear to overlap (28). Functional and anatomical connections between the dlPFC and other regions of the timing circuitry, namely the midbrain and striatum, have also been established (13, 108). The pre-SMA and right IFC also may play a role in time perception abilities (e.g., 44, 151, 253), though it has been suggested that the pre-SMA may be more important in motor-related timing tasks than purely perceptual tasks (e.g., 44). In general, the cortical regions activated by timing tasks seem to depend to a large extent on the type of task employed. Further research is necessary to better understand these differences across studies. Nevertheless, these frontal regions may all receive dopaminergic input from midbrain structures (90, 108) and project back to the striatum (3, 108). It is thus possible that these regions, independently or interactively, make up the corticostriatal inputs associated with the timing functions proposed by the SBF model. Network connectivity analyses combined with specific behavioral manipulations could help in understanding the role these cortical structures play in the core network subserving timing abilities.

## **5.2. Modulation of timing networks by emotional stimuli: Orienting and physiological arousal**

Dopamine (DA) plays a critical role in the SBF model and the dopaminergic inputs to the circuitry proposed in the SBF model are likely substrates of emotional distortions of time perception. Separable effects of tonic and phasic dopamine levels have been demonstrated using a variety of methods (e.g., 81, 224). The SBF model proposes that tonic DA levels in the frontal cortex are important in setting the tonic firing rate of cortical projections to the striatum. Increases or decreases in this rate could thus result in increases or decreases in the rate of cortical oscillations, resembling a pacemaker-like mechanism. At the same time, phasic dopaminergic signals may have more transient effects on timing circuitry. Phasic dopamine release to the cortex and striatum has been demonstrated in response to appetitive and aversive stimuli, cues that predict such stimuli, and novel/salient stimuli (e.g., 21, 22, 224, 226). Phasic burst firing of dopaminergic neurons results in changes in dopaminergic

concentrations in target areas that last up to a few seconds (217). While phasic dopaminergic firing is thought to play a role in starting timing processes, such phasic DA bursts may also mediate the transient physiological arousal component of temporal distortion induced by emotional stimuli. The input pathway inducing phasic bursting of dopaminergic midbrain neurons could influence the latency after stimulus onset that these neurons fire, with earlier bursting resulting in increases in temporal estimates. Alternatively, in the same way that tonic dopamine may change the rate of cortical oscillation frequencies, transient increases in dopamine levels might transiently increase the rate of cortical oscillations, resulting in short-lived increases in temporal estimates. The presentation of emotional cues has been associated with phasic changes in DA release in the prefrontal cortex, which may be the neural mechanism driving short-term increases in temporal overestimation (e.g., 50, 80). Phasic changes in dopamine neuron firing rates can transiently change DA concentrations in target regions for a few seconds (217). The transient release of DA and quick return to baseline levels would be consistent with studies of emotion and time perception showing transient overestimation effects of emotional stimuli that are not observed with longer durations.

Further consideration of the neural correlates of emotional processing suggests the initiation of dopaminergic phasic bursting may be triggered by input from the central nucleus of the amygdala. The amygdala is known to respond rapidly to salient and emotional stimuli (e.g., 259). The central nucleus of the amygdala (CE) projects to the dopaminergic midbrain and this pathway is thought to play a role in orienting responses (e.g., 22). Thus, amygdala projections to the midbrain, which project to cortical and striatal regions, could influence temporal distortions at short temporal intervals by either changing the latency to initiate timing or by transiently increasing cortical oscillation. Amygdalar inputs are a plausible candidate for the initiation of this process as the amygdala responds to both positive and negative stimuli, although the extent of responding may be greater or more reliable for negative stimuli (e.g., 110). Such a pattern of responding would be consistent with observations that both positive and negatively valenced arousing stimuli generally result in transient overestimations of temporal durations, with the magnitude of this effect typically larger for negative stimuli. A study in rats supports a role for the CE in modulating time perception after the presentation of an emotional stimulus by showing that a fear cue produced a transient decrease in temporal precision in wild type rats but produced different effects on timing in rats with CE lesions (77).

Increases in NE are associated with salient threat cues and physiological arousal (155), potentially implicating activity in the locus coeruleus (LC) in modulating temporal distortions associated with an initial increase in physiological arousal. Interestingly, lesions of the NEergic bundle but not the dopaminergic VTA have been associated with the ablation of SCRs (261), further suggesting a role of the NE system in modulating physiological arousal-driven effects on time perception. The plausible role of this system is further supported by significant evidence that this neuromodulatory system enhances perception (155). Further investigations would be necessary to explore how NE might interact with timing circuitry.

### 5.3 Modulation of timing networks by emotional stimuli: Resource-sharing

It is clear that emotion can influence attention and working memory and that attention and working memory are important for encoding stimulus durations. We propose that the neural regions supporting the maintenance of attention and working memory for timing processes may be modulated by the presence of emotional stimuli. Cortical oscillations have been shown to be important for working memory and attention processes (e.g., 16, 31, 112, 218). Recently, it has been suggested that timing signals and working memory signals may be present in different bands of cortical oscillation frequencies and that, under optimal conditions, these different oscillation frequencies are synchronized (107). The presentation of an emotional stimulus that enhances attention to timing processes may increase synchronization of these signals resulting in increased temporal estimates. On the other hand, an emotional stimulus that distracts from timing processes may result in an uncoupling of these cortical oscillations, resulting in a decrement to working memory processes supporting timing. At the same time, recent theories suggest the striatum and PFC work interactively to influence working memory and attention (41), which implies that emotional influences at the level of the striatum could also result in changes in the allocation of attention/working memory resources that could, in turn, modulate time perception.

Emotional distractors modulate neural activity in working memory and attention areas, including regions of the prefrontal cortex and anterior cingulate cortex (e.g., 8, 59, 61, 79, 139, 227, 262). The reciprocal structural and functional connectivity between regions associated with emotional processing and negative anticipation, such as the anterior insula and amygdala (32), and working memory related regions (e.g., 60, 120, 122, 186) make the insula and amygdala plausible regions to modulate working memory and timing processes after the presentation of an emotional stimulus. Both the insula and amygdala have previously been implicated in temporal distortions (e.g., 56, 258), further supporting their potential role in modulating time perception during emotional events. The role of the amygdala in particular is supported by evidence that lesions of this area reverse distortions in time perception for longer temporal intervals in rodents during the presentation of emotional cues, consistent with the proposed role of this region in modulating working memory/attention resources during emotional experiences (181).

While the amygdala in particular is implicated in the processing of positive and negative stimuli (e.g., 109, 110, 191) it is possible that different neural regions could drive activity in working memory/attention regions for positive and negative stimuli, for distinct kinds of emotions, or for distinct timecourses of emotional events. For example, neural dissociations have been shown for the processing of phasic and sustained fear in the amygdala and the bed nucleus of the stria terminalis (BNST). This research, largely conducted in non-human animals, has suggested that longer periods of fear/anxiety become increasingly reliant on BNST activity (51). The BNST also has extensive connections to areas implicated in working memory/attention and timing processes, including prefrontal regions and the striatum. Further work will be needed to assess the mechanisms by which emotion can modulate working memory/attention in service or to the detriment of timing processes.

## 6. Implications and future directions

Studies of emotion and time perception have supported the idea that time perception is flexibly modulated by context and experience. Timing researchers assume that such modulations reflect processes that allow individuals to adaptively respond to changes in their environment (e.g., 37, 229), though the relationship between distortions of time perception and subsequent behaviors remains largely speculative. However, in support of the idea that time perception can influence subsequent cognitive processes, Dirnberger et al. (56) found that emotional stimuli perceived as longer in duration were also subsequently remembered better. While this memory effect may have been driven by a distinct pathway from time perception, with both pathways separately enhanced by arousal processes, the possibility that the perceived duration of an emotional event could contribute to its prioritization in memory is an attractive hypothesis with important implications. In general, further research devoted to demonstrating that emotional distortions in time perception support adaptive responding to environmental pressures is important to argue against the idea that these distortions are a psychological byproduct of the operation of other cognitive processes.

Evidence supporting the adaptive role of emotional temporal distortions could be particularly relevant to the study of fear and anxiety disorders. Despite the growing literature on emotion induced temporal distortions, there have been few investigations of how time is perceived in populations exhibiting aberrant fear and anxiety responses (e.g., 25, 251). In spider phobics, temporal overestimation in response to threat-relevant stimuli is enhanced. This evidence raises the possibility that enhanced fear and anxiety in individuals with disordered processing of emotional experiences might be associated with temporal distortions of a magnitude that is no longer adaptive and may further contribute to maladaptive behavioral responses.

An intriguing hypothesis is that the relationship between time perception and emotion is bidirectional, such that modulation of the perceived duration of an event could influence the intensity of the emotion associated with it or could affect the ability to properly learn relationships between emotional events and other stimuli. Few studies have examined how time perception may influence the experience of emotion but preliminary evidence does support the bidirectional influence of emotion and time perception. Pomares et al. (210) demonstrated that misleading individuals about the duration of a painful event modulated the perceived intensity of the pain. Even though the duration of the pain was actually the same, when participants were told that the duration of the painful event was longer, they judged the intensity of the pain to be higher.

A bidirectional relationship between time perception and emotion modulation may also suggest that temporal distortions during emotional events could contribute to conditioned learning and deficits in such learning processes. Learning the temporal relationship between an aversive outcome and a predictor of threat is critical for conditioning (87, 250). Aberrant timing processes associated with emotional events in individuals with fear and anxiety disorders might contribute to deficits in conditioned learning, consequently resulting in the maladaptive behaviors associated with fear and anxiety disorders. For example, due to aberrant timing processes, a neutral event and an unrelated aversive event might inaccurately

be perceived as temporally related, contributing to the documented phenomenon of fear generalization in anxious individuals. Another possibility is that distortions in time perception could cause emotional events to seem more unpredictable, resulting in enhanced anxiety. Evidence supporting negative consequences of temporal distortions on the perception of unpredictability would have important implications, given the aversiveness of unpredictability (116) and the integrality of uncertainty in contributing to anxiety (e.g., 105, 129). If temporal distortions contribute to aberrant responding and learning, then cognitive interventions designed to normalize or reduce these distortions could potentially serve as the basis for a novel therapeutic option for individuals with fear and anxiety disorders. One study providing preliminary evidence for the efficacy of this idea found that paying attention to time as a form of emotion regulation, rather than paying attention to the emotion of affective images, reduced physiological arousal (184). More work will be necessary to substantiate the adaptive role of temporal distortions and their proposed role in maladaptive responding and behaviors in clinical populations. Nevertheless, such work has the potential to further advance the study of emotional memory and emotion-related disorders, in addition to advancing our understanding of the nature and importance of time perception to affective and cognitive processes (c.f., 128, 223, 248, 255, 265).

## Acknowledgments

This work was supported, in part, by a NSF Graduate Research Fellowship to JIL. We would like to thank Cindy Lustig (University of Michigan) for comments on the manuscript.

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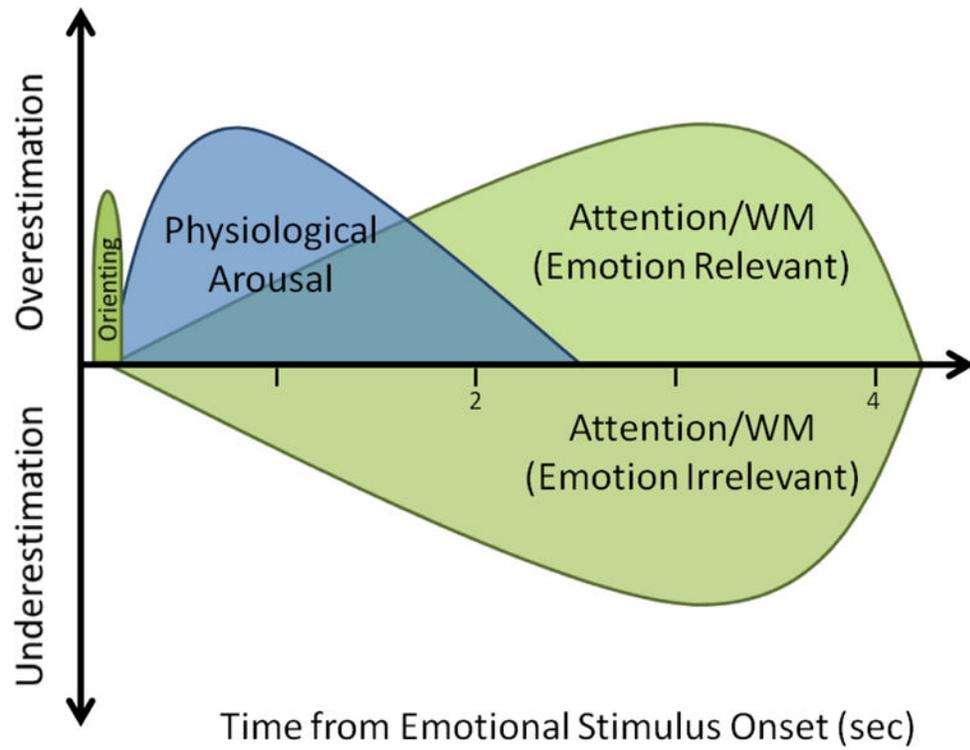
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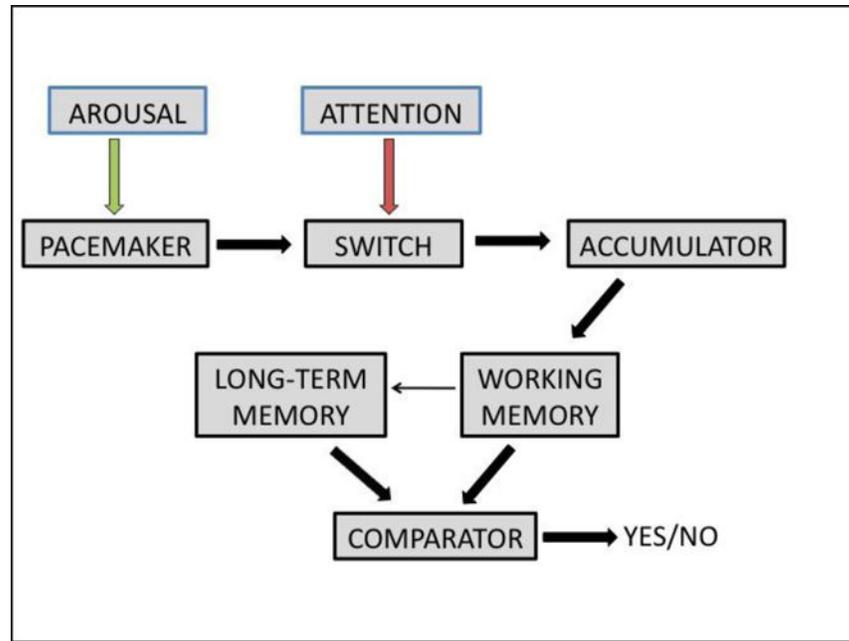
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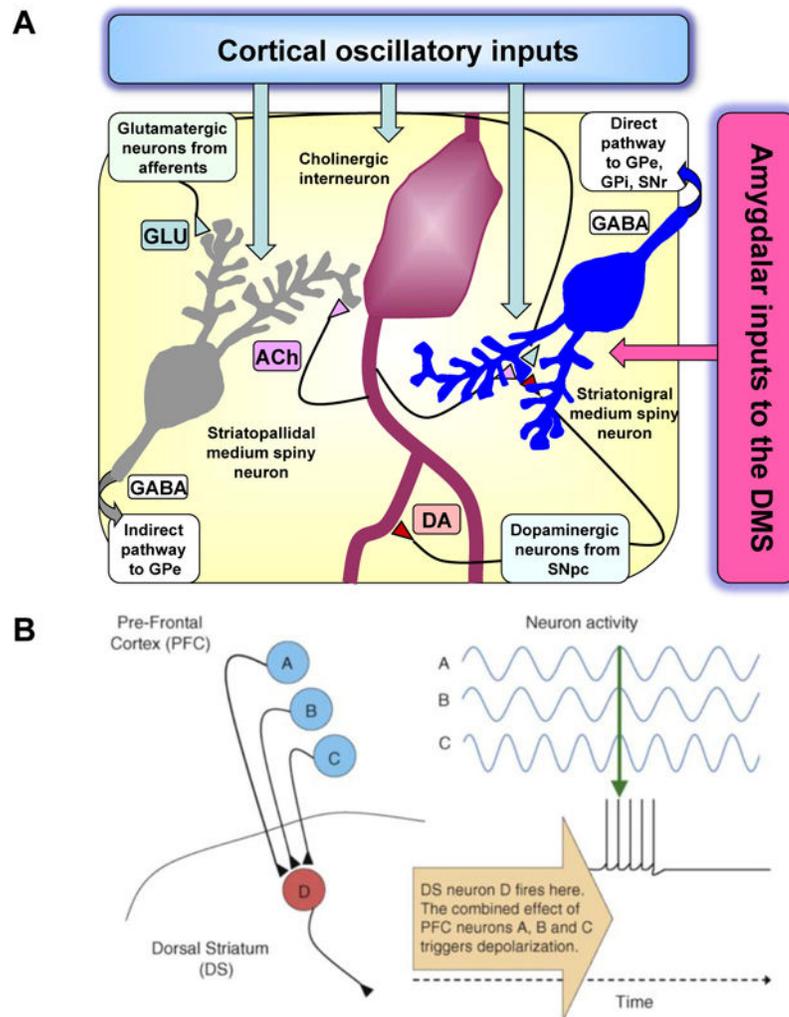
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**Fig. 1.** Proposed theoretical model of emotion-induced temporal distortions. This model illustrates the temporal dynamics underlying temporal distortions after the presentation of an emotional stimulus, the proposed relationship between arousal (blue) and attention (green) components during this evolving perceptual experience, and the importance of the way in which attention is directed in determining the influence of the attention components.



**Fig. 2.** Pacemaker-accumulator model of interval timing with the influences of arousal and attention added as proposed by the adherents of this type of information processing model. Colored arrows indicate enhancements of (green) and reductions of (red) temporal estimates. Adapted from Gibbon et al. (1984).



**Fig. 3.** **A)** Schematic representation of the relationship among oscillatory cortical inputs to striatal medium spiny neurons (MSNs), amygdalar inputs to the MSNs in the dorsomedial striatum (DMS) in the case of fear conditioning (54, 55), cholinergic interneurons, glutamatergic afferents, and dopaminergic axons projecting from the substantia nigra pars compacta (SNpc) to the striatum as specified by the Striatal Beat Frequency (SBF) model of interval timing (158). The direct output pathway to the globus pallidus – external (GPe) and internal (GPi) segments, and substantia nigra reticulata (SNr) as well as the indirect pathway to the GPe are indicated. Relevant neurotransmitters = acetylcholine (ACh), dopamine (DA),  $\gamma$ -aminobutyric acid (GABA), glutamate (GLU). **B)** Illustration of the coincidence detection property of striatal MSNs as specified by the SBF model of interval timing. In this model, the activation patterns of oscillatory neurons in the cortex (e.g. neurons A, B, and C) are monitored by MSNs (e.g. neuron D). These cortical neurons have patterns of activity that fire with different frequencies and converge onto MSNs. At the beginning of an interval, these oscillating neurons are synchronized and the status level of the MSNs reset by dopaminergic input from the ventral tegmental area and SNpc, respectively. The delivery of feedback at the target duration produces a pulse of dopamine thereby strengthening the

synapses in the dorsal striatum that are activated as a result of the beat- frequency pattern of these cortical neurons at that specific point in time as indicated by the green arrow. In this manner, mechanisms of long-term potentiation and long-term depression are used to strengthen and weaken synaptic weights in order to produce a record in memory of the target duration. Later, when the same signal duration is timed again, MSNs compare the current pattern of activation of these cortical neurons with the pattern stored in memory in order to determine when the target duration has been reached. When the clock and memory patterns match, as determined by coincidence detection, the MSNs fire to indicate that the interval has elapsed. Adapted from (1, 182).

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