IDENTIFYING NEURAL MECHANISMS AND BEHAVIORAL EFFECTS OF ANXIETY ON ATTENTIONAL CAPTURE

A Dissertation

by

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ABSTRACT

Attention research has long investigated the mechanisms by which sensory information is selectively filtered for neural representation. Models for visual selective attention initially formed a theoretical dichotomy in which goal-oriented or salience-driven mechanisms were argued as the predominant modes for attentional selection. However, this theoretical dichotomy was challenged when new experimental findings could not be reduced to goal-oriented or salience-driven mechanisms. These results were grouped into a new component of attentional control by an experience-driven mechanism and expanded models of selective attention into a theoretical trichotomy under the third label *selection history*.

In the context of attention research, threat has been investigated primarily by measuring rapid orienting towards threatening stimuli. Individuals with elevated state anxiety measured via self-report demonstrate increased attentional orienting towards threatening stimuli and enhanced attentional capture by physically salient stimuli. However, such findings are limited to attentional mechanisms toward the threatening nature of a stimulus and do not extend to more systemic changes in attentional control when the observer is in a threatened state. It is yet unknown whether elevated state anxiety globally modulates attentional capture through a core mechanism or whether such changes in observer state uniquely modulate different modes of attentional control. Furthermore, the mechanism by which threatening stimuli are afforded greater attentional priority in individuals with elevated state anxiety is still unclear.

Here, I investigate how attentional priority can be modulated by changing the state of an individual by experimentally inducing anxiety through the Threat of Shock (ToS) paradigm. I first present a series of behavior experiments that investigate how unpredictable threat modulates the three predominant mechanisms of attentional selection: attentional capture by reward history (selection history), color (salience-driven), and strategic goals. Then, I present a neuroimaging experiment that investigates how the neural mechanisms of processing threat interacts with mechanisms of attentional selection by previously-reward associated stimuli. I conclude by expanding on the core findings of this research and its implications concerning how changes in observer state modulates attentional control and how the identified mechanisms can be expanded to inform our understanding of attentional biases toward threatening stimuli.

DEDICATION

This dissertation is dedicated to my mother, Hyunhee Kim, and my father, Jonggook Kim. This written piece is a direct product of the only son you raised with love, sacrifice, wisdom, and prayer. I have long recognized and acknowledged that I would not be able to be here in this stage of life without your constant advice and I am delighted to be able to share in this accomplishment together. Although we do not verbally express it much, I know our family loves each other always. Thank you for supporting and guiding me in all aspects of life. I look forward to the additional memories we will create in the future as a family.

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1. INTRODUCTION

The world that we live in is a dynamically changing environment filled with numerous unique objects. While it would be ideal to perfectly perceive all the beautiful details of the world, we are limited by the representational capacity of the brain and its inability to fully process all external stimuli. To manage this limitation, the attention system selectively filters and identifies relevant sensory information to determine what is ultimately represented (e.g., Desimone & Duncan, 1995). Naturally, objects that are unattended fail to reach “identification” or “awareness” and are minimally (if at all) processed by other higher-order cognitive mechanisms such as decision making and memory storage (e.g., Broadbent, 1958; Most et al., 2001; Rensink et al., 1997). This selectivity component has been the foundation of attention research throughout its history.

How then does the attention system determine which stimuli or location should be attended to? The Biased Competition Theory of Attention poses that object representation in higher order brain networks is a result of a competition between sensory information, or in other words, a priority gain of representation of one object would result in a cost to another (Desimone & Duncan, 1995). As experimental evidence accumulated affirming the mechanism of biased competition in attentional selection, the definition has also been advanced to state that neuronal representation is a weighted averaged of all presented stimuli in which attention biases these weights in favor of the attended stimulus (e.g., Reddy et al., 2009). Even though biased competition is a mechanism occurring at the neuronal level by tuning neuronal receptive fields, biased competition was found to occur at multiple levels of processing including early visual up to higher-order levels. At each stage of processing, neurons were assumed to have a gain or cost in attentional priority by following a “priority map” (also called saliency or target map), or a two-dimensional map encoding specific features of objects (e.g., Itti & Koch, 2000, 2001; Koch & Ulman, 1985; Rutishauser & Koch, 2007; Zelinsky, 2008, 2012). Accordingly, the Biased Competition Theory postulates that attentional priority afforded to specific features of a target would continue to be integrated in later stages as well. Based on these early theoretical models of attentional selection, researchers would investigate how attentional priority is allocated at each stage of neuronal processing for decades to come.

1.1. The Formation of a Theoretical Dichotomy

In this section, I will briefly review the two predominant mechanisms of attentional selection that were established in the early history of selective attention: goal-oriented and salience-driven attentional selection. Goal-oriented attention (also known as top-down or endogenous attentional control) is commonly conceptualized as voluntary attentional priority allocated to features, objects, or regions in space based on the current selection goals of the observer. Salience-driven attention (also known as bottom-up or exogenous attentional control) is commonly conceptualized as involuntary attentional priority allocated to stimuli based on the saliency of its low-level features (i.e., color, shape). I will provide a brief historical account on the evidence found in support of each mode of attentional control and how these findings eventually formed a theoretical dichotomy that came to define initial models of selective attention.

1.1.1. Evidence for Goal-oriented Attentional Control

In the early 1970s and 80s, evidence for goal-oriented attentional control was popularly demonstrated in spatial cuing paradigms. Eriksen and colleagues investigated the deployment of attention guided by spatial cues by requiring participants to identify letter targets in a search array after a specific spatial location was cued, prior to presentation of the array (Eriksen & Collins, 1969; Eriksen & Hoffman, 1972, 1973). These early findings demonstrated that attention could be allocated to a cued location within a temporal window and that target identification was primarily determined by the attentional priority given to the location rather than other features. Then, Posner (1980) developed a spatial cuing task (commonly known as the Posner cuing task) to measure covert attentional shifts toward a cued spatial location (Posner, 1980; Posner et al., 1980). While these spatial cuing studies demonstrated that orienting attention towards a cued location ahead of the presentation of the target array biased information processing at the cued location, others also demonstrated that prior knowledge of specific features of the upcoming target in a search array decreases response time in visual search (e.g., Egeth et al., 1984; Wolfe et al., 1989). These early studies were the first evidence that prior knowledge of the observer was a critical component for voluntary attention allocation.

In addition, Jonides (1981) made a critical observation on a design element of the spatial cuing task and hypothesized that voluntary or automatic shifts of attention would depend on where the cue and stimuli were presented in the field of view. This hypothesis was framed on the theoretical basis that attention could be allocated like a “spotlight” or a circular region in visual space. His findings demonstrated that an arrowhead in the central point of fixation led to a voluntary, goal-driven shift of attention while an arrowhead in the periphery automatically drew attention (stimulus-driven) and first presented evidence that attention could be voluntarily or automatically biased. Thus, goal-oriented attention was largely conceived to be a voluntarily allocation of attention based on observer goals. However, Folk et al. (1992) utilized the contingent capture paradigm to demonstrate that an involuntary shift of attention could be contingent on the relationship between the cue and the target property and not due to specific features of the cue itself (Folk et al., 1992, 1994; Folk & Remington, 1998). These seminal findings became the backbone of a plethora of studies arguing for the prominence of goal-oriented attentional capture and its role in biased competition.

1.1.2. Evidence for Salience-driven Attentional Control

Also, in the early 1980s, researchers accumulated evidence for a different component of attentional priority allocation driven by the salient features of an object rather than observer goals. In a comprehensive series of experiments, Treisman & Gelade (1980) used a variety of experimental paradigms and manipulated multiple different features of stimuli to demonstrate that the detection and identification of singletons (stimuli that are unique) in a local dimension were due to the activation of their respective priority maps based on specific features (called feature maps). Thus, they proposed the feature-integration theory of attention which argues that attention is serially allocated toward stimuli within a set of independent feature maps by encoding the spatial location of objects that shared that feature (although they do not rule out the plausibility of top-down processing to also play a parallel role in selection). Interestingly, they do admit that although the individual results for each of their experiments could be alternatively interpreted, the collection of findings they present converge towards the proposed feature-integration theory.

Next, Pashler (1988) conducted a series of experiments using a boundary detection task and argued that neurons that are tuned to specific features of stimuli made local “within-dimension” comparisons. These findings supported the feature-integration theory of attention and led to the coining of the phrase “feature singleton” to be defined as a stimulus that is highly contrasting to its local stimuli in one feature dimension based on neuronal receptive fields. Amongst the many following studies investigating the role of feature singletons (i.e., color) in visual search to measure attentional capture by salient features, Bacon & Egeth (1994) interestingly demonstrated that attentional capture by a feature singleton only occurred when participants engaged in “singleton-detection mode”, arguing for the importance of the observer’s attentional control setting. Such studies began to form a debate on whether the saliency of stimuli is an important factor in the control of attention in comparison to observer goals.

The opposite claim was made by Theeuwes (1992) in which he argued that top-down guidance of attention was unnecessary for attentional selection of task-irrelevant information. Over multiple experiments, Theeuwes (1992) demonstrated that response times increased during visual search when a salient, but task-irrelevant color singleton was present, and that eye movements can be inadvertently directed to such stimuli at a rate that is higher than non-salient non-targets (e.g., Theeuwes et al., 1998, 1999). From these findings, he claims that saliency and not target identity captures attention and that the most salient singleton in the search array would ultimately gain the most attentional priority, challenging the prominence of goal-oriented attentional control raised by Folk and colleagues (e.g., Folk et al., 1992, Folk & Remington, 1998; Theeuwes, 1991, 1992, 1994). Over decades, the debate on how attentional priority is allocated for selection continued with both sides making claims almost as if the opposite side was completely misguided. While such strong claims have now acquiesced, the investigations on whether attentional priority is dominated by salience or goals goes on to this day (e.g., Anderson & Folk, 2012; Belopolsky et al., 2010; Luck et al., 2021; Sawaki & Luck, 2010; Luck et al., 2020; Wang & Theeuwes, 2020; Wolf & Lappe, 2020).

1.1.3. Divergent Neural Networks for Goal-oriented and Stimulus-driven Attentional Control

Beyond the data from behavior experiments, a robust collection of neuroimaging studies has discovered divergent neural networks for the control of goal-directed and stimulus-driven attention (see Corbetta & Shulman, 2002, 2008; Vossel et al., 2014; for reviews). Goal-directed attention is broadly known to be controlled by a dorsal frontoparietal system that integrates top-down, voluntary control giving attentional priority to specific features or locations. This network incorporates core regions within the dorsal parietal and frontal cortex such as the intraparietal sulcus (IPS), superior parietal lobule (SPL), and the frontal eye field (FEF) (e.g., Corbetta et al., 2000;

Hopfinger et al., 2000; Serences et al., 2004; Yantis et al, 2002). On the other hand, stimulus-driven attention is broadly known to be controlled by a ventral frontoparietal system that integrates bottom-up, involuntary control giving attentional priority to "pop-out" stimuli and to trigger shifts of attention. This network incorporates regions of the ventral network and frontal cortex including the temporoparietal junction (TPJ), the superior temporal sulcus (STS) and gyrus (STG), the middle frontal gyrus (MFG), inferior frontal gyrus (IFG), frontal operculum, and anterior insula (see Corbetta & Shulman, 2008, for a review). Validation of these regions as neural nodes for each network were conducted in "resting-state" functional connectivity and white matter structural connectivity neuroimaging studies (e.g., Fox et al., 2006; He et al., 2007; Umarova et al., 2010).

More interestingly, studies have investigated the interactions between these divergent neural networks. In a modified version of a contingent capture task, Serences et al. (2005) observed neural activation by both the location of the distractor (based on color) and by the peripheral locations in which attention was directed to (based on goals). The authors demonstrate an interaction between the dorsal and ventral networks of attention and argue that BOLD activation within the TPJ and VFC trigger a redeployment of attention. In fact, the TPJ of the ventral attention network has often been referred to as a "circuit-breaker" and activation within this region is associated with the reorienting of attention (Corbetta & Shulman, 2008). Furthermore, suppression of activity within the TPJ has been identified in top-down guided attentional processing tasks which has been claimed to protect against unwanted distraction (e.g., Shulman et al., 2003, 2007). On the other hand, neural activity within the TPJ has been identified in studies with salient nontargets that carry information about the target stimulus (e.g., Geng & Mangun, 2011; Serences et al., 2005). Furthermore, this reorienting of attention has shown to be blunted by using transcranial magnetic stimulation (e.g., Chica et al., 2011). Lastly, lesion and brain-damaged patient studies have also demonstrated that structural damage to one network has functional deficiencies in attentional roles that were supposed to be isolated in the other (e.g., Friedrich et al., 1998; Halligan et al., 2011; Mort et al., 2003). While distinct neural networks of attentional selection have been identified for prior goals and physical salience, the dynamic interplay between these networks argues that biased competition is a result of a balance between both networks for representation.

1.2. It Came in Like a Wrecking-Ball: The Advent of Selection History

Theories are models developed by scientists that try to best-estimate truth given the conclusions that the available data point to. Thus, naturally, theories are never perfect and are often revised when new evidence is found. The theoretical dichotomy introduced in the prior section was challenged when observed attentional biases in new studies could not necessarily be reduced to a goal-oriented or salience-driven component of attentional control. These findings supported an account in which attentional priority is allocated on the basis of past experience, either a prior history of attentional priority given to certain stimuli or locations or knowledge of associations between stimuli and outcomes, in which is now commonly known as *selection history*. While the early findings that did not fit the theoretical dichotomy failed to presume a new component of attentional priority (although see Anderson et al., 2011), the growing accumulation of evidence for experience-driven attention posed that the theoretical dichotomy of attention was outdated. Eventually, the field proposed a theoretical trichotomy of attentional control (e.g., Awh et al., 2012). In the following section, I will briefly review the evidence accumulated for this third component of attentional control and how experimental findings directly challenged the prior mold of a theoretical dichotomy.

1.2.1. Reward/Punishment History

One of the first examples of attentional selection that was neither goal-oriented nor stimulus-driven was found using reward. While many studies investigated the effect of receiving reward on attention, originally researchers perceived the modulatory effect of reward on attention as a type of motivating factor and naturally presumed it to be a sub-component of goal-oriented attentional control (e.g., Esterman et al., 2014, 2016; Navalpakkam et al., 2009, 2010; Pessoa, 2009). These conclusions were further corroborated when neuroimaging studies identified enhanced activation of the dorsal attention network to be linked with reward-associated stimuli and overlapped with the neural nodes of top-down attention (e.g., Jimura et al., 2010; Locke & Braver, 2008; Padmala & Pessoa, 2011; Pessoa & Engelmann, 2010; Small et al., 2005).

However, Anderson et al. (2011) demonstrated that attentional capture by previously-reward associated stimuli occurred even when it was task irrelevant and physically non-salient, directly challenging the claim that attentional capture by previously reward-associated stimuli could be reduced to a motivation or goal-oriented component of attentional capture. Here, Anderson et al. (2011) utilized a training phase to associate a color stimulus with reward. In the subsequent test phase, subjects completed a visual search task in which they were exposed to this task-irrelevant distractor. They found that attention was biased by the color distractor that was previously associated with reward even when it is task-irrelevant and physically non-salient, leading to the interpretation that such findings could not be reduced to a goal-oriented or salience-driven account of attentional control. This conclusion was replicated in other studies that also recognized the need to make reward a non-motivating factor by making it task-irrelevant during both the training and test phases (e.g., Bucker & Theeuwes, 2017; Le Pelley et al., 2015; Pearson et al., 2015). In addition, the effect of learned associations on attention were not limited to just reward learning. Stimuli that were previously associated with aversive outcomes such as electric shock were also shown to capture attention when appearing as task-irrelevant distractors (e.g., Anderson & Britton, 2020; Schmidt et al., 2015a, 2015b). Such experimental designs in which learned associations between stimuli and outcomes result in the capture of attention by valent stimuli, even when task-irrelevant and physically non-salient, provided the strongest initial evidence for an experience-driven account of attention.

1.2.2. Inter-trial Priming

Attentional priority given to or taken away from a stimulus on any given trial has shown to have a "lingering" effect on the following trial called inter-trial priming (e.g., Geyer et al., 2006; Kristjansson, 2006; Kristjansson et al., 2002; Kristjansson & Driver, 2008; Maljkovic & Nakayama, 1994, 1996; Wang et al., 2005). This trial-by-trial effect has been shown to effectively bias attentional priority to features and locations.

Originally, as in Jonides (1981), trial-by-trial effects were often interpreted in the context of a goal-oriented account of attention allocation. However, like the experimental designs that investigated the effect of reward history on attention, clever designs that dissociated the goal-oriented effects from the inter-trial priming effects argued otherwise. For example, experiments measuring inter-trial priming effects began to manipulate subject awareness. Despite giving prior knowledge that the target-defining feature would be manipulated trial-by-trial, subjects still demonstrated inter-trial priming effects leading to the conclusion that such priming effects were explicitly non-strategic (Hillstrom, 2000; Maljkovic & Nakayama, 1994). Furthermore, Theeuwes & Van der Burg (2007, 2011) further informed subjects on the prominent feature of the upcoming target singleton but found no beneficial effects of such prior knowledge. These experiments demonstrated that inter-trial priming effects persist even when they cannot be reduced to a modulation of goal-oriented attentional biases leading to an alternative conclusion that it fits under the umbrella of experience-driven attentional modulation.

1.2.3. Statistical Learning

When attention is repeatedly allocated toward a specific stimulus or location more frequently than others, researchers have shown that participants often learn this implicit attention bias in a phenomenon called statistical learning. Interestingly, Moray (1959) discovered that participants demonstrated increased attentional capture by their own name in an auditory stream. Although repeated exposure to each participant’s name was not specifically learned in the experimental setting, these findings showed that repeated prioritization of a specific stimulus would automatically capture attention even when it is task-irrelevant and non-salient. However, could one's name be argued to have "top-down" or motivational influence in grabbing attention? Thus, to experimentally demonstrate the effects of statistical learning, researchers utilized visual search tasks that incorporated a "high-probability location" where the target appeared more frequently. Although participants were unaware of such design manipulations, findings showed that increased attentional priority was allocated to this high-probability location (e.g., Geng & Behrmann, 2002, 2005; Jiang et al., 2013; Jiang & Swallow, 2013). Furthermore, this statistical learning effect was extended to situations in which the high-probability location was applied to the distractor rather than the target in visual search, producing facilitated ignoring of the stimuli appearing in the high-probability location (Wang & Theeuwes 2018a, 2018b, 2018c). Again, importantly, this learning effect occurred without any explicit knowledge about the distractor location contingencies (e.g., Failing et al., 2019a, 2019b; Wang & Theeuwes, 2018a). More interestingly, some studies have shown unique aspects of statistical learning that clearly differentiates itself from goal-oriented attentional control. For example, Jiang et al. (2013) demonstrated that statistical learning effects could last hours or even days and Jiang & Wagner (2004) showed that these learned, implicit biases could be transferred over to a different display. Such experimental evidence for statistical learning demonstrated characteristics that could be dissociated from goal-oriented attentional control.

1.2.4. Is Selection History Truly Different?

Not all researchers were keen to adopting the proposed change to a theoretical trichotomy. Ever since the change in taxonomy, some have argued that selection history still falls under the umbrella of goal-oriented attention (e.g., Egeth, 2018; Gaspelin & Luck, 2018b). Wolfe et al. (2006) raised the claim that priming is a form of accessing prior knowledge and not solely driven by experience. In contrast, Theeuwes et al. (2006) argues that these priming effects could be regarded as “bottom-up” since they are unaffected by voluntary control. However, I believe that the evidence provided in this section clearly shows a unique type of attentional priority allocation that cannot be reduced to goal-oriented or salience-driven attentional biases. Furthermore, I do agree with Gaspelin & luck (2018b) that such confusion and lack of agreement originates from the arbitrary definitions of terms used in the field of attention such as “top-down” and “bottom-up”. In addition, other experimental findings such as contextual cuing (e.g., Chun & Jiang, 1998, 2003) and attention bias to novel or in frequent stimuli (e.g., Folk & Remington, 2015; Neo & Chua, 2006; Horstmann & Ansorge, 2006, 2016; Johnston et al., 1990, 1993) have also challenged the original theoretical dichotomy and are argued to be modulated by experience-driven attention. Thus, there is a critical need to review all the evidence that can be classified under the term selection history and to define and distinguish each component of experience-driven attention from goal-oriented and stimulus-driven attention.

1.3. Suppression

As more evidence accumulated on how attentional priority could be allocated in either a goal-oriented, stimulus-driven, or experience-driven manner, arguments were no longer framed around the idea of one mechanism being the overall more dominant mechanism but rather the control of attention was characterized as the product of the interplay between a group of potential mechanisms that depended on the task or type of stimulus. While many of these studies demonstrated how attentional priority was allocated to a stimulus or location, Sawaki & Luck (2010) showed that attention could be actively down regulated in what they defined in the signal suppression hypothesis. Using event-related potential (ERP) studies, Sawaki & Luck (2010) showed that the "attend-to-me" priority signal that salient singletons automatically produce could be actively suppressed. In this section, I will briefly introduce the evidence in support of the signal suppression hypothesis and how these findings offered a new interpretation of biased competition.

1.3.1. Evidence for Inhibition

ERP studies have been a useful tool in psychophysiological studies of the control of attention given its high temporal precision. In attention studies, two components of the ERP are commonly measured: the N2pc and Pd (distractor positivity) which are sensitive indexes of covert deployment of visual attention and attentional suppression, respectively (Eimer, 1996; Luck & Hillyard, 1994; Hickey et al., 2009). In a series of experiments, Sawaki & Luck (2010) first demonstrated that the "attend-to-me" signal presented by salient irrelevant singletons were actively suppressed to prevent attentional priority to be deployed to these distractors, irrespective of attentional control settings. Other studies have also replicated the identification of the Pd component to be elicited by salient distractors that fail to capture attention (e.g., Gaspar & McDonald, 2014; Kiss et al., 2012; McDonald et al., 2013; Sawaki & Luck, 2010) and this measure was importantly found to be in conjunction with behavior (Gaspelin & Luck, 2018).

In addition to electrophysiological studies, behavior studies have also identified suppression of attentional priority using the capture-probe paradigm. In the capture-probe paradigm design, a memory-probe is interspersed among trials to assess whether participants are allocating attention evenly amongst all potential locations. Gaspelin et al., (2015) demonstrated that participants had reduced probe identification in the location of a salient distractor, demonstrating that attention allocation was actively being suppressed in that location. Furthermore, this finding was replicated in eye-tracking studies to extend the hypothesis to an oculomotor suppression effect (Gaspelin et al., 2017). Also, Gaspelin et al. (2017) demonstrated that the phenomenon of signal suppression occurred only when the attentional priority was allocated in a goal-oriented and not a stimulus-driven manner. If the target of the visual search array was not a shape singleton, participants engaged in “feature-search mode” to find the target and did not have slowed response times in the presence of the distractor. Rather, it was only when the visual search target was a shape singleton that participants used “singleton-detection mode”, or stimulus-driven attentional control, that occurred in slowed response times and active suppression of behavior.

Then, is signal suppression a mechanism of “top-down” attentional control given that active inhibition depends on the attentional set? Or perhaps, is signal suppression an experience-driven mechanism of control as seen in trial-by-trial manipulations of features to be ignored (Beck et al., 2018; Cunningham & Egeth, 2016; Moher & Egeth, 2012)? Much of the described studies suggest that stimuli are proactively suppressed in a particular location before the allocation of attention to that area. However, others proposed the opposing argument that attentional priority can be initially allocated but then quickly suppressed afterwards as described in the "search-and-destroy" hypothesis (Moher & Egeth, 2012) or the rapid disengagement hypothesis (Theeuwes, 2010; Theeuwes et al., 2000). Both behavior and electrophysiological studies have found evidence in support for these reactive mechanisms of attention allocation (e.g., Beck et al., 2018; Geng & Diquattro, 2010; Hickey et al., 2006; Moher & Egeth, 2012).

1.3.2. How Does This Change the Theoretical Trichotomy?

Gaspelin & Luck (2019) offered the signal suppression hypothesis as a "resolution to the attentional capture debate" in that it provides a mechanism for how both goal-oriented and stimulus-driven attention could compete for attentional priority. However, I disagree in that there was a such a debate in the first place. The large mass of evidence in support of goal-oriented, stimulus-driven and experience-driven attention had already made it evident that biased competition is a result of all mechanisms of attentional capture simultaneously competing for attentional priority, albeit the dominant mode of control depends on the particulars of the environment. Rather, the signal suppression hypothesis offers a new lens in conceptualizing the neural mechanisms of each component of attention control and how these networks interact to ultimately decide what is represented. However, the understanding of signal suppression is still relatively new. For example, the debate whether signal suppression is proactive, reactive, or a combination of both is still ongoing. Some have used the rapid disengagement hypothesis to strengthen their argument that top-down control cannot override stimulus-driven attentional capture (Theeuwes, 2004). Furthermore, the signal suppression hypothesis has primarily been investigated using physically salient stimuli in the context of goal-oriented control. Its mechanistic role in experience-driven attentional control is largely unexplored. The field is ripe to investigate such possibilities and I will attempt to apply the concept of signal suppression to the findings throughout this dissertation.

1.4. Threat and Attention

Detection of threat has long been conceived as a conserved evolutionary mechanism for survival. The study of attention bias to threat has primarily been examined in clinical contexts with the hope of treating pathological phobias and anxiety disorders. However, the inconsistency in translating research findings in this domain to clinical trials of pathological anxiety has called for a need to better understand the mechanisms of attention bias by threatening stimuli and elevated state-anxiety (see Mogg & Bradley, 2018, for a review). In this section, I will briefly review the majority of research that has focused on attentional orienting to threatening stimuli, how this narrow approach has limited progress in translating to the clinical setting and offer an alternative model to investigate attention bias under threat.

1.4.1. Orienting to Threat

Current working models of anxiety depict pathology as inappropriate and excessive activation of neural circuitry designed to be beneficially adaptive under threat (e.g., Brooks & Stein, 2015). Both pathologically anxious patients and individuals with elevated self-report measure of anxiety have demonstrated increased attentional priority for orienting to threatening stimuli, primarily in tasks measuring attention shift (see Bar-

Haim et al., 2007, for a meta-analysis). Thus, much research has focused on measuring attention bias to threat and orienting to threatening stimuli.

Threatening stimuli or stimuli associated with aversive outcomes have consistently been demonstrated to capture attention more than neutral stimuli, often impairing task performance (e.g., Most et al., 2005; Most & Wang, 2011; Mulckhuyse, 2018; Ohman & Mineka, 2011; Vuilleumier, 2005). These experimental paradigms have used a wide variety of stimuli such as fearful faces (Dimberg & Ohman, 1996; Eastwood et al., 2001; Eldar et al., 2010; Vuilleumier, 2005), threatening animals (e.g., snakes, spiders; Ohman et al., 2001; Ohman & Mineka, 2003), negative-valence images (Derryberry & Reed, 2002; Most et al., 2005; Quigley et al., 2012), or threatening words (Mathews & Macleod, 1985, 1994) to capture attention. In addition, studies manipulating learned associations between arbitrary stimuli and aversive outcomes have demonstrated that associative learning of threat can also automatically bias attention (e.g., Schmidt et al., 2015a, 2015b, 2015c; Wang et al., 2013, Chubala & Smith, 2009; Koster et al., 2004).

However, by what mechanism of biased competition does threatening stimuli gain attentional priority? Some findings have shown that orienting to threatening stimuli is an early process of attentional orienting in the visual system (e.g., Ohman & Mineka, 2001; Thigpen et al., 2017; Vuilleumier, 2005). However, do these findings indicate that low-level visual features are driving attentional orienting to threatening stimuli? Or perhaps, is threat avoidance a learned response from exposure to harm or a voluntary response for the goal of survival? Brown et al. (2020) used the classic contingent capture and emotion-induced blink paradigms in an RSVP task to provide evidence for involuntary attentional capture when adopting a search goal for threat. Also, Vromen et al. (2016) demonstrated that rapid orienting of attention to threatening stimuli only occurred when stimuli were goal relevant. These findings support the claim that orienting to threatening stimuli can be goal contingent. In contrast, Abado et al. (2020) argues that the physical saliency of the target (bird vs. spider) interacts with expectancy to manipulate attention bias. While some have attempted to resolve this debate (Ohman & Mineka, 2001), the mechanisms of biased competition regarding threat-related attentional biases are still unclear.

1.4.2. Distinguishing Between Fear and Anxiety in the Control of Attention

As depicted in the previous section, threatening stimuli readily capture attention and the observer is thereby rapidly oriented to a posing threat. However, are the mechanisms by which threat modulates attentional priority consistent when the posing threat is predictable or unpredictable? For example, are the changes in attentional priority experienced by a police officer directly facing the threat of an active gunman identical to the changes in attentional priority experienced by a resting gazelle when it hears the rustle of leaves signaling the threat of an unseen predator? Experimental paradigms have modeled these differences to predictable and unpredictable threat, which are associated with the mechanisms of fear and anxiety, respectively.

Fear and anxiety were once perceived as similar biological processes due to their overlapping physiological symptoms (e.g., Davis et al., 2010). However, key differences have been identified to establish them as different mechanisms. Fear is defined as an adaptive response to an imminent, predictable threat that begins rapidly and dissipates rapidly as the danger is removed. On the other hand, anxiety is defined as a sustained response to an unpredictable, or potential threat that leads to longer lasting arousal and vigilance (e.g., Davis et al., 2010*)*. Naturally, these physiological differences have been mapped onto distinct pathologies: one by elevated cued-fear reactivity (e.g., phobias) and the other by maladaptive, long-term state of anxiety (Vollebergh, 2001).

Hypotheses claiming that the neural networks involving fear and anxiety were independent began with identification of unique anatomical pathways, specifically in regard to the central (CeA) and medial (MeA) nuclei of the amygdala and the bed nucleus of the stria terminalis (BNST; Alheid et al., 1998; Alheid & Heimer, 1988; see also Davis et al., 2010, for a review). The dissociable effects of fear and anxiety were clearly demonstrated in the pain literature in which anxiety increased pain sensitivity while fear decreased it (Rhudy & Meagher, 2000). Furthermore, rodent studies using neurotoxic lesions and pharmacological agents used to block specific pathways were found to block only one of phasic or sustained fear responses (e.g., Dong et al., 2001; Hitchcock & Davis, 1986, 1991; Lee & Davis, 1997; McDonald, 1991; Weller & Smith, 1982). In addition, human studies that incorporated clinical populations of post-traumatic stress and panic disorders demonstrated that patients had dissociable effects of startle potentiation depending on whether they were under predictable or unpredictable threat (Grillon et al., 2008, 2009). Finally, anxiolytic medications were shown to be effective in reducing startle potentiation only when electric shocks were unpredictable (Grillon et al., 2009). These clinical and pharmacological studies validated the claim that the neural representations of fear and anxiety were independent of each other and demonstrated a need for an experimental paradigm to separately model fear and anxiety for psychophysiological measurement.

The role of anxiety and threat in attention has been a topic of broad research interest. Typical approaches include comparing the performance of individuals who differ in trait-level anxiety (e.g., Bar-Haim et al., 2007; Derryberry & Reed, 2002; Koster et al., 2005, 2006; Moser et al., 2012). Attention biases towards threat-related stimuli have shown to be more pronounced in anxious individuals (e.g., Bar-Haim et al., 2007; Derryberry & Reed, 2002; Shechner & Bar-Haim, 2016; Shechner et al., 2017). Furthermore, anxiety disorders have been linked to increased distractibility and impaired concentration (Eldar et al., 2010; Eysenck et al., 2007), including increased susceptibility to attentional capture by physically salient stimuli (Esterman et al., 2013).

Consistent with the historical focus of research on the correlation between heightened state-anxiety and attentional orienting to threatening stimuli, cognitive behavioral therapies have become the gold-standard for treating pathological anxiety (e.g., Beard, 2011; Kaczkurkin & Foa, 2015), specifically utilizing attention bias modification treatment (ABMT) (e.g., Hakamata et al., 2010; MacLeod et al., 2002). However, ABMT has been inconsistent and marginally effective in clinical trials (see Mogg & Bradley, 2018, for a review), calling into question the strategy of "threat-avoidance" and "positive-search" training to reciprocate altered neural circuitry (e.g., Amir et al., 2009; Waters et al., 2013). Mogg & Bradley (2018) specifically highlight the need to understand the multiple processes underlying anxiety and attentional biases (not just orienting to threat) and emphasize the lack of data in evidence-based cognitive perspectives of anxiety and threat-related attention as a barrier to effective treatment.

1.4.3. A Paradigm to Model Anxiety

One of the first experimental paradigms developed to model differences in anxiety and fear in humans was the No-shock, Predictable-shock, Unpredictable-shock (NPU) task, which measured startle potentiation while manipulating the probability of threat of shock (Schmitz & Grillon, 2012). In the predictable-shock block, electric shocks are 100% cue-contingent and are always presented at a predictable known time, designed to model the phasic, event-related effects of fear. In contrast in the unpredictable-shock block, electric shocks are presented at unpredictable times designed to induce elevated state-anxiety or “sustained fear”. Stemming from the NPU threat task, the Threat of Shock (ToS) paradigm was further developed to incorporate solely the unpredictable-shock block and has now been recognized as the gold-standard translational paradigm to measure the effects of elevated state-anxiety in a within-subjects design (e.g., Clark et al., 2012; Cornwell et al., 2007; Grillon et al., 2004, 2008). Importantly, increasing amounts of experimental evidence have demonstrated that experimental induction on anxiety, particularly through threat of electric shock, evokes neural circuitry and patterns of behavior characteristic of pathological anxiety (e.g., Robinson et al., 2011, 2013, 2014, 2015). Thus, the ToS paradigm provides a gateway to investigate the effects of anxiety on numerous cognitive processes including attention.

Before moving forward, it is important to recognize the differences in adaptive vs. pathological anxiety. Anxiety has long been understood as a conserved, adaptive mechanism to enable an organism to rapidly detect and orient to threat (e.g., Robinson et al., 2011, 2012). Current models of anxiety disorders have suggested that pathological anxiety is the brain's plastic response to excessive activation of these originally intended adaptive pathways and often arises when attentional biases for threat have become inappropriately chronic (e.g., Insel, 2014; Insel et al., 2010; see also Bar-Haim et al., 2007, for a meta-analysis). To determine whether the effects of adaptive anxiety can be interchangeable with the symptoms of pathological anxiety, Chavanne & Robinson (2020) conducted a meta-analysis to show that while both induced and pathological anxiety overlapped in symptoms and shared in patterns of neuronal activation, the compared brain activity were not completely identical and became further disassociated depending on the type of pathological anxiety. Thus, although the ToS paradigm has previously shown to emulate the neural circuitry of pathological anxiety, it is more accurately depicted as an intermediate model of adaptive anxiety (now referred to as *experimentally induced anxiety* throughout) more so than pathological anxiety. Regardless, elevated state anxiety is still one of the primary symptoms of all anxiety disorders and more research is needed to fill in the gap between experimentally induced and pathological anxiety.

Thus, the ToS paradigm provides an opportunity to investigate how attentional control is modulated under conditions of experimentally induced anxiety and the corresponding change in observer state. Prior studies examining the influence of threat on attention to non-threat-related stimuli have been limited to between-subject designs comparing attentional capture between individuals with high and low self-report measures of state anxiety (e.g., Esterman et al., 2013; Moser et al., 2012). Furthermore, the available studies investigating attentional capture between subjects with varying state anxiety levels only have utilized physically salient stimuli as critical stimuli. As described in the prior sections, the mechanisms of goal-oriented, salience-driven, and experience-driven (selection history) attentional control are dissociable, including with respect to the neural networks that have been identified in their control. It is unclear whether state modulations such as elevated state anxiety will globally influence attentional control through a common mechanism or whether each mode of attentional control will be uniquely modulated by experimentally induced anxiety. Some studies have examined attentional biases by manipulating the state of the observer through hunger (e.g., Hardman et al., 2013; Mogg et al., 1998; Placania et al., 2002). As seen with individuals with elevated state-anxiety when exposed to threatening stimuli, hungry individuals also showed increased attentional priority allocation towards food-related stimuli compared to control stimuli. In addition, individuals with pathological anxiety or elevated state anxiety have shown to have increased attentional biases toward threatening stimuli (see, Bar-Haim et al., 2007, for a meta-analysis). However, it is unclear whether enhanced attentional biases toward threatening or negatively valent stimuli are due to changes in perception of the stimuli as being increasingly salient or whether elevated state anxiety primes attention networks into a more goal-oriented mode of processing, perhaps for the sake of survival.

In the chapters that follow, I present experiments that investigate how attentional priority is modulated under a state of experimentally induced anxiety, using the ToS paradigm. For a comprehensive approach, I will utilize attention tasks that measure attentional biases toward physically salient, previously reward-associated, and goal-relevant stimuli to investigate how induced anxiety modulates each mode of attentional control. In addition, I will present a neuroimaging experiment on the effects of experimentally induced anxiety on reward-associated attentional capture. The findings from these experiments will shed light on whether changes in observer state, and specifically a state of anxiety, globally affects attentional processing mechanisms or if changes in observer state uniquely modulates different attention networks for optimal attentional selection. Furthermore, a better understanding of the mechanisms by which threat modulates attentional control will offer additional insights into how threatening or emotionally valent stimuli are processed under elevated state anxiety.

2. THREAT REDUCES VALUE-DRIVEN BUT NOT SALIENCE-DRIVEN ATTENTIONAL CAPTURE[1]

The relationship between the mechanisms underlying value-driven attention (reward history on attention) and attention to aversively conditioned stimuli is not known. One possibility is that each of these two sources of attentional priority are represented in dedicated neural and cognitive systems for reward and threat, respectively, which independently bias attention. By this account, the experience of threat would not be expected to interfere with the influence of reward on attention. A second possibility is that these two sources of attentional priority compete with one another, such that the processing of threat information interferes with value-based guidance. By this account, value-driven attentional capture should be reduced under conditions of threat, aligning with the dual competition framework (Pessoa, 2009). However, the arousal-biased competition hypothesis poses an alternative interpretation which postulates that negative arousal enhances high-priority visual signals at the expense of less-salient signals (Mather & Sutherland, 2011). If reward-associated stimuli are deemed high-priority, by this account value-driven attentional capture would be potentiated under threat. In contrast, if reward-associated stimuli are deemed low-priority under threat, then value-driven attentional capture would correspondingly be

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[1] Kim, A. J., & Anderson, B. A. (2020), Threat reduces value-driven but not salience-driven attentional capture. *Emotion*, 20, 874-889.

reduced under threat, albeit by a different neural mechanism posed by the dual-competition framework.

In this chapter, I will first present a series of five experiments that examines how threat modulates the influence of reward history and physical salience on the allocation of attention. The first three experiments investigate how attentional priority to previously reward-associated stimuli are modulated under threat using the value-driven attentional capture paradigm (Anderson et al., 2011) in combination with the Threat of Shock (ToS) paradigm (Grillon et al., 2004). We then validated our experimental design and procedure in the following two experiments by investigating how attentional priority to physically salient stimuli are modulated under threat using the additional singleton paradigm (Theeuwes, 1992), also in combination with the ToS paradigm (Grillon et al., 2004), given that attentional priority to physically salient stimuli is known to be elevated under threat (e.g., Lee et al., 2012, 2014; Mather & Sutherland, 2011; Sutherland & Mather, 2012, 2015).

2.1. Experiment 1

To quantify the effects of reward history on selective attention, we utilized the value-driven attentional capture paradigm in which a participant is rewarded for orienting towards a valuable stimulus during a training phase, and this reward-associated feature then serves as a task-irrelevant distractor during a subsequent test phase (Anderson et al., 2011). We measured attentional capture by previously reward-associated stimuli under conditions in which the threat of shock was and was not present. To test whether the effect of the threat of shock differed for participants with different proclivities towards anxiety and depression, we included a battery of questionnaires assessing relevant constructs (Beck et al., 1996; Carver & White, 1994; Ferreira & Murray, 1983; Patton et al., 1995). Our objective was to test between the competing accounts of threat and reward processing outlined above, and we did not have specific predictions concerning which outcome was more likely.

2.1.1. Methods

2.1.1.1. Participants

Thirty-eight participants (23 females), between the ages of 18 and 35 inclusive, were recruited from the Texas A&M University community. All participants were English-speaking, reported normal or corrected-to-normal visual acuity and normal color vision. All procedures were approved by the Texas A&M University Institutional Review Board and were conducted in accordance with the principles expressed in the Declaration of Helsinki. Written informed consent was obtained for each participant. The sample size was informed by a power analysis in which the power to detect value-driven attentional capture and the power to detect threat-dependent modulations in attentional capture were considered. The effect size for attentional capture by a high-value distractor was estimated from Anderson and Kim (2019), on which the design of the task was based ($d_z = 0.55$). The effect size for threat-dependent modulations in attentional capture was estimated at $\eta^2 = 0.09$ from Sutherland and Mathur (2012). At $\alpha = 0.05$, a sample size of at least 28 participants would provide $\beta > 0.80$ to detect each of the two effects.

2.1.1.2. Apparatus

A Dell OptiPlex 7040 (Dell, Round Rock, TX, USA) equipped with Matlab software (Mathworks, Natick, MA, USA) and Psychophysics Toolbox extensions (Brainard, 1997) was used to present the stimuli on a Dell P2717H monitor. The participants viewed the monitor from a distance of approximately 70 cm in a dimly lit room. Paired electrodes (EL500, BioPac Systems, Inc., Goleta, CA, USA) were attached to the left forearm of each participant, and electric shocks were delivered through an isolated linear stimulator under the constant current setting (STMISOLA, BioPac Systems), which was controlled by custom Matlab scripts. Eye-tracking was conducted using the EyeLink 1000 Plus system (SR Research Ltd., Ottawa, Ontario, Canada), and head position was maintained using a manufacturer-provided chin rest (SR Research Ltd.).

2.1.1.3. Individual Differences Assessments

All participants completed electronic implementations of the State-Trait Anxiety Inventory (STAI-state, STAI-trait; Ferreira & Murray, 1983), Beck Depression Inventory (BDI-II; Beck et al., 1996), Behavioral Activation/Inhibition System Inventory (BAS/BIS; Carver & White, 1994), and Barratt Impulsiveness Scale (BIS-11; Patton et al., 1995) before completing the experimental task. After the experimental task, participants again completed the STAI-state inventory to assess whether state anxiety was elevated from the threat of shock.

2.1.1.4. Stimuli

In the training phase, each trial consisted of a gaze-contingent fixation display, a stimulus array, and a feedback display (see Figure 1A). The fixation display consisted of a box (3.3° x 2.5° visual angle) at the center of the screen. Each circle in the search array was 4.5° visual angle in diameter. Stimuli located on the left and right sides were 9.3° visual angle from the meridian. Vertically, stimuli were 3.3° visual angle and 7.4° visual angle above and below the horizontal equator. Targets were red and green, and the colors of the non-targets were drawn from the set {blue, cyan, pink, orange, yellow, white} without replacement (Anderson et al., 2011, 2014). If the target was fixated within the timeout limit, a feedback display was presented consisting of the amount of monetary reward earned on the current trial (+10¢ or +2¢), and the total reward accumulated across all trials. If the target was not fixated within the timeout limit, the word "Miss" would appear in the feedback in place of the trial earnings. Fixating a non-target did not trigger any outcome, and it was possible to fixate a non-target before fixating the target within the timeout limit and still receive the target-associated reward.

In the test phase, before each block of trials, participants were presented with a display indicating whether shock was possible in that block. Each circle in the search array had a 4.5° visual angle diameter and diamonds were 4.1° x 3.7° visual angle. The target was defined as the unique shape. At the beginning of a possible shock block, the display would present the words "Possible Shock" along with a white box that contained an image of a lightning bolt. At the beginning of a no shock block, the display would present the words "No Shock" along with a white box that contained an image of a lightning bolt with a red hash over it. Each trial consisted of a gaze-contingent fixation display, a stimulus array, and a blank inter-trial-interval (see Figure 1B). The fixation display included the identical image referenced at the start of each block, either a white box with a lightning bolt or red hash covering the bolt. The locations of the stimuli and the colors of the non-targets were identical to the training phase. If participants were unable to fixate the target within the timeout limit, the word “Miss” would appear during the inter-trial-interval. During possible shock blocks, a small number of trials were added in which electric shock was delivered in place of the stimulus array.

2.1.1.5. Design

Both the training phase and the test phase were split into two runs, with each run consisting of 120 trials (240 trials total in each phase). In the training phase, the target was equally-often red and green. Each target color appeared in each stimulus position equally-often within a run, and trials were presented in a random order. For each participant, one of the color targets (counterbalanced) would yield a monetary reward of 10¢ on 80% of trials and 2¢ on 20% of trials (high-value target); the other color target would yield 2¢ on 80% of trials and 10¢ on 20% of trials (low-value target). In the test phase, block order was counterbalanced across participants. On half of the trials, one of the non-target shapes was rendered in the color of the former high-value target during the training phase (referred to as the distractor). The other half of trials did not contain either of the prior target colors from training (distractor-absent trials); the low-value color did not appear during the test phase, to maximize the trials-per-cell in the factorial design. The target was equally-often a diamond among circles and a circle among diamonds and was never red or green. Target and distractor position were fully crossed and counterbalanced, and trials were presented in a random order. In shock blocks, participants were shocked 2 times in 2 blocks, 3 times in 3 blocks, and 4 times in 1 block, with the assignment of number of shocks to blocks randomized. The pattern of shocks administered in the shock block across trials was pseudo-randomly determined with the constraint that shocks were never administered on consecutive trials nor on the last trial of a block. At the end of the experiment, participants were paid the total monetary reward obtained during the training phase.

2.1.1.6. Procedure

In the training phase, each trial began with the presentation of a white box that remained on-screen until the participant fixated on the box for 500 ms. The stimulus array would then be displayed for 1000 ms or until the target was fixated. Then the feedback display would appear for 1500 ms, indicating the monetary reward gained and the participant’s total earnings. Following the training phase, the participant was connected to the isolated linear stimulator and a shock calibration procedure was conducted for each participant to achieve a level that was “unpleasant, but not painful” (Murty et al., 2012; Schmidt et al., 2015a, 2017). In the test phase, each trial began with the presentation of the block display, indicating whether the following block would contain a potential electric shock or no chance of an electric shock. The block began once the experimenter pressed the space bar. Each trial began with the presentation of the identical image referenced in the block display. Fixation on the image for 500 ms triggered the stimulus array, which again remained on screen until participants fixated the target or 1000 ms elapsed, and the inter-trial-interval lasted 1000 ms.

Head position was maintained throughout the experiment using an adjustable chin rest that included a bar upon which to rest the forehead (SR Research). Participants were provided a short break between each run of the task in which they could reposition their head to maintain comfort. Eye position was calibrated prior to each block of trials using 9-point calibration (Anderson & Yantis, 2012), and was manually drift corrected by the experimenter as necessary (the next trial could not begin until eye position was registered within 1.1° of the center of the fixation cross for 500 ms; see, e.g., Nissens et al., 2017). During the presentation of the search array, the X and Y position of the eyes was continuously monitored in real time with respect to the six stimulus positions, such that fixations were coded online (Le Pelley et al, 2015).

2.1.1.7. Data Analysis

One participant withdrew from the experiment prior to completion and two participants were unable to be eye-tracked using our apparatus. Thus, 35 complete data sets were ultimately analyzed.

We measured which of the six shape stimuli was initially fixated on each trial, as well as whether the target was fixated before the timeout limit along with the time required to fixate the target (i.e., RT). Fixation of a stimulus was registered if eye position remained within a region extending 0.7° around the stimulus for a continuous period of at least 50 ms (100 ms on the target trigger the termination of the stimulus array; see, e.g., Le Pelley et al., 2015). Oculomotor capture was determined by comparing the probability of initially fixating the valuable distractor compared to the average of other non-target stimuli. RT was measured from the onset of the stimulus array until a valid target fixation was registered. RTs in fixating the target that exceeded three standard deviations of the mean for a given condition for a given participant were trimmed (Anderson & Yantis, 2012).

2.1.2. Results

A 2 x 2 analysis of variance (ANOVA) with distractor condition (present vs. absent) and block (shock vs. no shock) as factors was conducted over mean RT. There was no main effect of distractor condition, $F(1,34) = 3.01$, $p = 0.092$, no main effect of block, $F(1,34) < 0.01$, $p = 0.998$, and also no interaction, $F(1,34) = 0.16$, $p = 0.689$ (see Figure 2A). The same ANOVA conducted over oculomotor capture revealed a main effect of distractor condition, $F(1,34) = 8.20$, $p = 0.007$, $\eta^2 = 0.194$, but there was no main effect of block, $F(1,34) = 0.06$, $p = 0.802$, nor an interaction $F(1,34) = 0.15$, $p = 0.700$ (see Figure 2B). Post-hoc comparisons revealed that there were significantly more saccades to the distractor compared to a non-target within both the shock block, $t(34) = 2.65$, $p = 0.012$, $d = 0.65$, and the no-shock block, $t(34) = 2.45$, $p = 0.02$, $d = 0.60$.

Unsurprisingly given the lack of interaction effects between attentional capture and threat, no questionnaire measure was predictive of the difference in oculomotor capture between shock and no shock blocks (see Supplemental Table 1). State anxiety increased after the test phase, $t(34) = 6.67$, $p < 0.001$, $d = 1.7$, confirming the anxiety-provoking nature of the threat-of-shock manipulation.

2.1.3. Discussion

In Experiment 1, we found no effects of threat of shock on value-driven attentional capture. Eye movements were biased towards previously reward-associated stimuli, but the magnitude of this oculomotor bias did not differ between blocks with and without the threat of shock. State anxiety, as measured using the STAI, increased as a result of the test phase manipulation, suggesting that the threat of shock was effective in inducing a state of anxiety.

Fear is a response that occurs from predictable threat and is quick to dissipate, while anxiety results from the anticipation of an unpredictable threat and is longer-lasting. While null effects of the ToS paradigm on behavior have been documented (Robinson et al., 2015) as in our experiment, another possibility is that the no-shock blocks in the present experiment were not sufficiently long for anxiety to dissipate, especially given the alternating nature of shock and no-shock blocks (where future epochs involving shock could be anticipated). Unlike in the manipulation of fear in which the removal of the fearful stimulus quickly returns a person to a baseline state (Grillon et al., 1991; see also Davis et al., 2010, for a review), a state of anxiety may be “bleeding over” into no-shock blocks in the present experiment, compromising the effectiveness of the block manipulation. A global state of threat could be influencing capture across the entire task, in similar measure across blocks.

2.2. Experiment 2

In Experiment 1, there was no difference in capture between “shock” and “no shock” blocks, which on the surface is consistent with the idea that brain systems for value and threat influence attention independently. However, it is not evident whether our manipulation of anxiety through threat varied substantively between blocks. Potentially, anxiety instilled through the threat of shock during the “shock” blocks is unable to be turned off in quick succession and resulted in a global state of threat over the entirety of the test phase of Experiment 1. Thus, in Experiment 2, we recruited a new group of participants to complete an otherwise identical task, but without any threat of electric shock. All mention of shock was removed from the task. Of interest was whether the magnitude of value-driven attentional capture would differ from the magnitude observed in Experiment 1 where participants were sometimes under threat of shock.

2.2.1. Methods

2.2.1.1. Participants

Thirty-two participants (18 females), between the ages of 18 and 35, were recruited from the Texas A&M University community. All participants reported normal or corrected-to-normal visual acuity and normal color vision. All procedures were approved by the Texas A&M University Institutional Review Board and all study procedures were conducted in accordance with the principles expressed in the Declaration of Helsinki. Written informed consent was obtained for each participant.

2.2.1.2. Apparatus & Stimuli

The apparatus and stimuli were identical to Experiment 1, with the exception that the isolated linear stimulator was not used, and no shock-related images were presented.

2.2.1.3. Design & Procedure

The design and procedure were identical to Experiment 1, with the exception that the administration of electric shock and any references to electric shock, including in the instructions and images, were removed (see Figure 1C).

2.2.1.4. Data Analysis

Data were analyzed in the same manner as Experiment 1. Two participants were unable to be eye-tracked using our apparatus. Thus, 30 complete data sets were analyzed.

2.2.2. Results

A 2 x 2 ANOVA with distractor condition (present vs. absent) and experiment (Experiment 1 vs. Experiment 2) as factors was conducted over mean RT. We collapsed performance across “shock” and “no shock” blocks for Experiment 1 because there were no differences found between them. This ANOVA revealed a main effect of distractor condition, $F(1,63) = 12.06$, $p = 0.001$, $\eta^2 = 0.161$, but no effect of experiment, $F(1,63) = 2.40$, $p = 0.127$, or interaction, $F(1,63) = 1.85$, $p = 0.179$ (see Figure 3A). The same ANOVA conducted over oculomotor capture revealed a main effect of distractor condition, $F(1,63) = 34.60$, $p < 0.001$, $\eta^2 = 0.354$, and, critically, a significant interaction, $F(1,63) = 5.96$, $p = 0.017$, $\eta^2 = 0.086$. The main effect of experiment was not significant, $F(1,63) = 1.19$, $p = 0.175$ (see Figure 3B).

2.2.3. Discussion

In Experiment 2, we conducted the identical task as Experiment 1 but with no reference to electric shock. This allowed us to compare the magnitude of value-driven attentional capture between conditions with (Experiment 1) and without (Experiment 2) a threat manipulation. As in Experiment 1, robust value-driven attentional capture was observed, this time in both RT and eye movements. In addition, oculomotor capture was significantly greater in magnitude in Experiment 2 (as evidenced by the experiment by distractor condition interaction), indicating that the threat of shock generally suppressed attentional capture by previously reward-associated stimuli.

2.3. Experiment 3

In Experiment 1, we were unable to produce a within-subject effect of shock using the alternating block design. As previously discussed, we hypothesized that participants were unable to reduce their anxiety levels back to baseline in the no-shock blocks given the timeframe of block switches. Experiment 2 showed that the threat of shock was indeed having a significant effect on oculomotor capture, consistent with the idea that participants in Experiment 1 were completing the test phase under a global state of anxiety. Given the novelty of this finding, which contrasts with the effects of threat on the processing of physically salient stimuli (e.g., Esterman et al., 2013; Mather & Sutherland, 2011; Sutherland & Mather, 2012, 2015), we wanted to replicate and extend the evidence for this relationship. Therefore, in Experiment 3, we examined whether within-subject effects of anxiety on value-driven attentional capture would be evident when threat of shock was confined to a distinct epoch of the task, providing a clear boundary between threatening and non-threatening contexts. Instead of alternating blocks after 20 trials, we modified the design to have participants complete two otherwise identical implantations of the test phase in which the delivery of shock was and was not possible.

2.3.1. Methods

2.3.1.1. Participants

Thirty-two participants (18 females), between the ages of 18 and 35, were recruited from the Texas A&M University community. All participants reported normal or corrected-to-normal visual acuity and normal color vision. All procedures were approved by the Texas A&M University Institutional Review Board and all study procedures were conducted in accordance with the principles expressed in the Declaration of Helsinki. Written informed consent was obtained for each participant.

2.3.1.2. Apparatus & Stimuli

The apparatus and stimuli were identical to Experiment 1.

2.3.1.3. Design & Procedure

The design and procedure were similar to Experiment 1. However, we changed the design to have two training and test phases (see Figure 1D). Instead of an alternating block design of 20 trials, the test phase consisted of two blocks of 120 trials each, one with and one without the threat of shock (order counterbalanced between subjects). A training phase of 180 trials preceded each test phase. Such an alternating training-test design has been shown to have high test-retest reliability in measurements of value-driven attentional capture (Anderson & Kim, 2019). In addition, each participant was only connected to the isolated linear stimulator before the test phase of the “shock” block and was immediately disconnected from the device after completion of the "shock" block. After disconnecting the stimulator from the participant, they completed the post-task STAI state inventory before proceeding (in addition to at the beginning of the experiment).

2.3.1.4. Data Analysis

Data were analyzed in the same manner as Experiment 1, with the exception that the order of blocks (shock block first vs. no-shock block first) was included as a factor in the ANOVAs. Data from two participants were excluded from analyses because their accuracy was lower than 70% and two participants were unable to be eye-tracked using our apparatus. Thus, 28 complete data sets were analyzed.

2.3.2. Results

A 2 x 2 x 2 ANOVA with distractor condition (present vs. absent), block (shock vs. no shock), and order (shock block first vs. no-shock block first) as factors was conducted over mean RT. Unlike in Experiment 1, there was a significant main effect of distractor condition, $F(1,26) = 108.77$, $p < 0.001$, $\eta^2 = 0.807$. There was no main effect of block, $F(1,26) = 0.50$, $p = 0.485$, or order, $F(1,26) = 1.03$, $p = 0.321$. Importantly, there was a significant interaction between distractor condition and block, $F(1,26) = 4.35$, $p = 0.047$, $\eta^2 = 0.143$ (see Figure 4A), with attentional capture being reduced under threat of shock. A significant interaction was observed between block and the order of blocks, $F(1,26) = 11.20$, $p = 0.003$, $\eta^2 = 0.301$, reflecting the fact that participants were generally faster during the second block (regardless of whether that block involved shock of not). The order of blocks did not interact with distractor condition, $F(1,26) = 0.29$, $p = 0.593$, nor was the three-way interaction significant, $F(1,26) = 1.90$, $p = 0.18$.

The same ANOVA conducted over oculomotor capture revealed a main effect of distractor condition, $F(1,26) = 6.89$, $p = 0.015$, $\eta^2 = 0.21$. No other main effects or interactions were significant, *F*s < 1.7, *p*s > 0.2 (see Figure 4B). As in Experiment 1, state anxiety increased after the test phase of the shock block, $t(27) = 7.71$, $p < 0.001$, $d = 1.9$, confirming the anxiety-provoking nature of the threat-of-shock manipulation.

2.3.3. Discussion

In Experiment 3, we modified the design of Experiment 1 to facilitate assessment of the threat of electric shock within-subjects, separately training and then testing participants with and without the use of the isolated linear stimulator. Here, we found robust value-driven attentional capture and a significant effect of the threat manipulation on the response time measure, replicating reduced distractibility in a threatening context. The results provide converging evidence for the modulatory role of threat in reducing the magnitude of value-driven attentional capture.

In the present experiment, the measure of value-driven attentional capture sensitive to the threat manipulation was RT, which differs from Experiments 1-2 in which threat modulated oculomotor selection. Each of these measures have been consistently implicated in distraction by reward cues (e.g., Anderson et al., 2011, 2013, 2014; Anderson & Kim, 2019; Anderson & Yantis, 2012). In general, the RT cost associated with the distractor was also numerically much larger in Experiment 3 compared to the prior two experiments. The reason for this apparent discrepancy is unclear and reflects a limitation of the present study, although we do note that the implementation of the reward training, as well as the period over which attentional capture was measured both in relation to the threat manipulation and in relation to training, was quite different across experiments. Fewer trials of training preceded each epoch of the test phase in the present experiment, although the two total epochs of training resulted in more training trials overall. Given that each epoch of the test phase was only half as long as the test phase of Experiments 1-2, the test phase of Experiment 3 was likely less subject to extinction, which might explain the overall more robust attentional capture measured in this implementation. Any of these differences could have shifted the sensitivity of the paradigm to the effects of reward history on attention, although in each case some indication of attentional capture was significantly reduced under threat.

2.4. Experiments 4 & 5

Experiments 1-3 demonstrate reduced value-driven attentional capture under conditions of threat. This finding contrasts with previous demonstrations of increased attentional capture by physically salient stimuli in anxious individuals (Esterman et al., 2013; Moser et al., 2012) and more preferential processing of physically salient stimuli following induction of negative arousal (Mather & Sutherland, 2011; Sutherland & Mather, 2012, 2015). It is tempting to conclude that threat and anxiety influence value-driven and salience-driven attention differently, suppressing one while potentiating the other. However, it is unclear whether this is indeed the case, or whether a particular aspect of our experimental design led to fundamentally different results. To our knowledge, threat of shock has not been examined in the context of the additional singleton task (Theeuwes, 1992), which serves as the basis of our experimental paradigm.

Our goal here was to conceptually replicate findings supporting arousal-biased competition in the context of the processing of physically salient stimuli (Mather & Sutherland, 2011; Sutherland & Mather, 2012, 2015) and links between anxiety and increased attentional capture by physically salient stimuli (Esterman et al., 2013; Moser et al., 2012), but in the specific context of our visual search paradigm using a threat of shock manipulation. This would provide a more direct contrast to the findings of our prior experiments. Therefore, experiments 4 and 5 paralleled Experiments 1 and 2, but using physically salient color singleton distractors (see Theeuwes, 1992, 2010) in the absence of prior reward training. We hypothesized that threat of shock would magnify rather than suppress attentional capture by physically salient distractors, consistent with prior findings using different experimental tasks and different manipulations of threat and anxiety (Esterman et al., 2013; Moser et al., 2012). To maintain consistency with the prior experiments, we retained the rapid-switching block structure of Experiment 4 and anticipated the need for Experiment 5 to provide a comparison condition with no threat of shock. We chose this between-subjects manipulation of threat of shock, rather than the within-subjects approach adopted in Experiment 3, given that the interaction with threat was more robust in Experiments 1-2 and oculomotor indicators of attentional capture, including value-driven attentional capture, tend to have higher reliability as a dependent measure (Anderson & Kim, 2019).

2.4.1. Methods

2.4.1.1. Participants

Thirty-eight unique participants were recruited for both Experiment 4 and 5 (18 females and 20 females, respectively), between the ages of 18 and 35, from the Texas A&M University community. All participants reported normal or corrected-to-normal visual acuity and normal color vision. All procedures were approved by the Texas A&M University Institutional Review Board and all study procedures were conducted in accordance with the principles expressed in the Declaration of Helsinki. Written informed consent was obtained for each participant.

2.4.1.2. Apparatus & Stimuli

The apparatus was identical to Experiment 1. The stimuli were identical to Experiment 1 except for the colors of the shapes. On distractor-absent trials, all of the shapes were a single color (red or green, counterbalanced across participants). On distractor-present trials, one of the non-target shapes was shown in the other color (red or green), which constituted the physically salient distractor (see Figure 1E & 1F).

2.4.1.3. Design & Procedure

There were no training phases in Experiments 4 and 5. The design and procedure of Experiments 4 and 5 were identical to those corresponding to the test phase of Experiments 1 and 2, respectively.

2.4.1.4. Data Analysis

Data were analyzed in the same manner as Experiments 1 and 2. For Experiment 4, data from one participant was excluded because their accuracy was lower than 70%

for the task, two participants withdrew from the study prior to completion, one participant was unable to be eye-tracked using our apparatus, and data from one participant was identified as an outlier and removed from further analysis (capture score exceeded 2.5 SD of the mean). For Experiment 5, four participants were unable to be eye-tracked using our apparatus and data from one participant was identified as an outlier and removed from further analysis (using the same 2.5 SD criterion). Thus, 33 complete data sets were analyzed for each experiment.

2.4.2. Results

For Experiment 4, a 2 x 2 ANOVA with distractor condition (present vs. absent) and block (shock vs. no shock) as factors was conducted over mean RT. We found a main effect of distractor condition, $F(1,32) = 231.47$, $p < 0.001$, $\eta^2 = 0.879$, but there was no main effect of block, $F(1,32) = 1.38$, $p = 0.249$, and also no interaction, $F(1,32) = 1.85$, $p = 0.183$ (see Figure 5A). Post-hoc comparisons revealed that response times were significantly slower during distractor-present trials within both the shock block, $t(32) = 11.80$, $p < 0.001$, $d = 1.71$, and the no-shock block, $t(32) = 13.75$, $p < 0.001$, $d = 1.85$. The same ANOVA conducted over oculomotor capture revealed a main effect of distractor condition, $F(1,32) = 153.86$, $p < 0.001$, $\eta^2 = 0.828$, but there was neither a main effect of block, $F(1,32) = 0.06$, $p = 0.816$, nor an interaction $F(1,32) = 0.14$, $p = 0.708$ (see Figure 5B). Post-hoc comparisons revealed that there were significantly more saccades to the distractor compared to a non-target within both the shock block, $t(32) = 11.71$, $p < 0.001$, $d = 2.93$, and the no-shock block, $t(32) = 12.09$, $p < 0.001$, $d = 3.1$.

For Experiment 5, a 2 x 2 ANOVA with distractor condition (present vs. absent) and experiment (Experiment 4 vs. Experiment 5) as factors was conducted over mean RT. As in Experiment 2, we collapsed performance across “shock” and “no shock” blocks for Experiment 4 because there were no differences found between them. This ANOVA revealed a main effect of distractor condition, $F(1,64) = 446.75$, $p < 0.001$, $\eta^2 = 0.875$, but there was neither a main effect of experiment, $F(1,64) = 2.65$, $p = 0.108$, nor an interaction, $F(1,64) = 0.62$, $p = 0.433$ (see Figure 6A). The same ANOVA conducted over oculomotor capture revealed a main effect of distractor condition, $F(1,64) = 284.26$, $p < 0.001$, $\eta^2 = 0.816$. In addition, we found a marginal effect of experiment, $F(1,64) = 3.73$, $p = 0.058$, $\eta^2 = 0.055$, and a marginal interaction, $F(1,64) = 3.22$, $p = 0.078$, $\eta^2 = 0.048$. Importantly, this trend was in the opposite direction compared to our experiments of value-driven attentional capture (see Figure 6B), with capture being greater in magnitude during the experiment with threat of shock.

To statistically assess whether threat differentially modulates value-driven and salience-driven oculomotor capture, we conducted a follow-up 2 x 2 x 2 ANOVA with distractor condition (present vs. absent), presence of shock (shock vs. no shock), and type of distractor (valuable vs. physically salient) as factors and probed the three-way interaction. The three-way interaction was indeed significant, $F(1,127) = 6.79$, $p = 0.010$, $\eta^2 = 0.051$, confirming a significant difference in how threat modulates value-driven and salience-driven attentional capture.

2.4.3. Discussion

In Experiments 4 and 5, we examined how the threat of electric shock modulates attentional capture to physically salient stimuli in the additional singleton paradigm. We emulated the design and procedure of our experiments examining value-driven attentional capture (Experiments 1 and 2) but removed the training phase and replaced previously reward-associated distractors with physically salient color singleton distractors. We found a robust effect of the distractor for both RT and eye movements in Experiment 4, but again found no difference between blocks with and without the threat of shock in a rapid switching design. In anticipation of the anxiety “bleed-over” between blocks, we conducted Experiment 5 without the threat of shock to serve as a comparison condition (as in Experiment 2). A robust effect of the distractor was again observed in Experiment 5. Contrary to Experiments 1 and 2, however, the influence of shock on attentional capture trended in the opposite direction, with capture being greater in magnitude under threat of shock, consistent with arousal-biased competition (Mather & Sutherland, 2011; Sutherland & Mather, 2012, 2015). A significant three-way interaction across experiments confirmed that the impact of threat differently affects value-driven and salience-driven attentional capture; while the threat of shock suppressed attentional capture by previously reward-associated stimuli, it tended to increase attentional capture to the physical salience of objects.

2.5. General Discussion

In the present study, we used the value-driven attentional capture paradigm to assess the influence of threat-induced anxiety on attentional capture by reward-associated stimuli. We used the ToS paradigm to manipulate anxiety (Grillon et al., 2004). Experiments 1 and 2 demonstrated attenuated value-driven attentional capture when previously reward-associated stimuli are encountered in a threatening situation, and this basic pattern was replicated in Experiment 3. Changes in self-reported state anxiety confirmed the effectiveness of our threat of shock manipulation. On the other hand, in Experiments 4 and 5, threat of shock showed a trend towards *increasing* susceptibility to attentional capture by physically salient stimuli, consistent with prior reports (Esterman et al., 2013; Moser et al., 2012). Our findings reveal a striking dissociation in which the threat of electric shock suppresses oculomotor capture by reward cues, while increasing oculomotor capture by physically salient stimuli.

The threat of shock paradigm has reliably induced anxiety in both human and animal studies (see Davis et al., 2010, for a review). However, null effects of the threat of shock paradigm have also been reported in two different decision-making tasks utilizing a similar fast-alternating block design (Robinson et al., 2015; compare to Experiments 1 and 4 of the present study). Robinson et al. (2015) speculated that the threat of shock manipulation may not have been significant enough to elicit behavioral change; however, in the present study, between-experiment measures of oculomotor capture and a within-subject manipulation involving a longer epoch of no threat produced reliable effects of threat of shock. Therefore, we hypothesize that the null effect of threat within-subjects in Experiments 1 and 4 was due to the slow-dissipating nature of anxiety (Kalin & Shelton, 1989), which bled over into the no-shock blocks and produced a global state of anxiety. In utilizing the threat of shock paradigm, a fast-alternating block design may be suboptimal, and either a between-subjects manipulation or a manipulation involving an extended epoch with and without the threat of shock may be more robust.

Previous studies observing the effects of anxiety on attentional capture by physically salient stimuli have tended to find evidence for increased attentional capture (Esterman et al., 2013; Moser et al., 2012). These studies supported the theory that anxiety produces a vigilant state within an individual and results in heightened responsiveness to external events under threatening conditions (Armony & Dolan, 2002; Kalin & Shelton, 1989; Mogg & Bradley, 1999; Pourtois et al., 2004). The vigilance hypothesis of anxiety has also been supported in the context of attention to threatening facial expressions (Hahn & Gronlund, 2007; Sussman et al., 2016a, 2016b; Williams et al., 2005). Similarly, the arousal-biased competition hypothesis suggests that negative arousal enhances high-priority visual signals at the expense of less-salient signals, biasing perceptual processing more strongly in favor of physically salient stimuli (Mather & Sutherland, 2011). A state of heightened vigilance has also been shown to reduce errors in Go/No-Go tasks (Grillon et al., 2017), indicating that anxiety may be effective and beneficial in facilitating rapid and accurate information processing.

Previously reward-associated stimuli preferentially draw attention (e.g., Anderson et al., 2011), which is thought to in part reflect stronger signals evoked by previously reward-associated stimuli in the visual cortex (Anderson, 2016a, 2017; Anderson et al., 2014; Hickey & Peelen 2015, 2017). To the degree that such value-biased visual signals are processed in a similar fashion to differences in feature contrast, or to the degree that anxiety invokes a general tendency to monitor for unexpected visual events at the expense of goal-directed attention, more robust attentional capture by reward cues would be expected under conditions of threat. However, our results reveal the exact opposite pattern. We show that the processing of negative emotional information such as threat interacts with the ability of learned value to guide attention, aligning with the dual competition framework (Pessoa, 2009). This model proposes that task-irrelevant threat information competes for central processing resources with cognition, potentially impairing cognitive processes. Our findings are consistent with the idea that negative valence states interfere with value-based attentional guidance, competing for limited processing resources.

The nature of this hypothesized competition in the processing of emotionally valent information is unclear. Broadly, the processing of salient features of objects have been organized into an oculomotor control network, starting from neuronal activation in early visual areas V1 (Knierim & Vanessen, 1992) and V4 (Burrows & Moore, 2009) to later cortical areas such as the parietal cortex (Balan & Gottlieb, 2006), and the frontal eye field (Bichot & Schall, 1999; Moore et al., 2003; Thompson & Bichot, 2005), in addition to the superior colliculus (Fecteau, Bell, & Munoz, 2004). Likewise, value-driven attentional capture also recruits the early visual cortex, ventral visual cortex, and the posterior parietal cortex (Anderson, 2017; Anderson et al., 2014; Hickey & Peelen, 2015, 2017; Hopf et al., 2015; Serences, 2008). However, additional regions have been linked to value-driven attentional capture specifically, both in the basal ganglia (e.g., caudate tail; Anderson, 2016a, 2017; Anderson, Kuwabara, et al., 2016; Anderson et al., 2014; Kim & Hikosaka, 2013; Yamamoto et al., 2013) and in the limbic system (e.g., amygdala; Ousdal et al., 2014; Peck et al., 2013; Peck & Salzman, 2014). The processing of threat also recruits the amygdala (e.g., Cisler & Koster, 2010; Ohman, 2002, 2005). One possibility is that the reduced influence of reward associations on the control of attention under threat is a result of the competition between the processing of threat and value-dependent information processing within the limbic system and/or basal ganglia. Further consistent with this hypothesis, attention to emotional targets in a visual search task has been shown to activate both areas of the spatial attention network and the limbic system, including the amygdala (Mohanty et al., 2009). In addition, studies of non-human primates have identified projections from the basolateral amygdala to the caudate tail (Griggs et al., 2017), suggesting that amygdala-dependent processing and other regions involved in value-driven attention are interconnected.

An alternative possibility, not mutually exclusive with the prior, is that threat biases attention towards a more stimulus-driven mode of information processing in which salient external events more effectively drive selection. Learned value associations reflect internally generated bias signals, which may be generally suppressed when under threat. Interactions between different valence-dependent processing mechanisms in the control of attention are largely unexplored, and the present study suggests that this is an area of inquiry ripe for future investigation. The issue of the neural mechanisms underlying the influence of threat on value-driven attention will be returned to in Chapter 4.

Previously reward-associated stimuli have been consistently shown to compete effectively with a more physically salient target for attention under conditions without an explicit threat manipulation (e.g., Anderson et al., 2011, 2013, 2014; Anderson & Kim, 2019; Anderson & Yantis, 2012), suggesting that valuable stimuli have high attentional priority (Anderson, 2016a). In this sense, our findings suggest a limitation to the arousal-biased competition model of information processing (Mather & Sutherland, 2011; Sutherland & Mather, 2012, 2015). It seems not to be the case than any high-priority information is biased under states of negative arousal, as manipulated here via threat of shock. Rather, as outlined above, the kind of priority enhanced by threat and/or negative arousal may be restricted to stimulus-driven representations or might not translate to positively valanced representations.

In addition to supporting competition in the processing of reward and threat, our findings have other important theoretical implications. First, it is clear that value-driven attentional priority cannot be reduced to a change in the perceived salience of a stimulus at the sensory level. If this were the case, threat would be expected to influence attention to valuable stimuli and physically salient stimuli in the same manner, which is clearly inconsistent with our results. It seems more likely that distinctly valence-dependent representations contribute, at least in part, to the control of value-driven attention. In addition, our findings suggest that susceptibility to distraction is not a uniformly state-dependent phenomenon. Although the threat of shock creates an anxiety-induced state, this state of anxiety has a fundamentally different effect on the orienting of attention depending on the eliciting stimulus. That is, anxiety does not have general effect on distractibility that can be reduced to heightened vigilance, but rather, its effect appears to be contingent upon the nature of the distracting information. Future research might seek to investigate the influence of threat on other factors involved in the control of attentional control, such as selection history (Awh et al., 2012) and goal-contingent attentional capture (Folk et al., 1992).

The present study focused on the influence of threat on value-driven attention. The extent to which the competitive relationship observed in the present study is particular to value-driven attention, or the extent to which it reflects a broader principle of valence-dependent competition, is unclear. It is possible that the processing of negatively valenced information competes with the processing of positively valenced information more broadly, which would predict the same pattern of results for attention to aversively conditioned stimuli with and without a positive arousal manipulation. Another interesting question not addressed by the present study concerns the influence of threat on attention to aversively conditioned stimuli. Valence-dependent competition might predict enhanced attentional capture in this situation. Future research should explore these possibilities. Relatedly, it is unclear whether the observed pattern of results is particular to the influence of associative reward learning on attention, or whether attention to arguably more "hard-wired" positively valenced stimuli such as erotica (Most et al., 2005) would be similarly subject to threat-dependent suppression. Future research might also explore the influence of trial-by-trial modulations in threat and/or negative arousal on the capture of attention, potentially using pupil dilation or electrodermal activity (EDA) as an on-line indicator.

3. THE INFLUENCE OF THREAT ON THE EFFICIENCY OF GOAL-DIRECTED ATTENTIONAL CONTROL[2]

3.1. Introduction

In the previous chapter, I presented a series of experiments that examines how threat modulates the influence of reward history and physical salience on the allocation of attention. These findings raise an important question concerning the relationship between anxiety and goal-oriented attentional control. Findings relating anxiety to increased attentional processing of physically salient stimuli (Esterman et al., 2013; Moser et al., 2012) do not differentiate between enhanced distractor processing and decreased goal-directed attentional control. Attention might be preferentially deployed to physically salient stimuli because such stimuli are afforded greater attentional bias under threat, because goal-directed attention is less effective at suppressing the selection of such stimuli and enhancing the representation of potentially task-relevant stimuli that compete with salient stimuli for selection, or both. Furthermore, the findings of Chapter 2 indicate that it cannot be assumed that anxiety necessarily impairs goal-directed attentional control, and anxiety could potentially facilitate goal-directed attention via increased vigilance and arousal. Such facilitation could explain the reduced distraction under threat in that study, assuming that physically salient stimuli (but not reward cues)

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are special in their ability to bias attention under threat as might be predicted from the arousal-biased competition account (Mather & Sutherland, 2011). The manner in which anxiety influences the goal-directed control of attention therefore remains to be clarified.

In Chapter 3, we provide a direct test of the impact of anxiety on the efficiency of goal-directed attentional control. To this end, we employed a modified version of the Adaptive Choice Visual Search (ACVS) task developed by Irons and Leber (2016, 2018) that requires efficient environmental appraisal for performance maximization. To create an experimentally induced state of anxiety, we manipulated the threat of unpredictable electric shock (as in Chapter 2; see also, Schmitz & Grillon, 2012). If anxiety generally interferes with the goal-directed control of attention, visual search should be less efficient when under threat of electric shock, whereas if anxiety enhances the goal-directed control of attention, visual search should instead be more efficient under threat.

3.2. Methods

3.2.1. Participants

39 participants (27 females), between the ages of 18 and 35 inclusive (M = 19.1y, SD = 0.89y), were recruited from the Texas A&M University community. All participants were English-speaking, reported normal or corrected-to-normal visual acuity and normal color vision. All procedures were approved by the Texas A&M University Institutional Review Board and were conducted in accordance with the principles expressed in the Declaration of Helsinki. Written informed consent was obtained for each participant.

The sample size was informed by a power analysis. We estimated the effect size for detecting threat-dependent modulations in the control of attention from Experiment 3 of Chapter 2, which used the same threat-of-shock manipulation in a within-subjects design, which was $f = 0.408$. Using G*Power 3.1, a sample size of at least 18 participants would provide $\beta > 0.90$ at $\alpha = 0.05$ for a within-subjects test with two measurements (task performance under threat and no threat). We decided to obtain a final sample size (see Data Analysis) that matched the number of participants used in Experiment 3 of Chapter 2.

3.2.2. Apparatus

A Dell OptiPlex 7040 (Dell, Round Rock, TX, USA) equipped with Matlab software (Mathworks, Natick, MA, USA) and Psychophysics Toolbox extensions (Brainard, 1997) was used to present the stimuli on a Dell P2717H monitor. Responses were entered using a standard US-layout keyboard. The participants viewed the monitor from a distance of approximately 70 cm in a dimly lit room. Paired electrodes (EL500, BioPac Systems, Inc., Goleta, CA, USA) were attached to the left forearm of each participant, and electric shocks were delivered through an isolated linear stimulator under the constant current setting (STMISOLA, BioPac Systems), which was controlled by custom Matlab scripts.

3.2.3. Stimuli

Each trial consisted of a fixation display, the visual search display, and an inter-trial-interval (see Figure 7). The fixation display consisted of a box containing an image of either a lightning bolt (during the shock block) or a lightning bolt with a red hash over it (during the no-shock block) for 1000 ms. The visual search display was composed of

54 colored squares (each approximately 1.1° x 1.1° visual angle) arranged in three concentric rings around the center of the screen for 5500 ms. The inner (radius 7.3°), middle (radius 10.1°), and outer rings (radius 13.0°) were composed of 12, 18, and 24 squares, respectively, positioned equidistant from each other. Each search trial contained red, blue, and green color squares. Each square contained a digit between 2 and 9, subtending 0.4° x 0.4°. If no response was recorded within the given time limit, a feedback display was given displaying the words “Too Slow” for 1500 ms. Lastly, the inter-trial-interval displayed a blank screen for 1000 ms.

3.2.4. Design

We adapted the design of the ACVS task from Irons & Leber (2018) with a few modifications. In addition to 14 green squares, each trial contained either 13 red squares and 27 blue squares (red-optimal trials) or 27 red squares and 13 blue squares (blue-optimal trials). Participants were informed that one red and one blue square each contained a digit from 2 to 5 and that their task was to find and report one of these two target squares. That is, targets were defined by the combination of a color (red or blue) and a digit (2-5). Each trial contained both a red and blue target square, but only one of them had to be identified. The two digits used for targets on a given trial were always different from each other to allow the behavioral response to be diagnostic of which color target was found (e.g., 3 for red and 4 for blue). All other red and blue squares contained digits from 6 to 9. Green colored squares were irrelevant to the task and contained digits between 2 to 9 to prevent participants from searching based on digit identity without respect to color. All digits inside non-target squares were assigned randomly using the aforementioned constraints. Each target color (red or blue) would be the optimal (i.e., less numerous) target color for a length of 1, 2, 3, 4 or 5 trials, with each length occurring twice per target color per run. Each shock/no-shock block consisted of a total of 180 trials. After each run of 60 trials within a block, the participant was prompted to take a 20 second break. Which color began as the optimal color was fully counterbalanced, and the length of trials between switches in the optimal color was randomly selected without replacement from the aforementioned set of possibilities.

3.2.5. Procedure

All participants completed the state component of the State-Trait Anxiety Inventory (Ferreira & Murray, 1983) at the beginning of the experiment to assess baseline state anxiety. Next, participants practiced the ACVS task for 20 trials. All participants were given instructions on the ACVS task and were told to search through either the red or blue colored squares to find a target number on each trial. In addition, we emphasized the utility of searching through the less-prevalent target color (optimal strategy) on each trial to help ensure that baseline performance was moderately optimal, maximizing our ability to detect changes in optimality due to the threat manipulation; not emphasizing the presence of an optimal strategy can result in selection that is ~60% optimal (Irons & Leber, 2016), which would leave little room to detect a potential threat-related reduction in optimality. Responses were indicated by pressing the “Z”, “X”, “N”, and “M” keys for the digits 2 through 5, respectively. If participants did not choose the optimal target color at least 85% of the time during practice, the experimenter re-explained the task and the participant was required to redo the practice until meeting this minimum requirement.

Following practice, each participant completed both the shock and no-shock block, order counterbalanced. Before completing the shock block, each participant was connected to the isolated linear stimulator and a shock calibration procedure was conducted for each participant to achieve a level that was “unpleasant, but not painful” (e.g., Anderson & Britton, 2020; Kim & Anderson, 2020b). Following calibration, participants again completed the STAI-state questionnaire before completing the task to validate the anxiety-inducing nature of the threat of electric shock. During the shock block, participants were instructed that they would unpredictably receive periodic electric shocks over the course of the block. A shock was administered a total of nine times during each 60-trial run of the shock block, no fewer than two and no more than four times every 20 trials, and never consecutively without an intervening search trial. Each shock was delivered by inserting an additional “trial” in which, immediately following the fixation period, a 1000 ms blank screen occurred in place of the visual search task and a brief shock was administered (2 ms pulse at the calibrated intensity). To match the length and experience of the shock block, the no-shock block contained nine trials every run with the same blank screen but no shock. Following completion of the shock block, participants were disconnected from the stimulator and, if they completed the shock block first, given a short break to allow the anxiety-inducing nature of the stimulator to dissipate (see Chapter 2).

3.2.6. Data Analysis

We excluded data from participants who did not select the optimal target color significantly above chance level (selecting the optimal target on > 56.67% of trials, which corresponds to $p < 0.05$ via binomial test), reasoning that such participants would not be informative for the question of whether anxiety improves or impedes goal-directed attention if these participants were not influenced by the color manipulation. Such participants may have misunderstood the task or decided not to try to optimize performance as instructed. This exclusion resulted in 32 retained data sets which were ultimately analyzed in relation to the threat manipulation. Measures of interest were the probability of selecting the optimal target color and the probability of failing to find either target before the time limit expired, separately in the threat and no-threat blocks.

3.3. Results

State anxiety increased from the beginning of the experiment in anticipation of completing the shock block, $t(31) = 3.95$, $p < 0.001$, $d = 0.70$ ($M = 39.5$ vs. 32.3 for threat and no-threat blocks, respectively). Overall, participants robustly selected the optimal target color over the non-optimal target color during both the no-threat ($M = 80.4\%$, $SD = 9.7\%$) and threat blocks ($M = 85.1\%$, $SD = 7.9\%$). Missed trials occurred infrequently during both the no-threat ($M = 4.0\%$, $SD = 2.4\%$) and threat blocks ($M = 3.1\%$, $SD = 2.1\%$). Under threat, participants were significantly more optimal in their visual search, $t(31) = 3.43$, $p = 0.002$, $d = 0.61$, and also missed significantly fewer targets, $t(31) = -2.13$, $p = 0.041$, $d = 0.38$ (see Figure 8). The threat of shock did not cause participants to switch target colors more or less frequently overall, $t(31) = 0.46$, $p = 0.650$ ($M = 56.6$ vs. 57.3 times for threat and no-threat blocks, respectively). In addition, there were no differences in response time when searching for the optimal target under threat, *t*(31) = 0.474, *p* = 0.639 (*M* = 2507 ms vs. 2520 ms for threat and no-threat blocks, respectively).

To characterize whether the threat of shock improved the optimality of search immediately when the more prevalent color changed, we assessed performance on the trials where the optimal color switched and on the trials immediately prior to a switch (maximal opportunity to have adjusted to a change in the optimal target color). We found that the threat of shock improved performance immediately following a switch of the optimal target color, *t*(31) = 2.88, *p* = 0.007, *d* = 0.51, whereas performance ceased to differ by the trial preceding the next optimal color switch, *t*(31) = 1.48, *p* = 0.149. Similarly, we evaluated the frequency of switches in the found target color when the optimal color changed. We only included trials on which participants found the optimal color immediately preceding a switch in the optimal color, such that a switch in the target color found would reflect optimal performance. On trials immediately following a switch in the optimal color, participants were more likely to switch which target color they found under threat compared to no threat, *t*(31) = 3.13, *p* = 0.004, *d* = 0.55, whereas the likelihood of having switched was generally higher and ceased to significantly differ by the 5th trial following the switch, *t*(31)= 0.43, *p* = 0.670 (Figure 9).

3.4. Discussion

In the present study, we used the ACVS task (Irons & Leber, 2016, 2018) to assess the influence of threat-induced anxiety on the efficiency of goal-directed attentional control. The threat of unpredictable electric shock improved the frequency with which participants optimally allocated their attention to potential targets in a demanding visual search task. The experience of threat was additionally associated with fewer missed targets, further consistent with more efficient goal-directed attention. The beneficial impact of threat on attention was evident immediately following a change in the optimal target color. That is, under threat, participants were less likely to miss an opportunity to adjust their search goals to maximize performance. Altogether, goal-directed attentional control was facilitated by our threat manipulation.

One interpretation of these findings is that threat specifically enhanced the ability to appraise the environment and update search goals when task considerations changed. On the other hand, Irons & Leber (2018) argue that performance in the ACVS task is unrelated to one's attentional control ability per se but rather reflects the "strategic use" of attentional control. Although participants were instructed and trained to search optimally in our experiment, a second possibility is that participants were similarly capable of goal-directed attentional control with and without the threat of shock but were more willing or motivated to engage the optimal strategy under threat. These two possible mechanisms by which threat might be facilitating goal-directed attentional control are not mutually exclusive, and further research will be necessary to parse between them.

Prior studies evaluating the effects of experimentally induced anxiety on information processing have demonstrated at times conflicting results. Similar to the results found in the present study, threat-induced anxiety has been linked to improvements in cognitive processes such as assessing risk in decision-making and navigating ability (Clark et al., 2012; Cornwell et al., 2012). On the other hand, studies have also demonstrated impaired cognitive control as well as null effects from experimentally induced anxiety (Gillan et al., 2019; Robinson et al., 2013; Yang et al., 2018). Eysenck et al. (2007) proposed the Attentional Control Theory which postulates that anxiety devotes excessive resources to the detection of potential threat and "impairs efficient functioning of the goal-directed attentional system" (p. 336). However, the present study and recent studies such as those previously described demonstrate that the type of cognitive task and the processing mechanisms recruited by the task may determine the modulatory influence of threat. We examined the efficiency of goal-directed attention in visual search specifically and found evidence for an anxiety-related improvement, suggesting that although anxiety may impair certain cognitive functions, the ability to modulate the control of attention in a changing environment is in fact facilitated, perhaps owing to the importance of goal-contingent sensory information processing to adaptive behavior and survival.

In the context of other studies manipulating anxiety via threat of shock, at times divergent patterns of results have been observed with anxiety both facilitating and hindering performance under different task conditions (e.g., Cornwell et al., 2012; Grillon & Charney, 2011; Grillon, 2008; Hu et al., 2012; Lindstrom & Bohlin, 2012; Miu et al., 2008; Robinson et al., 2011, 2013; Vytal et al., 2013; Yang et al., 2018). Although the reasons for these discrepancies in the literature remain to be clarified, we note that our visual search task was low in working memory and cognitive demand and would benefit from more effective filtering of task-irrelevant information once an attentional strategy has been selected (restricting attention to the optimal color until the target is found), which is consistent with both dual competition (Pessoa, 2009) and attentional narrowing accounts (e.g., Easterbrook, 1959). We also note that the degree of anxiety may play a role, such that manipulations resulting in more pronounced anxiety could potentially impair performance in our task, consistent with the Yerkes-Dodson Law (Yerkes & Dodson, 1908); however, the threat of shock as manipulated in our experiment is a common approach in the study of anxiety, with the same threat-of-shock manipulation producing increased distraction by physically salient stimuli but reduced distraction by previously reward-associated stimuli (Chapter 2), leaving it an open question how such anxiety influences the goal-directed control of attention to which our study speaks.

It is important to note that the paradigm we used, the ACVS paradigm, specifically probed the efficiency of goal-directed attention in a dynamically changing environment, requiring vigilant monitoring of the visual field for changes in the complexion of the objects presented. This form of goal-directed attentional control may be especially facilitated by a state of anxiety, and a similar manipulation of anxiety-inducing threat might result in a different pattern of performance in a more sustained goal-directed attention task. Future research should examine the modulatory influence of threat-induced anxiety across a range of different goal-directed attention tasks to obtain a more complete picture of the manner in which anxiety influences the attention system.

Our findings have important implications for theories linking anxiety and negative arousal to the attentional processing of physically salient but affectively neutral stimuli (Esterman et al., 2013; Moser et al., 2012; Sutherland & Mather, 2012, 2015).

The present study suggests that such preferential processing of salient stimuli likely reflects greater attentional priority afforded to salient stimuli directly and specifically, rather than an indirect increase in the processing of salient stimuli due to less efficient goal-directed attentional modulation (i.e., a reduced ability to suppress salient signals and/or bias attention in favor of less salient but potentially relevant stimuli that compete for attention), as predicted by theories of arousal-biased competition (Mather & Sutherland, 2011). Our findings also lend insight into the seemingly paradoxical findings of Chapter 2 in which attentional capture by previously reward-associated stimuli was reduced under threat. The results of that study were interpreted as reflecting the consequence of competition between the processing of threat and reward. In addition to this potential explanation, to the degree to which arousal-biased competition is particular to physically salient stimuli rather than any stimulus that evokes a stronger response than competitors in an attentional priority map, the reduced attentional capture observed in Chapter 2 may reflect an anxiety-related increase in the efficiency of goal-directed attention that led to reduced distraction by reward cues.

4. AROUSAL-BIASED COMPETITION EXPLAINS REDUCED DISTRACTION BY REWARD CUES UNDER THREAT[3]

4.1. Introduction

The two prior chapters investigate how threat modulates both attentional capture and the efficiency of goal-directed attention allocation. Specifically, it was found that the threat of random, unpredictable electric shock increases susceptibility to attentional capture by physically salient stimuli (Chapter 2) and increases the efficiency of visual search in a goal-directed attention task (Chapter 3). The former of these findings is consistent with previous experiments investigating individuals with high trait-anxiety (Esterman et al., 2013; Moser et al., 2012) and the principle of arousal-biased competition by which negative arousal (heightened arousal evoked by a negatively-valenced event or state) biases attention more strongly toward already high-priority stimuli (Lee et al., 2012, 2014; Sutherland & Mather, 2012, 2015), and the latter of these findings suggests that elevated attentional priority under threat is not the product of less efficient goal-directed attention. In contrast, threat of shock was found to reduce attentional capture by previously reward-associated stimuli (Chapter 2). These findings indicate that there may be a fundamental mechanistic difference in how anxiety

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modulates different attention networks, with enhanced processing of physically salient stimuli but blunted processing of reward-related stimuli.

In this chapter, I will present a functional magnetic resonance imaging (fMRI) study that probes the modulatory influence of threat on the neural representation of former targets that were previously associated with reward. Participants first completed a training phase in which a color-defined target was paired with high reward. In the subsequent test phase, we measured the influence of this training on eye movements and stimulus-evoked responses in the brain, both with and without the concurrent threat of shock. We hypothesized an interaction in behavior by which oculomotor capture by the previously reward-associated former-target (distractor) is reduced under threat of shock, replicating previous results (Chapter 2). Also consistent with prior results, we predicted elevated distractor-evoked responses in regions of the brain previously linked to value-driven attention, including the value-driven attention network (VDAN): extrastriate visual cortex, frontal eye field (FEF), intraparietal sulcus (IPS), and caudate tail (Anderson, 2017; Anderson et al., 2014, 2017; Kim & Anderson, 2020a), in addition to the insula (Wang et al., 2015), ventral striatum (Meffert et al., 2018), and amygdala (Peck & Salzman, 2014; Ousdal et al., 2014). We further hypothesized that the threat of shock would be associated with increased stimulus-evoked responses in these regions, reflecting a global effect of arousal on visual information processing. Of particular interest in the present study was the interaction between distractor-evoked neural responses and threat. The Dual Competition framework (Pessoa, 2009) predicts reduced distractor-evoked responses under threat, mirroring the hypothesized pattern in behavior.

In contrast, the Arousal-Biased Competition model (Mather & Sutherland, 2011) predicts elevated distractor-evoked activity under threat, consistent with the influence of negative arousal on the processing of physically salient stimuli (Lee et al., 2014). Given the intuitive fit between the Dual Competition framework (Pessoa, 2009) and previously observed behavioral results (Chapter 2), we hypothesized reduced distractor-evoked responses under threat.

4.2. Methods

4.2.1. Participants

Forty-one participants were recruited from the university community. All participants were English-speaking and reported normal or corrected-to-normal visual acuity and normal color vision. Four participants withdrew from the experiment before completing the brain scans and one participant was not scanned because they did not meet the performance criteria for the behavioral task during their initial in-lab visit. Thus, thirty-six participants were fully scanned (18 female, ages 18-35 [M=22.9y, SD = 4.33y]), and eye-tracking data was collected from 27 of these participants (due to eye-tracker availability and technical difficulties in the scanning environment).

4.2.2. Task Procedure

Participants were scheduled for an initial in-lab visit for 1 hour and each eligible participant underwent fMRI in a single 1.5 hour session at the scan-center on the following day. During their initial appointment, participants came into the lab for consenting, MRI safety screening, screening for adequate performance on the behavioral tasks, and familiarization with the shock delivery protocol. Participants first completed the test phase task once under the threat of shock (to familiarize them with the task procedure without interfering with prior learning) and then the training phase task three times to establish learning of the stimulus-reward associations. During the fMRI session, participants completed two runs of the training phase and the test phase, an anatomical scan, and an additional two runs of the training phase and the test phase. One pair of test phase runs was performed under threat of shock (see *Design*) and is referred to as the *threat block*. Two runs of reward training were completed prior to each block of the test phase to mitigate possible extinction effects between the two blocks. Before entering the scanner, participants underwent a shock calibration procedure to achieve a level of shock that is “unpleasant, but not painful” (e.g., Anderson & Britton, 2019; Chapters 2 and 3) and were then disconnected from the shock device. Participants were reconnected to the shock device before beginning the test phase of the threat block and were immediately disconnected from the device after completion of the threat block. The anatomical scan was inserted after the first test phase to allow for the anxiety-inducing nature of the shock device to dissipate in participants who completed the threat block first, as seen in within-subject designs of the ToS paradigm (Chapter 2). Participants were compensated the total monetary reward accumulated at the end of the last training phase or the combined amount of $10/hr spent in the initial appointment session and $20/hr spent in the fMRI session, whichever amount was higher.

4.2.3. Apparatus

During the initial in-lab visit, all tasks were completed on a Dell OptiPlex 7040 computer (Dell, Round Rock, TX, USA) equipped with Matlab software (Mathworks, Natick, MA, USA), and Psychophysics Toolbox extensions (Brainard, 1997). Stimuli were presented on a Dell P2717H monitor. The participants viewed the monitor from a distance of approximately 70 cm in a dimly lit room. Paired electrodes (BioPac Systems, Inc., Goleta, CA, USA) were attached to the left forearm of each participant, and electric shocks were delivered through an isolated linear stimulator under the constant current setting (STMISOLA, BioPac Systems), which were controlled by custom Matlab scripts.

For the fMRI portion of the experiment, stimulus presentation was controlled by an Invivo SensaVue display system. The eye-to-screen distance was approximately 125 cm. Key responses were entered using Cedrus Lumina two-button response pads. MRI-compatible electrodes (BioPac Systems) were attached to the left ankle of each participant, and electric shocks was delivered through an STM100C controlled by an MP160 system (BioPac Systems) triggered by custom Matlab scripts via parallel port interface. An EyeLink 1000 Plus system was used to track eye position (SR Research Ltd.).

4.2.4. Design

We adopted the design of Experiment 3 of Chapter 2 with modifications for fMRI. Both the training and test phases were split into two runs, with each run consisting of 60 trials. In the test phase, the order of threat block first or no-threat block first was counterbalanced across participants. In each run of the threat block, participants were shocked 2, 3, or 4 times every 20 trials (order randomized) for a total of 9 times during the entire run. The pattern of shocks administered in the threat block across trials was pseudo-randomly determined with the constraint that shocks were never administered on consecutive trials nor on the last trial of a run. At the end of the experiment, participants were paid the total monetary reward obtained during the training phase (spanning both the in-lab and in-scanner portions of the experiment).

4.2.5. Training Phase

In the training phase, each trial began with a fixation display (1800 ms), followed by a search array (1200 ms), an inter-stimulus-interval (ISI) consisting of a fixation cross, a reward feedback display (1500 ms), and an inter-trial-interval (ITI) (see Figure 10). The fixation display consisted of a fixation cross (0.7° x 0.7° visual angle) at the center of the screen. The search array consisted of six colored circles, three on each side of the display. During the search array, participants were instructed to search for a target circle that was unpredictably red or green (each target color appeared equally-often) and report the identity of the letter inside of the target as X or V using the response pad. Letters inside the non-targets were randomly assigned from the pool of H, Y, L, N, and K (without replacement). The letter-report procedure was used to require foveation of the target (see Theeuwes et al., 1998, 1999), as not all participants could be tracked with the eye tracker, precluding the use of an explicitly gaze-contingent task (in which the only response was an eye movement) as in Chapter 2. Each target color appeared at every position equally-often across trials and the order of trials was randomized for each run. Each circle in the search array was 4.5° visual angle in diameter. Stimuli located on the left and right sides were 8.2° (upper and lower positions) and 10.6° (center positions) visual angle from the meridian. Vertically, stimuli appearing in the upper and lower positions were 8.2° visual angle above and below the horizontal equator. The colors of the non-targets were drawn from the set [blue, cyan, pink, orange, yellow, white] without replacement. The ISI lasted for 600, 1200, or 1800 ms (equally-often). For each participant, one of the color targets (counterbalanced) would yield a monetary reward of 25¢ on 80% of trials and 5¢ on 20% of trials (high-value target); the other color target would yield 5¢ on 80% of trials and 25¢ on 20% of trials (low-value target). Lastly, the ITI lasted for 900, 2700, or 4500 ms (exponentially distributed with the shortest time being the most frequent). The fixation cross disappeared for the last 200 ms of the ITI to indicate to the participant that the next trial was about to begin.

4.2.6. Test Phase

In the test phase, each trial began with a fixation display (1800 ms), followed by a search array (1800 ms) and an ITI (see Figure 10). The fixation display was identical to that of the training phase. During the search array, participants looked for the uniquely shaped target and performed the same letter-judgment task on the target. The color of the shapes was irrelevant to the task. On half of the trials, one of the non-target shapes was rendered in the color of the former high-value target during the training phase (referred to as the distractor). The other half of trials did not contain either of the prior target colors from training (distractor-absent trials); the low-value color did not appear during the test phase in order to maximize the trials-per-cell in the factorial design (as in Kim & Anderson, 2020a). The target was equally-often a diamond among circles and a circle among diamonds and was never red or green. The target appeared on each side of the screen equally-often for both distractor-present and distractor-absent trials, and on distractor-present trials the side of the distractor was unbiased with respect to the side of the target (2/5 same side, 3/5 opposite side, corresponding to five stimulus positions not occupied by the target). The size and positions of the stimuli were identical to the training phase, as was the set of non-target colors used. Lastly, the ITI lasted for 600, 2400, or 4200 ms (equally-often). The fixation cross disappeared for the last 200 ms of the ITI to indicate to the participant that the next trial was about to begin. On trials in which a shock was delivered, an additional “pseudo-trial” was inserted, and shock was administered after the fixation display in place of the search array, followed by the ITI. In the no-threat block, pseudo-trials were also included but without shock administration in order to maintain the timing and flow of the trials across blocks.

4.2.7. Eye-tracking

During the fMRI scan, head position was restricted using foam padding within the head coil, and eye-tracking was conducted using the reflection of the participant's face on the mirror attached to the head coil. Eye position was calibrated prior to each run of trials using 9-point calibration (Anderson & Yantis, 2012), and was manually drift corrected by the experimenter as necessary during the fixation display. As the modulatory influence of threat on attentional capture by previously reward-associated stimuli was previously observed in distractor-evoked eye movements (Chapter 2), we sought to replicate this behavioral effect by measuring eye position in the present study.

4.2.8. Analysis of Eye-tracking Data

Following each run, recorded fixation events were analyzed off-line using custom MATLAB scripts. Fixations within a 6.3° window centered on and extending beyond the boundary of a stimulus, made during the period of time that the search array was on the screen, were attributed to that stimulus. The window size was chosen to roughly maximize the margin for error in measured eye position without creating ambiguity in which stimulus was fixated. Fixations were analyzed using the output file from the EyeLink host computer, in which saccades were defined as occurring when velocity exceeded 35°/s and acceleration exceeded 9,500°/s^2 (see, e.g., Anderson & Yantis, 2012). We measured which of the six shape stimuli in the test phase was initially fixated on each trial (i.e., the first of the six stimuli fixated). Oculomotor capture was determined by comparing the probability of initially fixating the high-value distractor (number of trials on which the high-value distractor was fixated / all trials on which a high-value distractor appeared) compared to the average of other non-target stimuli (i.e., corrected for the number of non-targets present in the display). We focused our analyses on oculomotor capture, rather than saccadic reaction time (RT), given its superior reliability (Anderson & Kim, 2019) and its relation to threat-based modulation in prior research (Chapter 2).

The influence of threat on oculomotor capture was assessed by means of a 2 x 2 analysis of variance (ANOVA) with reward association (high-value distractor vs. other non-target) and block (threat vs. no threat) as factors. In the event of the hypothesized interaction, the nature of the interaction would be probed by comparing eye movements across blocks separately for the high-value distractor and other non-targets, to determine whether threat-related changes in fixations were specific to fixations on the high-value distractor or whether the accuracy of eye movements was affected more broadly (including eye movements to non-targets other than the high-value distractor).

Lastly, to verify whether our threat-of-shock modulation induced a state of heightened negative arousal in the threat block as intended, we compared pupil size between the threat and no-threat blocks as an indicator of arousal (Bradley et. al, 2008; Nassar et. al., 2012). Specifically, mean pupil size was measured during the 1800 ms fixation period at the beginning of each trial, averaged across all trials separately for each block, and then compared between blocks using Student's t-test. Furthermore, we correlated the difference in mean pupil size between blocks with the interaction term corresponding to oculomotor capture (difference in the difference scores from the above 2 x 2 ANOVA) to determine whether the magnitude of negative arousal as measured from pupil size was related to the influence of threat on oculomotor capture.

4.2.9. MRI Data Acquisition

Images were acquired using a Siemens 3-Tesla MAGNETOM Verio scanner with a 32-channel head coil. High-resolution whole-brain anatomical images were acquired using a T1-weighted magnetization prepared rapid gradient echo (MPRAGE) pulse sequence [150 coronal slices, voxel size = 1 mm isotropic, repetition time (TR) = 7.9 ms, echo time (TE) = 3.65 ms, flip angle = 8°]. Whole-brain functional images were acquired using a $T2^*$-weighted echo planar imaging (EPI) multi-band pulse sequence [56 axial slices, TR = 600 ms, TE = 29 ms, flip angle = 52°, image matrix = 96 x 96, field of view = 240 mm, slice thickness = 2.5mm with no gap]. Each EPI pulse sequence began with dummy pulses to allow the MR signal to reach steady state and concluded with an additional 6 sec blank epoch. Each run of the training phase lasted 504 sec and each run of the test phase (for both the threat and no-threat block) lasted 428.4 sec (including dummy pulses).

4.2.10. MRI Data Analyses

4.2.10.1. Preprocessing

All preprocessing was conducted using the AFNI software package (Cox, 1996). Each EPI run for each participant was motion corrected using 3dvolreg, utilizing the first image following the anatomical scan as a reference. The anatomical image was skull-stripped using 3dskullstrip and non-linearly registered to the Talairach brain (Talairach & Tournoux, 1988) using auto_warp.py. EPI images were coregistered to the corresponding anatomical image for each participant using align_epi_anat.py, and the EPI then converted to percent signal change normalized to the mean of each run. Lastly, EPI images were non-linearly warped to the Talairach brain by applying the warp parameters from the anatomical image using 3dQwarp, and then spatially smoothed to a resulting 5 mm full-width half-maximum smoothness using 3dBlurToFWHM.

4.2.10.2. Statistical Analyses

All statistical analyses were performed using the AFNI software package (Cox, 1996). We used a general linear model (GLM) approach to analyze the test phase data. The test phase was split into the threat and no-threat blocks and a separate GLM was conducted on each. Each GLM included the following task-based regressors: (1) target on left, distractor on same side, (2) target on left, distractor on opposite side, (3) target on right, distractor on same side, (4) target on right, distractor on opposite side, (5) target on left, no distractor, and (6) target on right, no distractor. The hemifield in which the stimuli appeared was included in the model in keeping with prior studies of value-driven attention, as some distractor-evoked activity is known to be modulated by this factor (e.g., Anderson, 2019; Anderson et al., 2014; Kim & Anderson, 2020a). Experience of shock (or the absence of shock on pseudo trials in the no-threat block) was included as a regressor of non-interest. Each of these regressors was modeled using 16 finite impulse response functions (FIRs), beginning at stimulus onset. Six degrees of head motion and drift in the scanner signal were modeled using nuisance regressors. Trials in which the participant failed to make a motor response were excluded from the analyses.

The peak beta value for each task-based regressor from 3-6 sec post stimulus presentation was extracted (Kim & Anderson, 2020a). We first looked for regions sensitive to both the reward and the threat manipulation, which would serve as candidate regions for threat-based modulation of distractor processing. To this end, we computed the intersection of the effects of distractor condition and threat. The main effect of threat was determined by contrasting task-based regressors corresponding to the threat vs. no-threat blocks. The effect of distractor condition was determined separately for each combination of distractor and target position with the effect of target position factored out. Specifically, we contrasted task-based regressors (a) 1 vs. 5, (b) 2 vs. 5, (c) 3 vs. 6, and (d) 4 vs. 6, collapsing across regressors corresponding to threat and no-threat blocks. This was done to preserve information about the position of the distractor, which is known to affect neural responses in the visual system (Anderson, 2017, 2019; Anderson et al., 2014; Kim & Anderson, 2020a). The results from each contrast were corrected for multiple comparisons using the AFNI program 3dClustSim, with the smoothness of the data estimated using the ACF method (clusterwise $\alpha < 0.05$, voxelwise $p < 0.005$). Significant clusters of activation for each individual contrast were identified, and regions of overlap between each distractor contrast and the main effect of threat were determined (intersection of the respective activation maps), and then collapsed across the four contrasts to determine the entire extent of overlap.

Next, we probed for interactions between distractor condition and threat within regions identified in the prior analysis (i.e., clusters of voxels in which both an effect of distractor and threat were identified) using a region of interest (ROI) approach, which served as our primary analysis of interest that would discriminate between the competing predictions outlined in the **Introduction**. Since the regions of the VDAN are well-established to play an integrated role in the value-driven control of attention (Anderson, 2017, 2019; Anderson et al., 2014, 2017; Kim & Anderson, 2020a), we planned *a priori* to collapse across any regions identified within this network for this analysis and, along with any of the other regions previously implicated in value-driven attention as outlined in our hypothesis (see **Introduction**), apply Bonferroni correction for multiple comparisons. We used an ROI approach with a leave-one-subject-out procedure to preserve independence (Esterman et al., 2010) so that we could extract conditional means (as in, e.g., Anderson et al., 2016) to examine the specific nature of the interaction (i.e., assess directionality). To this end, we extracted per-region conditional means from distractor-present and distractor-absent trials, separately for the threat and no-threat blocks using the AFNI program 3dmaskave, and then computed the interaction term for these conditional means via a 2 x 2 within-subjects ANOVA (computed in SPSS). This interaction analysis focused specifically on distractor-present trials where the target and distractor were presented in opposite hemifields (task-based regressors 2 and 4), to better isolate task-irrelevant information processing in keeping with prior studies on the neural correlates of value-driven attention (Anderson, 2017; Anderson et al., 2014).

Finally, to assess potential links between the behavioral effect of threat on distractor-evoked eye movements and brain activation, we entered the difference between the frequency of fixations on the critical distractor in no-threat and threat blocks as a covariate in a contrast comparing activation on distractor-present trials (collapsing across the four combinations of target and distractor position) between the no-threat and threat blocks. The interaction between distractor condition and the covariate was set up such that a significantly positive relationship would indicate that more blunted oculomotor capture by threat was associated with more reduced distractor-evoked activity under threat and a significantly negative relationship would indicate the opposite. This covariate analysis was corrected for multiple comparisons at the cluster level in the same manner as the other contrasts as described above.

4.3. Results

4.3.1. Behavior

During the training phase, eye movements were recorded to one of the six shape stimuli on 90.2% of trials (SD = 10.4%). On trials in which a fixation was made and the high-value color was the target, first fixations to the target were made 58.7% of the time (SD = 17.3%) and on low-value target trials, first fixations to the target were made

58.6% of the time (SD = 14.6%). The likelihood of the first fixation falling on the target did not differ with respect to target value, $t(26) = 0.11$, $p = 0.910$.

During the test phase, eye movements were recorded on 82.0% of trials (SD = 15.1%). During the threat block, first fixations to the distractor and non-target shapes occurred on average 17.3% (SD = 7.6%) and 10.3% (SD = 4.6%) of trials, respectively. During the no-threat block, first fixations to the distractor and non-target shapes occurred on average 20.7% (SD = 10.3%) and 10.1% (SD = 4.4%) of trials, respectively. There was a significant main effect of reward association, $F(1,26) = 25.03$, $p < 0.001$, $\eta^2 = 0.490$, main effect of block, $F(1,26) = 5.09$, $p = 0.033$, $\eta^2 = 0.164$, and interaction between reward association and block with attentional capture being reduced under threat of shock, $F(1,26) = 4.94$, $p = 0.035$, $\eta^2 = 0.160$ (see Figure 11), replicating the pattern of performance observed in Chapter 2. Probing the interaction, fixations on the critical distractor differed between the threat and no-threat block, $t(26) = 2.32$, $p = 0.029$, $d = 0.45$, but fixations on non-targets did not, $t(26) = -0.50$, $p = 0.624$.

4.3.2. Pupil Size

Measured pupil size was larger during the fixation period leading up to presentation of the stimulus array in the threat compared to the no-threat block, $t(26) = 2.56$, $p = 0.016$, $d = 0.49$, confirming the arousing nature of the threat manipulation. The correlation between this threat effect and the interaction term from the ANOVA on fixations was marginally significant, $r = 0.331$, $p = 0.09$.

4.3.3. Neuroimaging

First, we were interested in regions in which stimulus processing was sensitive to both the distractor and the threat manipulation. To this end, we computed the intersection of the effect of distractor and threat (see **Materials and Methods**). Each of the hypothesized regions were identified in this analysis, including the extrastriate visual cortex, FEF, IPS, and caudate tail (collectively, the VDAN), in addition to the insula, ventral striatum, and amygdala (see Figure 12 and 12-1).

We next tested for an interaction between value (distractor condition) and block within the aforementioned regions, which served as ROIs in a follow-up contrast (see Materials and Methods). First, focusing specifically on the regions of the VDAN, the interaction was significant, $F(1,35) = 8.74$, $p = 0.006$, $\eta^2 = 0.200$, which was sufficiently robust to pass correction for multiple comparisons (see Materials and Methods). Further probe of the interaction within the VDAN revealed that the interaction was individually significant within each region of the VDAN, attesting to the assumption that they form an integrated network (see Table 4.1 below). Surprisingly, the direction of this interaction was opposite that of the behavioral interaction, with the distractor evoking stronger activation under threat in each individual region (see Figure 13). No reliable interaction was evident in the insula or ventral striatum/amygdala (which formed one contiguous cluster; see Table 4.1 below). As a covariate (see Materials and Methods), the reduction in distractor fixations in the threat block was associated with reduced distractor-evoked activation under threat in the orbitofrontal and visual cortex, in addition to increased distractor-evoked activation under threat in the dorsolateral prefrontal and anterior cingulate cortex (Figure 14).

Table 4.1 Interaction Effect Between Threat and Reward-associated Distractor for Main ANOVA Contrast Conducted Over Voxel Activation in each ROI.

Regions of Interest	***F***	***p***	η^2
Visual Cortex	4.249	0.047	0.108
Frontal Eye Fields	9.980	0.003	0.222
Intraparietal Sulcus	6.985	0.012	0.166
Caudate Tail	8.041	0.008	0.187
Insula	0.370	0.547	0.010
Ventral Striatum + Amygdala	0.645	0.428	0.019

4.4. Discussion

In the present study, we used the value-driven attentional capture (VDAC) paradigm (Anderson et al., 2011) combined with a threat-of-shock manipulation (e.g., Davis et al., 2010; Schmitz & Grillon, 2012) to determine the neural mechanisms of reduced attentional capture by reward-associated stimuli under conditions of experimentally-induced anxiety. As in Chapter 2, our behavioral results reveal reduced oculomotor capture by previously reward-associated distractors under threat, and our neuroimaging data replicate the neural correlates of VDAC throughout the VDAN, including the extrastriate visual cortex, IPS, FEF, and caudate tail (Anderson, 2017, 2019; Anderson et al., 2014, 2016, 2017; Hickey & Peelen, 2015; Kim, & Anderson, 2020a). We also observed elevated stimulus-evoked activity under threat, consistent with enhanced sensory processing due to negative arousal. Surprisingly, we additionally observed an interaction within the VDAN whereby reward-associated distractors evoked particularly elevated responses under threat. Stronger effects of threat on distractor-evoked eye movements were associated with a more pronounced reduction in distractor-evoked activity in the orbitofrontal and visual cortex and a more pronounced increase in distractor-evoked activity in the frontal cortex, potentially reflecting a threat-related modulation of stimulus-evoked activity (Anderson, 2017, 2019; Anderson et al., 2014; O'Doherty, 2004) and cognitive control (Chao & Knight, 1995; Corbetta et al., 2008; Ochsner & Gross, 2005; Sanchez-Lopez et al., 2018), respectively. These findings suggest that reduced distractibility by reward cues under threat, as measured from behavior (eye movements), is not due to competition between positive and negative valence for limited information-processing resources, which would have predicted the opposite pattern, but are rather more aligned with the framework of Arousal-Biased Competition (ABC; Mather & Sutherland, 2011).

The ABC model is derived from theories of biased competition (Desimone & Duncan, 1995; Itti & Koch, 2000) and postulates that negative arousal biases perceptual competition in favor of already high-priority stimuli at the expense of less salient stimuli (Mather & Sutherland, 2011). That is, under states of negative arousal, the difference in the strength with which high priority and low priority stimuli are processed becomes even more pronounced. In this study, we uncover that negative arousal due to threat of shock increases activation within the VDAN by high-priority (by virtue of their associated value) distractors in an oculomotor task, as would be predicted by the ABC model. However, this pattern in the stimulus-evoked brain responses was associated with *reduced* attentional capture by the distractors as measured with eye movements, in contrast to the behavioral predictions arising from the ABC model. Our findings therefore call for a reinterpretation of the relationship between arousal-biased competition and perceptual processing, at least with respect to overt attention.

Arousal has been shown to improve task performance and reduce errors (e.g., Grillon et al., 2017). Prior investigations of the ABC model have demonstrated *increased* attentional processing of stimuli that already possess elevated attentional priority, often operationally defined in terms of physical salience (e.g., Lee et al., 2012, 2014; Sutherland & Mather, 2015). Heightened attention to such stimuli could be considered adaptive under these circumstances, as the introduction of a physically salient stimulus could signal a potential new threat that needs to be evaluated and responded to (e.g., Esterman et al., 2013). In contrast, the previously reward-associated stimuli used in our study were not physically salient and were known to be task-irrelevant, but still possessed elevated attentional priority by virtue of their learning history. One potential interpretation of our findings is that consistent with the ABC model, negative arousal preferentially biases stimulus representation in favor of stimuli that already have high priority. However, the influence of this bias on the orienting response is not obligatory, but rather contingent upon the nature of the eliciting stimulus. If the eliciting stimulus is survival-relevant, as in the case of physically salient stimuli, it will trigger an orienting response, but if the eliciting stimulus explicitly poses no potential danger, as in the case of a previously reward-associated stimulus, observers are able to use the arousal-biased signal to "mark" the stimulus for ignoring.

The signal suppression hypothesis has been proposed as a model of attentional selection in which priority signals can be suppressed during goal-directed, feature-based visual search (Gaspelin & Luck, 2018b; Sawaki & Luck, 2010). This model has been repeatedly validated in event-related potential studies showing active suppression of a physically-salient stimulus (see Gaspelin & Luck, 2019, for a review). Furthermore, this phenomenon has been demonstrated in studies of overt attention in which the frequency of oculomotor capture by distractors is reduced via suppressive mechanisms (Gaspelin et al., 2015; Gaspelin & Luck, 2018a; Ipata et al., 2006). The neural correlates of signal suppression are not well understood and have not yet been investigated using fMRI. Our behavioral results are consistent with the concept of signal suppression under threat, although it is important to note that any threat-related suppression of distraction was only partial such that the previously high-value distractors still drew eye movements to some degree across all conditions in our study. More generally, however, our findings clearly demonstrate that elevated stimulus-evoked responses in the brain can lead to enhanced ignoring as measured from behavior, which may prove to be an important principle in understanding mechanisms of signal suppression. In this regard, it is noteworthy that signal suppression seems to be particularly effective for stimuli that evoke strong responses in the visual system by virtue of their physical salience (Gaspelin et al., 2015; Gaspelin & Luck, 2018a, 2018b; Hickey et al., 2009), necessitating some relationship between mechanisms of suppression and elevated stimulus-evoked activity in the visual system. Our findings are also consistent with a prior report showing that parametrically increasing salience or associated value can under certain circumstances reduce the magnitude of distraction (Moher et al., 2015), further supporting the notion that suppression of behavioral distraction might at times be facilitated by strengthening the representation of a stimulus in the visual system.

Prior studies in support of the ABC model have utilized fear-conditioned startle reflexes as negative arousal (Lee et al., 2014; Sutherland & Mather, 2012) or negatively-valenced images (Lee et al., 2012) in the context of visual search. In our study, in contrast, negative arousal resulted from the threat of an unpredictable and aversive biological event. Both methodologies have produced results in support of the ABC model (Kim & Anderson, 2020b, Lee et al., 2012, 2014; Sutherland & Mather, 2012), but studies using startle reflexes have consistently demonstrated increased attentional capture while reduced attentional capture by reward cues has only been tested in the context of threat-of-shock. However, increased attentional capture by physically salient stimuli has been previously observed using the threat of shock paradigm (Chapter 2), arguing that the contrasting behavioral results are not a by-product of the methodology used to induce negative arousal. At the same time, an increasingly nuanced understanding of fear- and anxiety-associated neural networks have determined fundamental differences between cognitive processing during imminent vs. unpredictable threat (e.g., Davis et al., 2010), and so we restrict our conclusions to the influence of unpredictable threat.

Another way in which our study differs from prior studies supporting the ABC model is in the role of memory in the attentional priority of the distractor. In the present study, the distractors were preferentially attended by virtue of their status as previously high-value targets, which contrasts with the attentional priority of the physically salient stimuli frequently used in studies of arousal-biased competition (Lee et al., 2012, 2014; Mather & Sutherland, 2011; Sutherland & Mather, 2015), which is not memory-dependent. One possibility is that threat modulates access to, or the recruitment of, memory for the pertinence of stimuli, which may have impacted the influence of such memory on eye movements and/or stimulus processing in the visual system of the brain. It is also possible that our threat manipulation had a more direct impact on visual information processing, as hypothesized by the ABC model (Lee et al., 2012, 2014; Mather & Sutherland, 2011; Sutherland & Mather, 2015). Attention and memory are intricately intertwined (see Chun & Turk-Browne, 2007; Hutchinson & Turk-Browne, 2012, for reviews), although the specific role of the memory system in involuntarily directing attention to previously reward-associated stimuli remains to be clarified.

Prior rodent and human studies evaluating the neural correlates of sustained fear or adaptive anxiety have identified corresponding neural activity in the dorsal amygdala, particularly in the central extended amygdala (CeA) and bed nucleus of the stria terminalis (BNST; Alvarez et al., 2011; Davis et al., 2010). However, due to the small size of these neuronal populations and the limited spatial resolution, few fMRI studies have studied these regions under conditions of experimentally induced anxiety. In our task assessing overt attentional capture, we identified voxels activated under threat within the amygdala in the present study, but our whole brain analyses were limited in differentiating between the neuronal populations within the amygdala. Future research using targeted, higher-resolution imaging sequences coupled with analytical techniques such as multivoxel pattern analyses (MVPA) may provide further insight in piecing out the functional role of specific neuronal populations within amygdala in modulating anxiety in attention networks.

In the present study, we examined the neural processes by which threat reduces the distracting quality of previously reward-associated stimuli. Our neuroimaging results support the ABC model of neural processing but show that the resulting bias in the representation of visual stimuli need not magnify distraction as measured from behavior and can even reduce it, calling for a more nuanced interpretation of the functional role of ABC in the control of visual orienting. Our study extends the concept of arousal-biased competition in the brain beyond physically salient stimuli to stimuli that have elevated priority by virtue of learning history, as well as to negative arousal arising from the threat of an unpredictable and aversive biological event (as manipulated via threat-of-shock). Our findings have additional implications for the signal suppression hypothesis by demonstrating an explicit link between elevated stimulus-evoked responses in the visual system and reduced behavioral distraction and offer novel insights into why elevated attentional priority can at times seemingly paradoxically reduce the distracting quality of stimuli (Moher et al., 2015).

5. CONCLUSIONS

In this dissertation, I present a series of experiments investigating how unpredictable threat modulates attentional biases by previously-reward associated stimuli and physically salient stimuli in a visual search task, and also in a goal-oriented attentional control task. In the scope of research on the relationship investigating threat and attention, the approach taken here deviates from the norm; rather than investigating attentional orienting to threatening stimuli, I investigate how attention biases are modulated when altering the state of the observer by elevating state-anxiety through the Threat of Shock paradigm. The findings in Chapter 2 demonstrated that experimentally induced anxiety increases attentional capture by physically salient stimuli while reducing attentional capture by previously reward-associated stimuli. Furthermore, the results in Chapter 3 demonstrated that threat facilitates optimal attentional control in a goal-oriented attention task, improving efficiency and maximizing performance. Such converging evidence reveal that changes in observer state such as induced anxiety does not globally modulate processing of attention, but rather uniquely affect each component of attentional control. Furthermore, these findings demonstrate that negative arousal does not globally influence cognitive processing, but rather modulates each mode of attentional control by the mechanisms of biased competition both for in favor of and against certain stimuli given their priority.

In addition, the behavioral findings in Chapters 2 and 3 were ambiguous with respect to the mechanism by which experimentally induced anxiety modulates attentional control. It remained unclear whether reduced attentional capture by previously reward-associated stimuli was a consequence of the competition between networks processing attention and threat for neural resources (e.g., Pessoa, 2009) or a result of biased competition in which attentional priority toward such stimuli were reduced under threat (e.g., Mather & Sutherland, 2011). The findings in Chapter 4 supported the arousal-biased competition hypothesis in that reduced attentional capture by previously reward-associated stimuli was due to elevated stimulus-evoked activation in the visual system, consistent with other findings of increased attentional priority by physically salient stimuli (e.g., Lee et al., 2012, 2014; Mather & Sutherland, 2011; Sutherland & Mather, 2015); however, in contrast to physically salient stimuli, previously reward-associated stimuli were more easily ignored under threat. This suggests a central role for arousal-biased competition as a mechanism in threat-related modulations of information processing, although the consequence of such biased competition on the orienting response depends on the nature of the eliciting stimulus, potentially as a function of its survival relevance under threat (high for physical salience and low for reward-related stimuli).

The identification of a mechanism for attentional priority allocation under induced anxiety gives insight into understanding why threatening stimuli are rapidly oriented to under conditions of elevated state-anxiety. The arousal-biased competition hypothesis would support the notion that threatening stimuli are actively allocated more attentional priority under threat as a result of biased competition, which reflects the workings of a broader mechanism of attentional control that is not limited to the modulation of threat-related sitmuli. With attention bias modification treatment largely being unreliable as a treatment option for pathological anxiety, the findings from this dissertation suggest the potential for targetting specific mechanisms of attentional control to reduce attentional priority allocated towards threatening stimuli.

As mentioned earlier, it is hasty to translate the mechanistic findings of attentional biases under experimentally induced anxiety to pathology. However, the ToS paradigm acts as an effective intermediate tool to understand how experimentally induced anxiety modulates attention biases. Although the ToS paradigm has been validated as an appropriate model of experimentally induced anxiety, it still poses some limitations. It is unclear whether participants under threat of shock eventually habituate and no longer maintain a state of adaptive anxiety. However, analyses done with pupil size here support the claim that a state of induced anxiety was maintained over the span of a 1-hour experiment. Lastly, the scope of this dissertation does not cover the molecular signaling via neurotransmitter release in the related neural networks. Research into the dynamic interplay of noradrenergic signaling under negative arousal, local glutamatergic release for signal amplification, and dopamine release in association with reward-associated stimuli are ripe for future investigation.

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APPENDIX

FIGURES

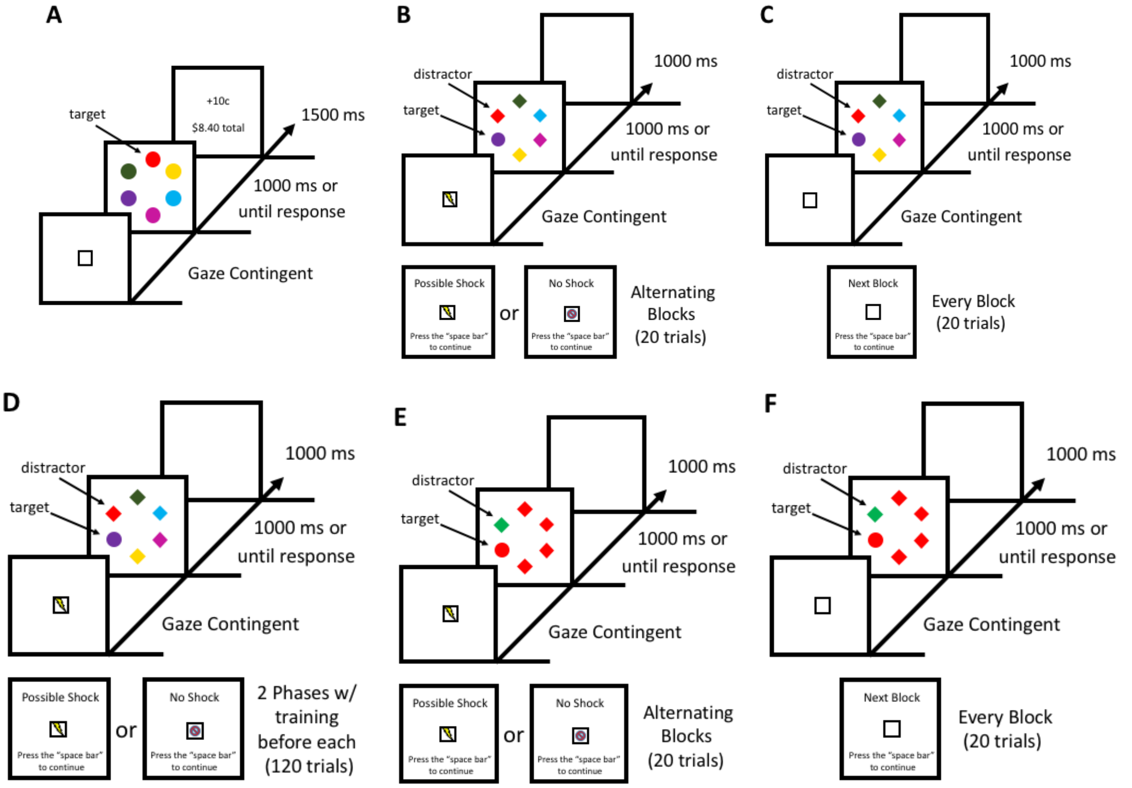

Figure 1. Sequence of trial events for experiments in Chapter 2. (A) Training phase for Experiments 1-3. The target was defined by color. Correct responses were followed by the delivery of monetary reward feedback. (B) Test phase of Experiment 1. The target was defined as the unique shape and no reward feedback was provided. (C) Test phase of Experiment 2, which mirrored Experiment 1 except that each block was the same and there was no reference to shock. (D) In Experiment 3, each of two 120-trial blocks of the test phase was preceded by a separate training phase. The stimuli were identical to Experiment 1. (E) In Experiment 4, there was no training phase and participants completed only the shape singleton search task with a color singleton as a distractor. The block design and procedure were identical to Experiment 1. (F) In Experiment 5, the same shape singleton search task as in Experiment 4 was completed without reference to shock.

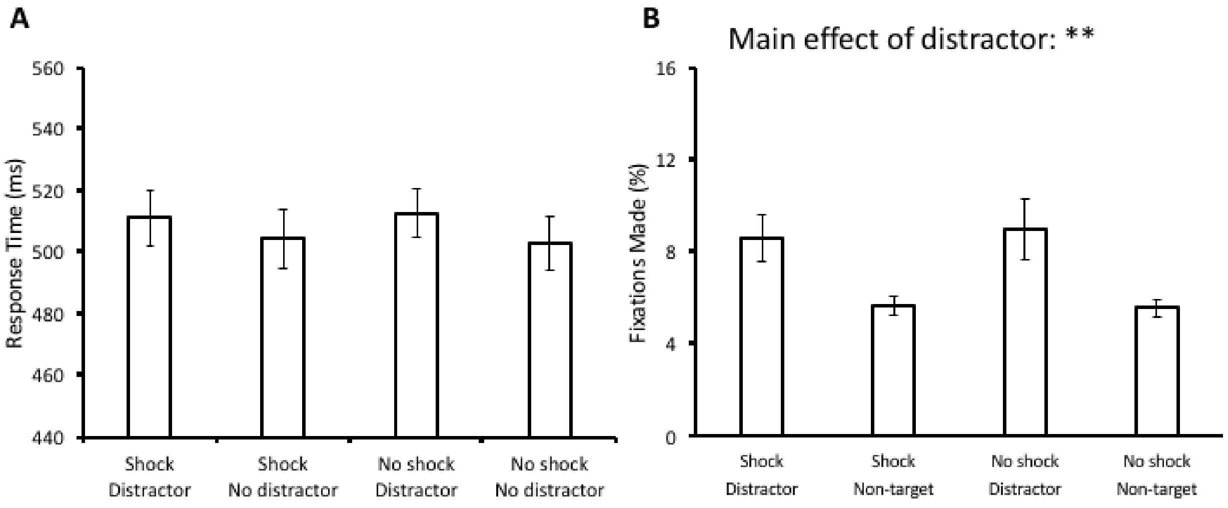

Figure 2. Response time (A) and fixation data (B) from the test phase of Experiment 1 in Chapter 2. Data are broken down by block (Shock vs. No shock) and distractor present vs. absent in (A) and fixations on the distractor vs. a non-target in (B). Error bars reflect the standard error of the mean. $^{**}p<0.01$

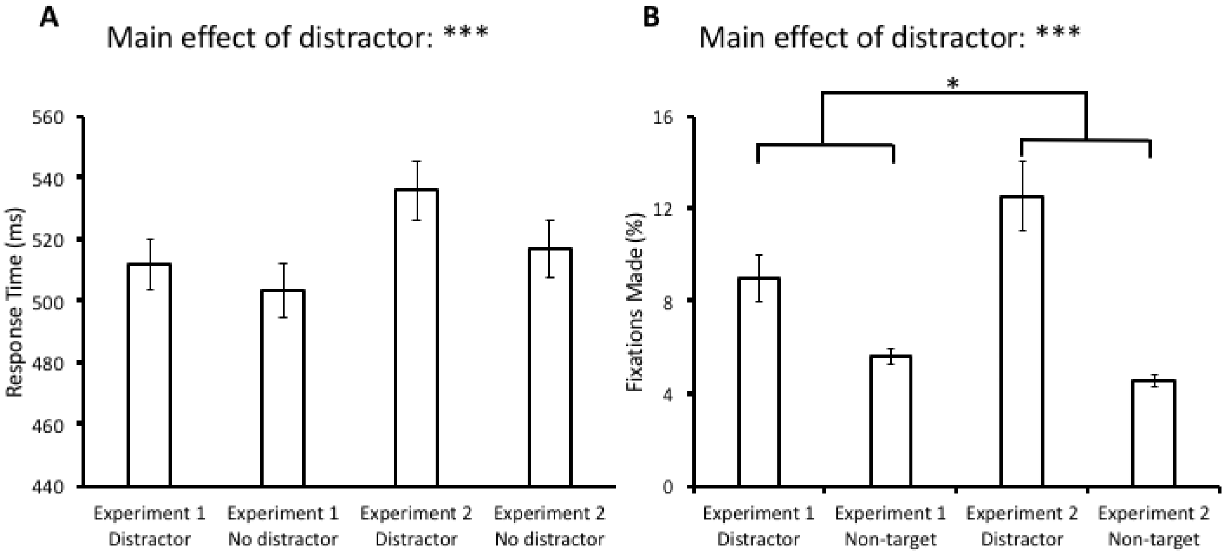

Figure 3. Comparison of response time (A) and fixations (B) between the test phase of Experiment 1 (collapsed across shock and no-shock blocks) and Experiment 2 in Chapter 2. Data are broken down by experiment and distractor present vs. absent in (A) and fixations on the distractor vs. a non-target in (B). Error bars reflect the standard error of the mean. $^{*}p<0.05$, $^{***}p<0.001$

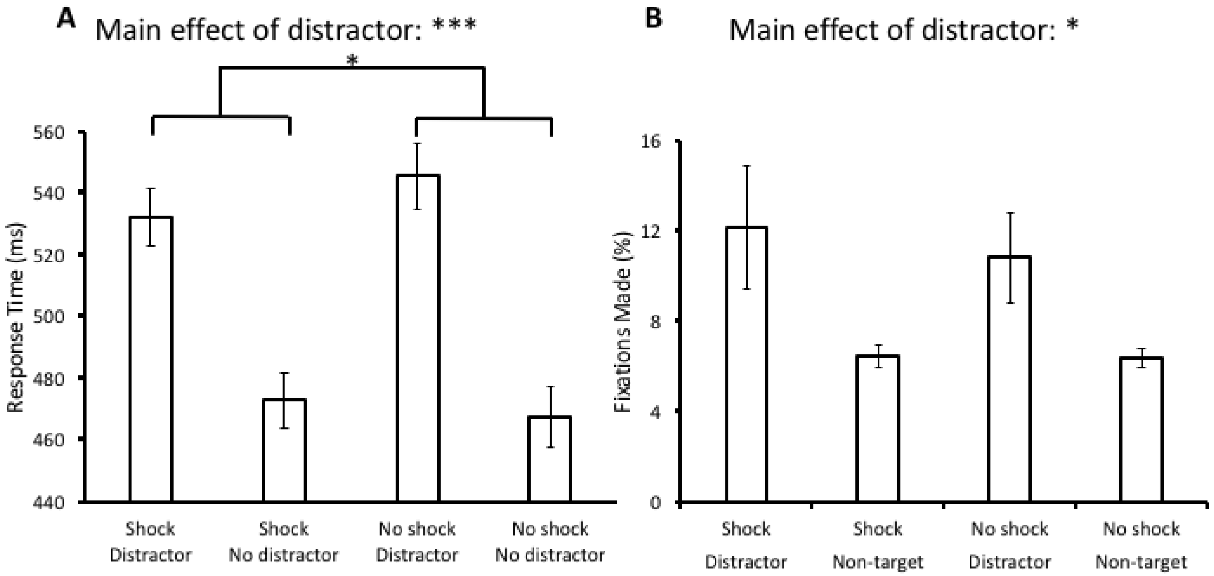

Figure 4. Response time (A) and fixation data (B) from the test phase of Experiment 3 in Chapter 2. Data are broken down by block (Shock vs. No shock) and distractor present vs. absent in (A) and fixations on the distractor vs. a non-target in (B). Error bars reflect the standard error of the mean. **p*<0.05, ****p*<0.001

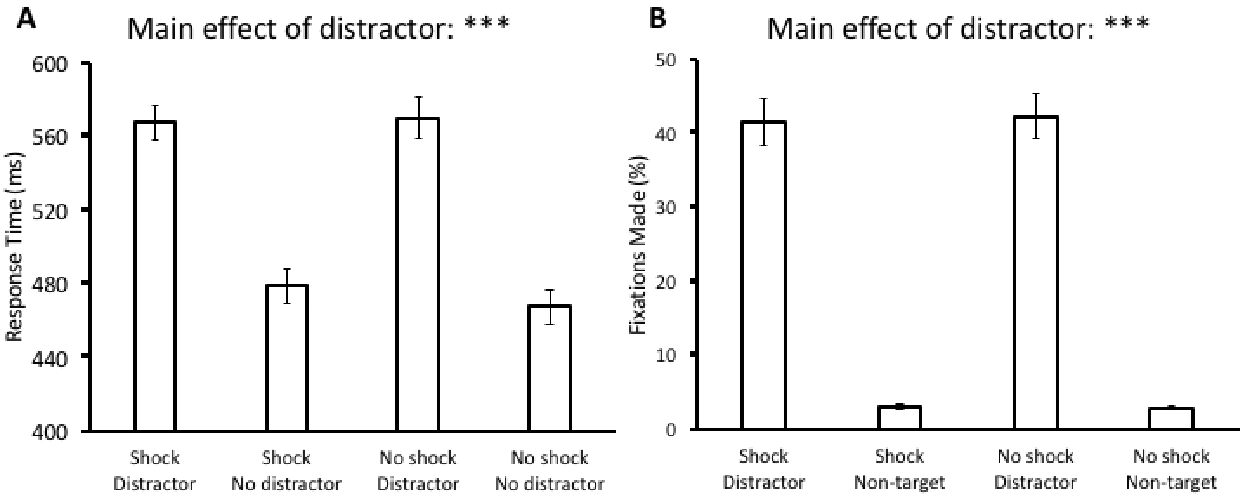

Figure 5. Response time (A) and fixation data (B) from the test phase of Experiment 4 in Chapter 2. Data are broken down by block (Shock vs. No shock) and distractor present vs. absent in (A) and fixations on the distractor vs. a non-target in (B). Error bars reflect the standard error of the mean. ****p*<0.001

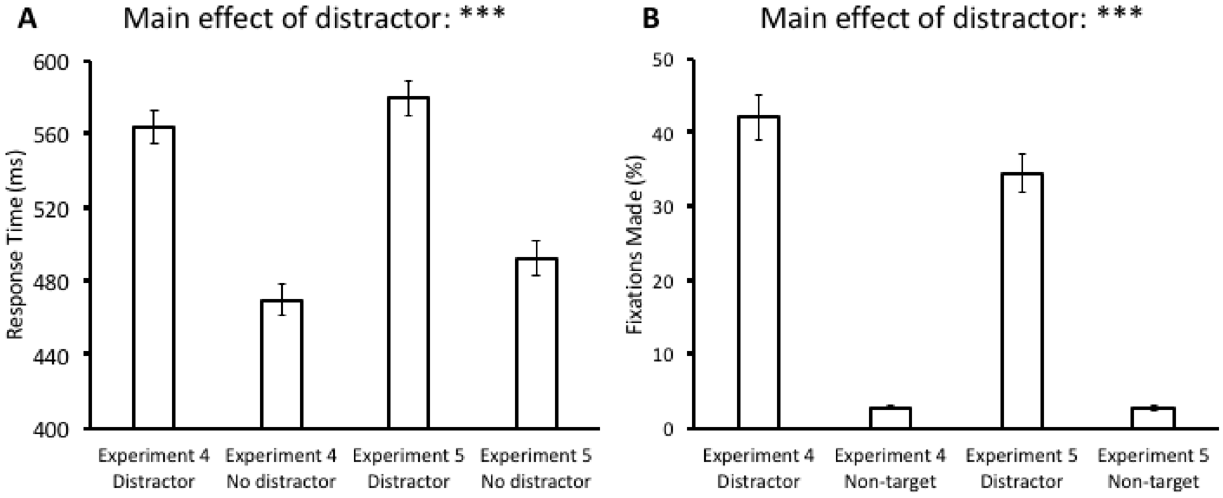

Figure 6. Comparison of response time (A) and fixations (B) between the test phase of Experiment 4 (collapsed across shock and no-shock blocks) and Experiment 5 in Chapter 2. Data are broken down by experiment and distractor present vs. absent in (A) and fixations on the distractor vs. a non-target in (B). Error bars reflect the standard error of the mean. ***$p<0.001$

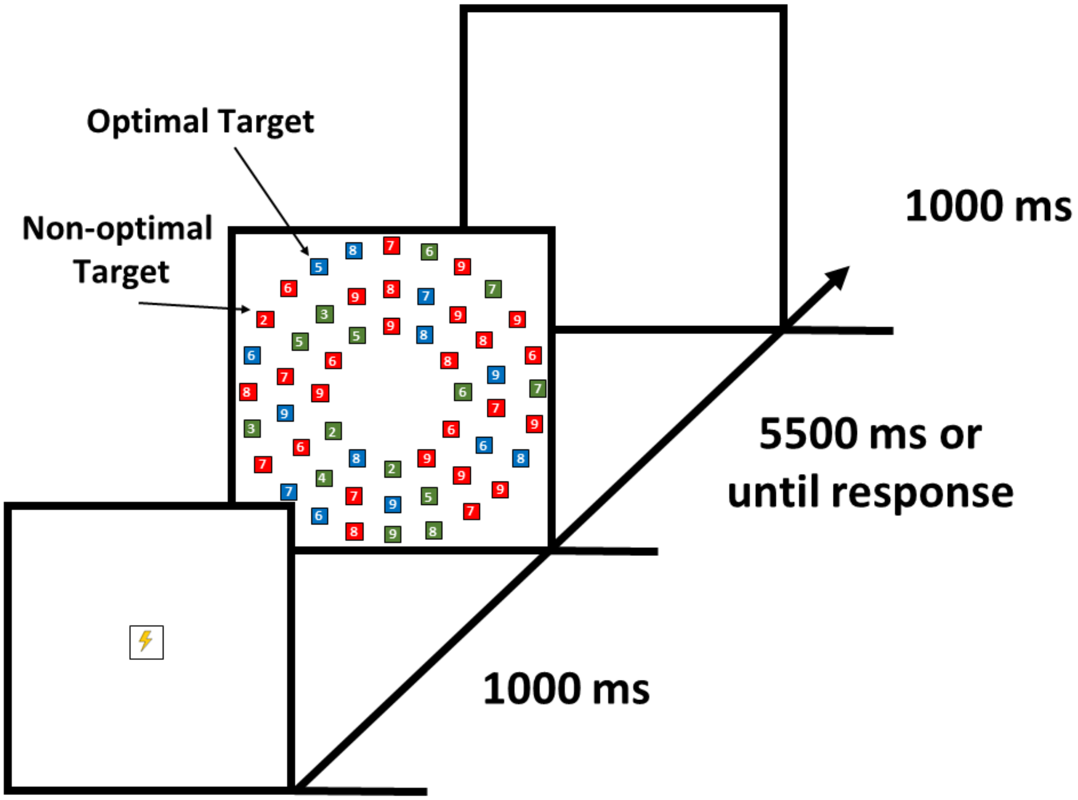

Figure 7. Sequence of trial events. Participants were shown a white box containing an image of a lightning bolt or one with a red hash over the lightning bolt, depending on whether they were completing the threat or no threat block, respectively. Then, the stimulus array would be displayed for 5500 ms or until a keyboard press was recorded. If participants did not indicate a response within the time-limit, a feedback display of "Too Slow" would be displayed for 1000 ms. Finally, the inter-trial-interval lasted 1000 ms.

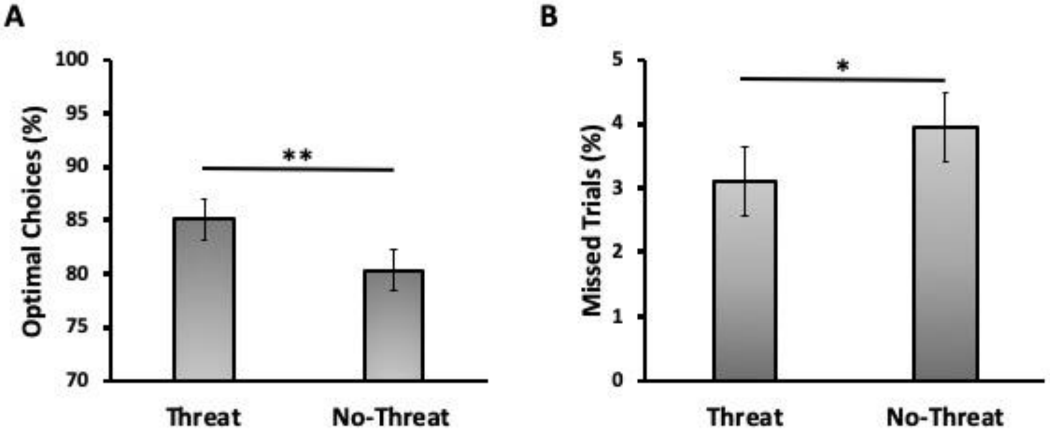

Figure 8. Behavioral performance with and without the threat of shock for experiment in Chapter 3. (A) Percentage of trials in which the optimal color target was chosen. (B) Percentage of trials in which a response was not recorded within the timeout limit. Error bars depict within-subjects confidence intervals calculated using the Cousineau method with a Morey correction. **$p < 0.01$, *$p < 0.05$

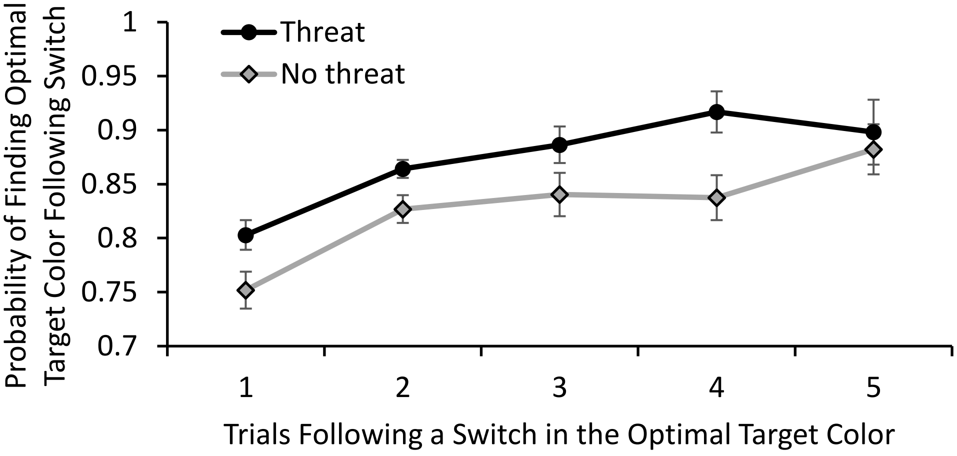

Figure 9. The probability of finding the optimal target color box as a function of the number of trials following a switch in the optimal target color, separately for threat and no-threat blocks. Error bars depict within-subjects confidence intervals calculated using the Cousineau method with a Morey correction.

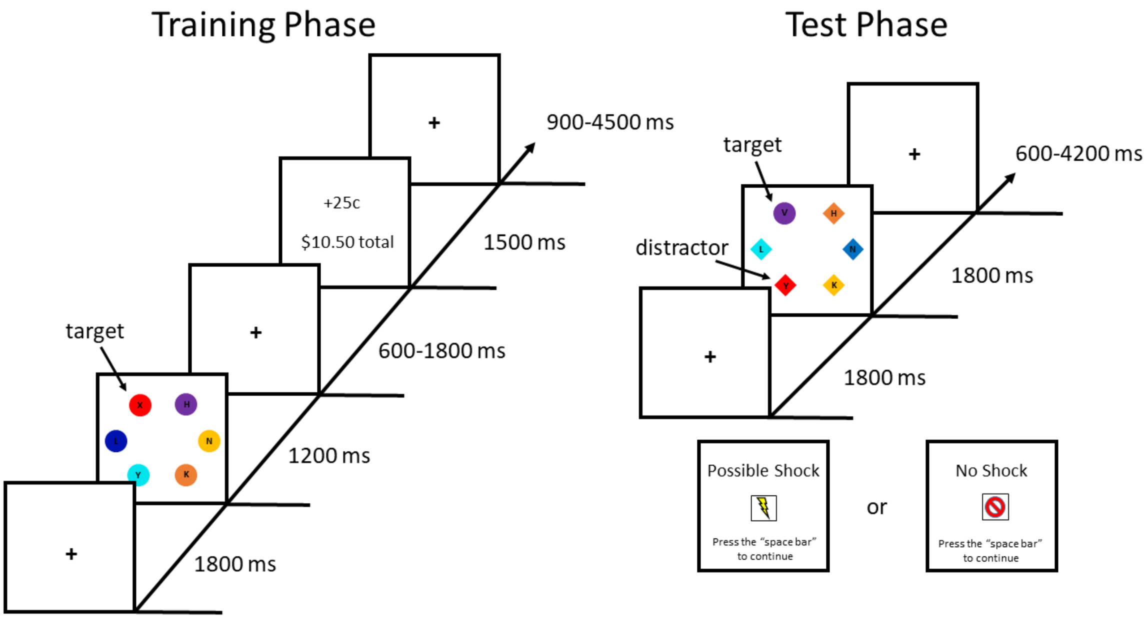

Figure 10. Sequence of trial events for experiment in Chapter 4. In the training phase, participants searched for a target defined by color (red or green, exact one of which was present on each trial) and correct responses were followed by the delivery of monetary reward feedback. In the test phase, participants searched for a target defined as the unique shape, and no reward feedback was provided. Half of the trials contained the previously rewarded color as a non-target distractor. The test phase was split into the threat and no-threat blocks in which it was possible to receive unpredictable eletric shocks or no chance of receiving shock, respectively.

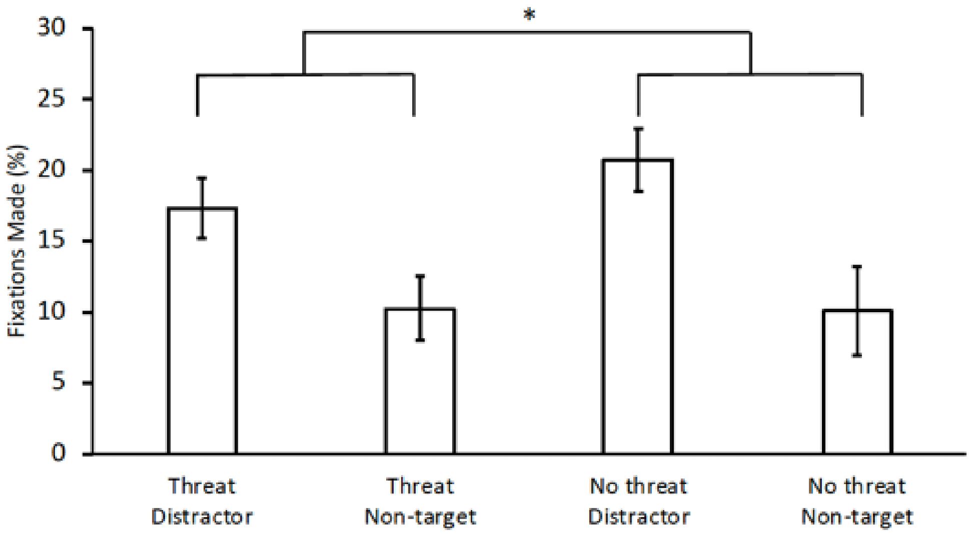

Figure 11. Oculomotor capture in the test phase of experiment in Chapter 4. Data are broken down by block (Threat vs. No-threat) and first fixations made each trial on the previously reward-associated distractor vs. a non-target. Error bars depict within-subject confidence intervals calculated using the Cousineau method with a Morey correction. **p*<0.05.

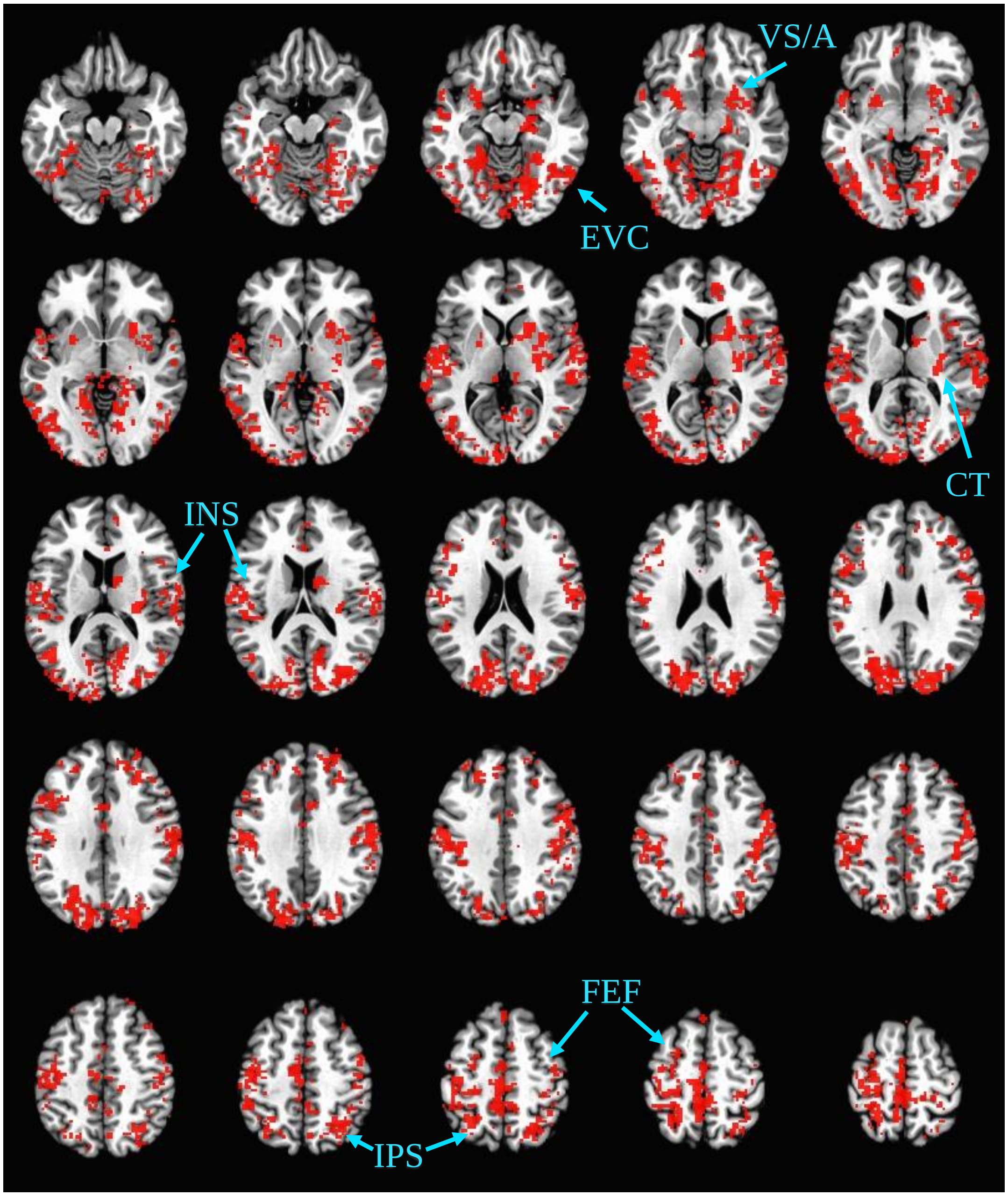

Figure 12. Montage of regions for which both an effect of threat and distractor condition was evident. Significant clusters were identified for each effect (clusterwise $\alpha < 0.05$, voxelwise $p < 0.005$) and the intersection of the resulting activation maps was computed and used for ROI definition (ROIs indicated with the labels and arrows). The intersection is shown across subjects using the leave-one-subject-out procedure to depict the full spatial extent of the ROIs used. The resulting activations are overlaid on an image of the Talairach brain. EVC = Extrastriate Visual Cortex, FEF = Frontal Eye Field, IPS = Intraparietal Sulcus, VS/A = Ventral Striatum / Amygdala, INS = Insula, CT = Caudate Tail.

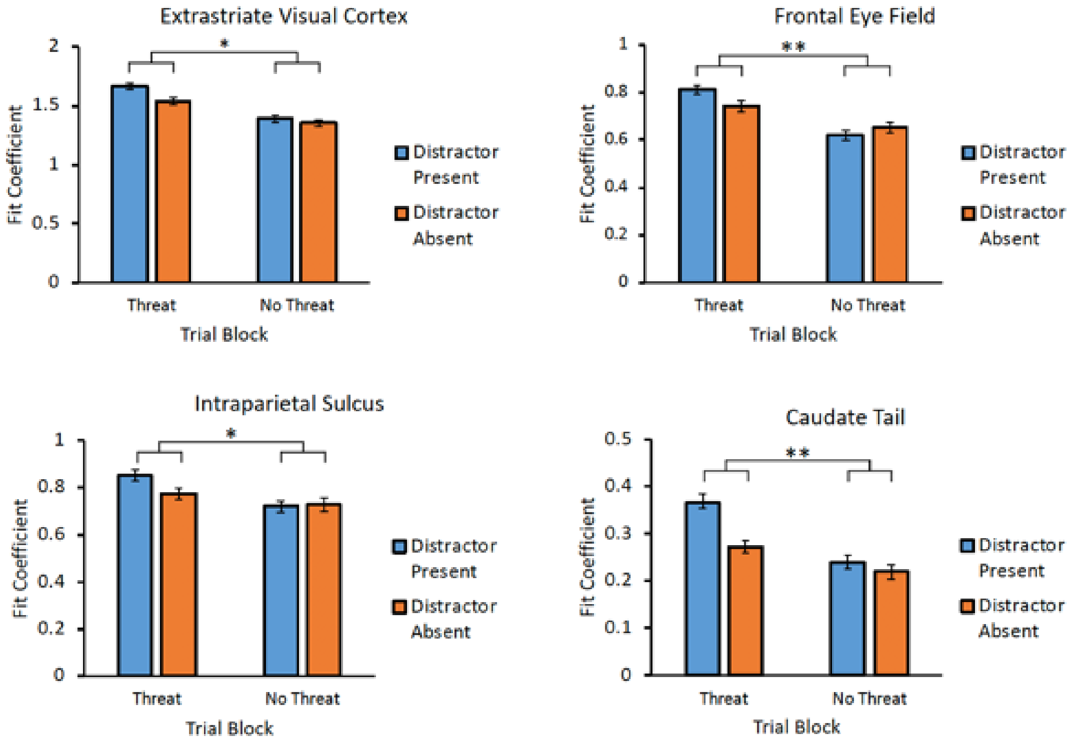

Figure 13. Interaction of threat (threat vs. no-threat) and distractor condition (present vs. absent) in the Extrastriate Visual Cortex, Frontal Eye Field, Intraparietal Sulcus, and Caudate Tail. Error bars depict within-subject confidence intervals calculated using the Cousineau method with a Morey correction. *$p<0.05$. **$p<0.01$

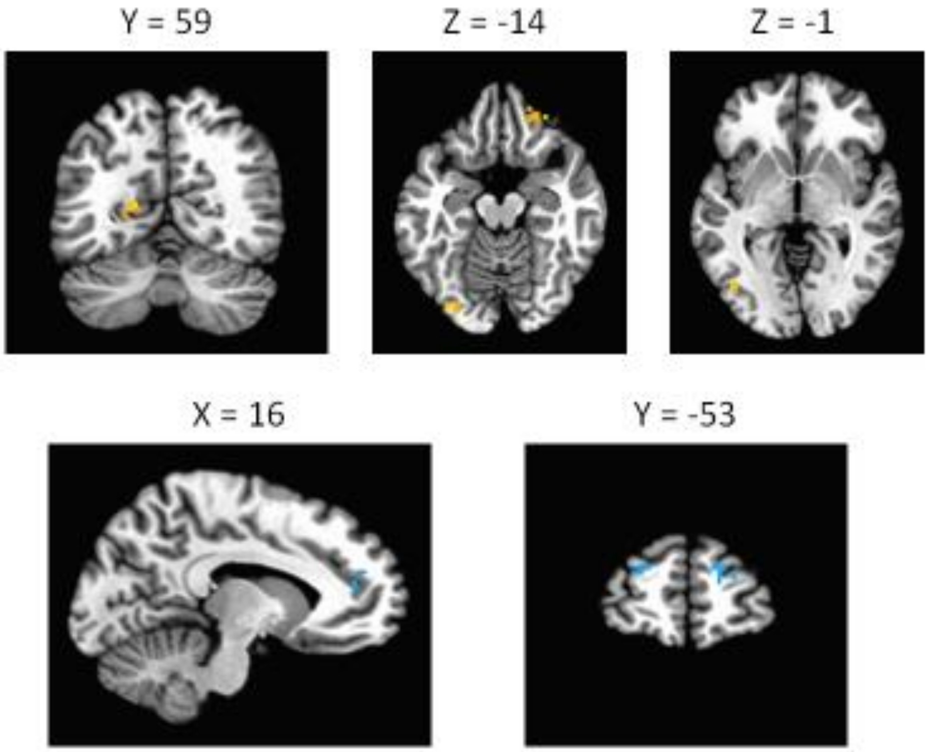

Figure 14. Significant clusters, overlaid on an image of the Talairach brain, where the modulation of distractor-evoked brain activity by threat was related to the influence of threat on oculomotor capture.