

Emotional Modulation of Time Perception

by

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Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
Psychology & Neuroscience in the Graduate School
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ABSTRACT

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Abstract

Our perception of time is not veridical but rather is consistently modulating by changing dynamics in our environment. Anecdotal experiences suggest that emotions can be powerful modulators of time perception; nevertheless, the 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 and their interaction from the perspective of affective and cognitive science. The aim of this dissertation was to more clearly examine the role of arousal and attention in driving emotion-induced temporal distortions by explicitly manipulating and measuring these constructs using well-established timing procedures within the context of affective manipulations induced via classical conditioning and drug administration. Measures of physiological arousal and subjective measures of top-down attention to emotional stimuli were assessed both within and across subjects. The findings reported here suggest that current models of time perception do not adequately explain the variability in emotion-induced temporal distortions. Instead these findings provide support for a new theoretical model of emotion-induced temporal distortions proposed in the current manuscript that emphasizes both the unique and interactive influences of arousal and attention on time perception, dependent on temporal dynamics, event relationships, and individual differences. Collectively, these findings may point to plausible neurobiological

mechanisms of emotion-induced temporal distortions and have important implications for our understanding of how emotions may modulate our perceptual experiences in service of adaptively responding to biologically relevant stimuli.

Dedication

To my extraordinary parents for their endless support.

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Acknowledgements

I would like to express my gratitude to my advisors, Kevin S. LaBar and Warren H. Meck for giving me the freedom to explore my academic interests while providing invaluable feedback and pushing me to think independently and critically. I would also like to thank the other members of my committee, R. Alison Adcock and Timothy J. Strauman for their support and guidance throughout my graduate career. I would like to acknowledge the members of the LaBar lab for their support and camaraderie over the years. In particular, I would like to thank Phil Kragel for his never-ending patience, support and delightful negativity and a big thank you to Matt Fecteau for his help with manuscript figures! I would also like to thank my former labmate, roommate, and forever friend Vishnu Murty for his helpful feedback on this manuscript. Thank you to Emma Wu Dowd and Anastasia Kiyonaga for keeping me motivated as I finished this manuscript at Brain Camp. I would like to thank the friends who sat with me in numerous coffee shops as I wrote this dissertation—your companionship (and seeing daylight outside the LSRC basement) was critical to my success. And finally, thank you to all my friends and colleagues in the Center for Cognitive Neuroscience for making these past five years truly unforgettable. Words cannot express how lucky I feel to have been able to share this journey with all of you. I cannot believe how fast the time flew by...

1. Introduction

The ability to perceive time is critical for adaptively navigating through our everyday lives. We utilize timing processes to assess 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”. 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 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.

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 (Hare, 1963; Langer, Wapner, & Werner, 1961; Thayer & Schiff, 1975; but see Falk & Bindra, 1954). 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 (Langer et al., 1961). 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 (Hare, 1963; Langer et al., 1961), or were compared to estimates of empty temporal intervals (Thayer & Schiff, 1975), rather than 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 by using standardized emotional stimuli, allowing for more mechanistic interpretations of resultant temporal distortions. Such studies have frequently interpreted their findings within the context of pacemaker-accumulator models of time perception (Gibbon, Church, & Meck, 1984; Treisman, 1963; Zakay & Block, 1997). However, a review of

the existing literature suggests that such interpretations have been limited by a variety of factors.

In this chapter, I will review the basic tenets of pacemaker-accumulator 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, I will argue that using pacemaker-accumulator models to interpret the extant literature on emotional effects on time perception is limiting due to different interpretations of pacemaker-accumulator models and different operational definitions of plausible temporal distortion mechanisms across timing and affective/cognitive science fields. After a review of the current literature, I will propose a new model of emotional influences on time perception that may provide a better framework for understanding underlying mechanisms of temporal distortions.

1.1. Pacemaker-Accumulator Models of Time Perception: Arousal, Attention, and Working Memory Mechanisms

Pacemaker-accumulator models of time perception (Figure 1; Gibbon et al., 1984; Treisman, 1963; Zakay & Block, 1997) posit that there are three main stages in making a temporally based judgment - clock, memory, and decision-making. During the clock phase, 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 passed during the timing of a particular interval. A switch controls the transfer of pulses from the pacemaker to the accumulator (Lejeune, 1998). When the switch closes, pulses

pass into the accumulator; pulses are blocked when the switch is open. In the memory phase, 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 phase, 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 expectancy 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 (Gibbon, 1977).

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 manuscript.

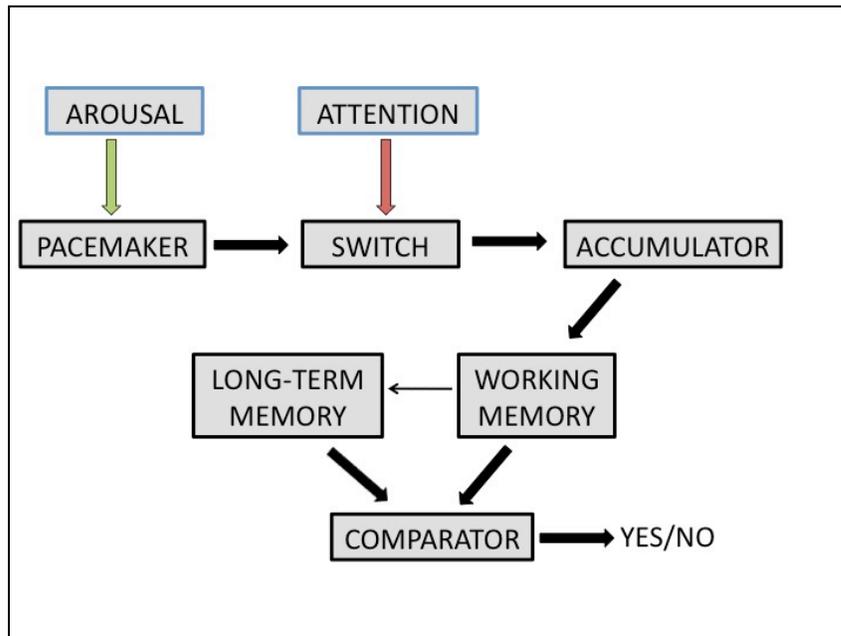


Figure 1: Information-processing model of interval timing with the influences of arousal and attention added as suggested by pacemaker-accumulator models. Colored arrows indicate enhancements of (green) and reductions of (red) temporal estimates. Adapted from Gibbon et al. (1984).

Within the time perception literature, arousal is often 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 a specific temporal interval. 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 (Gibbon, 1977).

Behavioral and pharmacological manipulations in humans and non-human animals have produced changes in clock speed that have been labeled as arousal effects, based on the operational definition of arousal as an increase in pacemaker rate or clock speed. Administration of dopaminergic drugs in non-human animal models has been shown to produce effects consistent with changes in pacemaker rate, demonstrating proportional shifts in timing functions (Meck, 1983). Methamphetamine, a psychostimulant that increases the effective level of dopamine in the synapse, also increases clock speed, resulting in overestimations of duration (Maricq & Church, 1983; Meck, 1983). In contrast, haloperidol administration, which decreases the effective level of dopamine in the synapse, decreases clock speed, resulting in underestimations of duration (Maricq & Church, 1983; Meck, 1983). Studies in humans have also shown changes in timing performance after dopaminergic manipulations (Arushanya, Baida, Mastiyagin, Popova, & Shikina, 2003; Lake & Meck, 2013; Rammsayer, 1993, 1997, 1999), consistent with changes in the speed of an internal clock. Increases in body temperature also result in proportional increases in temporal durations, whereas decreases in temperature result in underestimation of duration (Wearden & Penton-Voak, 1995). Lastly, visual flickers or auditory clicks preceding temporal judgments have been shown to increase the rate of the pacemaker (Droit-Volet & Wearden, 2002; Penton-Voak, Edwards, Percival, & Wearden, 1996). While these findings have been utilized 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 (Droit-Volet & Meck, 2007), 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 chapter.

Attention, on the other hand, 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 switch regulating the flow of pulses into the accumulator by alternating between an open and a closed state. 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. Latency effects are independent of stimulus duration, resulting in distortions of temporal estimates that are additive, rather than proportional, across stimulus durations (Lejeune, 1998; Meck & Benson, 2002). In other words, 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 should not affect temporal sensitivity (Gibbon & Church, 1984). On the other hand, if attention resources are divided throughout the timing of a stimulus, the switch is said to ‘flicker’ between an open and a closed state (Lui, Penney, & Schirmer, 2011; Lustig & Meck, 2001, 2011; Penney, Allan, Meck, & Gibbon, 1998;

Penney, Gibbon, & Meck, 2000). 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 performance were less likely to be observed.

Many studies provide evidence of temporal distortions resembling those predicted by attention models of time perception within the tradition of pacemaker-accumulator models (Buhusi & Meck, 2002, 2009; Zakay & Block, 1997). In rats, the presentation of a warning signal in a different modality from the stimulus to be timed led to underestimations of duration (Meck, 1984). This warning signal is thought to prepare the animal for timing the signal and, thus, when the signal is in a different modality, the need to reorient attention increased 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 certain temporal interval had elapsed, the rats responded later than the duration of the trained interval (Penney, Holder, & Meck, 1996). The magnitude of this effect across interval durations suggested an additive rather than a

proportional shift, thus 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., Arnsten & Contant, 1992; Robbins, 1984). On the other hand, studies have demonstrated 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 (Coull, Vidal, Nazarian, & Macar, 2004), supporting a flickering switch mechanism of temporal distortion.

More recent instantiations of pacemaker-accumulator models of time perception support an influence of resource-sharing on time perception but suggest 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 (Buhusi & Meck, 2009). 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, while 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 but directed either towards internal representations or external representations, respectively (Awh & Jonides, 2001; Chun, 2011; Gazzaley & Nobre, 2012; Kiyonaga & Egner, 2013). Based on such theories, the influence of resource-sharing on time perception should involve 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.

1.2 Complications with using Pacemaker-Accumulator Models as Framework for Emotional Timing Studies

The emotional timing literature has largely relied on pacemaker-accumulator 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, implementations of pacemaker-accumulator models have varied across studies, with different interpretations presented for 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.

1.2.1 Problems with interpretations of pacemaker and switch-like mechanisms

Problems with interpretations of emotional distortions of time perception within the pacemaker-accumulator 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 pacemaker-accumulator 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 (Droit-Volet, Brunot, & Niedenthal, 2004; Effron, Niedenthal, Gil, & Droit-Volet, 2006; Gil, Niedenthal, & Droit-Volet, 2007; Tipples, 2010).

A second interpretation of pacemaker-like effects has been focused on the scalar property of the pacemaker, such that increases in the pacemaker rate result in proportional increases in temporal estimates across durations (Droit-Volet, Bigand, Ramos, & Bueno, 2010; Droit-Volet et al., 2004; Droit-Volet, Fayolle, & Gil, 2011; Droit-Volet, Mermillod, Cocenas-Silva, & Gil, 2010; Gil & Droit-Volet, 2009, 2011a, 2012; Grommet et al., 2011). Nevertheless, differences in the temporal task employed have influenced interpretations in favor or against a pacemaker-like mechanism. For example, in Droit-Volet et al. (2004), 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 were interpreted as a switch latency or attention effect (Gil & Droit-Volet, 2011b; Grommet et al., 2011). However, considering the constraints associated with this procedure is important when testing for pacemaker-like effects across durations (Lake, LaBar, & Meck, 2014). 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 these comparisons 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 (Droit-Volet et al., 2004) or of suggesting that the lack of such an interaction is evidence against a pacemaker mechanism (Gil & Droit-Volet, 2011b; Grommet et al., 2011) is questionable when the magnitude of estimates are assessed within a single temporal range.

An alternative strategy when using a bisection procedure that has been implemented is the comparison of temporal distortion magnitudes at the point of subjective equality (PSE) across multiple duration ranges (Droit-Volet & Meck, 2007; Grommet et al., 2011; Lake et al., 2014; Merchant, Harrington, & Meck, 2013). Some emotional timing studies using this approach have interpreted such an analysis as support for a pacemaker-like mechanism when the magnitude of PSEs across duration ranges increases (Droit-Volet et al., 2011; Droit-Volet, Mermillod, et al., 2010). Nevertheless, other studies have not shown increases in the magnitude of PSEs across duration ranges (Droit-Volet, Bigand, et al., 2010; Gil et al., 2007; Grommet et al., 2011; Shi, Jia, & Muller, 2012). The lack of proportional effects has alternately been interpreted as evidence against a pacemaker-like mechanism (Droit-Volet, Bigand, et al., 2010; Grommet et al., 2011; Shi et al., 2012) or as evidence that a pacemaker-like effect is short-lived (Gil et al., 2007).

Other emotional timing studies have used temporal reproduction or estimation procedures and have explored proportional increases in temporal estimates across durations. These studies have frequently reported decreases in relative (compared to a neutral condition) or absolute (compared to physical duration elapsed) temporal overestimation with increases in temporal durations (Angrilli, Cherubini, Pavese, & Mantredini, 1997; Bar-Haim, Kerem, Lamy, & Zakay, 2010; Noulhaine, Mella, Samson, Ragot, & Pouthas, 2007), inconsistent with a strictly pacemaker-like mechanism. At the same time, studies using such methods have sometimes demonstrated that shorter

durations were overestimated while longer durations were underestimated (Lambrechts, Mella, Pouthas, & Noulhiane, 2011; Tamm, Uusberg, Allik, & Kreegipuu, 2014), regardless of their emotional content. Such a pattern of responses is consistent with Vierordt's law, which suggests that perceptions or judgments of durations are biased towards the mean of the temporal distribution (Gu & Meck, 2011). It is thus unclear if an interaction exists between the emotional content of a stimulus and such biases on temporal judgments or if such biases may obscure the influence of emotion on temporal estimates/reproductions.

In addition to differing interpretations of what constitutes a pacemaker effect, studies have relied on different definitions of switch-like effects within the context of pacemaker-accumulator models. The operation of a switch-like mechanism has been supported if temporal durations were underestimated for emotional compared to neutral stimuli (Tipples, 2010). On the other hand, other studies have allowed for a bidirectional influence of switch latency on time perception. Based on such assumptions, 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 increases or decreased temporal estimates (Grommet et al., 2011; K. H. Lee, Seelam, & O'Brien, 2011; Shi et al., 2012). Nevertheless, some pacemaker-accumulator 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 (Buhusi & Meck,

2009; Lejeune, 1998; Penney et al., 2000; Zakay & Block, 1997). These mechanisms have been largely ignored in much of the emotional timing literature, although some studies have recognized the potential influence of such factors (Lui et al., 2011; Matthews, He, Buhusi, & Buhusi, 2012).

From this brief overview, it is clear that dissociating pacemaker and switch-like mechanisms of distortion within the emotional timing literature has been limited by different interpretations of pacemaker-accumulator models. Incorporating all current views of the plausible manipulations of the pacemaker and switch suggests that dissociating the influence of these mechanisms 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 that this review highlights is that mechanistic interpretations of 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 while holding the other factor constant to more clearly demonstrate that the proposed mechanism was responsible for the observed effects. However, further investigation of emotional timing studies suggests that such manipulation/measurement of these factors might be complicated by the differing definitions of arousal and attention within and across the fields of time perception and affective science.

1.2.2 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 effects on time perception and 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 two multifaceted constructs with complicated interactions.

Many different processes are associated with arousal within an affective science perspective (Hanoch & Vitouch, 2004). Arousal is characterized by both central and peripheral effects on the nervous system (Ledoux, 2012). The activity and release of modulatory neurotransmitters in the brain associated with increased arousal have widespread effects on cognition and behavior (LeDoux, 2000). For example, arousal-related norepinephrine and acetylcholine release are thought to modulate memory and attention processes (Hasselmo & Sarter, 2011; Kensinger, 2009), as well as increase vigilant behaviors (Davis & Whalen, 2001). The hypothalamic-pituitary-adrenal (HPA) axis releases the hormone cortisol into circulation (Ledoux, 2012). At the same time, arousal causes changes in autonomic activity, shifting away from homeostasis towards the activation of the sympathetic nervous system, associated with changes in heart rate, pupil dilation, and skin conductance responses (SCRs). A cognitive component of arousal is also reflected by subjective ratings of arousal, which likely reflect appraisal-like assessments of affect intensity and biological relevance (Noulhaine et al., 2007).

Different arousal-related responses have unique time courses. Central release of neuromodulators generally occurs rapidly, while peak changes in HPA axis release of cortisol generally occurs minutes after the emotionally arousing event. Physiological changes are also relatively fast-acting, with differential responses evident within up to a few seconds from the onset of an emotional event. The relative time courses and relationships between emotion-related changes in physiological and subjective arousal have been debated within the field of affective science. While positive correlations between physiological arousal and subjective arousal processes are common (e.g., Salimpoor, Benovoy, Longo, Cooperstock, & Zatorre, 2009), studies have also shown that these processes can be separately modulated (Diskin & Hodgins, 2003; Gross, 1998; Papciak, Feuerstein, & Spiegel, 1985; Sloan, Strauss, Quirk, & Sajatovic, 1997), suggesting that they may reflect unique components of an emotionally arousing event.

The construct of attention is also multifaceted. Attention orienting is generally divided into exogenous and endogenous component processes (Corbetta & Shulman, 2002). Exogenous attention is stimulus-driven, reflexively captured by salient stimuli, and controlled by a ventral frontoparietal network, whereas endogenous attention is goal-directed, serving internally generated objectives or expectations and controlled by a more dorsal frontoparietal network (Corbetta & Shulman, 2002; Theeuwes, 1994; Yantis, 1993). These processes are also associated with unique time courses. Specifically, exogenous attention is fast-acting, while endogenous attention is somewhat slower-acting with latencies of about 100- 150 ms (Theeuwes, Atchley, & Kramer, 2000). After

attention orienting, cognitive processes are necessary to either shift attention away from a stimulus (Wager, Jonides, & Reading, 2004) or to maintain attention to it (Sarter, Givens, & Bruno, 2001). Cognitive processes underlying sustained attention are necessarily recruited more heavily as a temporal interval elapses (Coull, 1998).

In addition to the multifaceted nature of arousal and attention within affective/cognitive science, theories of emotional arousal and attention within this tradition suggest that while these constructs are unique, they frequently interact such that emotional arousal can influence attention (and vice versa), with the nature of these interactions modulated by a variety of factors, including the biological relevance of 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 (Kensinger, 2009; Mather, 2007; Mather & Sutherland, 2011). 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 (Ohman, Flykt, & Esteves, 2001). 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 (Mogg & Bradley, 1999). 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 results, while if attention to a negatively arousing stimulus distracts from the ability to perform a task, emotion can impair performance.

The influence of positively 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 (Fredrickson & Branigan, 2005). 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 (Brosch, Sander, Pourtois, & Scherer, 2008). Another explanation for the differences observed for studies of positive emotion could be the biological relevance of the emotional stimuli utilized (Vuilleumier & Huang, 2009). When high approach-motivated positive affect was induced (which was likely accompanied by enhanced arousal), a narrowing of attention was also observed (Gable & Harmon-Jones, 2008).

These attention cuing studies reflect rather fast-acting interactions between arousal and attention within the millisecond duration range, but, importantly, such

processes also interact at longer latencies during sustained attention (Coull, 1998; Sarter et al., 2001). Top-down attention control processes can modulate physiological arousal (Ochsner & Gross, 2005). At the same time, the volitional modulation of physiological arousal improves sustained attention performance (O'Connell et al., 2008), 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 task dimensions, such that arousal may enhance attention maintenance when the arousing stimulus is task-relevant, while the maintenance of attention to a neutral stimulus is impaired by a negatively arousing distractor (Dolcos & McCarthy, 2006).

In addition to the potential role of valence and/or the biological or task relevance of the emotionally arousing event in influencing how that event directs attention, the temporal dimensions of the task also 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 did not impair detection at an 800 ms lag (S. D. Smith, Most, Newsome, & Zald, 2006). 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, while longer lags (800-1000 ms) have improved accuracy (Bocanegra & Zeelenberg, 2009; Ciesielski, Armstrong, Zald, & Olatunji, 2010). 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 (Morriss, Taylor, Roesch, & van Reekum, 2013).

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 Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & van, 2007; Cisler & Koster, 2010; Puliafico & Kendall, 2006). Personality factors have also 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 (Derryberry & Reed, 1994). It has been suggested that these biases reflect self-relevance or familiarity (Compton, 2003). Individual differences in emotional recovery or automatic emotion regulation may also modulate the influence of emotionally arousing stimuli on attention at different time points (Morriss et al., 2013). Finally, 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 (Mather & Carstensen, 2003, 2005). Together this evidence supports the interactive relationship between emotional arousal and attention and its modulation by a variety of factors, namely biological/task relevance of the emotionally arousing stimulus, temporal dynamics, and individual differences.

1.2.3 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 the role of arousal in modulating emotion-driven temporal distortions. However, the evidence used to support this idea is varied. Firstly, 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 influence of arousal (Droit-Volet et al., 2004; Droit-Volet, Mermillod, et al., 2010; Droit-Volet, Ramos, Bueno, & Bigand, 2013; Gil & Droit-Volet, 2012; Grondin, Laflamme, & Gontier, 2014; Yamada & Kawabe, 2011). Complications resulting from such interpretations are multifold. Primarily, complications stem from different interpretations of what constitutes a pacemaker effect, as illustrated in Section 1.2.1. Specifically, different interpretations of pacemaker effects have led to different criteria

used to support the role of arousal in emotion-driven temporal distortions. At the same time, the assumption of a direct correspondence between the pacemaker and arousal does not require an explicit demonstration that changes in arousal actually change time perception. Interpretations in favor of or against the role of arousal have sometimes been based on nothing more than a demonstration that the presentation of an emotional stimulus increases or decreases temporal estimates (Fayolle & Droit-Volet, 2014; Gil & Droit-Volet, 2011b). Many studies have lacked a direct manipulation of arousal separate from other components of the emotional stimulus, including 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 (Folta-Schoofs, Wolf, Treue, & Schoofs, 2014). Almost all studies of emotional influences on time perception using emotional pictures or sounds have not reported controlling for basic perceptual features (Angrilli et al., 1997; Gil & Droit-Volet, 2012; Grommet et al., 2011; Grondin et al., 2014; Lui et al., 2011; Noulhaine et al., 2007; S. D. Smith, McIver, Di Nella, & Crease, 2011).

Other emotional timing studies have supported the contribution of arousal to emotion-induced temporal distortions not based on pacemaker-accumulator model predictions, but on subjective ratings of arousal (Angrilli et al., 1997; Buetti & Lleras, 2012; Droit-Volet et al., 2011; Droit-Volet, Mermillod, et al., 2010; Gil & Droit-Volet, 2012; Grommet et al., 2011; Lui et al., 2011; Mella, Conty, & Pouthas, 2011; Noulhaine et al., 2007; Shi et al., 2012; S. D. Smith et al., 2011) and/or physiological arousal

measures (Angrilli et al., 1997; Droit-Volet, Mermillod, et al., 2010; Mella et al., 2011) 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. Thus, concluding that arousal contributes to temporal distortions may reflect different underlying relationships depending on the component measure of arousal assessed.

Studies relying on different emotional stimuli have also had different interpretations of how distortions relate to arousal processes. Many studies using emotional faces have suggested that emotional arousal increases temporal overestimation, with the degree of overestimation related to the magnitude of arousal, as evidenced by greater overestimation with more arousing emotional expressions, such as fear and anger (Bar-Haim et al., 2010; Doi & Shinohara, 2009; Droit-Volet et al., 2004; Effron et al., 2006; Fayolle & Droit-Volet, 2014; Gil & Droit-Volet, 2012; Gil et al., 2007; Tipples, 2011; Young & Cordes, 2012, 2013). On the other hand, other studies, mainly using emotional pictures and sounds rated as high versus low arousal, have suggested that arousal may not have a singular, increasing influence on time perception but rather, the level of arousal may determine the underlying mechanism that drives temporal distortion (Angrilli et al., 1997; Buetti & Lleras, 2012; Noulhaine et al., 2007). For example, Angrilli et al. (1997) proposed the often cited idea that low levels of arousal favor the reliance on an attention mechanism, whereas high levels of arousal rely on an “emotion-

driven” mechanism. These studies have provided varying interpretations of how such effects might correspond to the mechanisms outlined by pacemaker-accumulator models.

Interpretations of what constitutes an arousal effect have also been based on the proposed time course of arousal effects. 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 latencies, and thus effects, occurring for shorter temporal durations could not be driven by arousal (Lui et al., 2011; Schirmer, 2011). On the other hand, 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 (Angrilli et al., 1997; Bar-Haim et al., 2010; Noulhaine et al., 2007). It is clear that these conflicting interpretations are the result of differing definitions of arousal and the subcomponents of arousal being considered.

Interpretations of what constitutes an attention effect have also 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 (Gil & Droit-Volet, 2011b; Tipples, 2010), whereas 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 (Grommet et al., 2011; K. H. Lee et al., 2011; Shi et al., 2012). It has also been proposed that attention effects could be driven by changes in both pacemaker rate and switch

latency effects (Lambrechts et al., 2011; Tse, Intriligator, Rivest, & Cavanagh, 2004). Attention effects have been supported for effects thought to reflect resource-sharing between emotional processes and timing (Faure et al., 2013; Matthews et al., 2012; Meck & Macdonald, 2007). All of these interpretations are in addition to the attention mechanisms which have been supported for low arousal emotional stimuli (Angrilli et al., 1997) or for temporal distortions occurring at short (Lui et al., 2011; Schirmer, 2011) or long durations (Angrilli et al., 1997; Bar-Haim et al., 2010; Noulhaine et al., 2007), as discussed above. Collectively, despite the unique interpretations of arousal and attention, this review demonstrates that, in contrast to theories of affective/cognitive science, emotional timing studies have largely assumed that arousal and attention are independent and unrelated processes.

On the other hand, a few studies have provided evidence that arousal and attention processes may interact to influence time perception. For example, Mella et al. (2011) 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. (2011) 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 (Droit-Volet, 2013; Gil & Droit-Volet, 2009, 2011a; Schwarz, Winkler, & Sedlmeier, 2013) but have not suggested 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 that these constructs reflect the same underlying processes mechanisms. Pacemaker-accumulator models of time perception do not currently allow for more detailed predictions for emotional effects on time perception that reflect the potential influence of different arousal or attention components and 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 influence temporal estimates. This assessment clearly demonstrates that more standardized operational definitions are necessary to assess the degree to which the different processes associated with emotional arousal and attention influence emotion-induced temporal distortions. To this end, measures of factors of interest 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.

1.2.4 A consideration of other proposed modulatory factors

The conflicting conclusions reviewed thus far across emotional timing studies and the differences outlined between pacemaker-accumulator models and theories of emotion and attention within the affective/cognitive science tradition suggest that pacemaker-accumulator 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 attention mechanisms of temporal distortions, researchers have also suggested emotion-driven temporal distortions may not be exclusively driven by such mechanisms (Droit-Volet, Fayolle, Lamotte, & Gil, 2013; Droit-Volet & Gil, 2009), 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, I 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 factors may help clarify the nature of emotion-induced temporal distortion mechanisms.

1.2.4.1 Valence

Multiple studies have reported differential effects of positive 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 (Angrilli et al., 1997; Buetti & Lleras, 2012; Droit-Volet, Fayolle, et al., 2013; Mereu & Lleras, 2013; Noulhaine et al., 2007; S. D. Smith et al., 2011; Yamada & Kawabe, 2011). Nevertheless, differences in physiological arousal responses to positive and negative stimuli are sometimes found despite stimuli being rated as equally arousing (e.g., Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Pastor et al., 2008), 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 (McGraw, Larsen, Kahneman, & Schkade, 2010). This 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 (IAPS; Lang, Bradley, & Cuthbert, 1999) and the International Affective Digitalized Sounds System (IADS; Bradley & Lang, 1999), which both use bipolar scales of valence and arousal. On the other hand, differences in the biological relevance of negatively and positively valenced stimuli utilized may differentially influence attention during the timing task. As noted previously, high approach-motivated positive affect stimuli have similar influences on attention as highly arousing threat-relevant negative stimuli (Gable & Harmon-Jones, 2008).

1.2.4.2 Biological Relevance

The influence of biological relevance in modulating attention is also likely to underlie different effects of specific emotions with equivalent arousal levels on time perception. For example, Tipples (2008) found that angry faces were overestimated compared to fear faces with comparable levels of reported subjective arousal. The author suggested 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 (Droit-Volet & Meck, 2007; Gil, Rousset, & Droit-Volet, 2009; Grondin et al., 2014; Shi et al., 2012; but see Gil & Droit-Volet, 2012). While disgust is a biologically relevant and adaptive emotion, it serves a biological function distinct from other negative emotions (Chapman & Anderson, 2012) and thus may elicit a unique influence on temporal distortion. A role for disgust in differentially modulating attention has been proposed (Gil & Droit-Volet, 2012; Gil et al., 2009). 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, likely 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 (Doi & Shinohara, 2009). 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 also serve as biologically relevant signals of approaching and receding objects and have been shown to engage defensive mechanisms (Bach, Neuhoff, Perrig, & Seifritz, 2009; Schiff, Caviness, & Gibson, 1962). 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 have presented looming objects and required participants to press a button when they believed the object will "collide" with them, explicitly requiring a self-relevant focus. In such studies, 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 (Gray & Regan, 2006).

Furthermore, looming threats appear to move faster in approach than do non-threatening objects, suggesting the importance of the evaluation of threat to one's person in driving the distortions (Brendel, DeLucia, Hecht, Stacy, & Larsen, 2012; Brendel, Hecht, DeLucia, & Gamer, 2014; Vagnoni, Lourenco, & Longo, 2012). The underestimation of time-to-contact estimates has been shown to positively correlate with fear ratings (Vagnoni et al., 2012). At the same time, spider and snake phobics underestimated time-

to-contact estimates compared to a control group (Brendel et al., 2014). 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 such effects may be driven by distortions in time perception (Brendel et al., 2012; Brendel et al., 2014). This proposal is supported by evidence that looming objects are overestimated in duration compared to receding subjects (Tse et al., 2004; van Wassenhove, Buonomano, Shimojo, & Shams, 2008; Wittmann, van Wassenhove, Craig, & Paulus, 2010).

Evidence for differential effects of approach and avoidance signals on time perception have also 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 (Neuhoff & McBeath, 1996), 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 (Lake et al., 2014). 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 (Craig, 2009; Schirmer, 2011;

Wittmann & van Wassenhove, 2009; Wittmann et al., 2010), it seems more parsimonious that such stimuli may modulate time perception via changes in arousal and attention.

1.2.4.3 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 (Nicol, Tanner, & Clarke, 2013), 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 driven by different influences of emotions on attention across the adult lifespan (Mather & Carstensen, 2003).

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 (Bar-Haim et al., 2010; Buetti & Lleras, 2012; Droit-Volet et al., 2011; Tipples, 2011). Similarly, greater temporal overestimation has been observed for spider phobics (Watts & Sharrock, 1984), with the magnitude of this effect correlated with individual differences in the degree of self-reported fear (Buetti & Lleras, 2012). Such individual differences are consistent with enhanced attention biases towards threat in anxious and fearful individuals (Amir, Elias, Klumpp, & Przeworski, 2003; Bar-Haim et al., 2007; Cisler & Koster, 2010).

Considering individual difference measures may be useful in studying emotional influences on time perception for a variety of reasons. Firstly, 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.

1.3 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 distortions in time perception, but that these constructs do not necessarily map directly onto pacemaker and switch mechanisms. The utility in pacemaker-accumulator 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 time perception. The current review of the existing literature on emotional distortions of time perception suggests that the reliance on such models has led to complications in interpretation driven by attempts to define emotional effects by the mechanisms outlined by these models and different interpretations of how these mechanisms relate to the constructs of arousal and attention. As pacemaker-accumulator models have also been criticized for their neurobiological implausibility (Matell & Meck,

2004), the utility in adhering to such models for understanding underlying emotion-driven temporal distortions is unclear. I 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.

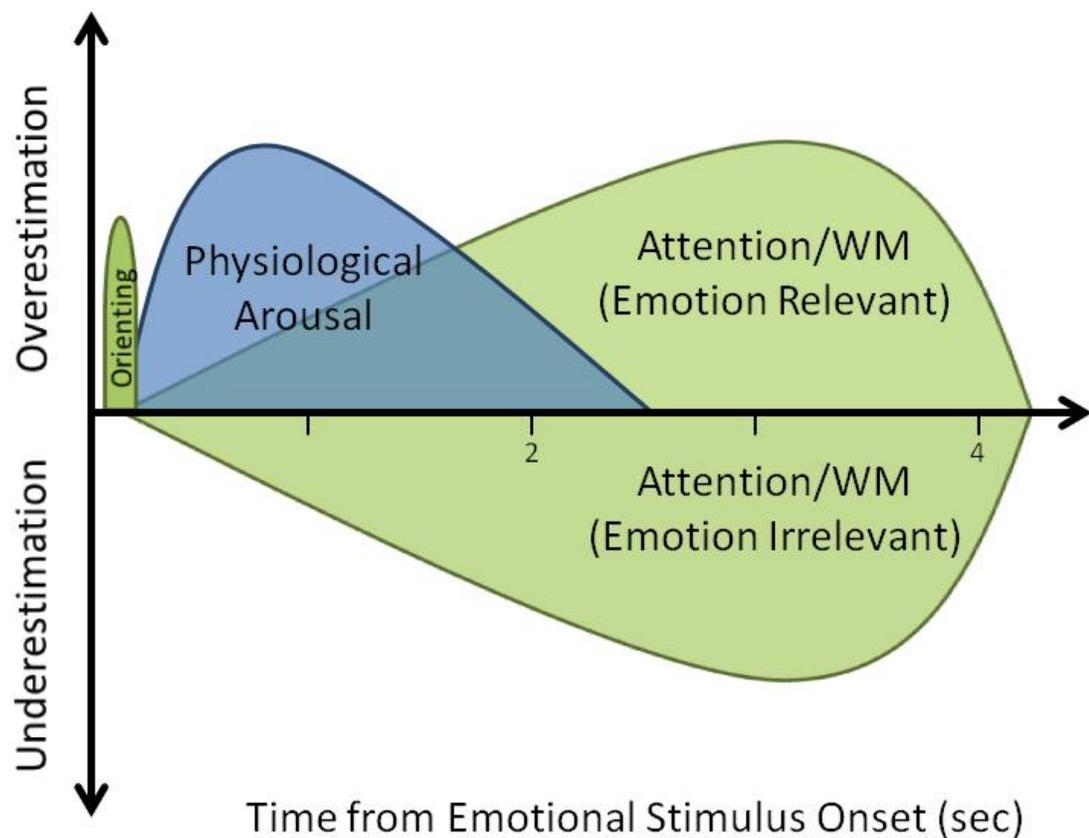


Figure 2: Proposed theoretical model of emotion-induced temporal distortions. This model illustrates the temporal dynamics underlying temporal distortions after the presentation of an emotional stimulus, the proposed relationship between arousal (blue) and attention (green) components during this evolving perceptual experience, and the importance of the way in which attention is directed in determining the influence of the attention components.

A critical component of this new model is the consideration of the time elapsed since the onset of the emotional event. I 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 (Enns, Brehaut, & Shore, 1999; Seifried & Ulrich, 2011; Yeshurun & Marom, 2008). As orienting responses can be modulated by emotion (Brosch, Pourtois, Sander, & Vuilleumier, 2011; Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2004), emotional arousal might modulate the magnitude of this initial influence on time perception. Next, I 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., Angrilli et al., 1997; Bar-Haim et al., 2010; Droit-Volet et al., 2004; Fayolle & Droit-Volet, 2014; Noulhaine et al., 2007; Tipples, 2011). After a few seconds, physiological arousal effects may not be as clear given the ephemeral increase in physiological arousal associated with brief emotional events which return to baseline after a few seconds have elapsed. More dynamic or intense emotionally arousing events may extend the duration of physiological arousal effects (Droit-Volet et al., 2011).

During this second phase, time perception may become increasingly influenced by the interaction of physiological arousal processes with more cognitively driven

processes involved in directing the 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 (Schwarz et al., 2013). I propose that such an imbalance may depend on the duration since the emotional stimulus onset, such that physiological effects may be stronger initially, with attention control processes becoming increasingly engaged as time elapses (Coull, 1998). The necessity of such controlled cognitive processes is highlighted by their role in both emotion appraisal/regulation (Ochsner & Gross, 2005) and in timing multi-second durations (Lewis & Miall, 2006). 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 which 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, while if it is not emotion-relevant, 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 after the window of threat has passed. While the distinctions between these three phases are supported by evidence in the existing literature on emotional timing, these hypotheses remain to be explicitly tested.

In addition to this new theoretical model, I propose complementary guidelines for the study of emotional influences on time perception. Firstly, 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.

Secondly, it is recommended 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, if possible, 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 correlations, it is difficult to conclude that these dimensions, rather than other differences between presented stimuli, drive resulting temporal distortions. Such correlations may be possible 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.

Thirdly, I 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 contribute 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.

1.4 The present manuscript

In the remaining chapters, I will assess the validity of this new theoretical model of emotional influences on time perception while addressing many of the outstanding questions in the study of emotion and time perception. Across Chapters 2-4, I will

address the hypothesis that the effects of physiological arousal and emotion-driven attention on time perception have interacting influences on time perception that depend on 1) the temporal dynamics of the emotional manipulation and task, 2) the way that the emotional stimuli direct attention, and 3) individual differences. I will address these predictions by explicitly manipulating or measuring clearly defined components of arousal and attention based on affective and cognitive science traditions and the proposed theoretical model.

In Chapter Two, I will consider how phasic signals of threat predicting aversive outcomes influence time perception. In this study, I will explore how the modulation of working memory and attention processes contributes to resulting distortions. I will also assess the unique contributions of physiological arousal and individual differences in top-down attention to threat. In Chapter Three, I will further explore the influence of phasic threat stimuli on time perception by considering whether attention effects on time perception are indeed correlated with physiological arousal. In this chapter, I am particularly interested in whether the duration of an emotional experience modulates the influence of physiological arousal on resulting temporal distortions. In Chapter Four, I will assess how changes in tonic dopamine levels influence the perception of time and how such effects are modulated by individual differences in drug-induced positive affect. In the final chapter, I will return to the newly proposed theoretical model and assess the degree to which the studies described support the model. Additionally, I will consider how these proposed mechanisms might be neurally instantiated based on the described

studies, the neurobiologically plausible striatal beat frequency model of interval timing, and other existing time perception and affective and cognitive neuroscience evidence. Finally, I will address possible implications of the described effects of emotion on time perception and suggest avenues for further exploration of such interactions.

2. Threat anticipation and imminent threat differentially modulate the perception of time

2.1 Introduction

Imagine you are walking home alone late at night when you suddenly hear a noise behind you. You turn around and see the dark shadow of an imposing figure with a weapon in his hand moving towards you. You freeze. You dread his approach. In what feels like no time at all he is in front of you. The rest of the encounter lasts only a few seconds as he demands for your wallet and then disappears, but it feels like those moments went on forever. This example illustrates how the anticipation and experience of threat may modulate our perception of time.

The anticipation of threat is a dynamic process associated with an evolving neural network (Mobbs et al., 2007) mediating a series of behaviors and cognitive processes based on both spatial and temporal threat proximity (Fanselow, 1994). Recently, the importance of temporal dynamics in threat anticipation processes has been emphasized, particularly the role of unpredictability or uncertainty in enhancing anxiety (Grupe & Nitschke, 2013). Given that unpredictability or uncertainty of the timing of a threatening event necessarily increases as the duration until such an event increases, temporal dynamics may be important in advancing our understanding of threat anticipation processes. While timing plays a critical role in threat-related processes, our perception of time is not veridical, particularly during emotional events. Studies of time perception have generally found that threatening stimuli are overestimated in duration (Droit-Volet

& Meck, 2007). However, no investigations have directly compared how threat proximity modulates the perception of time. Understanding how time is perceived during different phases of threat processing may have important implications given that phasic versus anticipatory fear may correspond to distinct clinical disorders, with phasic fear processes more strongly associated with phobic disorders and sustained fear processes more strongly associated with anxiety-related disorders (Davis, Walker, Miles, & Grillon, 2010).

Delay and trace conditioning may serve as useful tools for manipulating threat imminence given the differences in their temporal dynamics. In delay fear conditioning, the presentation of an intrinsically aversive unconditioned stimulus (US) is contiguous with the offset of an initially neutral stimulus (conditioned stimulus, CS). On the other hand, in trace conditioning, an empty trace interval elapses after the CS offset and prior to the delivery of the US. Thus, if the CSs in delay and trace conditioning procedures are matched, the proximity of threat following the CS will differ between these two procedures, such that delay conditioning would represent a more imminent threat phase, whereas trace conditioning would represent a more anticipatory threat phase. Consistent with the idea that threat proximity modulates cognitive and neural processes, these two procedures are supported by distinct psychological and neural mechanisms. In rodents, impaired acquisition of trace, but not delay, conditioning has been demonstrated by lesions or deactivations of the anterior cingulate, hippocampus, and medial prefrontal cortex, regions implicated in attention, timing, awareness, and working memory

(Chowdhury, Quinn, & Fanselow, 2005; Clark & Squire, 1998; Gilmartin, Miyawaki, Helmstetter, & Diba, 2013; Han et al., 2003). The importance of such cognitive processes in trace, but not delay, conditioning is further supported by behavioral and neuroimaging evidence in humans. For example, behavioral evidence has demonstrated that acquisition of trace conditioning is reduced to a greater degree than delay conditioning when participants simultaneously completed a working memory task, suggesting that trace conditioning relies more heavily on working memory processes (Carter, Hofstetter, Tsuchiya, & Koch, 2003). Neuroimaging studies have also supported greater recruitment of the hippocampus and dorsolateral prefrontal cortex in trace versus delay conditioning (T. Cheng, Disterhoft, Power, Ellis, & Desmond, 2008; Haritha, Wood, Ver Hoef, & Knight, 2013; Knight, Cheng, Smith, Stein, & Helmstetter, 2004). Based on such evidence, we hypothesized that the greater recruitment of cognitive processes at longer latencies from an aversive outcome would modulate the influence of threat on time perception.

In the current study, we utilized conditioned stimuli within the context of an ordinal comparison task to determine whether threat imminence modulates time perception. In the Delay condition, participants were presented with a neutral stimulus followed by either a threat (CS^+) or neutral (CS^-) cue and were asked to judge whether the comparison stimulus was longer or shorter in duration than the preceding cue. An aversive outcome (electrical stimulation) sometimes followed the offset of comparison stimulus on threat trials, whereas a neutral outcome (non-aversive tactile stimulation)

sometimes followed the offset of the comparison stimulus on neutral trials. In the Trace condition, participants were presented with a threat (CS⁺) or neutral (CS⁻) cue followed by a comparison stimulus and were asked to judge whether the comparison stimulus was longer or shorter in duration than the preceding cue. Aversive and neutral outcomes again were sometimes delivered at the offset of the comparison stimulus on CS⁺ and CS⁻ trials, respectively. The trace interval created a period of threat anticipation. In both Delay and Trace conditions, neutral outcomes were presented on CS⁻ trials in order to control for anticipatory or expectancy processes more generally (Fortin, 2003) and to more specifically assess the influence of threat-related processes. To avoid the potentially confounding influence of awareness in the acquisition of trace vs. delay conditioning (Weike, Schupp, & Hamm, 2007), we utilized an instructed fear-conditioning paradigm in which participants were instructed prior to the task on the contingencies between CSs and USs. Instructed fear conditioning has been shown to elicit similar arousal responses as learned fear conditioning (Olsson & Phelps, 2004).

Given that both the physiological and subjective processes associated with emotion are thought to modulate time perception (Noulhaine et al., 2007), we hypothesized that these processes might underlie imminent (Delay) and more distal threat (Trace) effects on time perception. To examine these processes, we assessed the influences of physiological arousal, measured via online skin conductance responses (SCRs), and of cognitively mediated threat anticipation, measured via a subjective arousal rating of electrical stimulation, on temporal judgments. We hypothesized that

physiological arousal would be associated with the overestimation of temporal durations during imminent threat (Delay condition), given that highly arousing, threatening stimuli generally increase temporal estimates (Droit-Volet & Meck, 2007). On the other hand, we predicted that the recruitment of cognitive processes for anticipating a more distal threat during the Trace condition would reduce the resources available for timing, as these processes rely on similar cognitive resources (Buhusi & Meck, 2009; Matthews et al., 2012). We expected this resource-sharing to be manifested in individual differences in the degree to which participants devoted attention to anticipating the aversive US (electrical stimulation). Specifically, we hypothesized that greater attention to the aversive US (reflected in higher arousal ratings of the electrical stimulation) would predict greater underestimation of temporal durations during threat anticipation, as cognitive resources are directed away from task relevant timing.

It has been argued that differences between delay and trace conditioning are driven by differences in the duration of US anticipation (Moustafa et al., 2013). This idea is supported by evidence that while shorter delays can be processed rather automatically, longer temporal durations require the recruitment of cognitive processes (Lewis & Miall, 2003a, 2003b). However, even when the durations of CSs and USs have been matched in conditioning procedures, differences between delay and trace conditioning have been observed (Haritha et al., 2013; Herbert, Eckerman, & Stanton, 2003), suggesting that these two procedures may reflect different relative stages of threat imminence, with delay conditioning perceived as a more imminent cuing of threat and trace conditioning

perceived as a more anticipatory cuing of threat, requiring the maintenance of attention/working memory to an internal representation of the CS-US relationship (Carter et al., 2003; Han et al., 2003). Based on this idea, we anticipated that if a threat cue directly predicted an aversive outcome, it would be interpreted as an imminent threat cue, even if the relative duration until the US matched the CS-US duration in the trace conditioning procedure, whereas the empty interval between a CS and US in trace conditioning would result in more anticipatory threat processes and require more cognitive resources. In other words, we expected that even if longer delay conditioned cues also recruit cognitive processes, these processes may not modulate time perception in the same way as threat anticipation would in trace conditioning. To test this hypothesis, we included a Long Delay condition that was the same in structure as the Delay condition, except the durations of CS⁺ and CS⁻ cues were extended to better match the CS-US interval duration in the Trace condition. In this way, we were able to assess whether or not observed differences in time perception were driven exclusively by the duration until the aversive US or due to differences between delay and trace conditioning in supporting distinct stages of threat processing prior to the US.

2.2. Methods

2.2.1 Participants

One hundred and eighty healthy Duke University students provided written informed consent and either received course credit or monetary compensation (\$10/hr) for participation. Individuals were excluded from analyses if they were skin conductance

non-responders (responded on $\leq 10\%$ of all trials) or demonstrated poor temporal sensitivity. The exclusion of 39 participants (~22% of participants) based on SCR non-responding is consistent with previous investigations (Venables & Mitchell, 1996). As we were specifically interested in the influence of threat anticipation over neutral anticipation, we also excluded individuals who did not demonstrate greater arousal to the CS+ versus the CS- (23 participants, approximately 12% of participants) to ensure that the intensity of the aversive reinforcer was greater than that of the neutral reinforcer. The final sample consisted of 105 participants (60 females; 18-26 years, mean = 19.4; SD = 1.57). Participants were assigned to either the Delay (n = 35), Long Delay condition (n = 35) or Trace condition (n = 35). The study protocol was approved by the Duke Medical Center Institutional Review Board.

2.2.2 Stimulus Materials

Stimuli were delivered using Presentation Software (Neurobehavioral Systems, Albany, CA). Participants wore BOSE QuietComfort® 15 Acoustic Noise Cancelling® headphones at all times to minimize auditory distractions. The stimuli to be timed were blue, green, and gray squares (3" x 3"). For each participant, an ascending staircase procedure was used to calibrate the 15 ms aversive electrical stimulation, delivered to the flexor surface of the dominant wrist, to a level determined by the participant to be annoying but not painful. The 15 ms non-aversive tactile stimulation (pictured in Figure 3), a TSP190 Haptic Stimulation Transducer, was delivered to the extensor surface of the dominant wrist. The device deploys a metal plunger that mechanically stimulates a 1.5

mm diameter surface area of skin and was calibrated for each participant to minimize plunger force while ensuring reliable perception. A MP-150 BIOPAC system (Goleta, CA) was used to deliver aversive electrical stimulation and neutral tactile stimulation and record SCRs.

2.2.3 Timing Task and Procedure

All participants completed an ordinal-comparison timing task (Figure 3). Each trial began with 2500 ms of fixation followed by a 500 ms blank screen, after which the standard square was presented. In the Delay and Trace conditions, the standard was presented for 800 ms. In the Long Delay condition, the standard was presented for 2000 ms. A blank screen was then presented with a duration jittered between 400-600 ms, followed by a second comparison square. In the Delay and Trace conditions, the comparison was presented for either 600, 700, 800, 900 or 1000 ms. These durations were chosen based on theories suggesting that subsecond durations are processed automatically without requiring top-down attention/working memory-related processes (Lewis & Miall, 2003a, 2003b). In the Long Delay condition, the comparison was presented for either 1500, 1750, 2000, 2250, or 2500 ms. These durations were chosen to approximately match the CS-US interval duration in the Trace condition, which varied between 1800 and 2400 ms (CS duration + variable interstimulus interval + variable comparison stimulus duration), and to match the proportional relationship between the standard and comparison intervals in the Delay and Trace conditions (i.e., $(1000-600)/800 = (2500-1500)/2000$). After a 200 ms blank screen, a response screen prompted

participants to judge whether the second comparison square was longer or shorter in duration than the preceding ‘standard’ square. Participants were given as much time as necessary to make a response but were instructed to respond as quickly and accurately as possible. Response mappings were counterbalanced across participants.

Imminent threat (Delay conditioning) and threat anticipation (Trace conditioning) were created within the context of an ordinal comparison task by manipulating whether or not the first or second square provided information about the trial type (indicated by the square colors). In the Delay and Long Delay conditions, the standard was always a gray square and the comparison was either a green or blue square. In the Trace condition, the standard was either a green or blue square and the comparison was always a gray square. The blue/green squares indicated whether that trial was a threat (CS^+) or a neutral (CS^-) trial. CS^+ s were paired with electrical stimulation (aversive US) at a 50% rate. CS^- s were paired with non-aversive tactile stimulation (non-aversive US) at a 50% rate. All other CS presentations were not paired with stimulation. Unlike typical discrimination conditioning procedures in which CS^- cues are unpaired with reinforcement, we paired CS^- cues with a neutral reinforcer to control for general anticipatory processes, allowing us to compare the effects of aversive versus neutral anticipation. Stimulation (aversive or non-aversive US) was delivered at the offset of the comparison square in all conditions.

To minimize any differential effects of awareness between Delay and Trace conditioning procedures (Clark & Squire, 1998; Weike et al., 2007), participants were explicitly informed prior to completing the timing task of the relationships between the

green and blue squares and the type of stimulation they predicted (aversive electrical stimulation or non-aversive tactile stimulation). Color assignment was counterbalanced between subjects. Participants completed a total of 80 CS⁺ and 80 CS⁻ trials. For both trial types, comparison squares were presented 16 times at each duration (Delay: 600, 700, 800, 900, 1000 ms; Long Delay: 1500, 1750, 2000, 2250, or 2500 ms). Half of these presentations were followed by stimulation. The task was divided into four equal runs. Trials were presented semi-randomly such that no more than three of the same trial type (CS⁺ or CS⁻) were presented in a row and no more than three consecutive CS⁺ or CS⁻ trials were followed by the corresponding stimulation (aversive and non-aversive US, respectively) to ensure vigilance to threat was maintained across the experiment.

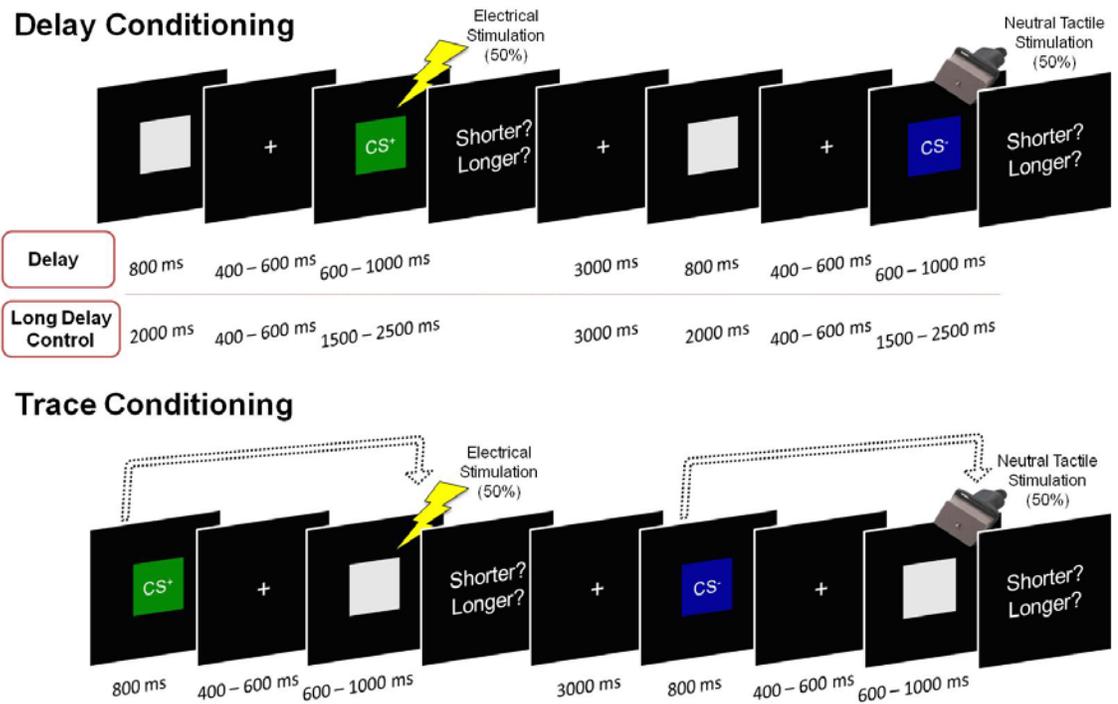


Figure 3: Trial structure for Delay, Long Delay and Trace conditioning procedures. Across all conditions, participants were required to judge whether the second of two presented squares was longer or shorter in duration than the previous square. CS⁺ trials were followed by electrical stimulation at the offset of the second square (50%) while CS⁻ trials were followed by neutral tactile stimulation at the offset of the second square (50% rate). Durations in the Long Delay condition were chosen to match the CS-US interval in the Trace condition. In the Delay and Long Delay conditions CSs were presented as the second square, whereas in the Trace condition CSs were presented as the first square.

Four practice trials with stimulation were completed before the experiment began to ensure participants understood the task. After completing the experiment, participants rated the aversive US and non-aversive US on 9-point Likert scales of arousal (1 = completely unaroused, 9 = completely aroused) and valence (1 = completely unhappy, 9 = completely happy) and completed a final questionnaire.

2.2.4 Timing Performance Analysis

The proportion of “longer” responses given for each comparison square duration for CS⁺ and CS⁻ trials were separately calculated for each participant. Trials on which response times were 3 SDs above or below the participant’s mean were excluded. Point of subjective equality scores (PSEs) and Weber fraction values (WFs) were estimated from these raw scores using a maximum likelihood function to fit logistic functions to individual participant data. Importantly, only trials unpaired with stimulation were included in analyses to remove the potentially confounding effects of stimulation on perception or decision-making. PSE values were divided by the standard duration (Delay/Trace: 800 ms; Long Delay: 2000 ms) such that underestimation is reflected by PSE ratio scores > 1 and overestimation is reflected by PSE ratio scores < 1. PSE ratio scores and WF values were analyzed in separate 2x3 mixed ANOVA with Trial Type (CS⁺ vs. CS⁻) as a within-subject factor and Conditioning Procedure (Delay, Long Delay, Trace) as a between-subject factor. Planned comparisons between the different conditioning procedures (Delay vs. Trace, Delay vs. Long Delay, and Trace vs. Long Delay) were conducted in three 2x2 (Trial Type x Study) mixed ANOVAs in order to test the hypotheses that differences in threat imminence in delay and trace conditioning procedures would differentially influence time perception and that temporal distortions in the Long Delay condition would distort time perception in a similar manner to the Delay rather than Trace condition, which would support the idea that the phase of threat

imminence (the relationship between CSs and USs), rather than the CS-US duration, modulates time perception.

2.2.5 Skin Conductance Responses (SCRs) Analysis

SCRs were recorded from the hypothenar eminence of the nondominant hand. SCRs were calculated with the Autonomate analysis program (Green, Kragel, Fecteau, & LaBar, 2014) coded in MATLAB (MathWorks, Natick, MA) using the criteria reported by Dunsmoor, Mitroff, and LaBar (2009). Briefly, SCRs were scored as responses if the trough-to-peak occurred 1-4 s after stimulus onset, the response lasted 0.5-5.0 s, and the amplitude was >0.02 microsiemens. SCRs that did not meet these criteria were scored as zeros. SCRs were manually verified by a trained scorer. SCRs were square root transformed and range-corrected by dividing responses by the largest recorded SCR (Lykken & Venables, 1971) for each participant. We assessed the relationship between SCRs and responses in a $2 \times 2 \times 3$ mixed ANOVA with Trial Type (CS^+ vs. CS^-) and Response (Shorter vs. Longer) as within-subject factors and Conditioning Procedure (Delay, Long Delay, and Trace) as a between-subject factor. As shorter responses are accurate and longer responses are inaccurate for the short comparison durations, while shorter responses are inaccurate and longer responses are accurate for the long comparison durations and we wanted to ensure that any resulting differences in SCRs observed in performing this analysis were not driven by only a subset of the comparison duration levels. There were not enough inaccurate responses at the extreme comparison duration levels to add Comparison Duration Level as an additional within subject factor,

thus we ran the same analysis for just the shorter comparison duration levels (1, 2 and 3) and for just the longer comparison duration levels (3, 4, and 5) to ensure that any resulting SCR differences were observed across all comparison duration levels. Four subjects did not make any shorter responses on either CS⁺ or CS⁻ trials for the longer comparison duration levels and were excluded from this analysis. We also compared SCRs in response to CS⁺ and CS⁻ across comparison duration levels in a 2x5x3 mixed ANOVA with Trial Type (CS⁺ vs. CS⁻) and Comparison Duration Level (1, 2, 3, 4, 5) as a within-subject factor and Conditioning Procedure (Delay, Long Delay, Trace) as a between-subject factor. Finally, we assessed the relationship between SCRs and accuracy in a 2x2x3 mixed ANOVA with Trial Type (CS⁺ vs. CS⁻) and Accuracy (Accurate Response vs. Inaccurate Response) as within-subject factors and Conditioning Procedure (Delay, Long Delay, Trace) as a between-subject factor. In this last analysis, only trials from comparison levels 1, 2, 4, and 5 were included because the 3rd comparison duration level was equal to the duration of the standard.

2.2.6 Individual Differences Analysis

All correlations were conducted using Pearson's correlations unless otherwise stated. We conducted correlational analyses for PSE ratio difference scores (CS⁺ - CS⁻ trials) and subjective shock arousal ratings separately for each conditioning procedure. We utilized this subjective arousal rating of the aversive US as an operationalized measure of attention devoted to the anticipation of threat based on previous work which has supported the idea that subjective arousal ratings reflect "enhanced attention to the

detection of self-relevant emotional event (Noulhaine et al., 2007).” In other words, subjective arousal ratings are thought to reflect the operation of cognitive processes involved in emotional appraisal and sustained attention when emotional stimuli are deemed relevant to the individual. To validate the operational definition of the subjective arousal rating for electrical stimulation as a measure of top-down attention directed towards anticipating the aversive US, we conducted additional correlations of this measure with response time (RT) differences between CS⁺ and CS⁻ trials for each conditioning procedure.

2.3 Results

2.3.1 PSE Ratios and WF Values

The average proportion of longer responses across comparison durations are shown for the Delay, Trace and Long Delay conditions in Figure 4A-C. A 2x3 (Trial Type x Conditioning Procedure) mixed ANOVA of PSE values indicated a main effect of Trial Type $F(1, 102) = 5.989, p = .016, \eta_p^2 = .055$ and a main effect of Study, $F(2, 102) = 3.187, p = .045, \eta_p^2 = .059$. These main effects were qualified by a Trial Type x Study interaction, $F(2, 102) = 3.548, p = .032, \eta_p^2 = .065$, suggesting that the relationship between CS⁺ and CS⁻ trials differed across conditioning procedures. Actual PSEs for CS⁺ and CS⁻ trials in all three conditioning procedures are given in Table 1.

Table 1: Average PSE values

Conditioning Procedure	CS⁺ trials	CS⁻ trials
Delay	767.60 (12.39)	815.89 (11.71)
Trace	808.08 (13.45)	805.25 (11.29)
Long Delay	1914.31 (25.13)	1947.64 (30.08)

Note. Data are reported as mean (*SEM*).

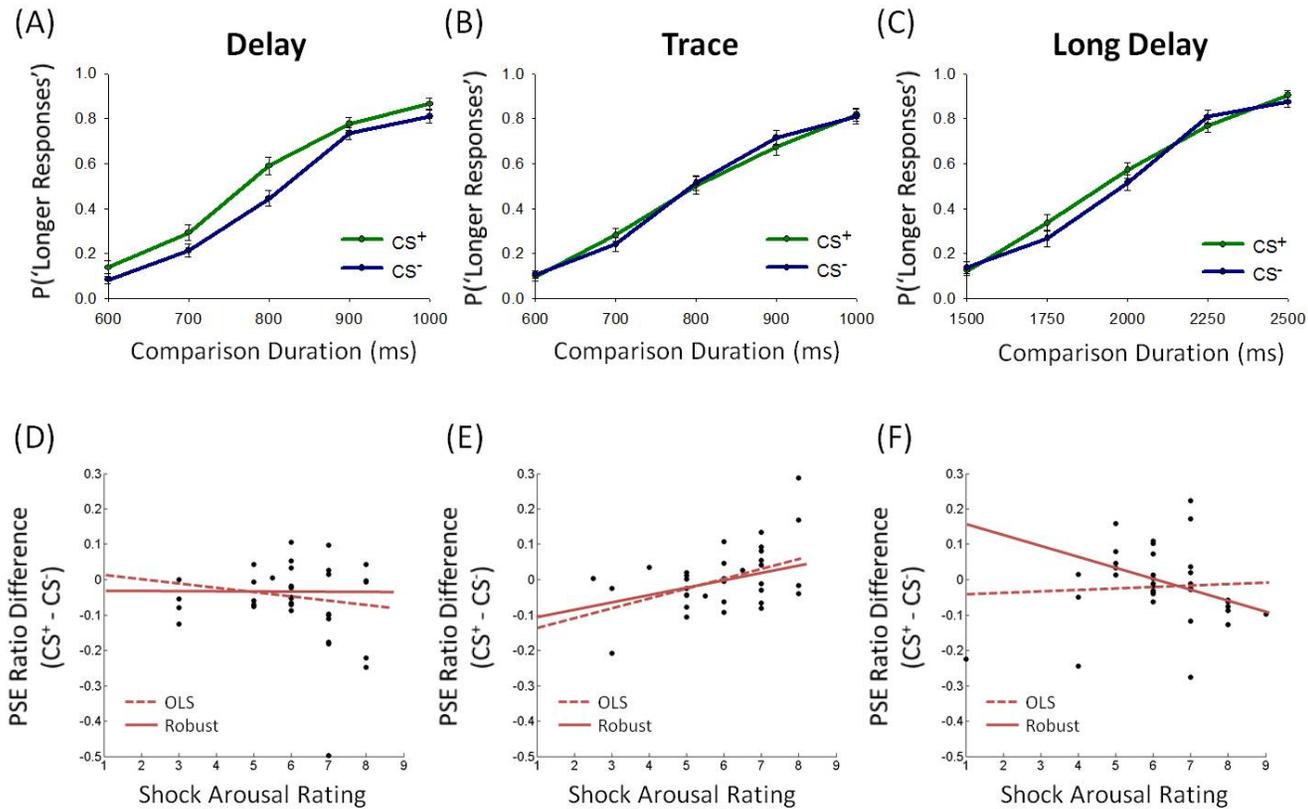


Figure 4: Average proportion of longer responses for CS+ versus CS- trials across comparison durations in the Delay, Trace, and Long Delay conditions (A-C) and correlations between shock arousal ratings and difference scores for point of subjective equality ratios on CS+ minus CS- trials across Delay, Trace, and Long Delay conditions (D-F). Dashed correlation lines reflect ordinary least squares regression lines; solid lines reflect robust regression lines to account for outliers, particularly in the Long Delay condition. Error bars represent SEM.

To further explore the relationships between CS⁺ and CS⁻ trials across experiments we conducted three 2x2 mixed ANOVAs of PSE values for Delay vs. Trace, Trace vs. Long Delay and Delay vs. Long Delay. The comparison between Delay and Trace conditions revealed a main effect of Trial Type $F(1, 68) = 5.651, p = .020, \eta_p^2 = .077$, qualified by a Trial Type x Conditioning Procedure interaction $F(1,68) = 7.142, p = .009, \eta_p^2 = .095$, supporting our hypothesis that differences in threat imminence in delay and trace conditioning procedures would differentially modulate time perception during threat versus neutral anticipation. Follow-up analyses revealed that significant differences between CS⁺ versus CS⁻ trials were only observed in the Delay condition, $t(34) = -3.210, p = .003, Cohen's d = .68$, indicating overestimation of durations on CS⁺ versus CS⁻ trials, consistent with previous studies that have found that threat increases temporal estimates (e.g., Bar-Haim et al., 2010; Droit-Volet, Mermillod et al., 2010; Tipples, 2011). Temporal estimates on CS+ trials were also overestimated in the Delay condition compared to the Trace condition $t(68) = -2.213, p = .030, Cohen's d = .53$. Interestingly, PSEs for CS⁺ trials in the Delay condition were also significantly greater than 1, $t(34) = -2.616, p = .013$, indicating that these trials were not only significantly overestimated compared to a neutral condition but also to physical time (the duration of the standard stimulus).

The comparison of Delay vs. Long Delay procedures indicated a main effect of Trial Type $F(1, 68) = 8.675, p = .004, \eta_p^2 = .11$, such that CS⁺ trials were overestimated compared to CS⁻ trials, supporting the idea that, despite a longer CS-US interval, threat anticipation in the Long Delay procedure did not have a significantly different influence

on time perception than the Delay procedure. No other effects were significant. Finally, the comparison of the Trace vs. Long Delay procedure only revealed a main effect of Study, $F(1,68) = 6.203, p = .015, \eta_p^2 = .084$, indicating that durations in the Long Delay procedure were overestimated compared to the Trace condition, regardless of Trial Type. PSE values for CS⁺ and CS⁻ trials in each conditioning procedure are plotted in Figure 5.

A 2x3 (Trial Type x Conditioning Procedure) mixed ANOVA of WF values did not reveal any significant effects, suggesting that neither the trial type nor type of conditioning procedure influenced temporal sensitivity.

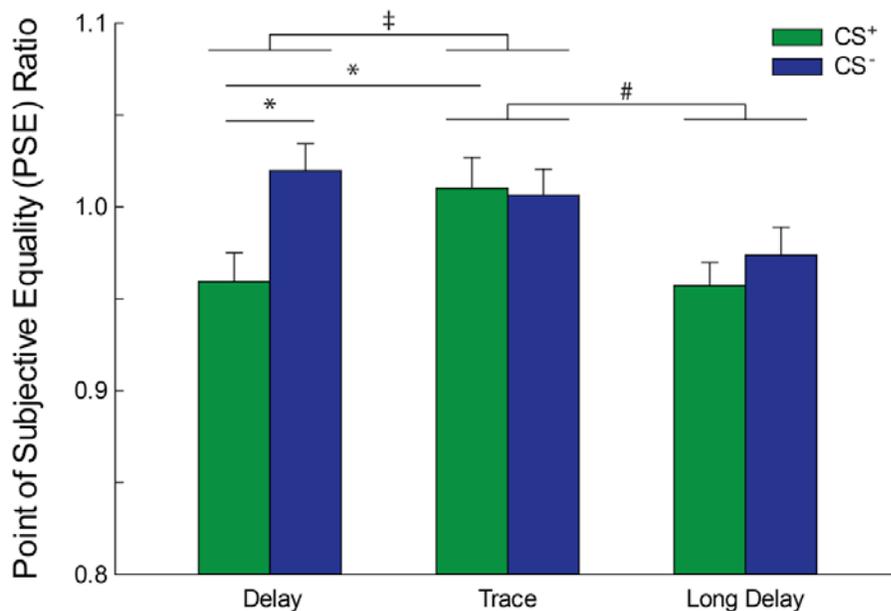


Figure 5: Mean point of subjective equality (PSE) ratio scores for CS⁺ and CS⁻ trials in the three conditioning procedures. Values >1 reflect underestimations of comparison stimulus durations compared to the standard stimulus duration, whereas values <1 reflect overestimations of durations compared to the standard stimulus duration. ‡ Interaction between study and trial type between Delay and Trace conditions. * Significant overestimation of CS⁺ Delay versus CS⁻ Delay and versus CS⁺ Trace. # Main effect of conditioning procedure between Trace and Long Delay conditions. All $P < .05$, error bars represent SEM.

2.3.2 SCR Values

To examine whether participant temporal judgments were associated with trial level fluctuations in SCRs in response to CSs across conditions, we conducted a 2x2x3 (Trial Type x Response x Conditioning Procedure) mixed ANOVA of SCR averages. Contrary to our prediction, we found a main effect of Response, $F(1,102) = 10.528, p = .002, \eta_p^2 = .094$, wherein SCRs were greater for ‘longer’ than ‘shorter’ responses (Figure 6), suggesting that physiological arousal was associated with overestimation across all conditioning procedures. As participants were selected for study inclusion based on greater SCRs for CS⁺ vs. CS⁻ trials, we predictably also found a main effect of Trial Type, $F(1,102) = 120.266, p < .001, \eta_p^2 = .54$. Nevertheless, this main effect was qualified by a Trial Type x Study interaction, $F(2,102) = 3.965, p = .022, \eta_p^2 = .072$. *Post-hoc* two-tailed t-tests on SCR difference scores (CS⁺ - CS⁻) revealed significantly larger SCR differences in the Trace condition compared to the Delay condition, $t(68) = -2.130, p = .037, \text{Cohen's } d = 0.47$, and the Long Delay conditions, $t(58.932) = 2.01, p = .049, \text{Cohen's } d = .48$. No differences between the Delay and Long Delay conditions were observed, $t(68) = 2.01, p = .807$. No other main effects or interactions were significant.

Due to empty cells we could not test the Response effect across all comparison duration levels but separate exploratory analyses for shorter (1, 2, 3) and longer (3, 4, 5) comparison duration levels both replicated the main effect of Response (shorter comparison levels: $F(1,102) = 7.107, p = .009, \eta_p^2 = .065$; longer comparison levels: $F(1,98) = 8.491, p = .004, \eta_p^2 = .08$), suggesting that this effect was consistent across

comparison durations. A 2x5x3 (Trial Type x Comparison Duration Level x Conditioning Procedure) did not reveal any main effects or interactions with Comparison Duration Level. Finally, a 2x2x3 (Trial Type x Accuracy x Conditioning Procedure) analysis revealed no differences in SCRs for accurate versus inaccurate responses. These analyses support the idea that the SCR differences we observed for shorter versus longer durations do not reflect differences across comparison stimulus durations or differences between correct and incorrect responses, but instead reflect biases in temporal estimation.

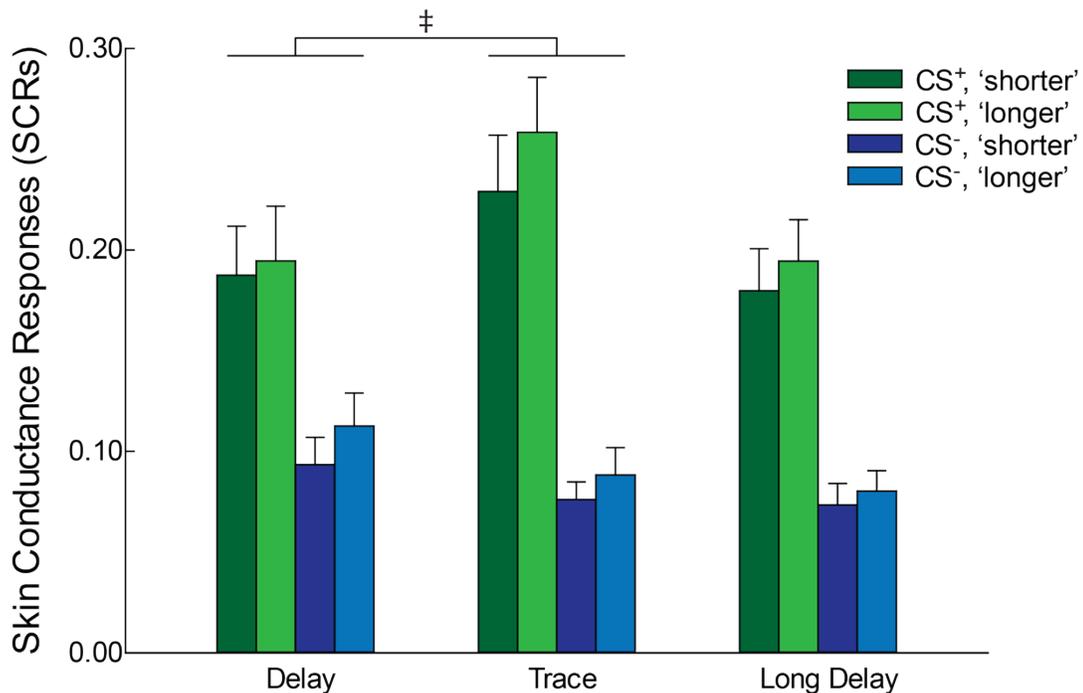


Figure 6: Skin conductance responses (SCRs) for CS⁺ and CS⁻ trials on which participants responded that the comparison duration was shorter or longer than the preceding standard stimulus across conditioning procedures. A main effect of Response indicated that across conditions participants showed greater SCRs on trials for which they subsequently judged the comparison stimulus as longer. A main effect of Trial Type indicated greater SCRs on CS⁺ versus CS⁻ trials. An interaction between Delay and Trace conditions indicated that the difference between CS⁺ and CS⁻ trials was larger in the Trace versus Delay condition.

2.3.3 Individual Differences

To test the hypothesis that longer CS-US ISIs in the Trace and Long Delay Conditions would recruit attention/working memory processes but differentially modulate CS⁺ and CS⁻ temporal estimates across participants according to the relative phase of threat imminence they reflected, we ran correlational analyses between Shock Arousal and PSE ratio difference score (CS⁺ - CS⁻). This correlation was significant in the Trace condition, $r = .456$, $p = .006$, such that higher subjective ratings of shock arousal predicted greater underestimation of CS⁺ versus CS⁻ trials (Figure 4E), consistent with our hypothesis that cognitive processes supporting threat anticipation would distract attention from timing processes. This effect appears to have been largely driven by the relationship between shock arousal and PSE ratios on CS⁺ trials, $r = .337$, $p = .048$. The correlation between Shock Arousal and PSE difference score was not significant in the Long Delay condition, $r = -.060$, $p = .72$. However, further examination of this relationship suggested that non-significant outliers might have contributed to this null effect. To better account for the influence of these outliers, we conducted a robust regression in MATLAB for the Long Delay condition which revealed, in contrast to the Trace condition, a significant negative relationship between Shock Arousal and the PSE Difference Score, $p = .001$, such that higher subjective ratings of shock arousal predicted greater overestimation of CS⁺ versus CS⁻ trials (Figure 4F), supporting the idea that, despite matching the CS-US duration from the Trace condition, cognitive processes engaged during Long Delay conditioning differentially modulated time perception in a manner consistent with the direction of temporal bias observed in the Delay condition.

Importantly, individual differences in shock arousal ratings in the Trace and Long Delay conditions were both positively correlated with an average RT difference score ($CS^+ - CS^-$), Trace: $r = .367, p = .030$; Long Delay: $r = .351, p = .038$. Neither the correlation of Shock Arousal with the PSE difference score (Figure 4D) or RT difference score was significant for the Delay condition.

2.4 Discussion

In this study, we found evidence to support our hypothesis that delay and trace conditioning, supporting unique stages of threat processing, differentially modulate the perception of time and that the directionality of such threat-related effects may depend on the interaction of physiological arousal and cognitive processes supporting threat anticipation. In line with our predictions, we found that imminent threat resulted in the overestimation of temporal durations in delay conditioning procedures, whereas more anticipatory threat processes, to the extent that cognitive processes were recruited during trace conditioning, predicted the underestimation of temporal durations. Our findings are thus consistent with behavioral and neural dissociations between proximal and distal threat-related processes (Fanselow, 1994) and suggest that, while timing is important in learning to appropriately respond to threat (Boulangier Bertolus et al., 2014; Diaz-Mataix, Ruiz Martinez, Schafe, LeDoux, & Doyere, 2013; Shionoya et al., 2013), stimuli presented prior to a predicted aversive outcome are not perceived veridically.

Beyond demonstrating the effect of threat proximity on time perception, we provided evidence that the threat-related temporal distortions we observed were driven by changes in physiological arousal and cognitive processes supporting threat anticipation.

We provided novel evidence that across all three conditioning procedures, higher physiological arousal, as indexed by trial by trial fluctuations in SCRs, was associated with a propensity to judge durations as longer. Given that CS⁺s are associated with greater physiological arousal than CS⁻s, these findings suggest that physiological arousal underlies the overestimation biases in time perception we observed, consistent with studies reporting the overestimation of temporal durations for brief emotionally arousing stimuli (e.g., Bar-Haim et al., 2010; Dirnberger et al., 2012; Droit-Volet et al., 2004; Fayolle & Droit-Volet, 2014; Shi et al., 2012; Tipples, 2008, 2011; Young & Cordes, 2013). While previous studies of emotion and time perception have assessed temporal distortions across different arousal levels, collecting online measures of physiological arousal allowed us to more sensitively assess the role of physiological arousal in temporal distortions at the trial level.

We also used a subjective arousal rating of electrical stimulation to operationalize the cognitive processing dedicated to anticipation of the aversive US, based on the idea that subjective arousal ratings reflect the engagement of attention processes directed towards a self-relevant emotional event (Noulhaine et al., 2007). The validity of this measure was supported by the positive relationship we observed between the electrical stimulation arousal rating and RT difference score in the Trace and Long Delay (but not the Delay) condition, as slower RTs are generally thought to reflect the engagement of attention (e.g., Theeuwes, 1991; Weissman, Roberts, Visscher, & Woldorff, 2006). This correlation is thus consistent with our hypothesis that attention devoted to the anticipation of an aversive US at longer CS-US interval durations would capture and hold attention.

The demonstration that this correlation was positive for the Trace and Long Delay conditions suggests that cognitive processes were similarly engaged in service of anticipating an aversive US in both conditions.

However, the differences in how these anticipatory processes distorted time perception in the Trace and Long Delay conditions, despite their similar engagement of cognitive resources, suggests that the relationship between the CS and US was critical in determining the direction of temporal distortions resulting from threat-related processing. This differential modulation supports the idea that influence of threat processing on time perception does not solely depend on the absolute duration of time until the US but rather, reflects differences in the stage of threat processing according to the relationship between the CS and US. In the Trace condition, we believe more cognitive processes were engaged in service of anticipating the US, resulting in greater attention directed away from timing processes. In this condition, participants were asked to time a neutral comparison stimulus while also maintaining the temporal relationship between the CS and US, requiring the sharing of cognitive resources between these two processes. This effect demonstrates that the degree to which individuals devoted attention resources towards maintaining the CS-US relationship determined the degree to which attention resources were taken away from timing the comparison stimulus, resulting in temporal underestimation (Buhusi & Meck, 2009). Resource-sharing models of time perception (Buhusi & Meck, 2009) have suggested that timing relies on working memory/attention processes that are limited in capacity and must be shared between timing and other cognitively demanding processes. These models predict that the saliency of distractors is

proportional to their resulting influence on temporal estimates. Our current evidence supports this resource-sharing account by demonstrating that the degree to which attention was directed to US anticipation in the trace condition determined the magnitude of temporal underestimation.

On the other hand, while top-down cognitive processes also appear to have been engaged in the Long Delay condition, the comparison stimuli in this condition provided direct information about whether and when the aversive US might be delivered and therefore, no division of cognitive resources was required to support threat-related processes. Thus, recruited attention processes were devoted to maintaining attention to the CS⁺, with the degree to which these processes were recruited predictive of the degree of temporal overestimation. In other words, maintaining the temporal relationship between the CS and US did not conflict with timing the duration of the CS as it did in the Trace condition, likely because the duration until the aversive outcome and the duration of the comparison stimulus were one in the same. The fact that the direction of temporal estimation in the Long Delay and Trace conditions differed supports our idea that they reflect different stages of threat processing, despite the fact that the CS-US durations were matched. Consistent with this interpretation, we did not observe any significant differences in timing performance in the Delay and Long Delay conditions. Collectively these findings suggest that physiological arousal and threat-directed attention may synergistically drive overestimation biases during imminent threat, while more anticipatory threat processes distract attention from timing resulting in greater temporal underestimation driven by competition between arousal and attention processes.

Previous evidence has suggested that waiting for an inescapable event can be aversive and that individuals differentially value shorter waiting periods of threat versus lower intensities of aversive outcomes (Berns et al., 2006). Such evidence suggests that the individual differences in our study may also reflect such differential preferences. However, as we did not manipulate anticipation duration or aversive outcome intensities within subjects we cannot assess the degree to which such a preference trade-off may have contributed to the current findings. Future work should consider how the relationship between the duration of threat anticipation and the intensity of an aversive outcome might interactively modulate time perception.

Previous studies have sometimes reported differences in learning rate or the magnitude of conditioned responses in delay versus trace conditioning procedures, demonstrating that learning is slower or conditioned responses are smaller in trace versus delay conditioning or with longer CS-US intervals (Herbert et al., 2003; Kamin, 1961; Knight et al., 2004; Raybuck & Lattal, 2014 but see Haritha et al., 2013). It could thus be argued that differences in acquisition between procedures could explain why we did not observe a significant PSE difference between CS⁺ and CS⁻ trials in the Trace or Long Delay condition. Nevertheless, various lines of evidence argue against this possible explanation. Firstly, all participants were explicitly instructed as to the relationships between CSs and USs, therefore all individuals should have been aware of the stimulus contingencies. Awareness was confirmed in a post-experiment written questionnaire. Additionally, individuals were excluded from analyses if they did not demonstrate greater SCRs to CS⁺ versus CS⁻ trials, thus all included participants demonstrated physiological

evidence of learning the CS-US relationships. Further evidence that the Delay was not characterized by better CS-US learning, more participants were excluded from the Delay ($n = 11$) than from the Trace condition ($n = 6$) or the Long Delay condition ($n = 6$) for not demonstrating physiological evidence of learning. Finally, our SCR analyses suggest that the differences between temporal estimates across conditions were not due to overall greater differences in SCR responses in the Delay condition, as we actually observed greater SCR differences in the Trace condition.

Another important alternative explanation for the results we observed is that the effects observed in the Trace condition were driven by differences in encoding the standard stimulus, rather than the engagement of attention processes during threat anticipation. In the Delay condition, we demonstrated that CS^+ s were overestimated in duration compared to CS^- s. In a similar manner, the CS^+ as the standard in the Trace condition may have also been overestimated in duration resulting in the relative underestimation of the comparison stimulus. Individual differences in this effect may have, in turn, driven the underestimation bias associated with increasing subjective arousal ratings of electrical stimulation. To rule out this alternative explanation, we ran a control experiment with an additional 35 participants (see Supplemental Findings in section 2.6). This control experiment did not support the idea that the underestimation bias was driven by a difference in encoding the CS^+ versus CS^- as the standard.

It is important to note that our current findings are unaccounted for by pacemaker-accumulator models of time perception. While our study revealed physiological arousal effects at shorter and longer latencies from CS^+ onset, the effect of physiological arousal

at longer latencies did not result in a significant overestimation bias for CS⁺ versus CS⁻ trials in Trace or Long Delay conditions, suggesting that physiological arousal effects did not scale with duration and, thus may have had only transient influences on time perception. Such findings suggest that physiological arousal effects on time perception are categorically distinct from clock speed/pacemaker-like effects, which are expected to increase across temporal durations. At the same time, our findings suggest an influence of top-down attention to threat in distorting time perception for longer CS-US interval durations, with the directionality of this influence dependent on whether or not such processes direct attention towards or away from timing. In other words, increases or decreases in temporal estimates depend on whether or not attention to threat conflicts or is compatible with timing processes. While such a mechanism is most adequately described by resource-sharing accounts of time perception, timing models have not explicitly considered how the time course of events may modulate resource-sharing. The transient influence of physiological arousal on temporal estimates and the influence of attention resource-sharing, with effects dependent on how attention is directed, that we observed in this study are consistent with predictions of the theoretical model of emotion-driven temporal distortions proposed in Chapter 1.

The current findings have important implications for our understanding of delay and trace conditioning and how they can be utilized to study threat-related processes. Historically, the importance of cognitive differences between delay and trace conditioning has been based on the proposed role of awareness in trace conditioning, supporting the idea that these two procedures may serve as important models of

nondeclarative and declarative memory, respectively (Clark, Manns, & Squire, 2001, 2002; Clark & Squire, 1998; Weike et al., 2007). As such, researchers have investigated differences in the neural mechanisms of these two processes to understand the processes that support these two forms of learning. At the same time, our current findings suggest that delay and trace conditioning may also be important for understanding different phases of threat-related processing. Specifically, we propose that delay conditioning may be implemented as a model of imminent threat during which defensive behaviors are engaged, while trace conditioning may be implemented as a model of threat anticipation processes, when threat has been detected (as signaled by the threat cue) but is not yet imminent, often associated with freezing behavior (Fanselow, 1994). If examined in this matter, studying these two conditioning procedures may help us understand underlying stages of threat processing. Given that different forms of threat processing are thought to differentially contribute to fear and anxiety disorders, our current findings may also have important implications for our understanding of aberrant processes in these clinical disorders. There have been limited investigations of how threat contributes to temporal distortions in individuals with higher levels of fear and anxiety (Bar-Haim et al., 2010; Buetti & Lleras, 2012; Watts & Sharrock, 1984). Nevertheless, the demonstration that different phases on threat processing differentially modulate time perception suggests the possibility that time perception may play an adaptive role in supporting such processes. Thus, further investigations might consider if temporal distortions contribute to aberrant threat processes in clinical populations (Lake & LaBar, 2011).

2.5 Summary

The current findings suggest that different mechanisms may be involved in temporal distortions according to the stage of threat processing, with the overestimation of shorter durations driven by physiological arousal in imminent threat and estimates of longer durations driven by the recruitment of top-down attention resources for anticipating the arousing event. At the same time, we provided evidence that top-down attention resources do not have a fixed relationship to timing processes, but rather their influence depends on whether these processes are compatible or in conflict with timing processes. The current study improves upon previous investigations by relying on well-established properties of conditioning procedures to investigate mechanisms underlying emotional distortions of time perception. This investigation demonstrates the utility of explicitly manipulating and measuring specific components of arousal and attention in order to understand the influence of such components on the subjective experience of time and suggests that emotional influences on time perception are not fully accounted for by current models of time perception.

2.6 Supplemental Experiment: Encoding Control

In the trace conditioning experiment, we found that subjective arousal ratings of electrical stimulation predicted the underestimation of temporal durations during threat anticipation. We interpreted this finding as a demonstration of resource-sharing between attention/working memory processes supporting threat anticipation and timing processes. Nevertheless, an alternative possibility is that the effects observed in the Trace condition were driven by differences in encoding the standard stimulus between CS⁺ and CS⁻ trials,

rather than the engagement of attention processes during threat anticipation. To rule out this alternative explanation, we ran a control experiment that was identical to the Trace procedure, except the USs were presented at the offset of the CSs (the standard squares), removing the anticipation of threat during the comparison stimulus. If differences in encoding drove the positive correlation we found in the Trace condition between subjective arousal ratings of electrical stimulation and the PSE difference score, we expected to observe the same effect in this control experiment.

2.6.1 Methods

Fifty-four additional participants provided written informed consent and either received course credit or monetary compensation (\$10/hr) for participation. The same exclusion criteria were imposed, resulting in a final sample of 35 participants (21 females; 18-31 years, mean = 20.3; SD = 2.78). The experimental procedure was identical to that for the trace condition except electrical stimulation was delivered at the offset of the standard stimulus rather than at the offset of the comparison stimulus.

2.6.2 Results

We did not observe a significant difference between PSE values on CS⁺ versus CS⁻ trials, $t(34) = .133$, $p = .895$ (Figure 7A). WF values were significantly lower for CS⁺ versus CS⁻ trials, $t(34) = -2.166$, $p = .037$, *Cohen's d* = 0.38. While there was not a significant correlation between PSE Difference Scores and Shock Arousal, there was a significant correlation between Threat PSEs and Shock Arousal, $r = -.437$, $p = .009$, suggesting that increased subjective shock arousal predicted the overestimation of temporal durations (Figure 7B).

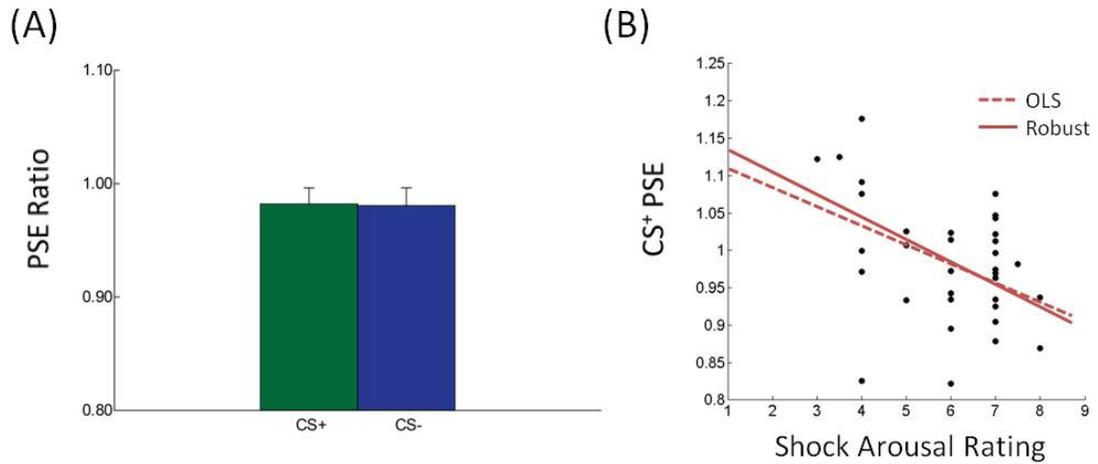


Figure 7: (A) No difference between PSE ratios for CS+ versus CS- trials in the encoding control task. (B) A significant negative correlation between PSE ratio difference scores and subjective shock arousal suggest that comparison durations were increasingly overestimated in duration as subjective arousal in response to shock increased.

2.6.3 Discussion

The results of this experiment suggest that differences in encoding on CS⁺ and CS⁻ trials were not responsible for the positive correlation between subjective arousal to the US and temporal underestimation. Interestingly, the relationship between Shock Arousal and temporal estimation reversed in this control condition, wherein the US was delivered after the standard stimulus rather than after the comparison stimulus. This evidence supports our conclusion that the bias towards underestimation associated with the subjective US arousal rating was driven by attention processes recruiting for anticipating the US, rather than by differences driven by the CS⁺ versus CS⁻ at encoding.

3. Physiological arousal modulates the influence of attention on time perception

3.1 Introduction

Emotional effects on cognition and behavior allow us to adaptively respond to stimuli in our environment. Given that emotions are particularly powerful drivers of temporal distortions, the modulatory role of emotion on time perception suggests that emotion-induced temporal distortions may serve a biologically relevant function. Such an adaptive role of temporal distortions may be particularly pertinent during the processing of aversive or threatening stimuli, for which inappropriate anticipation or timing processes could have negative consequences. Supporting the idea that threat-induced distortions are adaptive, temporal overestimations of emotionally arousing, aversive images relative to subsequent neutral images have been associated with enhanced memory for aversive stimuli and reduced memory for subsequent neutral stimuli (Dirnberger et al., 2012), which may point to a role for threat-driven temporal distortions in prioritizing threat-relevant stimuli in service of learning and memory. These implications of threat-induced temporal distortions support further investigation of this perceptual phenomenon.

Despite growing interest in the modulation of time perception by threat-relevant stimuli, the cognitive mechanisms underlying this perceptual phenomenon remain unclear. Current studies of time perception generally suggest that emotional arousal increases temporal estimates, whereas attention distraction decreases temporal estimates (Bar-Haim et al., 2010; Droit-Volet et al., 2004; Effron et al., 2006; Gil et al., 2009).

However, these models fail to account for how arousal processes might interact with attention processes to influence time perception, as well as how such interactions may dynamically change during and after an emotional experience.

Findings within the affective science tradition clearly support the interaction of threat-related arousal and threat-driven attention. For example, the presentation of threatening stimuli as targets within visual search paradigms has been shown to facilitate target detection, whereas when such stimuli serve as distractors they impede target detection, confirming the ability of emotional arousal to modulate attention (e.g., Ohman et al., 2001; Schmidt, Belopolsky, & Theeuwes, 2014). Conversely, attention has also been shown to modulate arousal responses. Goal-directed processes or manipulations of attention load reduce emotional processing, as evidenced by reduced arousal-related neural responses to emotional stimuli, particularly in the amygdala (Blair et al., 2007; Hsu & Pessoa, 2007; Pessoa, Padmala, & Morland, 2005; Silvert et al., 2007).

Theories of emotional arousal and attention further support the idea that interactions between these two processes modulate perception. For example, the arousal-biased competition model suggests that arousal biases perception in favor of processing high priority stimuli, enhancing the magnitude of perceptual gains associated with bottom up and top-down attention factors (Mather & Sutherland, 2011). In support of this idea, Phelps, Ling, and Carrasco (2006) demonstrated that the presentation of fearful faces within an attention cueing task enhances contrast sensitivity beyond the magnitude expected from additive or independent influences of arousal and attention. This effect supports the interactive modulation of perception by arousal and attention by

demonstrating that contrast sensitivity was enhanced for task-relevant (and thus high priority) stimuli. Further investigations have also supported the interactive role of emotion and attention on perception (Bocanegra, Huijding, & Zeelenberg, 2012; T. H. Lee, Baek, Lu, & Mather, in press).

While it is clear that arousal and attention interact, an examination of the current literature suggests that the nature of this interaction may depend on the temporal dynamics associated with emotion. Emotional experiences unfold over time and are associated with multiple stages of processing and regulation (Eimer & Holmes, 2002; Esslen, Pascual-Marqui, Hell, Kochi, & Lehmann, 2004; Jackson et al., 2003), suggesting that attention may be differentially modulated across time by emotional arousal. Consistent with this idea, many studies suggest that emotional arousal impairs attention processing at short temporal latencies (~50 – 500 ms) from stimulus onset (Bocanegra & Zeelenberg, 2009; Ciesielski et al., 2010; Muller, Andersen, & Keil, 2008; Schupp et al., 2007), whereas emotional arousal facilitates attention processing at later stages (~400-1000 ms) of processing (Bocanegra & Zeelenberg, 2009; Ciesielski et al., 2010; Padmala & Pessoa, 2008; Schupp et al., 2007). However, studies using relatively longer emotional stimulus presentations have also shown impairing affects of emotional arousal on attention up to a few seconds after emotional stimulus offset (Morriss et al., 2013; Muller, Andersen, & Hindi Attar, 2011). Some studies have also suggested that emotional arousal facilitates attention processes at short temporal latencies (Phelps et al., 2006; Selinger, Dominguez-Borras, & Escera, 2013). While the dynamics underlying emotional

arousal and attention interactions require further clarification, these studies support the idea that emotional arousal and attention interactions may differ across time.

Consideration of the potential interactions between arousal and attention in modulating time perception during threatening events has been limited. However, a study by Mella et al. (2011) provides preliminary support for such an interactive role of these processes in driving threat-related temporal distortions. In this study, negative sounds were presented and participants were instructed to pay attention to the emotional intensity of the stimulus, pay attention to its duration, or split attention between these two processes. This top-down attention manipulation influenced physiological arousal, as measured via skin conductance response (SCRs), such that SCRs were greater when participants were instructed to pay attention to emotional intensity. At the same time, physiological arousal seemed to partially predict temporal estimates, such that greater physiological arousal responses were associated with increased temporal estimates. This study thus supports the influence of attention in modulating arousal to drive subsequent changes in time perception. However, the possible role of arousal in influencing attention to distort time perception has yet to be explored.

A possible influence of arousal in driving attention is suggested by emotional timing studies that have demonstrated differential modulations of time perception over time. Studies have generally found that threat-relevant, emotionally arousing stimuli are overestimated in duration for short temporal durations, an effect that has largely been attributed to the influence of arousal (Droit-Volet, Meck, & Penney, 2007; Gil & Droit-Volet, 2012). Interestingly, these emotion-driven temporal distortions are diminished for

emotional stimuli of longer durations or for stimuli presented after emotional events (Angrilli et al., 1997; Bar-Haim et al., 2010; Lui et al., 2011; Noulhaine et al., 2007). These diminished temporal distortions have been attributed to decrements in attention to timing processes due to the recruitment of emotional appraisal or regulation processes. While it is unclear from such studies what drives the later recruitment of emotional appraisal and/or regulation processes, the decrement in physiological arousal that accompanies successful emotion regulation (Jackson, Malmstadt, Larson, & Davidson, 2000) suggests that these processes may be interactive in modulating time perception at later latencies from emotional stimulus onset.

Emotional appraisal and regulation can be consciously or automatically recruited in response to a threat-relevant arousing event (Gross & Thompson, 2007; Mauss, Bunge, & Gross, 2007; Phillips, Ladouceur, & Drevets, 2008). Emotion regulation processes are recruited at longer latencies from emotional stimulus onset (Jackson et al., 2003), and rely on cortical areas, particularly the prefrontal cortex and subgenual cingulate (Drevets, Savitz, & Trimble, 2008; Quirk & Beer, 2006). As such, emotion regulation processes may compete for attention resources with task-relevant or goal-oriented processes, including timing. Competition for cognitive resources between emotional regulation and timing processes at longer latencies from emotional stimulus onset is consistent with resource-sharing models of time perception, which suggest that limited attention/working memory resources must be divided across ongoing processes (Buhusi & Meck, 2009). Diverting cognitive resources away from timing processes has consistently been shown to reduce temporal estimates (Brown, 1985).

If emotional distortions in time perception at longer latencies from emotional stimulus onset reflect the recruitment of emotion regulation processes in response to increased emotional arousal, such distortions could have important implications for individuals with anxiety. It has been demonstrated that individuals with anxiety demonstrate enhanced sensitivity to emotional distractors and exhibit deficits in executive control, suggesting that they might show greater impairments in resource-sharing, resulting in greater temporal underestimation. On the other hand, individuals with anxiety have been shown to automatically engage in suppression regulation techniques, which in turn, have been associated with greater reports of anxiety and larger, longer lasting physiological responses (Bishop, Duncan, Brett, & Lawrence, 2004). A prolongation of the emotional experience may extend the overestimation influence of arousal observed at shorter temporal latencies, reducing the magnitude of temporal distortions. Exploring how threat-induced temporal distortions are modulated by anxiety might provide further insight into the aberrant processes underlying such disorders.

In this study, we were interested in assessing the possible role of physiological arousal in modulating the resource-sharing of attention between timing and emotion regulation processes after the presentation of a threat-related distractor. In Experiment 1, we examined how a task-irrelevant threatening distractor predicting immediate reinforcement would influence time perception for a subsequent neutral stimulus. We predicted that the recruitment of automatic emotion regulation processes to down-regulate the emotional response after the threat had passed would decrease temporal estimates of the comparison tone, consistent with a resource-sharing mechanism that

would divide attention or cognitive resources between emotion regulation and timing processes. Critically, we hypothesized that both a physiological arousal individual difference measure and a measure of trial level fluctuations in physiological arousal would be associated with increased underestimation, supporting the role of physiological arousal in modulating attention to drive temporal distortions at longer latencies from emotional stimulus onset. In Experiment 2, we aimed to more directly test our interpretation that the effects observed in Experiment 1 were driven by the manipulation of attention by presenting reinforcement after the comparison tone. We hypothesized that this manipulation might enhance the threat-relevance of the neutral comparison tone, subsequently increasing its prioritization and changing the predictive relationship between arousal responses and the modulation of time perception. Given the plausible implications of irregular threat-induced modulations of time perception for anxious individuals, we investigated the relationship between threat-driven temporal distortions and trait anxiety across both studies.

3.2 Experiment 1

To investigate whether physiological arousal modulates attention resource-sharing at longer temporal latencies from emotional stimulus onset, we examined how a task-irrelevant conditioned threat cue predicting an immediate aversive outcome would influence time perception for a subsequent neutral stimulus. Participants completed an ordinal comparison task in which they were presented with two tones and were instructed on each trial to judge whether the second tone was longer or shorter in duration than the first tone. The conditioned cues (CS+ and CS-) were presented between the two tones on

every trial. We were interested in how such cues influenced the perceived duration of the comparison tone. We chose to examine the influence of a threatening stimulus on time perception after the stimulus offset, as modulations of perception after the offset of a stimulus can more conclusively be attributed to regulation rather than reactive processes (Jackson et al., 2003). Based on resource-sharing models of time perception (Buhusi & Meck, 2009) and previous evidence that emotional overestimation effects on time perception are short-lived (Angrilli et al., 1997; Bar-Haim et al., 2010; Noulhaine et al., 2007), we hypothesized that at longer latencies from emotional stimulus onset, emotional regulation processes would compete with timing processes for attention resources. Given that threat-relevant stimuli are typically prioritized in attention (Lobue & DeLoache, 2008; Ohman et al., 2001), we predicted that such competition would take resources away from timing processes, resulting in the underestimation of temporal durations.

To examine whether the magnitude of this effect was modulated by physiological arousal, we computed an independent individual difference measure of threat-driven physiological arousal, collected during a conditioning phase prior to the timing task, in addition to collecting physiological arousal responses during the timing task.

Physiological arousal was assessed via the recording of phasic skin conductance responses (SCRs) to threat and neutral conditioned cues. We predicted that increased arousal would increase the prioritization of regulating emotion in attention, which would be supported by evidence that individual differences in the magnitude of threat-driven physiological arousal (greater differences in SCR responses to threat versus neutral cues) would increase temporal underestimation. At the same time, we predicted that

fluctuations in SCRs on a trial level basis would also predict timing judgments, such that larger SCR responses would be associated with greater underestimation responses. Using previously neutral, conditioned cues as threatening distractors allowed us to avoid potentially confounding factors that may have contributed to temporal distortions in previous studies of emotional effects on time perception, such as complexity (Folta-Schoofs et al., 2014).

Finally, we were also interested in exploring the possible influence of trait anxiety on temporal distortions. As individuals with higher levels of anxiety demonstrate greater impairments in goal-directed processes during the presentation of emotionally arousing distractors (Bishop et al., 2004), the magnitude of temporal underestimations may be enhanced by trait anxiety. On the other hand, studies of emotion regulation strategies in anxious individuals have found that such individuals report spontaneously utilizing suppression strategies to regulate their emotional responses more than healthy controls (Gross & Levenson, 1993, 1997). Interestingly, such enhanced attempts at emotion regulation have somewhat counterintuitively been associated with greater reports of anxiety, higher ratings of aversiveness for emotional stimuli, and enhanced physiological arousal. Such evidence may suggest that the reactive phase of emotional processing is extended in such individuals, delaying the successful recruitment of emotion regulation processes. As initial reactive influences of physiological arousal increase temporal overestimation (as demonstrated in Chapter 2), trait anxiety might alternatively be associated with a decrement in temporal underestimation. The unique hypotheses for how trait anxiety might influence emotion regulation and emotional reactivity to modulate

time perception allowed us to explicitly test which of these two possible mechanisms might be driving observed temporal distortions.

3.2.1 Methods

3.2.1.1 Participants

Fifty-two healthy adults provided written informed consent and received monetary compensation (\$10/hr) or course credit for participation. As we were interested in how learned threat influences time perception, skin conductance non-responders (skin conductance responses, SCRs, recorded for $\leq 10\%$ of all trials during conditioning) and non-learners (SCRs for neutral trials \geq SCRs for threat trials during conditioning) were excluded from analyses. The final sample consisted of 38 participants (20 females; 18-28 years, mean = 20.13; SD = 2.34). All participants demonstrated explicit knowledge of the relationship between cues and reinforcement after conditioning. The study protocol was approved by the Duke Medical Center Institutional Review Board.

3.2.1.2 Stimulus Materials

Stimuli were delivered using Presentation Software (Neurobehavioral Systems, Albany, CA). Tones (400 Hz sine waveforms with 3 ms linearly ramped rise/fall times) were delivered dichotically using BOSE QuietComfort® 15 Acoustic Noise Cancelling® headphones. Blue and green squares (3"x3") signaled threat and neutral trials. All participants completed trait anxiety scale of the Spielberger State-Trait Anxiety Inventory (STAI, Spielberger, 1983).

For each participant, an ascending staircase procedure was used to calibrate the 15-ms aversive electrical stimulation (ES), delivered to the flexor surface of the dominant

wrist, to a level considered annoying but not painful. The 15-ms non-aversive tactile stimulation (TS, pictured in Fig. 8), a TSP190 Haptic Stimulation Transducer, was delivered to the extensor surface of the dominant wrist. The device deploys a metal plunger that mechanically stimulates a 1.5 mm diameter surface area of skin and was calibrated to minimize plunger force while ensuring reliable perception. ES, TS, and SCRs were controlled using a MP-150 BIOPAC system (Goleta, CA).

3.2.1.3 Conditioning Task and Procedure

Participants were pseudo-randomly presented with 10 blue and 10 green squares for 3000 ms (Fig. 8A). One square color was paired with ES at a 50% rate. The other square color was paired with non-aversive TS at a 50% rate. All other square presentations were not paired with stimulation. Stimulation was delivered at the offset of the blue/green square. Cue color/stimulation type pairings were counterbalanced between subjects. A 9-12 s jittered fixation period followed each trial. It is important to note that typical discriminatory conditioning paradigms pair one conditioned stimulus (CS^+) with an aversive event while another conditioned stimulus (CS^-) remains unpaired. In the current study, we paired a neutral cue with a non-aversive outcome at the same rate as the threat cue (CS^+) was paired with an aversive outcome. This procedural decision was made to control for general arousal/anticipatory effects in order to more specifically capture threat-related arousal effects.

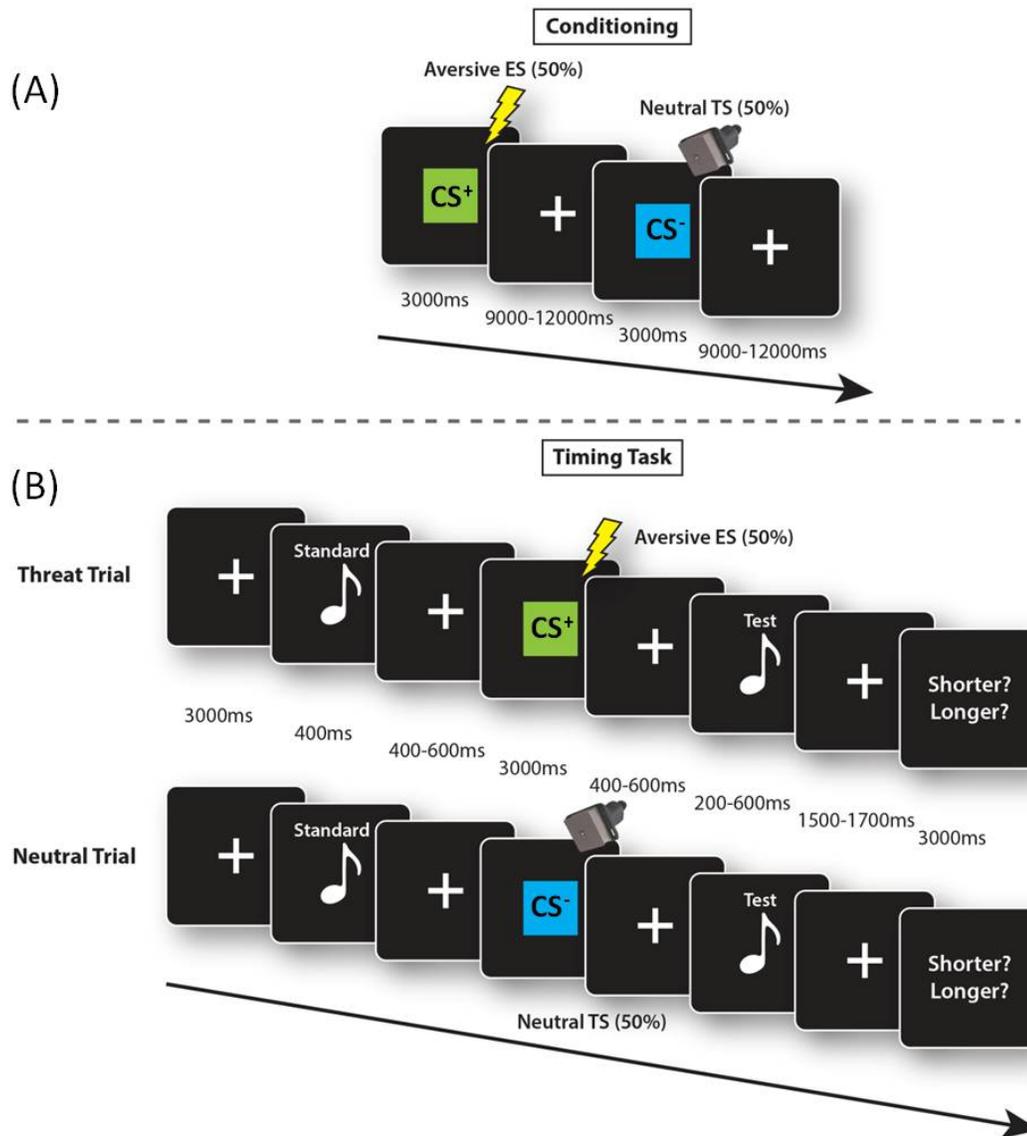


Figure 8: Example trial sequences for Experiment 1 conditioning and timing phases. (A) Conditioning Phase: green and blue squares presented with one colored square followed immediately by aversive electrical stimulation (ES) on 50% of trials and the other colored square followed immediately by neutral tactile stimulation (TS) on 50% of presentations. Participants were instructed to indicate via key press whether they expected ES, TS, or were unsure as soon as a square was presented. (B) Timing Task: 400 ms standard tone presented, followed by one of the two colored squares from the conditioning phase, and then a test tone of varying duration. Stimulation (ES or TS) was delivered at the offset of the colored squares on 50% of trials. A response screen asked participants to indicate whether the test tone was ‘longer’ or shorter’ in duration than the standard tone.

To increase attention to cue color/stimulation type contingencies, participants were instructed to indicate, as quickly as possible upon the presentation of a colored square, if they expected to receive ES, TS, or were unsure. Participants were informed that the cue color/ stimulation type pairing would not change during the experiment. After conditioning, participants rated the ES and TS on 9-point Likert scales of arousal (1 = completely unaroused, 9 = completely aroused) and valence (1 = completely unhappy, 9 = completely happy) and were asked to indicate how frequently each cue type was followed by ES and TS.

3.2.1.4 Timing Task and Procedure

After the conditioning phase, participants completed an ordinal-comparison timing task (Fig. 8B). After 3000 ms of fixation, each trial began with a standard tone (400 ms). A threat or neutral cue (blue or green square) was presented 400-600 ms after standard tone offset for 3000 ms. Stimulation (ES or TS) was delivered at cue offset. Test tones (200, 300, 400, 500 or 600 ms) were presented 400-600 ms after cue offset. After a variable wait period (1500 - 1700 ms after test tone offset), a response screen prompted participants to judge whether the test tone was 'longer' or 'shorter' in duration than the standard. Participants completed 4 practice trials without stimulation to ensure participants understood the task. A total of 80 threat and 80 neutral trials were presented. For both trial types, each test tone duration was presented 16 times. Half of these presentations were followed by the corresponding stimulation type. The task was divided into 4 equal runs. After the timing task, participants were again asked to rate the ES and

TS on 9-point Likert scales of arousal and valence and indicate how frequently each cue type was followed by ES and TS.

3.2.1.5 Timing Performance Analysis

The proportion of longer responses given for each test tone duration for threat and neutral trials were calculated for each participant (Figure 9A). Point of subjective equality scores (PSEs) were estimated from these raw scores using a maximum likelihood function to fit logistic functions to individual participant data. Only trials unpaired with stimulation were included in analyses to remove the potential confound of stimulation delivery on decision-making. Underestimation is reflected by PSE scores > 400 ms and overestimation is reflected by PSE scores < 400 ms, where 400 ms is the point of objective equality (equal to the actual duration of the test tone).

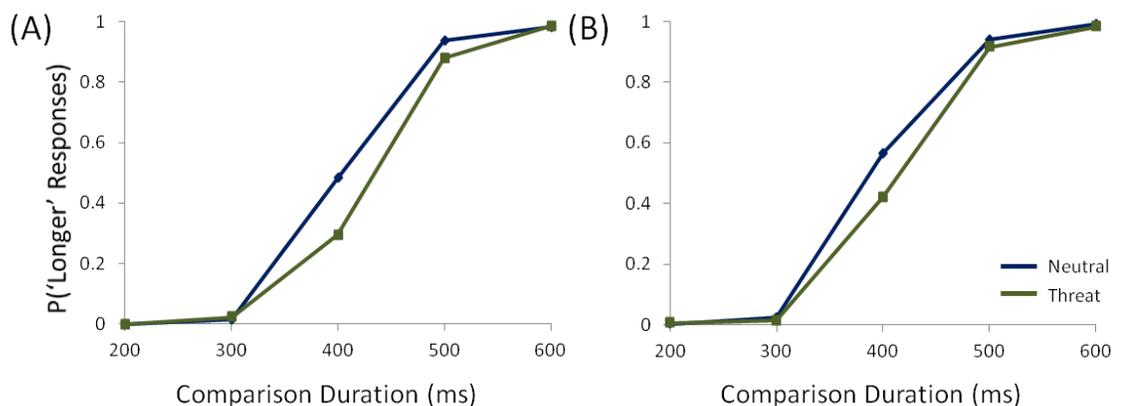


Figure 9: Average proportion of longer responses made during threat and neutral trials (A) in Experiment 1 and (B) in Experiment 2.

3.2.1.6 Skin Conductance Responses (SCRs) Analyses

SCRs were recorded from the hypothenar eminence of the nondominant hand palm. SCRs were calculated with the Autonomate analysis program (Green et al., 2014)

in MATLAB (MathWorks, Natick, MA) using the criteria reported by Dunsmoor et al. (2009). Briefly, SCRs were scored as responses if the trough-to-peak occurred 1-4 s after stimulus onset, the response lasted 0.5-5.0 s, and the amplitude was >0.02 microsiemens. SCRs that did not meet these criteria were scored as zeros. SCRs were manually verified by a trained scorer. SCRs were range-corrected separately for conditioning and timing phases by dividing responses by the largest recorded SCR in that phase (Lykken & Venables, 1971).

3.2.2 Results

3.2.2.1 Subjective Ratings

A 2x2 repeated measures ANOVA of arousal ratings in response to ES (conditioning: $M = 5.1$; test: $M = 5.4$) and TS (conditioning: $M = 1.8$; test: $M = 1.9$) after the conditioning and test phase confirmed that participants perceived ES as more arousing than TS, $F(1,37) = 451.605, p < .001$, with no change in subjective ratings across experimental phase or interaction between stimulation type and study phase, p 's > .1. A separate 2x2 repeated measures ANOVA of valence ratings in response to ES (conditioning: $M = 4.8$; test: $M = 4.2$) and TS (conditioning: $M = 5.8$; test: $M = 5.9$) after conditioning and test phases confirmed that participants perceived ES as more aversive than TS across experimental phase, $F(1,37) = 33.269, p < .001$. A significant interaction between stimulation type and study phase, $F(1,37) = 9.144, p = .005$, indicated that after the test phase ES was rated significantly more aversive than after the conditioning phase, $t(37) = 3.064, p = .004$.

3.2.2.2 Timing Task Performance

We found a significant difference between PSE values for neutral and threat trials, $M = 4.8$, $t(37) = -3.914$, $p < .001$, *Cohen's d* = .71, such that threat trials, $M = 424.41$, $SE = 4.88$, were underestimated compared to neutral trials, $M = 402.67$, $SE = 5.1$. No difference between WF values was observed, $t(37) = -1.118$, $p = .271$, suggesting temporal sensitivity was not differentially affected on threat and neutral trials.

3.2.2.3 Individual Differences Analyses

Threat PSE scores were positively correlated with SCR differences from the conditioning phase, $r = .395$, $p = .014$, such that greater differences in SCRs to threat versus neutral cues predicted greater underestimation on threat trials (Figure 10A). Correlational analyses also revealed a negative correlation between Threat PSE scores and trait anxiety, $r = -.336$, $p = .039$, such that greater trait anxiety predicted less underestimation on threat trials (Figure 10B), consistent with the hypothesis that greater anxiety would extend the duration of emotional reactivity, delaying successful emotion regulation. No correlation was observed between Neutral PSE scores and trait anxiety.

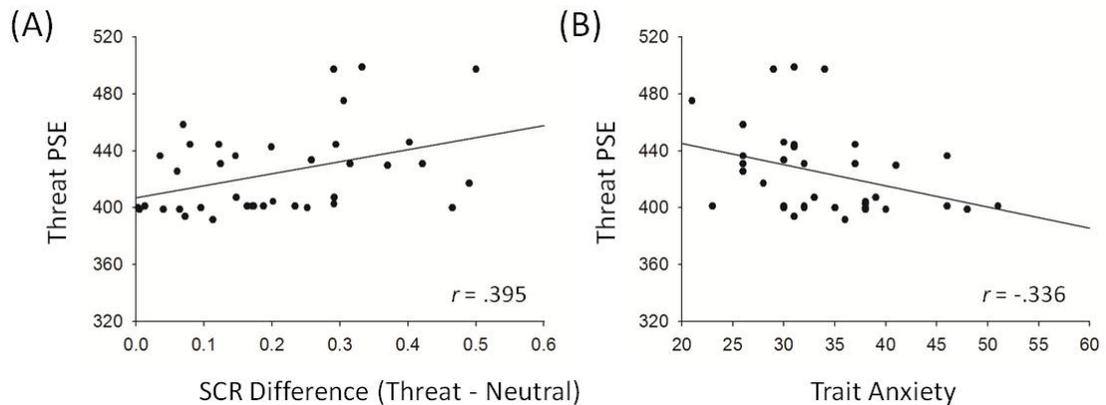


Figure 10: (A) Greater skin conductance responses to threat (CS⁺) versus neutral (CS⁻) cues predicted greater underestimation on threat trials. (B) Greater trait anxiety predicted less underestimation on threat trials.

3.2.2.4 SCR Analyses

To assess the relationship between SCRs and subsequent timing judgments, we conducted a 2x2 (Trial Type x Response) repeated measures ANOVA of SCRs. As we selected participants based on greater SCRs to threat versus neutral trials, we unsurprisingly found a main effect of Trial Type, $F(1,37) = 24.522$, $p < .001$, $\eta p^2 = .399$. There was a trend for a main effect of Response, $F(1,37) = 3.938$, $p = .055$, $\eta p^2 = .098$ and a trend for a Trial Type x Response interaction, $F(1,74) = 3.238$, $p = .080$, $\eta p^2 = .080$. Planned comparisons confirmed that SCRs were larger when participants responded shorter versus longer on threat trials, $t(37) = 2.263$, $p = .030$, *Cohen's d* = 0.17, but not on neutral trials.

3.2.3 Discussion

This study confirmed our hypothesis that threat-related arousal would interact with attention processes to predict the underestimation of a subsequently presented neutral stimulus, supporting the diversion of attention by threat at the expense of task

relevant processes. The underestimation effect we observed is in line with previous evidence of temporal underestimation at longer latencies from emotional stimulus onset (Angrilli et al., 1997; Bar-Haim et al., 2010; Lui et al., 2011; Noulhaine et al., 2007) and supports a resource-sharing mechanism, whereby attention resources were redirected from task-relevant timing processes towards processing of a threat-relevant emotionally arousing distractor. Because such effects occurred after the offset of the emotional stimulus, we believe they reflect the recruitment of emotion regulation processes, rather than emotional reactivity *per se*.

Supporting the idea that the diversion of attention resources from timing was driven by physiological arousal, we found that greater differences in SCRs to threat versus neutral cues during conditioning predicted greater temporal underestimation on threat trials in the timing task. We also found that trials on which comparison tone durations were judged as shorter versus longer than the standard tone were associated with greater SCRs. This effect was significant only for threat trials. Such specificity may reflect the modulatory role of threat-specific physiological arousal, rather than a more general physiological arousal process. Based on such evidence, we conclude that the temporal underestimation of the comparison tone was driven by a threat-related arousal modulation of attention resources.

Interestingly, in the current experiment we found that the magnitude of temporal distortion for the comparison tone was diminished for individuals with higher trait anxiety scores. Such findings may suggest that the duration of emotional reactivity is extended in individuals with higher trait anxiety, such that physiological arousal-driven

overestimation biases, which are frequently found at shorter latencies from emotional stimulus onset (Droit-Volet & Meck, 2007), may contribute to temporal estimates in anxious individuals at this later time point. The extended duration of emotional reactivity may delay the successful regulation of emotion, thus emotional regulation processes may not compete with timing processes as much as in individuals with lower trait anxiety. While this is one possible interpretation of the current findings, others are possible. One plausible alternative mechanism for the reduced magnitude of temporal underestimation in high trait anxious individuals could be an influence of fear generalization. In fear generalization, learned fear responses are transferred to new stimuli (Dunsmoor, Prince, Murty, Kragel, & LaBar, 2011; Dunsmoor, White, & LaBar, 2011). While such processes may be adaptive in certain contexts, it has been proposed that individuals with anxiety may demonstrate enhanced fear generalization, contributing to the perpetuation of their anxieties, as stimuli that are non-threatening elicit fear responses (Lissek et al., 2005; Lissek et al., 2009). If time perception reflects the prioritization of stimuli in attention, the reduced underestimation of the comparison tone may reflect generalization of fear such that the comparison stimulus is perceived as threat-relevant. Nevertheless, we did not observe a relationship between SCR responses on neutral trials with anxiety, suggesting that the reduction in underestimation we observed was not driven by an increase in underestimation on neutral trials.

To summarize, the relationships we observed between threat-related arousal and time perception support our proposal that increased physiological arousal modulates resource-sharing of attention to timing processes. We suggest that the recruitment of

emotional regulation processes, in proportion to the magnitude of the initial physiological response, were responsible for the diversion of attention resources. We also believe that the reduction of temporal underestimation in trait anxious individuals may reflect the extension of an initial emotional reactivity response, potentially delaying the successful recruitment of emotional regulation processes. Nevertheless, we did not directly manipulate the experience or duration of emotion within this experiment. Thus, to further explore the idea that the duration of an emotional experience would change the nature of arousal and attention interactions in the modulation of time perception, we manipulated when the aversive outcome was expected in Experiment 2, such that the duration of threat anticipation was extended.

3.3 Experiment 2

3.3.1 Introduction

In this experiment, we were interested in further exploring how physiological arousal and attention interact to drive temporal distortions and specifically to address whether the duration of an emotional experience modulates the interaction of arousal and attention in driving temporal distortions. While static emotional images have typically been associated with temporal underestimations or reductions in the magnitude of temporal overestimation at longer latencies from emotional stimulus onset (Angrilli et al., 1997; Bar-Haim et al., 2010; Lui et al., 2011), the presentation of dynamic longer emotional stimuli were shown to result in temporal overestimation even at longer latencies from the stimulus onset (Droit-Volet et al., 2011; but see Noulhaine et al., 2007). This effect suggests that extending the duration of an emotional experience by a

more powerful emotional manipulation may change the contribution of physiological arousal to attention resource-sharing in driving temporal distortions. To more explicitly test this hypothesis, we implemented a trace conditioning procedure in which threat cues were paired with aversive outcomes delivered after an empty trace interval. In the timing task, this temporal gap between cue offset and stimulation delivery was maintained such that stimulation was delivered *after* the neutral tone to be timed. This modification of the previous experimental design created a period of threat anticipation from the presentation of the threat cue until the test tone offset. The anticipation of threat in trace conditioning procedures is thought to recruit attention and working memory resources to maintain the relationship between the cue and predicted aversive outcome (Carter et al., 2003; Han et al., 2003). As such, we predicted that resource-sharing might still be necessary between threat anticipation and timing processes and thus, the duration of the comparison tone might still be underestimated. However, we hypothesized that this manipulation would extend the duration of the emotional experience, as anticipation of threat had to be maintained across the timing of the comparison stimulus, such that the transition from an initial physiological arousal-driven overestimation effect, as demonstrated in Chapter 2, to an attention resource-sharing effect on time perception would be delayed. In this case, we predicted that physiological arousal might better predict a reduction in the magnitude of temporal underestimation.

3.3.2 Methods

3.3.2.1 Participants

Sixty-one healthy adults provided written informed consent and received monetary compensation (\$10/hr) or course credit for participation. The same exclusion criteria were implemented as in Experiment 1, except one additional participant was excluded for not demonstrating explicit knowledge of cue color/stimulation type pairings. Such explicit knowledge is argued by some to be critical for successful trace conditioning (Weike et al., 2007). The final sample consisted of 38 participants (17 females; 18-33 years, mean = 20.68; SD = 3.21). The study protocol was approved by the Duke Medical Center Institutional Review Board.

3.3.2.2. Conditioning and Timing Tasks

The conditioning task and procedure were identical to those in Experiment 1 except that stimulation (ES and TS) was delivered pseudo-randomly 700-1500 ms after cue offset (to approximate the trace intervals in the subsequent timing task) (Figure 11A). The timing task and procedure were identical to those in Experiment 1 except that stimulation was delivered at test tone offset (Figure 11B).

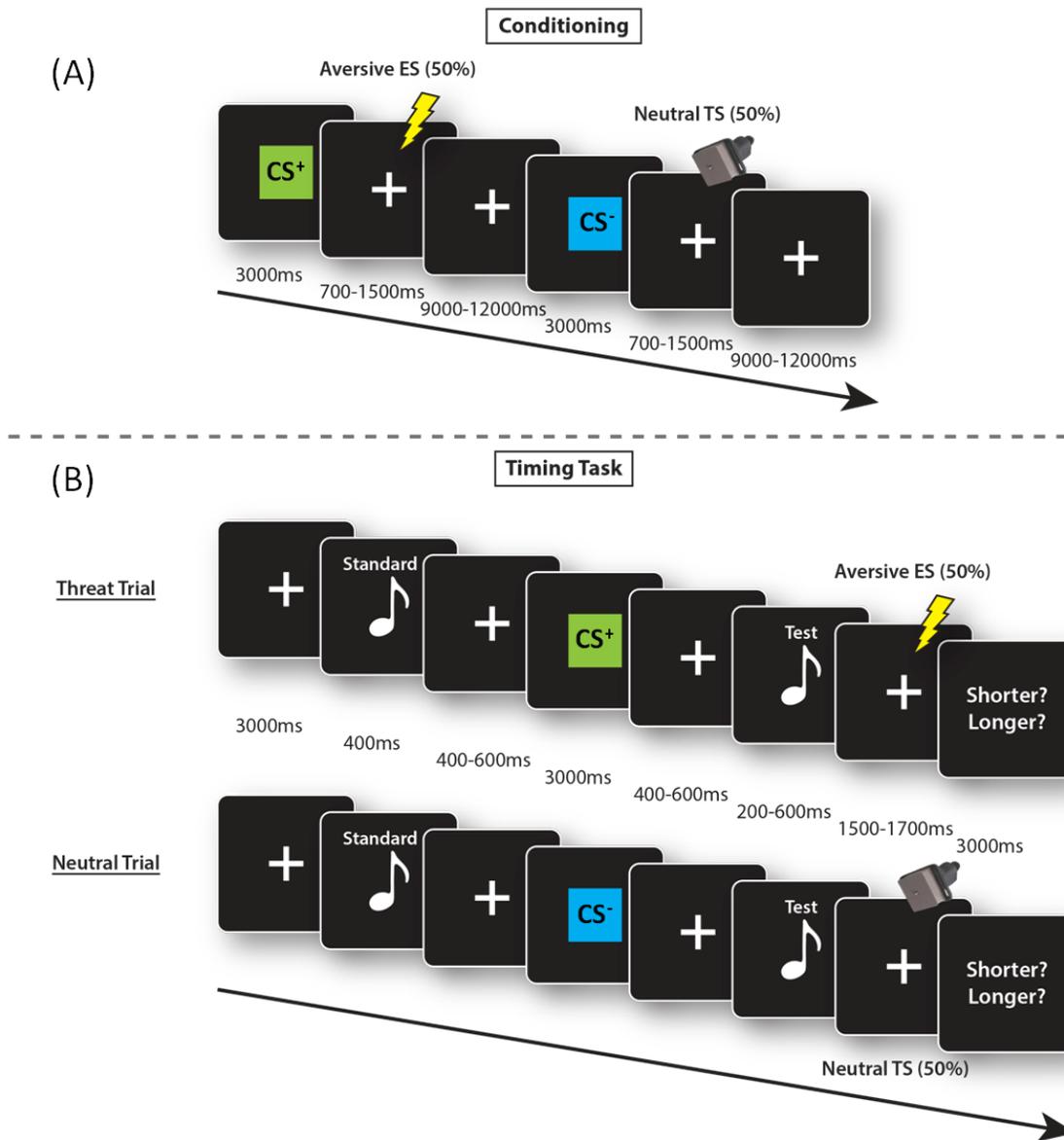


Figure 11: Example trial sequences for Experiment 2 conditioning and timing phases. (A) Conditioning Phase: same as Experiment 1 except stimulation (ES & TS) delivered after a variable 700-1500 ms trace interval. (B) Timing Task: Same as Experiment 1 except stimulation (ES & TS) delivered at comparison tone offset.

3.3.2.3 Analyses

The same analyses were performed for Experiment 2 as were conducted for Experiment 1. The average proportion of longer responses made on threat and neutral

trials are shown in Figure 9B. Between-experiment contrasts were conducted to ensure that our samples were comparable on a number demographic and individual difference measures (age, electrical stimulation level, state anxiety, and arousal/valence ratings of ES) prior to analyses across Experiment 1 and 2. We ran two separate 2x2 mixed ANOVAs with Trial Type as a within-subject factor and Experiment as a between-subject factor for PSE and WF values. To compare SCRs across experiments, we conducted analyses of SCRs as described in Experiment 1 with Experiment as a between-subject variable. We also compared RT values for threat versus neutral trials across experiments in a 2x2 mixed ANOVA with Trial Type as a within-subject factor and Experiment as a between subject factor.

3.3.3 Results

3.3.3.1 Subjective Ratings

A 2x2 repeated measures ANOVA of arousal ratings in response to ES (conditioning: $M = 5.2$; test: $M = 5.4$) and TS (conditioning: $M = 2.2$; test: $M = 2.2$) after the conditioning and test phase confirmed that participants perceived ES as more arousing than TS, $F(1,37) = 99.998, p < .001$, with no change in subjective ratings across experimental phase or interaction between stimulation type and study phase, $p's > .1$. A separate 2x2 repeated measures ANOVA of valence ratings in response to ES (conditioning: $M = 4.4$; test: $M = 3.8$) and TS (conditioning: $M = 5.6$; test: $M = 5.6$) after conditioning and test phases confirmed that participants perceived ES as more aversive than TS across experimental phase, $F(1,37) = 67.572, p < .001$. No main effects or interactions with experimental phase were observed, $p's > .05$.

3.3.3.2 Timing Task Performance

PSE values on threat trials were significantly underestimated compared to neutral trials, $t(37) = -2.138, p = .039, \text{Cohen's } d = .40$. WF values did not differ between trial types, $t(37) = -.573, p = .570$.

3.3.3.3 Individual Differences Analyses

Consistent with our hypothesis, PSE difference scores were negatively correlated with SCR differences in the conditioning phase, $r = -.443, p = .005$, such that greater differences in SCRs for threat and neutral cues predicted less underestimation on threat trials. This effect was driven by PSE scores on threat trials, $r = -.323, p = .048$ (Figure 12). No correlation between trait anxiety and PSE values were observed.

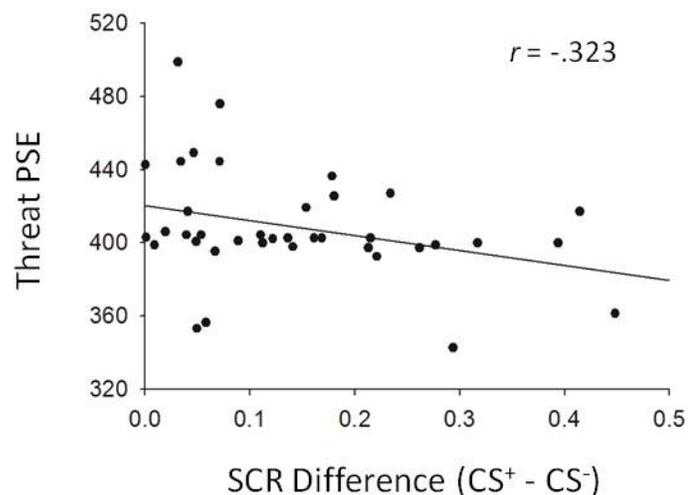


Figure 12: Greater SCRs to CS⁺ versus CS⁻ cues predicted less underestimation on threat (CS⁺) trials.

3.3.3.4 SCR Analyses

A 2x2 ANOVA (Trial Type x Response) of SCRs only revealed a main effect of Trial Type, $F(1,37) = 16.110, p < .001, \eta_p^2 = .303$.

3.3.3.5 Comparing Experiments 1 & 2: Demographic and Individual Difference Measures

A comparison of shock level values between Experiments 1 & 2 revealed that participants in Experiment 2 set the electrical stimulation level significantly higher than participants in Experiment 1, $t(74) = 3.475, p = .001, \text{Cohen's } d = .80$. Nevertheless, participants did not report differences in subjective arousal or valence in response to electrical stimulation, *all p's* > .1. Participants also did not differ in age or trait anxiety between the two experiments, *all p's* > .05.

3.3.3.6 Comparing Experiments 1 & 2: Timing Task Performance

A 2x2 (Trial Type x Experiment) mixed ANOVA of PSE values did not reveal a significant main effect or interaction with Experiment. To assess the potential influence of shock level differences between the experiments, we ran the same analysis with Shock Level as a covariate. No main effect or significant interaction with Shock Level was observed. A 2x2 (Trial Type x Experiment) mixed ANOVA of WF values did not reveal any significant main effects or interactions. To assess the potential influence of shock level differences between the experiments, we ran the same analysis with Shock Level as a covariate. No significant main effects or interactions were observed.

3.3.3.7 Comparing Experiment 1 & 2: SCR Analyses

To examine the relationship between SCRs and subsequent timing judgments across experiments, we conducted a 2x2x2 (Trial Type x Response x Experiment) mixed ANOVA of SCRs (Figure 13). We found a main effect of Trial Type, $F(1,74) = 40.378, p < .001, \eta_p^2 = .353$ and a main effect of Response, $F(1,74) = 5.140, p = .026, \eta_p^2 = .065$.

These main effects were qualified by a Trial Type x Response interaction, $F(1,74) = 5.884$, $p = .018$, $\eta_p^2 = .074$. Follow up analyses demonstrated that SCRs were larger when participants responded shorter versus longer on threat trials only, $t(75) = 2.822$, $p = .006$, *Cohen's d* = 0.14, consistent with the findings in Experiment 1. No other main effects or interactions were observed.

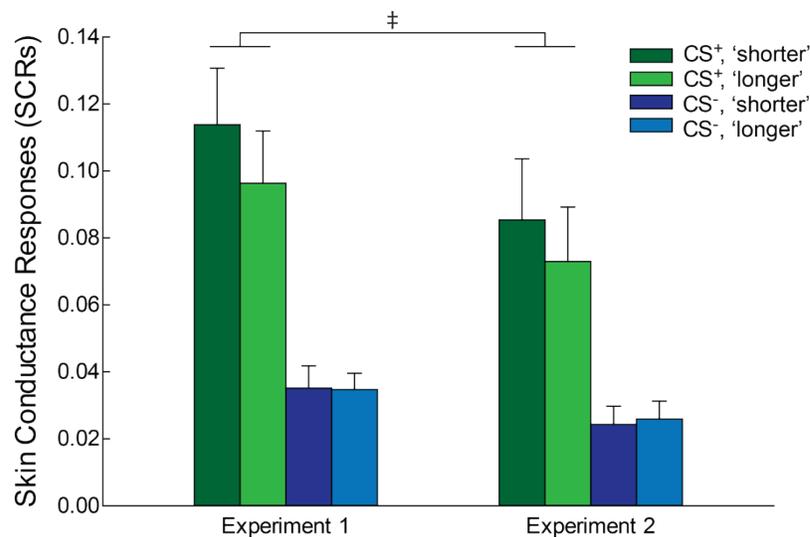


Figure 13: SCRs for CS⁺ and CS⁻ trials for which participants judged the comparison tone as shorter or longer than the preceding standard tone in Experiment 1 and 2. A main effect of Trial Type indicated that SCRs were greater on CS⁺ versus CS⁻ trials. An interaction between Trial Type and Response indicated that SCRs were greater for trials on which comparison tones were judged as shorter versus longer for CS⁺ trials only.

3.3.4 Discussion

In this experiment, we replicated the underestimation effect we observed in Experiment 1. While null effects are difficult to interpret, the fact that we did not observe any significant differences in PSEs between these two studies suggests that attention processes may have been similarly diverted from timing processes in both Experiment 1

and 2. Interestingly, despite the direction of this main effect, we found that threat-related physiological arousal differentially biased temporal estimates in Experiment 2 from the relationship we reported in Experiment 1. Specifically, we found that when an aversive outcome was expected *after* the test tone to be timed, greater threat-related physiological arousal predicted less temporal underestimation. We propose that this effect was driven by the extension of a physiological arousal-driven anticipation response prior to an aversive outcome, which biased temporal estimates in the opposing direction from attention resource-sharing. Such an influence of physiological arousal is consistent with studies demonstrating an overestimation of temporal durations associated with emotionally arousing stimuli at short latencies from emotional stimulus onset. Essentially, we believe this correlation may reflect a shift in the balance between physiological arousal and attention resource-sharing across individuals.

The fact that we found an overall underestimation effect on threat versus neutral trials and did not observe any differences in the relationship between trial fluctuations in SCRs and temporal judgments between the current experiment and Experiment 1 suggests that our manipulation of the duration of emotional reactivity was not strong enough to overcome the distracting influence of the threat cue on attention. The fact that participants rated ES as only moderately arousing and aversive may explain why it was only possible to observe the effects of threat anticipation on performance using an individual difference measure. A more potent manipulation of anticipation might overcome the underestimation bias of the threat cue though such a manipulation might be difficult to achieve in a laboratory setting. Overestimation of duration during the

expectation of an aversive outcome has previously been supported in the literature (Droit-Volet, Mermillod, et al., 2010), consistent with the direction of the effects we observed in the current experiment. However, in this study by Droit-Volet and colleagues, all threat trials were followed by an aversive outcome, which leaves open the possibility that the observed effects were driven by the delivery of aversive reinforcement, rather than the effects of anticipation. At the same time, our findings for the current threat anticipation manipulation appear to conflict with those we observed in Chapter 2 in the trace conditioning procedure. However, many procedural differences exist between these two experiments which could have driven the different effects we observed, including the modality of the stimuli to be timed, the task-irrelevant nature of anticipation in the current study, the duration of the stimuli to be timed and the threat cues, and the duration of time elapsed from threat cue presentation until the presentation of the stimulus to be timed. Further work on threat anticipation effects on time perception is thus necessary to further explore the underlying mechanisms and resulting consequences for temporal distortions.

3.4 General Discussion

Our findings across Experiments 1 and 2 suggest that threat-induced biases in temporal estimates are driven by the interaction between physiological arousal and attention processes. These experiments extend theories of emotion and attention by demonstrating that arousal and attention interact to modulate not only basic perceptual phenomena but also the more dynamic perception of time. Given that time perception necessarily evolves over time, time perception may be particularly well-suited for

examining the dynamic relationship between arousal and attention across the time course of emotional reactive and regulatory processes.

By measuring physiological arousal and correlating this measure with performance, we demonstrated in Experiment 1 that physiological arousal could drive the underestimation of temporal durations, suggesting it may play a role in modulating attention at later processing stages in the time course of an emotional response. We believe this finding represents an important advance in the study of emotional timing by demonstrating that threat-related physiological arousal does not exclusively result in overestimation biases as has been implicitly assumed based on pacemaker-accumulator models of time perception but instead, may also interact with attention to drive the underestimation of temporal durations. We interpret the observation that the relationship between physiological arousal and the direction of temporal biases reversed when we manipulated the duration of threat anticipation as evidence that the influence of physiological arousal on temporal estimates dynamically changes across the time course of an emotional response. Specifically, we propose that initial reactive processes to an emotional event support the overestimation of temporal durations while at later processing stages, the magnitude of threat-driven physiological arousal may potentially drive the recruitment of emotion regulation and appraisal processes to mitigate the emotional response after the threat of an aversive outcome is determined to have passed. This interpretation is consistent with that of previous studies that have demonstrated a reduction in the magnitude of threat-related temporal overestimation for longer temporal durations (Angrilli et al., 1997; Bar-Haim et al., 2010; Noulhaine et al., 2007). As we

increased the duration of threat anticipation from Experiment 1 to Experiment 2, we believe this manipulation extended the duration of the initial reactive phase, such that emotional regulation processes were not recruited until later in the trial. Thus, in Experiment 2, the prolongation of the emotional experience was associated with physiological arousal biases towards decreasing, rather than increasing the magnitude of temporal underestimation. The relationship between trait anxiety and temporal estimation in Experiment 1 also supports the idea that an initial reactive emotional phase may have been extended in more anxious individuals, consistent with the deficits in the successful engagement of emotion regulation that have been demonstrated in anxious populations (Amstadter, 2008). Our findings thus suggest that current theories of emotional influences on time perception be adapted to reflect the temporal component of threat-induced arousal influences on time perception.

While we propose that the manipulation of threat anticipation across Experiment 1 and 2 and the trait anxiety findings reflects the extension of an initial emotional reactivity phase, further work will be necessary to more conclusively demonstrate that the emotional experience was, in fact, extended. Within the current experimental design, one way to more directly test this possibility would be to examine the magnitude of physiological arousal during the comparison tone. For example, if individuals with high trait anxiety showed greater physiological arousal, as measured via skin conductance levels, during the presentation of the comparison tone than individuals with lower anxiety scores, such findings could support the idea that the duration of the emotional experience was extended in such individuals. A similar analysis could be performed by comparing

physiological arousal (via skin conductance levels) during the comparison tone presentation in Experiment 1 versus Experiment 2 to support the idea that the duration of the physiological response determined the modulatory role of physiological arousal across these two studies. Such analyses are ongoing.

In general, our findings support current theories of how threat-related, emotionally arousing stimuli direct attention. Specifically, such stimuli are thought to interact with attention to increase the perception of high priority stimuli, with priority status determined by contextual parameters (Mather & Sutherland, 2011). In Experiment 1, we believe the threatening distractor was given highest priority status, consistent with studies that have shown that emotional distractors are prioritized over task-relevant processes (with low attention loads) (Schmidt et al., 2014). In Experiment 2, while the underestimation of the comparison tone suggests that the threatening distractor was still prioritized over the comparison tone, the manipulation of threat anticipation may have increased the priority of the comparison stimulus in individuals who experienced a prolonged period of emotional reactivity, as the comparison tone became a proximal temporal predictor of the aversive outcome, resulting in a small perceptual gain for the comparison tone. We believe our findings support the idea that temporal distortions may reflect an enhancement in perception driven by the prioritization of threat-relevant stimuli. Future studies might further examine this possibility by comparing temporal estimates for both a threat-relevant, emotionally arousing distractor and a subsequent neutral stimulus within the same experimental design. Evidence of a proportional trade-

off in temporal estimates would further support the idea that temporal distortions reflect the relative prioritization of presented stimuli.

In Experiment 2, despite the proposed manipulation of the duration of an initial emotional reactivity phase, we still observed a main effect of temporal underestimation. This finding may suggest that the threat anticipation manipulation we conducted was not strong enough to overcome the distracting influence of the threat cue. The fact that participants only rated ES as moderately arousing and aversive may explain why it was only possible to observe the effects of threat anticipation on performance using an individual difference measure. A more potent manipulation of anticipation might overcome the underestimation bias of the threat cue, though such a manipulation might be difficult to achieve in a laboratory setting. However, the study by Droit-Volet et al. (2011) suggests that more dynamic emotional stimuli, such as video clips, may extend the duration of emotional reactivity. Nevertheless, future investigations would need to control for potential confounding factors during the presentation of more complex emotional manipulations, as other factors besides the emotional content in such stimuli may contribute to temporal distortions, such as complexity (Folta-Schoofs et al., 2014) or the dynamic nature of the stimuli themselves (Fayolle & Droit-Volet, 2014). The influence of threat expectation in modulating temporal distortions has previously been shown to result in temporal overestimations of duration (Droit-Volet, Mermillod, et al., 2010) using aversive tones, rather than ES, as an aversive reinforcer, suggesting that it may be possible for threat anticipation to overcome the distracting influence of the threat cue itself. However, in this study, all threat trials were followed by an aversive outcome,

which leaves open the possibility that the reported effects on time perception may have been, at least partially, driven by the delivery of aversive reinforcement, rather than purely driven by the anticipation of threat. Further work perhaps parametrically manipulating the potency of threat anticipation might be useful in further understanding the underlying mechanisms and resulting consequences of threat anticipation on time perception.

It is interesting to note that in the current study we did not observe any effects of our threat manipulation on WF values. This is interesting in light of the fact that emotional stimuli have been shown to modulate sensitivity in other perceptual domains, such as sensitivity to contrast (e.g., T. H. Lee et al., in press; Phelps et al., 2006). This finding supports the idea that emotional stimuli adaptively modulate perceptual features in distinct ways in order to adaptively respond to danger (Bocanegra & Zeelenberg, 2009). Biases in perception, rather than changes in sensitivity to a particular stimulus dimension, have been shown for other perceptual phenomenon such as perceived loudness, perceived height, and perceived distance from an emotional stimulus (Siegel & Stefanucci, 2011; Stefanucci & Storbeck, 2009).

While we have interpreted our findings as evidence of an influence of emotional distraction on temporal processing for the subsequent neutral comparison tone, using similar procedural designs, studies have suggested that emotional distractors can impair working memory for a previously presented item (Dolcos & McCarthy, 2006). Such evidence may alternatively suggest that our current findings were driven not by changes in the perception of the comparison tone but due to distortions in working memory for the

duration of the standard tone. While we cannot rule out this possibility, we believe this possible mechanism of distortion is less likely. As the duration of the standard stimulus was the same on every trial, it is likely that participants were able to form a more stable representation of the standard stimulus in long-term memory and were able to compare this representation to the comparison tone. Additionally, we found that manipulating the time point at which aversive stimulus could be expected following the emotional distractor between Experiment 1 and 2 modulated the direction of the relationship between temporal estimates and physiological arousal. If the effects we observed were driven by a distortion in the representation of the standard stimulus, manipulating whether the aversive outcome was delivered before or after the comparison tone should not have influenced temporal judgments. Finally, another study which reported an underestimation effect using an ordinal comparison procedure similar to that of the current study (Lui et al., 2011) also demonstrated an underestimation effect using a temporal reproduction task in which no standard stimulus was presented prior to the emotional distractor, supporting the argument that the subsequent neutral stimulus was the locus of the emotional distractor effect.

The findings of this study may have important implications for our understanding of the mechanisms that dynamically modulate threat-driven changes in perception. In particular, such effects may be relevant to our understanding of aberrant arousal and attention responses in anxious populations. If temporal distortions reflect the relative priority level of presented stimuli, the fact that we observed a reduction in temporal underestimation in higher anxiety individuals may suggest that such individuals have

deficits in properly prioritizing stimuli within the context of threat-related experiences. Such aberrant processes, in turn, could contribute to deficits in fear learning that have been observed in anxious populations (Lissek et al., 2005; Lissek et al., 2009). Further research will be necessary to more definitely test this hypothesis.

3.5 Summary

In this study, we found that physiological arousal effects on time perception were modulated by the duration of threat anticipation. In contrast to predictions of current theories of time perception that suggest that arousal results in the overestimation of time, we found in Experiment 1 that threat-induced arousal predicted the *underestimation* of temporal durations, suggesting that threat-induced arousal modulates the diversion of attention resources from timing processes. In this experiment, we also found that the magnitude of temporal underestimation of the threat-irrelevant comparison stimulus following the presentation of a threatening cue was minimized by trait anxiety, which we believe may have been the result of an extended period of emotional reactivity and a reduction in the successful recruitment of emotion regulation processes. Consistent with this idea, we found in Experiment 2 that manipulating the duration of threat anticipation such that the aversive outcome was not expected until after the comparison tone reversed the relationship between physiological arousal and time perception, such that higher physiological arousal predicted *less* underestimation of the test tone. We believe this effect may also have reflected an extended duration of emotional reactivity and a delay in the recruitment of emotion regulation processes as the threat of an aversive outcome persisted through the timing of the comparison tone. These findings have important

consequences for studies of emotional influences on time perception, as they suggest an important role for context and temporal dynamics in modulating the effects of emotional stimuli on the perception of time. At the same time, these findings may have important implications for our understanding of aberrant processing of and responding to threat in anxious populations.

4. Differential effects of amphetamine and haloperidol on temporal reproduction: dopaminergic regulation of clock speed and modulation of attention by positive emotion

4.1 Introduction

Dopamine (DA) plays an integral role in the modulation of multiple cognitive processes. While its importance in timing and time perception is well established (Allman & Meck, 2012; Coull, Cheng, & Meck, 2011), studies examining the effects of dopaminergic (DAergic) drug administration on timing processes in humans have been limited. Previous work with rats and mice has shown that indirect DA agonists, such as cocaine and methamphetamine, result in the overestimation of time, as indicated by horizontal leftward shifts in the psychophysical functions relating the probability of a response to signal duration (e.g., Abner, Edwards, Douglas, & Brunner, 2001; Buhusi & Meck, 2002; Cevik, 2003; R. K. Cheng, Ali, & Meck, 2007; R. K. Cheng, Hakak, & Meck, 2007; R. K. Cheng, MacDonald, & Meck, 2006; Cheung et al., 2006; Chiang et al., 2000; Maricq & Church, 1983; Maricq, Roberts, & Church, 1981; Matell, Bateson, & Meck, 2006; Matell, King, & Meck, 2004; Meck et al., 2012). In contrast, the administration of DA receptor antagonists, such as haloperidol and raclopride, lead to an underestimation of time, as indicated by horizontal rightward shifts in psychophysical functions (e.g., Buhusi & Meck, 2002; R. K. Cheng & Liao, 2007; Drew, Fairhurst, Malapani, Horvitz, & Balsam, 2003; Lustig & Meck, 2005; MacDonald & Meck, 2005, 2006; Maricq & Church, 1983). Taken together, these results suggest that systemic changes in effective DA levels modulate the speed of an internal clock in the multiple-

seconds range (Buhusi & Meck, 2005; Gu & Meck, 2011; Jones & Jahanshahi, 2011).

These findings are consistent with the striatal beat frequency (SBF) model, which predicts that tonic changes in DA levels modulate cortical oscillation frequencies, resulting in biases in time perception (Allman & Meck, 2012; Matell & Meck, 2004).

In line with rodent studies, pharmacological challenges in humans have resulted in temporal distortions consistent with changes in clock speed (Arushanya et al., 2003). Rammsayer (1993, 1997, 1999) has found that DA antagonists impair time perception in the range of milliseconds and seconds, attributing these effects to DAergic modulation of the basal ganglia, a structure believed to play an integral role in timing processes and, specifically, in the regulation of clock speed (Meck, 2006a, 2006b). The importance of DAergic input to the basal ganglia in timing performance is supported by a recent study showing that DA precursor depletion reduced activity in the putamen which, in turn, predicted impairments in timing performance (Coull, Hwang, Leyton, & Dagher, 2012). Additionally, patients with Parkinson's disease (PD), a disorder characterized by the degradation of DAergic input to the striatum, demonstrate temporal processing deficits when tested off medication. These deficits are frequently ameliorated with administration of the DA precursor levodopa (l-dopa) and/or DA agonists (e.g., apomorphine) (Artieda, Pastor, Lacruz, & Obeso, 1992; Jahanshahi et al., 2010; Malapani et al., 1998), although effects may be dependent on the dose and other factors affecting optimal DA levels (Allman & Meck, 2012; Pouthas & Perbal, 2004; Rakitin, Scarmeas, Li, Malapani, & Stern, 2006). Similar restorative effects of l-dopa on timing behavior have been observed in rats with lesions of the substantia nigra pars compacta (Meck, 1996, 2006b). Taken

together, investigations of DAergic modulation of timing performance in humans support the role of DAergic signals in mediating temporal distortions by influencing activity in cortico-striatal circuits (for reviews see Allman & Meck, 2012; Coull et al., 2011; Jones & Jahanshahi, 2011).

Nevertheless, an understanding of how pharmacological manipulations of effective DA levels influence time perception in humans has been limited by a number of factors. First, studies have largely measured temporal accuracy (e.g., Rammsayer, 1993, 1997, 1999; Weiner & Ross, 1962), without assessing whether DAergic drugs result in systematic shifts in psychometric timing functions when ‘train vs. test’ comparisons are made, evidence of which would be consistent with changes in clock speed (Meck & Benson, 2002). Additionally, few studies have compared the effects of both DA agonists and antagonists within the same individuals (Buhusi & Meck, 2002; Maricq & Church, 1983). Lastly, direct comparisons between the timing performance of humans and non-human subjects have been limited by the fact that the majority of human studies have not used the types of duration reproduction tasks typically used in studies with lower animals, e.g., the peak-interval (PI) procedure (Church, Meck, & Gibbon, 1994; Maricq et al., 1981).

While the PI procedure using durations in the multiple-seconds range (e.g., 7–21 s) has rarely been studied with the administration of DAergic drugs in humans (Lustig & Meck, 2005; Malapani et al., 1998), many human studies have successfully implemented this timing procedure in other contexts (e.g., Hinton & Meck, 2004; Levin et al., 1998; Levin et al., 1996; Lustig & Meck, 2005; Malapani, Deweer, & Gibbon, 2002; Rakitin et

al., 1998; Rakitin, Stern, & Malapani, 2005; Wearden & McShane, 1988). Notably, some discrepancies in timing performance between human and non-human subjects on the PI and other timing procedures have been demonstrated (Lejeune & Wearden, 2006; Rakitin et al., 1998; Wearden & Lejeune, 2008; Wearden & McShane, 1988). While the mechanisms underlying the performance divergence between humans and non-human animals on the PI procedure remain unclear, these cross-species differences leave open the possibility that humans may not demonstrate the characteristic leftward and rightward shifts in psychometric functions associated with the administration of DA agonists and antagonists, respectively, that are observed in nonhuman animal studies.

Indirect evidence suggests that the influence of DAergic drugs on mood changes may have important consequences for temporal processing in humans through its modulation of working memory and attention processes. At sufficient dosages, DA agonists increase drug-liking scores and reports of drug-induced euphoria (Drevets et al., 2001; McCloskey, Palmer, & de Wit, 2010), while DA antagonists can decrease elation (Brauer & De Wit, 1997). At the same time, positive mood has been shown to influence executive functioning (Mitchell & Phillips, 2007), purportedly through associated changes in DA (Ashby, Isen, & Turken, 1999; Dreisbach et al., 2005). The direction of positive mood-induced effects may depend on the type of task assessed. For example, positive mood is thought to enhance cognitive flexibility and thus, may improve performance on tasks that rely on the integration of novel information and set switching (e.g., Ashby et al., 1999; Dreisbach, 2006; Dreisbach & Goschke, 2004). However, it has been argued that positive moods recruit cognitive resources for rumination on mood-

relevant thought (Mitchell & Phillips, 2007; Seibert & Ellis, 1991), which may come at the expense of processes that rely on these same limited cognitive resources, such as directed attention and working memory (Cools & D'Esposito, 2011). In line with this idea, enhanced positive affect has been shown to increase distractibility and reduce the maintenance of task-related information (Dreisbach, 2006; Dreisbach & Goschke, 2004).

While few studies have examined the effects of mood on interval timing (Droit-Volet et al., 2011; Droit-Volet & Meck, 2007), changes in attention and working memory capacity have consistently been shown to influence performance on timing tasks in humans (Brown, 1985; Gamache, Grondin, & Zakay, 2011; Lustig & Meck, 2001, 2005; Macar, Grondin, & Casini, 1994). Individuals with ADHD, a disorder characterized by attention and working memory deficits, demonstrate deficits in temporal processes (Barkley, Murphy, & Bush, 2001; A. Smith, Taylor, Rogers, Newman, & Rubia, 2002). Timing in the multiple-seconds range requires attention and working memory (Buhusi & Meck, 2009; Lejeune, 1998; Lewis & Miall, 2003a; Macar & Vidal, 2009; Thomas & Weaver, 1975), processes which are largely supported by prefrontal regions. Attention-sharing between temporal and non-temporal tasks is thought to divide attention resources, resulting in temporal underestimation in healthy participants (Macar et al., 1994). As positive mood is associated with increased distractibility and reduced maintenance resources (Dreisbach, 2006; Dreisbach & Goschke, 2004), the induction of a positive mood by a DA agonist might similarly recruit attention resources, diminishing the resources available for temporal processing.

Further supporting the potential for DA-induced positive mood to influence time perception, DA administration has been shown to modulate performance on tasks requiring working memory and attention processes (Floresco & Magyar, 2006; Jones & Jahanshahi, 2011). Based on such evidence, it has been suggested that DAergic modulation of attention and working memory can influence temporal accuracy (Rammsayer, 1999). Using variable feedback probabilities, Lustig and Meck (2005) found that rightward shifts in timing functions increased with the number of trials since feedback. Supporting the role of DA in modulating working memory, this study found that rightward shifts associated with the decay of feedback effects were enhanced with the administration of the DA receptor blocker haloperidol.

As positive moods impair directed attention and working memory and these processes, in turn, are important in influencing timing performance, we hypothesized that DA agonist-induced euphoric feelings may modulate interval timing performance. The potential for DA-induced euphoria to modulate time perception through changes in working memory and attention is further supported by evidence that DA agonist induced drug liking scores are correlated with a behavioral measure of lapses in attention at baseline (e.g., McCloskey et al., 2010). In this study, we assessed whether individual differences in drug liking scores (and attention lapses at baseline) predicted the effects of DA agonists on temporal processing. In the PI procedure, attention distraction shifts psychometric timing functions to the right (Buhusi & Meck, 2009), producing a shift in the opposite direction of the canonical leftward shift resulting from an increase in clock speed (Buhusi & Meck, 2002; Meck, 1996). To demonstrate dissociations in temporal

processing based on reports of drug-liking, we tested human participants under DA agonist (d-amphetamine), antagonist (haloperidol), and placebo conditions with a PI timing procedure, using target durations of 7-s and 17-s. We predicted that participants reporting ‘low’ or no drug-induced euphoria would demonstrate the typical clock-speed pattern of temporal distortions observed in rodent studies, wherein DA agonists induce increases in clock speed, resulting in proportional leftward shifts in psychometric timing functions and DA antagonists induce decreases clock speed, resulting in proportional rightward shifts in psychometric timing functions (Meck, 1996). On the other hand, we predicted that participants reporting ‘high’ levels of drug-induced euphoria in response to DA agonists would demonstrate rightward shifts in psychometric functions, suggesting attention distraction from the timing task. As moderate levels of DA antagonists generally do not significantly decrease mood ratings (Brauer & de Wit, 1996, 1997; Brauer, Goudie, & de Wit, 1997), timing performance under the influence of DA antagonists for individuals particularly sensitive to the euphoric effects of DA agonists was difficult to predict.

4.2 Methods

4.2.1 Healthy Participants

Twenty-two healthy volunteers (10 female; mean age = 23.5 years, range = 18–34 years) participated in the study. The local Institutional Review Board approved the experimental protocol, and written informed consent was obtained from each participant prior to the study. Participants reported no history of psychiatric illness or clinical treatment for drug abuse.

4.2.2 Simple reaction time task

The simple reaction time (SRT) task from the Automated Neuropsychological Assessment Metrics (Reeves et al., 2006) was used to assess lapses in attention and was administered prior to PI training. For the SRT, participants were required to press a key on a computer keyboard as quickly as possible following the presentation of a blue rectangle (6.4 cm wide×5.1 cm long) in the center of the computer screen at random intervals with a mean of 7 s. From the distribution of reaction times, the mean deviation of the individual reaction times from the modal reaction time was calculated for each participant. The deviation from the mode was used due to its resistance to variations in the shape of RT distributions while remaining sensitive to the skew in the right-hand tail of the distribution (McCloskey et al., 2010; Spencer et al., 2009).

4.2.3 Peak-interval (PI) timing procedure

Participants were tested on two target durations (7 s and 17 s) using PI timing procedures similar to those described by Hinton and Meck (2004), Lustig and Meck (2005), and Rakitin et al. (1998). The two target durations were presented during separate blocks of trials during sessions that were scheduled between 2 and 4 pm. Each experimental session began with five training trials, during which participants viewed a computer-presented blue rectangle (6.4 cm wide×5.1 cm long) that changed color to magenta at the target time independent of responding. These initial training trials were followed by trials during which participants viewed the blue rectangle and indicated when they thought the target duration had elapsed. Participants were instructed to make multiple responses on each trial, bracketing the target duration by starting to respond

slightly before the target and stopping slightly after. In addition, participants were instructed not to use any external timing device and to avoid counting or sub-dividing the interval in any way (i.e., no rhythmical behavior). After making their last spacebar response for that trial, participants could press the “Enter” key to terminate the trial. Otherwise, the trial would terminate automatically at three times the target duration. At the end of the trial, participants were either given feedback or began the next trial after a randomly varied ITI with a mean of 5 s. During this training phase, graphical feedback indicating the accuracy and precision of the participant’s performance was presented by displaying response histograms plotted on a relative time scale during the ITI following a random 50% of trials. Approximately 15 trials with feedback were presented during this training phase. All participants were trained with feedback on the PI timing procedure early in the session, approximately 10 min after initial drug administration, before appreciable drug had been distributed.

All participants were then tested without feedback approximately 1 h after initial drug administration, by which time asymptotic drug levels in the brain should have been reached. The later part of the session was used for analysis of drug effects and compared to both the earlier session performance and placebo sessions. In each block of trials, participants were asked to reproduce the duration (7 s or 17 s) of the blue rectangle as in the training session. There were 30 trials for each of the two target durations. Responses were summed into 1-s bins for each participant in order to produce a response distribution as a function of signal duration. The midpoint between the first and last response (response window) was used to determine the peak time and served as an index of the

accuracy with which participants timed the target durations. The first and last bins just below a threshold of 50% of the maximum number of responses per bin defined the width of the response function at half the maximum height (spread). The maximum number of responses at the peak time (peak rate) was used as a measure of general arousal (Rakitin et al., 1998).

4.2.4 Drug administration

Participants were administered d-amphetamine (20 mg oral—gelatin capsule), haloperidol (2 mg oral—gelatin capsule), or placebo (plain gelatin capsule) with a 6 oz cup of water approximately 10 min before training with the PI procedure began. Placebo and drug sessions were given in a random order and separated by at least two days. The order in which target durations were presented was counterbalanced across participants and treatment condition. Drug doses were chosen for their mild subjective and behavioral effects in healthy subjects and to limit side effects (Berger et al., 1996; Brauer, Cramblett, Paxton, & Rose, 2001; Brauer & De Wit, 1997; de Wit, Crean, & Richards, 2000; Mahler & de Wit, 2005; Wachtel, Ortengren, & de Wit, 2002).

4.2.5 Drug effects questionnaire

Following each condition, participants completed a visual analogue scale (VAS) to indicate their overall liking of the drug effects on a 100 mm scale (VAS; 0=dislike a lot, 50=neither like nor dislike, 100=like a lot) and attempted to identify the class of drug they received, e.g., placebo, stimulant, or sedative (McCloskey et al., 2010).

4.2.6 Statistical analyses

Data were analyzed using analysis of variance to evaluate group differences and linear regression to assess the correlation between independent variables. Adjustments for potential confounding variables were made using partial correlation analysis. Statistical analysis was performed with StatView (version 5.0; SAS Institute, Cary, NC) and SuperANOVA (version 1.11; Abacus Concepts, Inc., Berkeley, CA) statistical packages. Values of $P \leq 0.05$ were considered significant. This alpha level was adjusted to 0.025 for within group effects, and then divided by the number of post-hoc comparisons when testing for differences with placebo.

4.3 Results

In our analysis, we examined the relationship between baseline lapses in attention (as measured by the mean deviation of the individual reaction times from the modal reaction time obtained in the SRT task) and the VAS ratings of drug liking following the administration of 20 mg of d-amphetamine. We expected to replicate the negative association between baseline attention lapses and drug-liking scores for d-amphetamine (McCloskey et al., 2010). The correlation between the SRT measure of attention and the VAS rating of drug liking was significant, $R^2 = 0.60$, $p < 0.001$, as illustrated in Figure 14A. This variation in drug liking also allowed us to compare the mean horizontal shift in peak time averaged over the 7-s and 17-s target durations following 20 mg of d-amphetamine. The correlation between the SRT measure of attention and % peak shift was significant, $R^2 = 0.48$, $p < 0.001$, as was the correlation between the VAS rating of drug liking and % peak shift, $R^2 = 0.70$, $p < 0.001$, as illustrated in Figure 14B and 14C,

respectively. When adjusted for attention, the partial correlations between drug liking and % peak shift remained significant, $R^2 = 0.44$, $p < 0.001$, whereas when adjusted for drug liking, the correlation between attention and % peak shift was diminished, $R^2 = 0.02$, $p > 0.05$.

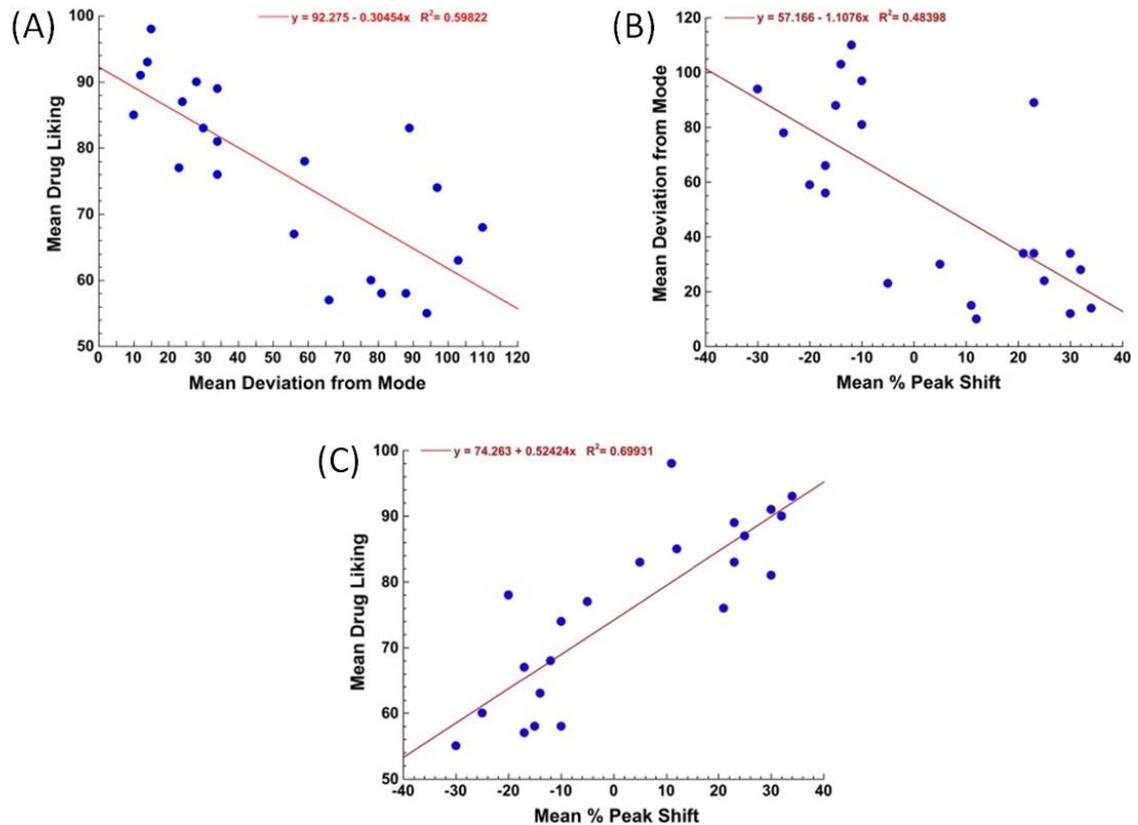


Figure 14: (A) Correlation between individual differences in mean deviation of reaction times from the modal reaction time obtained in the simple reaction time (SRT) task and the drug-liking index for d-amphetamine obtained from the visual analogue scale (VAS; 0 = dislike a lot, 50 = neither like nor dislike, 100 = like a lot). (B) Correlation between individual mean percent shifts in peak times for the 7 s and 17 s peak-interval (PI) functions following 20 mg d-amphetamine administration and the drug-liking index. (C) Correlation between individual mean percent shifts in peak times for the 7 s and 17 s peak-interval (PI) functions following 20 mg d-amphetamine administration and the simple reaction time (SRT) task used to assess lapses of attention.

Participants were subsequently divided into ‘low’ ($M = 83.73$, $SD = 17.68$) and ‘high’ ($M = 23.46$, $SD = 9.33$) levels of baseline attention for further analysis of shifts in peak time using a median split for the mean deviations from the mode reaction time. Importantly, the ‘low’ baseline attention participants demonstrated a leftward shift in peak times for 7-s and 17-s target durations following the administration of d-amphetamine relative to the baseline and placebo sessions, whereas the ‘high’ attention participants demonstrated a rightward shift in peak times following the administration of d-amphetamine. As expected from the negative correlation observed between attention lapses and drug liking, these two attention groups differed significantly from each other in terms of drug liking, $F(1,20) = 100.29$, $p < 0.001$.

The normalized PI timing functions for participants that exhibited either leftward or rightward shifts for d-amphetamine are illustrated in Figure 15A and Fig. 15B, respectively. The corresponding placebo and haloperidol peak functions are also plotted in the same figures. Interestingly, the participants that demonstrated leftward shifts in their 7-s and 17-s timing functions for d-amphetamine showed rightward shifts for haloperidol. Moreover, these leftward and rightward shifts were significant and proportional to the target durations as revealed by a within-subject ANOVA. A significant main effect of Drug and a non-significant effect of Duration was observed when shifts in peak time under d-amphetamine or haloperidol were normalized to the peak times obtained for placebo sessions, Drug $F(1,10) = 37.98$, $p < 0.001$; Duration $F(1,10) = 0.91$, $p > 0.05$; Drug \times Duration interaction = 0.74, $p > 0.05$ —with post-hoc tests indicating that the d-amphetamine and haloperidol conditions for both 7-s and 17-s

target durations were reliably different from placebo sessions, p 's < 0.05 . In contrast, participants that demonstrated rightward shifts in their 7-s and 17-s timing functions for d-amphetamine showed no reliable effects for haloperidol. Moreover, these rightward shifts following d-amphetamine administration were significant and proportional to the target durations as revealed by a within-subject ANOVA. A significant main effect of Drug and a non-significant effect of Duration was observed when shifts in peak time under d-amphetamine or haloperidol were normalized to the peak times obtained for placebo sessions, Drug $F(1,10) = 24.43$, $p < 0.001$; Duration $F(1, 10) = 0.58$, $p > 0.05$; Drug \times Duration interaction = 1.85, $p > 0.05$ —with post-hoc tests indicating that only the d-amphetamine condition for both 7-s and 17-s target durations was reliably different from placebo sessions, p 's < 0.01 .

Mean normalized response rate functions for 7-s and 17-s target durations under placebo conditions plotted as a function of relative time, i.e., normalized by the observed peak times for individual participants, are shown in Figure 16. Peak functions for different target durations should superimpose when plotted on a relative time scale if the scalar property holds, i.e., variability in timing grows proportional to the mean of the interval being timed. The high degree of superposition observed in the mean 7-s and 17-s placebo peak functions averaged over all participants provides strong support for the scalar property of interval timing and argues against participants using a chronometric counting/sub-dividing strategy (R. K. Cheng & Meck, 2007; Clement & Droit-Volet, 2006; Hinton & Rao, 2004; Meck & Malapani, 2004; Rakitin et al., 1998).

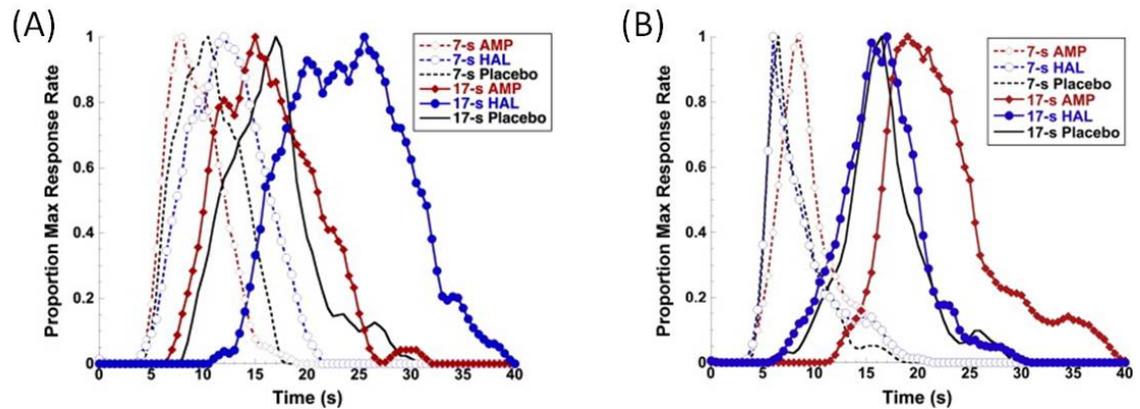


Figure 15: Mean normalized response rate functions for 7 s and 17 s target durations as a function of 20 mg d-amphetamine, placebo, and 2 mg haloperidol for (A) participants that showed ‘high’ levels of attention lapses in the SRT task, ‘low’ levels of drug liking for d-amphetamine, and leftward shifts of peak functions following d-amphetamine administration and (B) participants that showed ‘low’ levels of attention lapses in the SRT task, ‘high’ levels of drug liking for d-amphetamine, and rightward shifts of peak functions following d-amphetamine administration. The proportional leftward shifts in peak time for dopamine agonists and proportional rightward shifts in peak time for dopamine antagonists in (A) are representative of a ‘clock-speed’ pattern, whereas the proportional rightward shifts in peak time for dopamine agonists and little or no effect on peak time for dopamine antagonists in (B) are representative of the ‘attention’ pattern.

Eighteen percent of participants identified placebo as a stimulant, whereas 86% identified 20 mg of d-amphetamine as a stimulant. Participants identified haloperidol as a placebo 73% of the time, and as a sedative or a stimulant 23% and 9% of the time, respectively. These drug classifications did not differ reliably as a function of whether participants demonstrated a leftward or rightward shift following d-amphetamine administration. Overall levels of responding in the PI procedure did not distinguish these two groups of participants. No reliable differences between male and female participants were observed for any of the behavioral measures reported above, p 's > 0.05. Finally, we examined the relationship between the average spread of the 7-s and 17-s peak functions

obtained during the placebo session with the VAS rating of drug liking following the d-amphetamine session. The correlation between these measures was found to be significant, $R^2 = 0.73$, $p < 0.001$, indicating that sensitivity to signal duration was negatively correlated with drug liking.

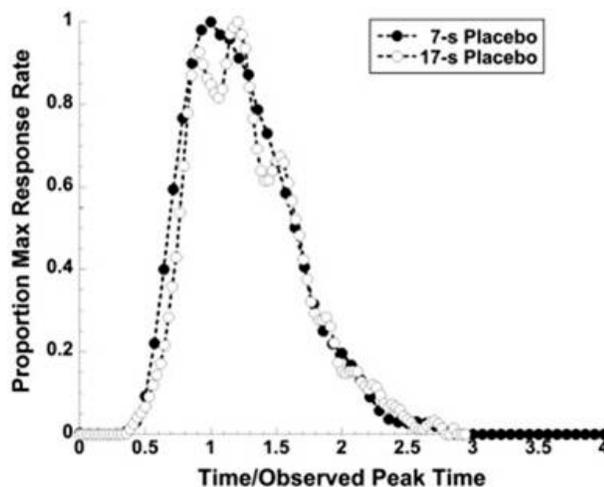


Figure 16: Mean normalized response rate functions for 7 s and 17 s target durations under placebo conditions plotted as a function of physical time normalized by psychological time. The degree of superposition observed in the mean 7 s and 17 s placebo peak functions, averaged over all participants, supports the scalar property of interval timing.

4.4 Discussion

In this study, we demonstrated that drug-liking scores in response to d-amphetamine administration predicted the direction of shifts in timing functions using the PI procedure. Individuals reporting ‘low’ drug-liking scores demonstrated proportional leftward shifts in timing functions consistent with the clock speed increases frequently described in rodent studies (Abner et al., 2001; Buhusi & Meck, 2002; Cevik, 2003; R. K. Cheng, Ali, et al., 2007; R. K. Cheng, Hakak, et al., 2007; R. K. Cheng et al., 2006; Cheung et al., 2006; Chiang et al., 2000; Maricq & Church, 1983; Maricq et al., 1981;

Matell et al., 2006; Meck, 1983, 1996, 2006b). On the other hand, participants with 'high' amphetamine-liking scores showed proportional rightward shifts in timing functions. We suggest that this rightward shift reflects reduced attention to time as a result of the reallocation of attention resources, such that attention is split between timing processes and non-temporal aspects of the drug effect associated with euphoria and positive mood induction. According to resource allocation models (Buhusi & Meck, 2009; Casini & Macar, 1999; Gamache et al., 2011), reductions in attention and/or other cognitive resources allocated to the "to-be-timed" signal result in the need for more physical time to elapse before the subjective target duration is reached. The results reported here suggest that individual differences in sensitivity to the euphoric effects of d-amphetamine modulate interval-timing performance as a function of resource allocation (Buhusi & Meck, 2002).

Converging lines of evidence point to the role of baseline DA levels in determining individual differences in executive functioning and drug-induced euphoria, suggesting that variability in baseline DA may help explain the individual differences observed in the current study. Many researchers have supported an inverted U-shaped relationship between tonic DA levels in the prefrontal cortex and performance on executive functions such as working memory and attention (Cohen, Braver, & Brown, 2002; Goldman-Rakic, 1998; Goto, Otani, & Grace, 2007; Kroener, Chandler, Phillips, & Seamans, 2009). Such claims have been sustained by animal studies which have directly or indirectly modulated DA levels in the PFC cortex and observed that a limited range of DA level increase improves working memory/attention performance while too low or too

high levels impair performance (Arnsten & Goldman-Rakic, 1998; Cai & Arnsten, 1997; Lidow, Koh, & Arnsten, 2003; Sawaguchi, Matsumura, & Kubota, 1988; Zahrt, Taylor, Mathew, & Arnsten, 1997). Human genetic polymorphisms influencing tonic DA levels in the PFC also predict performance on working memory related tasks (Diamond, Briand, Fossella, & Gehlbach, 2004; Egan et al., 2001). Taken together, this research suggests that working memory and attention likely depend on baseline DA levels in the PFC and thus, administration of DAergic drugs may have differential effects on performance depending on initial DA levels.

Based on such evidence, it is possible that in the current study, individuals demonstrating greater baseline lapses in attention and subsequent lower drug-liking scores had lower levels of baseline DA in the prefrontal cortex compared to those individuals demonstrating superior performance on the SRT task and reporting 'higher' drug-liking scores. This assumption fits well with subsequent performance during the administration of d-amphetamine, where individuals with low drug liking scores (and presumably lower baseline DA levels) showed temporal overestimation while those with higher drug-liking scores showed temporal underestimation, consistent with impaired working memory/attention. These findings follow the predictions of the inverted U-shaped modulation of executive function by DA. If high drug-liking individuals had higher baseline levels of DA, further increases by the administration of DAergic drugs may have pushed DA levels above optimal levels for temporal processing.

Nevertheless, more recent studies have painted a more complex picture of the neural regions underlying working memory and attention processes, implicating tonic DA

levels in both the PFC and striatum. Specifically, it has been suggested that these two regions may play interacting roles, with the PFC controlling flexibility and the striatum controlling updating processes (Cools & D'Esposito, 2011). Evidence that the administration of bromocriptine, a dopamine agonist, modulated frontal-striatal connectivity, such that connectivity was enhanced in individuals with low working memory capacity, whereas connectivity was diminished in individuals with high working memory capacity (Wallace, Vytlačil, Nomura, Gibbs, & D'Esposito, 2011) supports the importance of DA levels in modulating frontostriatal interactions during working memory performance and provides further support for the inverted U shaped function of dopamine in modulating working memory performance.

Similarly, timing differences observed in the current study may have been driven by a differential balance between clock speed and attention-related processes, mediated by DA levels in both cortical and striatal regions. This idea is supported by a recent study showing that timing performance was influenced by genetic polymorphisms affecting baseline DA levels in the cortex and striatum (Balci, Wiener, Cavdaroglu, & Branch Coslett, 2013). Interestingly, this study found that performance depended not on global DA levels, but on the balance between DA levels in the cortex and striatum. It is possible that groups with 'high' and 'low' drug-induced euphoria differed in this balance and this physiological interaction may help to explain why some studies report disruption or rightward shift in timing following DA agonist treatment (Balci et al., 2008).

The proposed relevance of the striatum to the current findings is further supported by studies which have shown that DA agonist-induced drug liking scores are positively

correlated with baseline DA levels in the ventral striatum (Drevets et al., 2001; Martinez et al., 2003). Based on such findings, differences in tonic DA levels in the striatum may have driven the temporal underestimation effect in individuals reporting high drug-liking scores by disrupting communication between the PFC and other regions responsible for task relevant processing (van Schouwenburg, den Ouden, & Cools, 2010). This proposed role of striatal DA levels in modulating drug-induced euphoria and working memory performance would again be consistent with an inverted U-shaped function, as individuals with higher drug induced euphoria had fewer attention lapses at baseline but demonstrated attention distraction or working memory deficits during timing after the administration of d-amphetamine. Together, the observed findings support the idea that there are optimal levels of DA in prefrontal and striatal regions which support performance on executive control tasks (Cools & D'Esposito, 2011).

Additional support for the idea that the rightward shift in timing functions after d-amphetamine administration was mediated by enhanced drug-induced euphoria comes from considering our DA antagonist findings. Those individuals demonstrating a rightward shift in their timing function in response to 20 mg d-amphetamine did not show a significant temporal shift after 2 mg haloperidol administration. As haloperidol did not significantly increase or decrease drug-liking scores, a shift in either direction based on mood changes would not be expected—at least within this dose range (Brauer & de Wit, 1996). At the same time, individuals showing the canonical leftward temporal shift due to d-amphetamine administration showed a rightward shift in response to haloperidol, supporting previous clock speed effects in rodents (Buhusi & Meck, 2002; R. K. Cheng

& Liao, 2007; Drew et al., 2003; MacDonald & Meck, 2005, 2006; Maricq & Church, 1983; Meck, 1983, 1986, 1996). The interaction between tonic DA levels in the prefrontal cortex and striatum may also explain the differences observed in the current study for dopamine antagonist administration, though further efforts will be necessary to clarify the effects observed here.

The differences in timing performance variability during the placebo condition may also support the idea that individuals in the current study differed in baseline DA levels. Greater temporal precision is associated with a faster internal clock and as increases in clock speed are generally associated with increases in DA levels (Coull et al., 2011; Matell et al., 2006; Matell et al., 2004), evidence of greater temporal precision during the placebo condition in those individuals reporting higher-drug induced euphoria and demonstrating rightward shifts in timing further suggests that these individuals had either higher baseline levels of DA or greater sensitivity to DA in corticostriatal circuits at baseline. Future studies that could directly measure baseline levels of DA activity would help to support the current idea that individual differences in drug-induced euphoria and temporal distortion can be predicted by baseline executive functioning and may stem from differences in baseline DA levels within prefrontal regions supporting attention and working memory.

Despite the evidence provided suggesting the centrality of DAergic modulation in mediating the drug-induced euphoria and timing distortions reported here, this explanation is likely still an oversimplification of the processes underlying the individual differences observed in this study. For example, other neuromodulators, such as

serotonin, GABA, glutamate, and norepinephrine, have also been found to influence time perception and to interact with DA in complex ways (Asgari et al., 2006; Coull et al., 2011; Jung & Shim, 2011; Wiener, Lohoff, & Coslett, 2011), which is important in light of the fact that both d-amphetamine and haloperidol influence the release of catecholamines and other neuromodulators. Consequently, some of the effects we have observed may also be influenced by these other neuromodulators (Matell & Meck, 2004; Smythies, Edelstein, & Ramachandran, 2012).

Another important caveat to the proposed DA mechanism(s), is the argument that DA may not directly modulate the euphoric feelings associated with the administration of d-amphetamine (Berridge, 2007). Alternatively, it has been argued that opioids mediate these feelings of euphoria. An opioid receptor gene polymorphism has been shown to modulate amphetamine-induced euphoria (Dlugos et al., 2011) and multiple studies have found that DA antagonists fail to fully block the euphoric effects of DA agonists (Brauer & de Wit, 1996, 1997). Future studies will be necessary to better tease apart the neuropharmacology underlying these reported phenomena. Nevertheless, our results suggest that these drug-induced mood and cognitive changes are correlated. We note that the present study was limited by only using a single dose of d-amphetamine and haloperidol and we were thus unable to show dose-dependent responses within participants, which would have enabled us to further test the proposed inverted U-shaped relationship between DA and the processes underlying task performance.

In conclusion, we found that baseline levels of attention, presumably dependent on baseline DA levels in the prefrontal cortex and striatum, predicted subsequent drug-

liking scores. We propose that these drug-induced positive feelings mediate changes in DAergic drug-related temporal distortions via an attention-distraction mechanism. These findings support the idea that positive moods can impair performance on tasks requiring directed attention and working memory (Lustig, Matell, & Meck, 2005; Lustig & Meck, 2005). Because greater baseline lapses in attention are considered a facet of impulsivity, it has been suggested that individuals with greater impulsivity would be more likely to take drugs and, as a result of receiving relatively low levels of pleasure from drug-taking, may be driven to increase drug intake. If true, this would have important implications for the study of temporal processing and drug addiction. As we find temporal distortions that are correlated with drug-induced euphoria they may prove to be of increasing clinical relevance (Wittmann, Leland, Churan, & Paulus, 2007; Wittmann & Paulus, 2008).

4.5 Summary

Humans exhibit dopaminergic regulation of interval timing in the multi-second range by displaying either one of two patterns of behavior. The first pattern is revealed by the indirect DA agonist d-amphetamine (20 mg—oral) producing proportional leftward shifts of the timing functions and with DA antagonist haloperidol (2 mg—oral) producing proportional rightward shifts. This symmetrical pattern of results suggests that clock speed is regulated (within limits) by the effective level of DA, i.e., d-amphetamine increases clock speed and haloperidol decreases clock speed (Meck, 1983, 1996; Williamson, Cheng, Etchegaray, & Meck, 2008). The second pattern is revealed by d-amphetamine producing proportional rightward shifts of the timing functions with haloperidol producing no reliable effect. This asymmetrical pattern of results is consistent

with an explanation in which attention toward the stimulant-induced euphoria produced by d-amphetamine diminished the resources available for temporal processing, thereby diminishing any drug-induced changes in clock speed. The result of increased competition and time-sharing between these two dimensions (e.g., attention towards feelings of euphoria versus attention towards the passage of time) led to the underestimation/overproduction of temporal intervals (Buhusi & Meck, 2009; Fortin et al., 2009; Macar et al., 1994). We believe these results reflect individual differences in baseline DA levels and we propose that DA-related increases in positive feelings may modulate time perception via the interaction of prefrontal and striatal regions.

5. General Discussion

In this manuscript, the findings from three studies were reported which support a new theoretical model of emotional distortions of time perception, outlined at the beginning of the manuscript. These studies examined two of the proposed phases of emotional distortions on time perception: the physiological arousal and resource-sharing attention phases. In Chapter 2, using an online measure of physiological arousal, we found that ‘longer’ responses were associated with greater SCRs than ‘shorter’ responses during the presentation of emotionally arousing threat cues signaling aversive outcomes. Consistent with the predictions for the physiological arousal phase of the theoretical model, this finding supported an influence of physiological arousal in driving temporal overestimations of duration within a short temporal window after emotional stimulus onset. However, a main effect of overestimation was not evident across all study conditions, specifically in those conditions with a longer ISI between the CS and US. We believe this diminished overestimation effect is consistent with the model prediction that a separate attention mechanism operates at longer latencies from the onset of an emotional stimulus. The evidence for an influence of physiological arousal on temporal estimates across study conditions demonstrates the utility of collecting online measures of physiological arousal in studying emotional influences on time perception, as this measure was able to capture an underlying mechanism of distortion not evident via the simple assessment of main effects, which has been the typical means of assessing the influence of emotional stimuli in studies of time perception.

The increased variability in emotional effects on time perception during longer temporal windows of threat anticipation was partially explained by an individual difference measure of subjective arousal, reflecting the operation of top-down attention/working memory resources to maintain the relationship between the CS and US, consistent with the resource-sharing attention phase of the theoretical model. Specifically we found that when the comparison stimulus was not related to the aversive outcome, greater attention was devoted towards anticipating the aversive outcome versus the stimulus to be timed, resulting in reduced temporal estimates. Alternatively, when the comparison stimulus was related to the anticipated outcome, greater attention directed towards anticipating the aversive outcome predicted more attention resources being devoted to the stimulus to be timed, resulting in greater temporal estimates. The ability to detect this effect using an individual difference measure, despite the lack of a main effect on time perception in either of the two conditions with longer CS-US ISIs (Trace and Long Delay), again illustrates the utility of using explicit measures of interest to probe potential influences on timing performance, rather than relying on the directionality of main effects. This finding also supports the use of individual difference measures as an important means to uncover underlying mechanisms of temporal distortion that may have subtle or variable influences on time perception across individuals. However, it is important to note that the variability in the effects we observed at longer CS-US ISIs were likely the result of the moderately arousing nature of the emotional manipulation and more potent manipulations (which may be difficult to perform in a laboratory

environment) would likely result in more potent and less variable effects across individuals.

In Chapter 3, we were interested in further exploring how the physiological arousal and resource allocation phases of the theoretical model of emotional distortions on time perception can be modulated. Specifically, we tested the hypothesis that top-down attention resources recruited at longer temporal latencies distract attention from timing processes and are driven by physiological arousal. We also examined whether the duration of emotional reactivity and the delay of successful emotion regulation modulates this attention effect. Consistent with the idea that physiological arousal influences the recruitment of attention resources, we found that ‘shorter’ responses were associated with greater SCRs than ‘longer’ responses, suggesting that at longer temporal latencies from emotional stimulus onset, physiological arousal can bias responses towards underestimation, likely through the modulation of attention. Specifically, I believe our findings suggest that physiological arousal influences the subsequent recruitment of top-down emotion regulation processes, such that greater physiological arousal recruits greater emotion regulation/appraisal processes. This interpretation is consistent with the prediction of the new theoretical model of temporal distortion that the recruitment of attention processes is dependent on physiological arousal responses. At the same time, in support of the idea that the duration of emotional reactivity modulates biases towards overestimation, presumably by extending the physiological arousal phase, we found that higher trait anxious individuals showed a reduced underestimation bias, suggesting a reduced ability to successfully regulate emotional responses after the presentation of an

emotional cue. We also found that directly manipulating the duration of the emotional experience by increasing the duration of threat anticipation also reduced the underestimation bias.

The argument that presenting the aversive reinforcement after the neutral stimulus to be timed in Chapter 3 extended the duration of the emotional experience may seem to conflict with the findings we reported for the Trace condition in Chapter 2, which we interpreted as evidence that less attention was directed to the neutral stimulus presented prior to the delivery of an aversive outcome. Nevertheless, multiple methodological differences could account for these differences. Firstly, the amount of time that elapsed between the CS+ and US was significantly longer than the duration of time that elapsed between the presentation of the comparison stimulus and the US, especially when compared to the same durations in the Trace condition of Chapter 2. Given that temporal dynamics seem to play an important role in modulating time perception, these differences may have contributed to the differences across studies. Alternatively, modality differences between the two experiments could also have contributed to the observed differences. Other differences in the experimental designs of these two studies, particularly the presentation of the emotional cue as a task-irrelevant distractor in Chapter 3 versus as the standard stimulus in the Trace condition on Chapter 2 may also have contributed to the directionality of these findings. Further work will be necessary to distinguish between these possibilities.

Finally, in Chapter 4, we were interested in assessing whether or not the attention processes are differentially allocated when modulated by positive affect. Our findings

suggested that, similar to the effects of negative affect on attention, attention to positive affect distracted participants from timing a biologically irrelevant stimulus, resulting in the underestimation of temporal estimates. This finding suggests that the resource-sharing attention phase of the new theoretical model of emotional distortions of time perception may be valence-independent.

Further work will be needed to more fully test the predictions made by this model. For example, the potential role of valence in modulating temporal estimates will need to be further explored in each proposed phase. It will also be important to demonstrate that this model generalizes to other negatively valenced emotional stimuli besides threat. At the same time, the studies reported in Chapters 2 and 3 excluded participants who did not show SCR responding to cues and who did not demonstrate physiological evidence of learning. Thus, the included sample represents a subset of the tested population and it is unclear how such individuals might differ from the population at large. Analyses are currently in progress to address this question. Finally, as I have pointed out, the relationship between arousal and attention has yet to be fully explained. Future studies might benefit from collecting baseline measures of attention and arousal, in addition to collecting online measures of these two constructs to understand how individual differences in these components may vary and how their interaction may contribute to time perception.

5.1 Plausible Neural Mechanisms

In addition to further exploring the validity of the proposed theoretical model of emotional distortions of time perception, I 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 (Dirnberger et al., 2012; Faure et al., 2013; Gan, Wang, Zhang, Li, & Luo, 2009; Matthews et al., 2012; Meck & Macdonald, 2007; Tamm et al., 2014; Tipples, Brattan, & Johnston, 2013). A neurobiologically plausible model of time perception, namely the striatal beat frequency model (SBF), 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 input and outputs of neural timing systems. In this section, I will briefly review SBF model and potential neural mechanisms of distortion within this model framework will be outlined that would be consistent with the theoretical model of emotional distortions of time perception proposed at the beginning of this manuscript.

5.1.1 Striatal Beat Frequency Model

The SBF model of time perception accounts well for much of the pharmacological and psychological empirical data on timing (Figure 17; Matell & Meck, 2000; Matell & Meck, 2004). The model proposes that time perception is largely mediated by connections between the striatum, cortex and thalamus, with the dorsal striatum, specifically, crucial for proper timing abilities (Meck, 1996). According to this model, the beginning of a stimulus to be timed is signaled 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 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 since the cortical synchronization event. Each medium spiny neuron 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 (Mirenowicz & Schultz, 1994). Striatal output influences activity of the thalamus via a direct and 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 (Allman & Meck, 2012). The direct and indirect pathways are suggested to

play a role in the start, stop, and resetting of the timing process (Matell & Meck, 2004).

Further research is necessary to elaborate the proposed roles of these pathways.

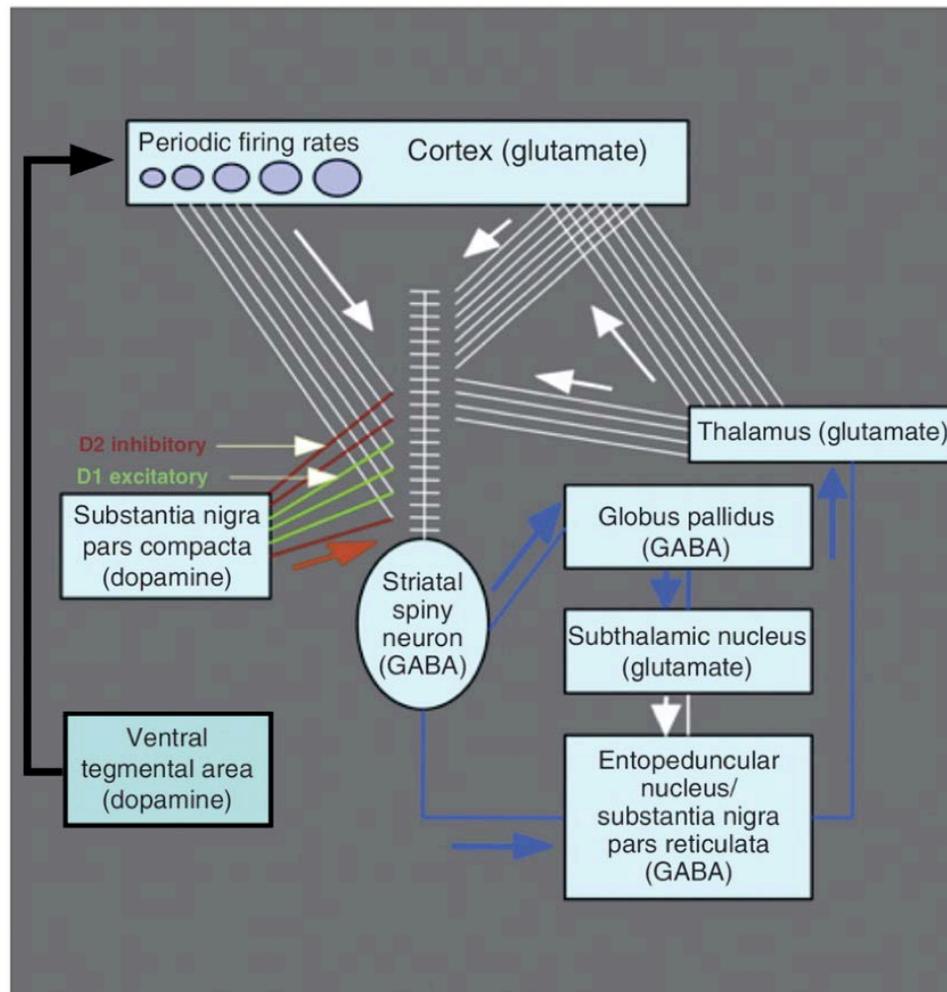


Figure 17: Striatal Beat Frequency model of interval timing. Adapted from Allman & Meck (2012).

As the SBF model is largely based on animal research, it does not specify the precise regions of the human cortex that may be involved in timing. Various lines of evidence have implicated regions of the lateral frontal cortex (Coull et al., 2011; Lewis, 2002; Lewis & Miall, 2006; Macar et al., 2002; Wiener, Turkeltaub, & Coslett, 2010),

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 (Coull et al., 2011). The importance of the dlPFC in time perception (Lewis, 2002; Lewis & Miall, 2006) is supported by its role in working memory and attention (Curtis & D'Esposito, 2003; Kondo, Osaka, & Osaka, 2004; Murty et al., 2011), as the processes underlying these functions appear to overlap (Buhusi & Meck, 2009). Functional and anatomical connections between the dlPFC and other regions of the timing circuitry, namely the midbrain and striatum, have also been established (Ballard et al., 2011; Haber & Knutson, 2010). The pre-SMA and right IFC also may play a role in time perception abilities (Coull et al., 2011; Macar et al., 2002; Wiener et al., 2010), though it has been suggested that the pre-SMA may be more important in motor-related timing tasks than purely perceptual tasks (e.g., Coull et al., 2011). 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 (Gaspar, Stepniewska, & Kaas, 1992; Haber & Knutson, 2010) and project back to the striatum (Alexander, DeLong, & Strick, 1986; Haber & Knutson, 2010). 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.

5.1.2 Modulation of Timing Networks by Emotional Stimuli- Orienting and Physiological Arousal Phases

Dopamine (DA) plays a critical role in the striatal beat frequency (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 (Floresco, West, Ash, Moore, & Grace, 2003; Schultz, 1998). 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. Alternatively, 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 (Bromberg-Martin, Matsumoto, & Hikosaka, 2010a, 2010b; Schultz, 1998; Wittmann & Paulus, 2008). Phasic burst firing of dopaminergic neurons results in changes in dopaminergic concentrations in target areas that last up to a few seconds (Roitman, Stuber, Phillips, Wightman, & Carelli, 2004).

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 also transiently increase the rate of cortical oscillations, resulting in short-lived increases in temporal estimates. A phasic dopamine driven effect on cortical oscillations would be consistent with studies of emotion and time perception showing transient overestimation effects of emotional stimuli that are not observed with longer durations.

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 (Darvas, Fadok, & Palmiter, 2011; Feenstra, Vogel, Botterblom, Joosten, & de Bruin, 2001). Phasic changes in dopamine neuron firing rates can transiently change DA concentrations in target regions for a few seconds (Roitman et al., 2004). The transient release of DA and quick return to baseline levels may explain why effects of physiological arousal on time perception are observed at shorter but not longer latencies from cue presentation.

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. The central nucleus of the amygdala (CE) projects to the dopaminergic midbrain and this pathway is thought to play a role in orienting responses (Bromberg-Martin et al., 2010b). Thus, amygdala projections to the midbrain which, in turn, project

to cortical and striatal regions could influence temporal distortions at short temporal interval by either changing the latency to initial 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 (Hamann, Ely, Hoffman, & Kilts, 2002; Zald, 2003). Such a pattern of responding would be consistent with observations that both positive and negatively valenced arousing stimuli result in transient overestimations of temporal durations, with the magnitude of this effect typically larger for negative stimuli. A recent study in rats supported 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 rats with CE lesions showed alterations in this emotional distortion of time (Faure et al., 2013).

Increases in NE are also associated with salient threat cues and physiological arousal (Markovic, Anderson, & Todd, 2014), 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 (Yamamoto, Arai, & Nakayama, 1990), 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 (Markovic et al., 2014). Further investigations will be necessary to further explore the

neural mechanisms underlying the physiological arousal related distortions of time perception we and others have reported.

5.1.3 Modulation of Timing Networks by Emotional Stimuli- Resource-Sharing Phase

It is clear that emotion can influence attention and working memory and that attention and working memory are important for encoding stimulus durations. I propose that the neural regions supporting the maintenance of working memory and attention 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 (Bauer et al., 2012; Calderone, Lakatos, Butler, & Castellanos, 2014; Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Roux & Uhlhaas, 2014). 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 (Gu, Laubach, & Meck, submitted). 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 (Cools & D'Esposito, 2011), suggested that emotional influences at the level of the striatum

could also result in changes in the allocation of attention/working memory resources which could in turn modulate time perception.

Emotional distractors modulate the activity in working memory and attention areas, including regions of the prefrontal cortex and anterior cingulate cortex (Anticevic, Repovs, & Barch, 2010; Dolcos, Iordan, & Dolcos, 2011; Dolcos & McCarthy, 2006; Levens, Devinsky, & Phelps, 2011; Shafer et al., 2012). The reciprocal structural and functional connectivity between regions associated with emotional processing and negative anticipation, such as the anterior insula and amygdala (Carlson, Greenberg, Rubin, & Mujica-Parodi, 2011), and working memory related regions (Dolcos et al., 2013; Kanske, Heissler, Schonfelder, Bongers, & Wessa, 2011; Kim et al., 2011; Menon & Uddin, 2010) make the insula and amygdala plausible target regions for the modulation of working memory and timing processes after the presentation of an emotional stimulus. Supporting the potential role of these two regions in modulating time perception during emotional events, a recent study found that both the insula and amygdala showed greater activity when aversive images were incorrectly versus correctly estimated (Dirnberger et al., 2012). 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 (Meck & Macdonald, 2007).

While the amygdala in particular is implicated in the processing of positive and negative stimuli (Hamann & Mao, 2002; Hamann et al., 2002) it is also possible that

different neural regions could similarly drive activity in working memory/attention regions for positive and negative stimuli, or even for distinct kinds of emotions. 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 become increasingly reliant on BNST activity (Davis et al., 2010). This neural region 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.

5.2 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. While the relationship between distortions of time perception and subsequent behaviors remains largely speculative, in support of the idea that time perception can influence subsequent cognitive processes, Dirnberger et al. (2012) found that emotional stimuli that were perceived as longer were also subsequently remembered better. While this memory effect could 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 that should be further explored. 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 (Buetti & Lleras, 2012; Watts & Sharrock, 1984). 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.

At the same time, 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. Specifically, it was shown that misleading individuals about the duration of a painful event modulated the perceived intensity of the pain (Pomares, Creac'h, Faillenot, Convers, & Peyron, 2011). 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. Alternatively, in a study in which participants listened to emotional sounds and were instructed to pay attention to their duration, rather than their emotional content, they showed reduced temporal overestimation and reduced emotional arousal. Such studies point to the flexibility in time perception as a means for regulating emotional experiences, which could lead to novel interventions for individuals with fear and anxiety related disorders. For example, if participants were trained to pay attention to the duration of an emotional event and were able to regulate the degree to which their perception of its duration was distorted, then the magnitude of its emotional impact might be reduced.

A bidirectional relationship between time perception and emotion modulation also suggests that temporal distortions during emotional events could contribute to conditioned learning and deficits in such processes. Learning the temporal relationship between an aversive outcome and a predictor of threat is critical for conditioned learning (Gallistel & Gibbon, 2000). Aberrant timing processes associated with emotional events in individuals with fear and anxiety disorders might then 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 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 that supported the negative

consequences of temporal distortions for emotional learning would have important implications given the aversiveness of unpredictability (Herry et al., 2007) and the integrality of uncertainty in contributing to anxiety (Grupe & Nitschke, 2013; Lake & LaBar, 2011). 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 (Mella et al., 2011). 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 emotion and emotion-related disorders in addition to advancing our understanding of the nature and importance of time perception.

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Biography

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Publications

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