SCOPE OF REWARD HISTORY EFFECTS ON VISUAL ATTENTION

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A Dissertation

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MING-RAY LIAO

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Chair of Committee,	Brian A. Anderson
Committee Members,	Darrell A. Worthy
	Jessica L. Yorzinski
	Joseph M. Orr
Head of Department,	Mindy E. Bergman

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ABSTRACT

In order to examine the scope of reward history effects on attention, I conducted four experiments and am planning on conducting two more. Reward history effects on attention (i.e., value-driven attentional capture; VDAC) are a persisting source of attentional bias that can overcome cognitive control and contribute to maladaptive biases in patients with substance use disorder. Before VDAC can contribute to clinical interventions, however, we as a field need more understanding of its effects in more ecologically valid conditions. In chapter two, I found that reward history extends to oculomotor behavior that biases the direction of eye movements in both unguided and guided search. In chapter three, I found that the neural correlates of value-driven spatial orienting include the conventional value-driven attentional network and regions that have been linked to value-driven feature-based orienting, but also regions that have been implicated in the processing of scene, space, and object information. In my fourth chapter, I found that reward history effects for multi-feature objects are limited to the reward-associated features and do not imbue non-predictive features with elevated priority. My last experiment chapter employed a reversal learning paradigm to demonstrate a temporal disconnect between reward learning and the acquisition of reward history effects on attention, as there was a notable delay before participants updated their biases towards the most currently reward-associated feature. The results inform us about the extent of reward history effects on attention that extend beyond traditional visual search paradigms and provide insight into the challenges of overcoming maladaptive attention.

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1. INTRODUCTION

The world we inhabit is comprised of endless streams of dynamic objects that constantly bombard our perceptual system. Without the ability to filter though the environment for specific objects to process, we would be paralyzed by the sheer amount of information available. Attention, the ability to select relevant information for representation and further processing (e.g., Desimone & Duncan, 1995), is crucial for ensuring survival and wellbeing (e.g., Anderson, 2013). Consequently, attention has often been conceptualized as a zero-sum game where unattended objects fail to influence later stages of cognition such as decision-making and memory formation (see Dux & Marois, 2009 and Jensen et al., 2011 for reviews).

Attention is widely understood to constitute a limited resource, but how does an organism determine what to pay attention to? Desimone and Duncan's (1995) *Biased Competition Theory* posits that attention arises from competition between different sources of sensory information, where the source with the most priority is given the most representational weight, which allows it to win the competition for selection. This theory is substantiated by evidence at multiple stages of information processing from the neuronal level up to higher-order levels, where the competition is represented within a spatial priority map that reflects the features and weights of objects in space (Sprague & Serences, 2013; Moran & Desimone, 1985; see also Kastner & Ungerleider, 2001 for review). The Biased Competition Theory has thus become an important framework that has guided investigations into selective attention for the past few decades.

1.1. Theoretical Trichotomy of Attentional Control

In this section, I will set the stage for our current understanding of the mechanisms of selective attention, which arises from the interaction between the goals of the observer, physical properties of the visual environment, and past experiences of the observer. Goal-driven attention

(i.e., top-down or endogenous attention) is characterized by the voluntary prioritization of task-relevant information (e.g., Moran & Desimone, 1985). Stimulus-driven attention (i.e., bottom-up or exogenous attention) refers to an involuntary allocation of attentional priority to information based only on its physical property (e.g., color or shape; Reynolds & Desimone, 2003). Finally, selection history (or experience-driven attention) refers to an independent source of attentional priority that involuntarily accumulates over time from experience (Anderson et al., 2021). I will summarize the dichotomy between goal- and stimulus-driven attention that preceded models of attention that include selection history, how experience-driven attention came to be understood, and neural evidence to reinforce the three components as independent sources of attentional priority.

1.1.1. Historical Dichotomy in Attentional Control

Before the advent of selection history, attentional control was thought to originate from a source either endogenous or exogenous to the observer. Support for goal-driven attention began with results from spatial cueing paradigms that provided evidence for deliberate attentional allocation (Eriksen & Collins, 1969; Eriksen & Hoffman, 1972, 1973). The most prominent study (Posner, 1980; see also Posner et al., 1980) demonstrated that attention can be deployed in advance to specific locations in anticipation for an upcoming target. When a peripheral cue that preceded the target location 80% of the time was presented, response times (RTs) in target identification were faster when the cue predicted target locations (valid cues) and slower when the cue did not (invalid cue). Follow-up studies with a centrally presented cue reflected the same pattern of results (Jonides, 1981), but were found to be slow (taking ~300ms) compared to cues appearing in the same location as the target (~50-100ms) reflecting a potential difference

between endogenous and exogenous attention – stimulus-driven attention is rapid and involuntary while goal-driven attention is slow and under volitional control (Carrasco, 2011).

Top-down allocation of attention can also extend to features like a particular color, where selection can be restricted to the target-defining color to facilitate visual search (Egeth et al., 1984; Irons et al., 2012; Reynolds et al., 1999; Wolfe et al., 1989; Wolfe, 1994). Like in classical spatial cueing paradigms, the prioritization of a particular color can lead to distraction by non-targets that share that feature because they compete for selection (Anderson & Folk, 2010, 2012b; Folk & Anderson, 2010; Folk, Leber, & Egeth, 2002; Folk & Remington, 1998; Folk et al., 1992). This was demonstrated saliently with a contingent capture paradigm where the facilitation and impairment of selection by precues depended on how similar the color of the precue was to the target (Folk et al., 1992, 1994; Folk & Remington, 1998). Although participants were able to rapidly orient attention based on an endogenous priority, it is more likely that the contingent capture paradigm reflects both voluntary and involuntary attentional control where the instantiation of goal-relevant features is voluntary while the allocation of attention to abrupt targets is not (see also Anderson & Folk, 2010, 2012b; Folk & Anderson, 2010; Folk, Leber, & Egeth, 2002; Folk & Remington, 1998; Folk et al., 1992).

Although the initial deployment of attention has been shown to depend on goals or task-relevant features, physically salient stimuli have been shown to capture attention despite being entirely task-irrelevant (e.g., Itti & Koch, 2001; Theeuwes, 1992, 1994; Yantis & Jonides, 1984). Physical salience is defined with respect to the difference in contrast between a stimulus and the surrounding environment, including other stimuli (e.g., abrupt flash of bright light somewhere dim or loud noises somewhere quiet; Egeth et al., 1972; Jonides & Yantis, 1998; Theeuwes, 1994). Using a singleton visual search task where participants searched for a circle among

squares, Theeuwes (1992) showed that even with extensive training, participants remain distracted by the presence of a uniquely colored distractor. The field of attention for the past few decades, and even now, has been dominated by debates in support of either goal-driven or stimulus-driven attention (e.g., Anderson & Folk, 2012; Belopolsky et al., 2010; Sawaki & Luck, 2010; Luck et al., 2020).

1.1.2. Neural Evidence for Independent Components of Attention

The persistence of the dichotomy can be partly attributed to the apparent divide in neuroimaging results for either goal-driven or stimulus-driven attention (see Corbetta & Shulman, 2002; Corbetta et al., 2008; Vossel et al., 2014 for reviews). Neural activity for task-relevant features (e.g., a particular location in space, color, or object) is enhanced during search (Bichot et al., 2005; Moran & Desimone, 1985; Roelfsema et al., 1998), or in anticipation of target onset (Beck & Kastner, 2009; Chelazzi et al., 1998; Luck et al., 1997; Stokes & Duncan, 2014). On the other hand, neuronal responses have been shown to be driven by pop-out stimuli that are more physically salient (Geng & Mangun, 2009; Hickey et al., 2006, 2010; Reynolds & Desimone, 2003; Schubö, 2009). Beyond stimulus-evoked neural activity, the dichotomy also persists into the two main neural networks that mediate selective attention – the dorsal frontoparietal network and the ventral frontoparietal attention network (see Corbetta & Shulman, 2002, 2008; Vossel et al., 2014; for reviews).

The dorsal frontoparietal network is associated with endogenous attention and includes the superior parietal lobule (SPL), the intraparietal sulcus (IPS), and the frontal eye field (FEF; Corbetta et al., 2000; Hopfinger et al., 2000; Serences et al., 2004; Yantis et al., 2002). Findings from functional magnetic resonance imaging (fMRI) studies have suggested that activity in the FEF and IPS reflect an attentional priority map that modulates neural activity in the visual cortex

to drive selective attention to stimuli with the highest priority (Sereno et al., 2001; Silver & Kastner, 2009; see also Fecteau & Munoz, 2006 and Zelinsky & Bisley, 2015 for corresponding findings in homologue regions in Macaques). This relationship is verified in animal models where microstimulations to the FEF increased V4 activity and improved target detection (Armstrong & Moore, 2007; Moore and Armstrong, 2003; Moore & Fallah, 2001; Noudoost et al., 2010), and LIP (homologue of IPS) inactivation led to impairments in selective attention (Balan & Gottlieb, 2009; Liu et al., 2010; Wardak et al., 2004). The ventral frontoparietal network is associated with exogenous attention and includes the temporoparietal junction (TPJ), inferior parietal lobule (IPL), the superior temporal sulcus (STS) and gyrus (STG), the middle (MFG) and inferior frontal gyrus (IFG), and anterior insula (Corbetta & Shulman, 2002, 2008; Husain & Nachev, 2007). Patients with lesions to the parietal cortex exhibit deficits in stimulus-driven attention such as inability to detect salient events (e.g., oddball targets or novel stimuli; Corbetta et al., 2000; see also Marois et al., 2000) as well as difficulties in sustaining attention and vigilance (Husain & Nachev, 2007; Malhotra et al., 2009). Neuroimaging studies have corroborated the importance of the ventral network in stimulus-driven attention where participants are required to orient to exogenous cues or away from exogenous cues (Chambers et al., 2004; Peelen et al., 2004; Shulman et al., 2009, 2010).

Multiple salient and task-relevant objects exist at the same time in our natural environment, and as is apparent from behavioral studies (e.g., Folk et al., 1992), exogenous and endogenous attention often operate simultaneously to compete for selection. This relationship is reflected in brain activation, as although the dorsal frontoparietal and ventral frontoparietal networks have distinct specializations, they interact depending on the cognitive demands. So how does our attention system orient between endogenous and exogenous attention? Evidence

from neuroimaging studies have suggested that the IPS and FEF applies a top-down filter onto stimulus-driven processing in the ventral attention network, and the TPJ acts as the "circuit-breaker" to orient attention from the endogenous to the exogenous salient stimuli (Corbetta et al., 2008). Chica et al. (2011) substantiated this relationship with a transcranial magnetic stimulation study showing that deactivating the TPJ interfered with orienting to nonpredictive peripheral cues, while deactivating the IPS interfered with both endogenous and exogenous attention. DiQuattro and Geng (2011) observed similar findings in a study where participants can use a salient nontarget to reorient their attention. They used dynamic casual modeling on connectivity data and found that the TPJ and IFG represented the contextual relevance of the salient nontarget (i.e., reorient away from this) and translated that into an attentional control signal through the FEF. Additionally, when the nontarget was no longer salient, the FEF actually inhibited the TPJ, further supporting the dynamic and flexible recruitment of regions in both networks depending on the task at hand. Despite neural evidence for two independent sources of selective attention, researchers over time began to notice certain findings that could not fit within the existing dichotomy – heralding the beginning of selection history.

1.1.3. A New Dawn: Selection History

Discrepancies within the historical dichotomy of attentional control began in the domain of auditory attention with the dichotic listening task (Moray, 1959). While attending to one audio stream, participants will pick up the unattended audio stream if it contains their name, breaking through goal-directed attention despite not being physically salient. This was the prelude to many findings in visual attention where selection was afforded to stimuli neither task-relevant nor physically salient. One example of such selection is priming, which refers to the general phenomenon where a prior stimulus continues to exert some influence on future trials

(Kristjansson, 2006; Maljkovic and Nakayama, 1994, 1996; Treisman, 1992; see Kristjansson & Campana, 2010 for a review). The most classic example of priming in the control of attention is the 'priming of pop-out' effect where participants searching for a feature-defined target (i.e., specific color) were more efficient when they searched for a target with the same feature on the preceding trial. Critically, this priming effect persisted even when it conflicted with the task requirement to select a target with a different feature value (i.e., different color).

For years, selection history effects like priming were conceptualized as either endogenous effects because they do not arise only from the stimuli (Wolfe et al., 2003), or as exogenous effects because they could not be overridden by voluntary control (Theeuwes et al., 2006). Some other examples of selection history effects include **novelty**, where participants preferentially attended to unexpected or unusual stimuli (Folk & Remington, 2015; Horstmann and Ansorge, 2006, 2016; Horstmann and Herwig, 2016; Horstmann, 2002; Neo and Chua, 2006; Retell et al., 2015), **task-irrelevant positively or negatively valent** stimuli that were afforded more attentional priority than neutral stimuli (e.g., Most et al., 2005; Most et al., 2007; Vuilleumier, 2005), effects of involuntary **long-term memory** like **statistical regularities** where greater attentional priority was allocated to locations where the target is more likely to appear (or vice versa, less attentional priority to where distractors were more likely to appear; Wang & Theeuwes, 2018a, b, c), or the **persistence of specific visual search strategies** (Leber & Egeth, 2006a, b; Leber et al., 2009; Liao et al., 2020), and the effect of learned associations such as reward history (Anderson, 2016a; Failing & Theeuwes, 2017; Le Pelley et al., 2015) and aversive conditioning (Anderson & Britton, 2020; Schmidt et al., 2015a, b; H. Kim & Anderson, 2021) among others (e.g., scene memories and semantic associations; Moores et al., 2003; Stokes et al., 2012; Summerfield et al., 2006). The findings from these studies supported the formation

of experience-driven attention as the third source of attentional selection, independent from goal- and stimulus-driven attention (Anderson, 2021; Awh et al., 2012).

1.2. Current Stage of Reward History

Effects of reward have often been shoehorned as a matter of motivation (e.g., Esterman et al., 2014; Esterman et al., 2016; Pessoa, 2009), and further corroborated with neuroimaging findings where the presence of reward-associated stimuli enhanced activation in the dorsal attention network (e.g., Esterman et al., 2017; Pessoa and Engelmann, 2010). Using a decision-making task with trial-by-trial ratings of subjective value, however, Serences (2008) showed that reward history was a better predictor than subjective value for activations within early regions of visual cortex that represent low-level stimulus features. Although outside of the realm of visual attention, this finding was especially interesting in that it suggested that reward history was independent from a participant's conscious appraisal of the choice's value. Various studies also showed that reward history persisted into extinction to compete for attentional selection (Della Libera & Chelazzi, 2009; Della Libera et al., 2011; Peck et al., 2009). Conflicting findings in the context of reward history (Anderson et al., 2011a; Hickey et al., 2010), along with the discrepancies mentioned above that did not fit existing theories of attentional control, prompted an expansion that included the component of selection history (Awh et al., 2012). Given the focus of this dissertation on reward history effects on attention, I will dedicate the section that follows to providing a historical overview and trajectory of this literature this particular component of selection history.

1.2.1. The Past and Present of Reward History

Reward is undoubtedly important for the survival and wellbeing of organisms, with many species having an innate motivation to maximize reward, be it food, those related to

reproduction, or even secondary or extrinsic rewards like money. The role of reward in learning and future behaviors was first proposed by Thorndike (1911), which inspired classical and operant conditioning that still prevail in contemporary research. Both types of conditioning can be considered forms of reinforcement learning, or the method by which associative learning occurs, which allows an organism to learn the optimal behavior in an environment by maximizing the reinforcer (i.e., food; Sutton & Barto, 1998). The key difference between the two is how much agency is afforded to the organism. In classical conditioning (or Pavlovian conditioning), the organism learns to associate the automatic or unconditioned response with a neutral stimulus without any explicit or meaningful action, because the reinforcer automatically follows (Pavlov, 1927). On the other hand, in operant conditioning (or instrumental learning), the organism learns explicit behavior(s) to receive the reinforcer (Skinner, 1938; Thorndike, 1911). Reinforcement learning, through either classical or operant conditioning, is the mechanism behind reward history effects on attention where features become associated with reward and receive elevated priority that competes for attentional selection (Kim & Anderson, 2019a).

Although motivation is relevant to an understanding of the control of attention, it is beyond the scope of what will be discussed here. It is important, however, to note that motivation was conceptualized as an innate mechanism to increase executive control (Pessoa, 2009). Reward, in turn, was a method to increase motivation and thus, increase goal-directed behavior (Robbins & Everitt, 1996; Schultz, 2000). Engelmann and Pessoa (2014), for example, varied the magnitude of reward to manipulate motivation in a spatial attention task and found that reward-induced motivations improved orienting and reorienting of exogenous attention as well as increasing perceptual sensitivity. Shortly afterwards, findings started to emerge that hinted at a more important role for reward in attention. In Hickey et al. (2010), for example, participants

searched for a shape-defined target among salient distractors and exhibited faster responses when the target color was presented in a color that was paired with high reward on the prior trial and slower responses when this was true of the salient distractor. They also measured different event-related potentials (ERPs) and found elevated N2pc, an increase in negative ERP amplitude 200 to 300ms after stimulus onset that indexes visuospatial attention, for both targets and distractors in high-value colors. Based on these findings, the authors posited that reward increases the salience of the associated object to better compete with goal-driven attention for attentional selection (see also Hickey & van Zoest, 2012). This concept was not without precedent, as the incentive salience theory actually proposes the same thing (albeit with more emphasis on the role of dopamine; Berridge & Robinson, 1998). It was not until 2011, however, that reward history became a definitively independent component of attentional control.

Anderson et al. (2011) directly investigated how reward history effects of attention conformed with neither goal-driven nor stimulus-driven attention, necessitating that researchers revise their theories of attentional control. The authors designed a two-part experiment in which participants first learned to associate a color with reward (i.e., training phase), before performing a visual search task (i.e., test phase) under extinction where the reward-associated color appeared as an irrelevant distractor. Critically, the color of all stimuli in the search array in the test phase were similarly salient (and counterbalanced), and the target was defined by its unique shape. Theories of attentional control up until this point predicted that the reward-associated distractor should hold the same amount of priority as the other nontargets, but the findings revealed that it continued to compete with the target, which was both physically salient and task-relevant. The finding that attention could be independently driven by value (i.e., value-driven) has been replicated by other researchers (e.g., Bucker & Theeuwes, 2017; Le Pelley et al., 2015; Pearson

et al., 2015) and extended to learned associations between stimuli and aversive outcomes (e.g., Anderson & Britton, 2019; H. Kim & Anderson, 2021; Nissens et al., 2017; Schmidt et al., 2015).

Since then, value-driven attentional capture (VDAC) has been demonstrated across a variety of stimulus features including color (Anderson et al., 2011a; Le Pelley et al., 2015), orientation (Laurent et al., 2015; Theeuwes & Belopolsky, 2012), shape (Della Libera & Chelazzi, 2009: Della Libera et al., 2011), object category (Donohue et al., 2016; Hickey et al., 2015), semantics (Grégoire & Anderson, 2019), and even within the auditory domain (Anderson, 2016c; A. J. Kim et al., 2021a, b). Although statistical learning has been able to shape spatial attention (e.g., Jiang, 2018; Jiang et al., 2013; Jiang et al., 2015), sometimes even flexibly depending on task demands (e.g., Britton and Anderson, 2020), reward history effects on spatial attention seem to rely on relational information within real-world scenes (Anderson & Kim, 2018a, b; see also Jiang et al., 2015; Won & Leber, 2016). Interestingly, reward seems to also modulate priming (Hickey et al., 2014), suggesting that selection history effects can interact amongst each other, or that short-term effects (e.g., inter-trial priming) and longer-term relationships (e.g., reward history) can influence each other.

1.2.2. Neural Components of Reward History

I have reviewed some of the rich and varied effects that reward history can have on attention, but how is reward history represented in the brain? In this section, I will describe the more general role of dopamine (DA) in learning and motivated behaviors relevant to reward history, before going into the neuroimaging results that will provide an understanding behind the neurobiology of this phenomenon. Electroencephalogram (EEG) recordings, especially the N2Pc ERP component, has proven extremely useful and serves as a well validated method to explore

reward history effects on attention (e.g., Bachman et al., 2020; Hickey et al., 2010). One such study found that reward associations did not speed up attentional orienting but increased the strength of stimulus processing when compared to physical salience (Bachman et al., 2020). However, EEG cannot reliably record neural activity that occurs beneath the surfaces of the brain, and given the importance of subcortical structures in this phenomenon (Anderson et al., 2014; Anderson et al., 2016; Anderson et al., 2017; Yamamoto et al., 2013), the neuroimaging findings I explore will be restricted to fMRI studies.

As was alluded to earlier, reward history is acquired on a trial-by-trial basis over time through reinforcement learning, and more specifically, through reward prediction-errors (RPE; Chang et al., 2016; Schultz, 2015). An organism will continuously expect a certain outcome from a stimulus or an action, and the greater the difference between the actual and expected outcome, the greater the increase in firing rate of DA neurons within the ventral midbrain. Since DA-mediated RPE drives learning, in this scenario, it has been called the teaching signal, and is the mechanism in which reward history is acquired. Using Position Emission Tomography (PET), researchers have confirmed the role of DA in both the acquisition of reward history, as well as its persisting effect on distraction (Anderson et al., 2016; Anderson et al., 2017). DA release in the right anterior caudate was associated with attentional biases towards reward-predictive cues during the acquisition of reward history (Anderson et al., 2017), and DA release within the caudate and posterior putamen during test phase, in which the previously reward-associated cue served as a task-irrelevant distractor, predicted VDAC (Anderson et al., 2016). Not all functions in the brain are related to DA release, and thus findings from fMRI studies related to reward history are equally important.

The presence of previously reward-associated stimuli evokes elevated activity in the caudate tail, ventral visual, and early visual cortex (Anderson et al., 2014; Anderson et al., 2016; Anderson et al., 2017; Barbaro et al., 2017; Donohue et al., 2016; Hickey & Peelen 2018, 2019; Kim & Hikosaka, 2013; Serences, 2008; Serences & Saproo, 2010; Yamamoto et al., 2012, 2013; see Anderson, 2019 for a review). Anderson (2019) provided a unifying account for these findings with a proposed value-driven attentional network. In the proposed pathway, early, feature-selective visual cortex sends a value-dependent priority signal along dorsal and ventral visual pathways that culminates in the parietal cortex and the caudate tail. Information from multiple sources is aggregated and weighted in a spatial priority map in the parietal cortex and superior colliculus (SC).

As mentioned in a section above, there are multiple priority maps in the brain, and there could also be multiple maps that guide value-driven attention. Zénon and Krazulis (2012) found that by inactivating SC, spatial attention was impaired, while leaving attentional modulations in the cortex intact; thus, providing direct evidence of an independent priority map. LIP (Peck et al., 2009) and FEF (Bichot & Schall, 1999; Ding & Hikosaka, 2006) may potentially serve as priority maps for reward history, but since their role has not been dissociated, they could just reflect priority maps in either the parietal cortex or SC. Depending on the task demands, however, other regions like the amygdala, anterior cingulate cortex, and anterior insula may also be involved (Hickey et al., 2010; Ousdal et al., 2014; Peck & Salzman, 2014; Wang et al., 2015). Unlike other components of selection history, there is a rich source of knowledge regarding reward and attention in either a learning capacity or when it persists and continues to capture attention (but see Kim et al., 2021).

1.3. Attention and Reward History in Abnormal Behavior

The automatic influence of reward history on attention can be adaptive and promote survival by detecting valuable or rewarding opportunities without voluntary control (Anderson, 2021a). However, abnormal levels of attentional biases towards reward-associated stimuli can become maladaptive and even clinically relevant (Anderson, 2016b; Anderson, 2020b). In this section I will first outline the relationship between reward history and clinical syndromes (attention-deficit hyperactivity disorder; ADHD, depression, addiction, and risky behavior), before focusing on the utility of reward history as a model for drug-dependence and highlighting the need for a deeper understanding of reward history.

1.3.1. Reward History in Clinical Disorders

The magnitude of reward history effects on attention varies among individuals but exists on a continuum that can become problematically strong or weak. Anderson (2021b) offered an integrative framework to understand abnormal and clinically relevant expressions of value-driven attentional capture. In this account, excessively strong VDAC, or hypersensitivity to reward history effects on attention, is related to addiction and risky behaviors. Patients suffering from drug-dependence and populations with a history of risky behaviors have been shown to exhibit stronger VDAC compared to controls (Anderson et al., 2013; Anderson et al., 2016). This was further corroborated by Albertella et al. (2019) who found that resistance in reversal learning of reward cues correlated with risky alcohol use. Although reward history persists in neurotypical populations, neurotypicals are better able to utilize cognitive control to reorient their attention in lab experiments, which may translate to an ability to avoid compulsive behaviors that can lead to deleterious outcomes. On the other hand, insufficient reward history

effects on attention are related to depression and attention-deficit hyperactivity disorder (ADHD).

A characteristic symptom of depression is blunted reward processing (see Henriques & Davidson, 2000 for review), so although a decrease in VDAC was expected, it was still surprising that individuals with moderate to severe depression did not exhibit any attentional capture towards previously reward-associated stimuli (Anderson et al., 2014b). As this particular population still exhibited biased attention for former targets (Anderson et al., 2017), another component of selection history, it seems that reward history simply failed to influence attention. The outcome here is slightly different to those with diagnosed ADHD. Sali et al. (2018) employed children with ADHD to perform the VDAC task and rewarded them during the test phase to maintain motivation and engagement. They found, however, that VDAC rapidly extinguished in those with ADHD compared to controls, demonstrating a preference for immediate rewards over long-term reward associations (Patros et al., 2016). Taken together, it is clear that reward history relates to a variety of psychopathology and could be potentially useful as a model to understand clinical disorders. Owing to an abundance of symptomatic overlap, the clearest utility currently for reward history is in understanding and potentially treating drug-dependence.

1.3.2. Utility of Reward History in Clinical Interventions

A prominent explanation for drug-dependence is the incentive-salience theory, which posits that a Pavlovian learning mechanism links stimuli or contexts (conditioned stimulus, CS) with the properties of the drug (unconditioned stimulus, US), which over time affords the CS exaggerated motivational value, or incentive salience (Pavlov, 1927; Robinson & Berridge, 1993). This salience persists despite the drug no longer being rewarding or pleasant, and even

after withdrawal symptoms have subsided (Robinson & Berridge, 1993; Berridge & Robinson, 2016) because learning has imbued the cue with the motivational properties linked to the US. Attentional biases are an indicator of incentive salience (Berridge, 2012), and the magnitude of attentional biases towards drug-related stimuli is predictive of relapse (Carpenter et al., 2006; Cox et al., 2002; Marissen et al., 2006; Powell et al., 2010; Waters et al., 2003), and patients abstaining from a substance of abuse continue to exhibit persisting attentional biases towards related drug cues (Field & Cox, 2008; Field et al., 2013; Marissen et al., 2006; Stormak et al., 1997). This inability to reorient away from a drug-related cue can be modeled by the VDAC (or other reward history-related) paradigm.

Like drug-related cues for drug-dependent populations, reward history effects have been shown to persist (past six months) after initial learning (Anderson & Yantis, 2013) and even transfer to tasks outside of visual search (e.g., Anderson et al., 2012). PET studies have identified the striatum as a region of interest for both cue-evoked drug craving (Volkow et al., 2003; Wong et al., 2006) and attentional biases towards monetary rewards (Anderson et al., 2016, 2017; see also Yamamoto et al., 2013), indicating a shared mechanism of habit learning (Anderson, 2016b). This is further supported by Luijten et al. (2012) who showed that neural activity to drug-related cues was reduced after the availability of dopamine was restricted with dopamine antagonists.

Cognitive-Behavioral Therapy (CBT) is the most common form of treatment for drug-dependence and focuses on identifying maladaptive behavioral patterns, enhancing self-control, and coping with cravings (Mchugh et al., 2010). CBT often incorporates extinction learning and attention bias modification to help patients reorient their attention effectively (Heitmann et al., 2018; Kaplan et al., 2011; Torregrossa & Taylor, 2013). Despite the importance of cognitive

control in curbing addiction, conventional CBT has not been effective at treating addiction (Heitmann et al., 2018; Kaplan et al., 2011; Torregrossa & Taylor, 2013). Additionally, there have been some studies that fail to predict relapse from the magnitude of attentional capture from drug-related cues (Field et al., 2013; Waters et al., 2003), emphasizing the continued demand for more research into addiction-related attentional biases. However, drug-dependent populations are difficult to recruit, and research with them may not be the most fruitful if we still do not fully understand how a healthy brain successfully reorients attention. Since VDAC can model the persisting incentive salience of drug cues in patients with drug dependence, we can uncover potential mechanism to treat substance use disorder by understanding how to overcome or extinguish VDAC.

1.4. The Present Study

Reward history effects on attention emerged recently, and we still have much to learn before being able to effectively inform clinical interventions. Some studies have extended reward history effects from basic visual features to complex objects (e.g., Donohue et al., 2016) and regions in space (Anderson & Kim, 2018a, b), but the extent of its effects remain unknown. Investigations into boundary conditions could lead to a never-ending endeavor, but it is at least important to understand scenarios that are relevant to everyday life. Visual search can get even more abstract than quadrants in a scene, becoming sequences or patterns of eye movements in baggage screening in security contexts (Kramer et al., 2019; Mitroff et al., 2018). On the other hand, visual search can involve searching for objects defined by a conjunction of simple features, which may be important when picking your favorite candy based on color and shape instead of shape alone. These are both situations that are vastly different than the modified singleton search

task employed in Anderson et al. (2011a), and the brain should theoretically adapt to the increased complexity accordingly.

In the chapters that follow, I present experiments that investigate the scope of reward history effects on attention. I will utilize a variety of modified VDAC paradigms to understand the extent of reward history effects in oculomotor behavior and conjunction features, as well as fMRI to uncover how the brain represents multiple valuable stimuli. Furthermore, I will use neuroimaging to uncover how the brain supports reward history in the context of spatial orienting to understand the neurobiology behind value-driven attention for more complex features. Lastly, I will explore one potential mechanism to counteract persisting reward history effects on attention.

2. REWARD HISTORY MODULATES EYE MOVEMENTS*

2.1. Introduction

Although reward history has been shown to impact a variety of stimulus features (e.g., Anderson et al., 2011a; Anderson & Kim 2018a, b; Della Libera & Chelazzi, 2009; Donohue et al., 2016; Laurent et al., 2015; Theeuwes & Belopolsky, 2012), the influence of reward learning on the oculomotor system itself has not been investigated. Saccades are rapid, ballistic movements of the eye that change the point of fixation, which can be triggered reflexively (Purves et al., 2012); this allows us to foveate stimuli of potentially high interest, maximizing our ability to process these stimuli with high visual acuity.

Reward seems to have a direct influence on both the speed and direction of saccade programming (Bendiksby & Platt, 2006; Bucker et al., 2015; Ikeda & Hikosaka, 2003; Kawagoe et al., 1998; Milstein & Dorris, 2007, 2011; Takikawa et al., 2002; Theeuwes & Belopolsky, 2012; Yamamoto et al., 2013). Even though a target remained on the display, the animals would consistently generate initial errant saccades to a task-irrelevant location in space previously associated with reward. In this situation, the reward-associated region is devoid of stimuli but still able to elicit saccades (Sohn & Lee, 2006). Additionally, human participants exhibited increased peak saccade velocity on potential reward trials (Chen et al., 2014).

Directional saccades reflect an overt behavior, which might be subject to biases arising from reinforcement learning. However, it remains unclear whether reward learning can bias the generation of eye movements in a particular direction, separately from the particular region of space to which they are made. The present study was designed to address the question of whether reward learning can bias the direction of eye movements per se. In the present study, I provided monetary incentives to encourage participants to orient towards a specific cardinal direction (i.e.,

*Parts of this chapter are adapted with permission from Liao and Anderson, 2020a

high-value direction). The high-value direction was decoupled from specific regions of space by having participants fixate initially at the center of the screen, and then to one of four cardinal directions before a decision-making task occurred. The decision-making task consisted of saccading to one of four peripheral targets, placed with random jitter in each of the four cardinal directions from the point of current fixation. Saccading to a target in one direction was associated with more reward (probabilistically) than saccading to a target in any of the other directions. In this task, the initial saccade from central fixation is, in principle, analogous to the different contexts (scenes) in Anderson & Kim's (2018 a/b) paradigm, as it separated the rewarded direction from a specific spatial location on the screen.

Here I examine whether participants could robustly learn which direction was the optimal direction in which to orient during training, and whether such learning would transfer to performance in an unrewarded visual search task. To this latter end, I measured eye movements after training in both an unguided (visual foraging, Experiment 1) and guided (saccade to a shape-defined target, Experiment 2) visual search task, given the potential distinction between the two as evident in value-driven attention to spatial locations (see Anderson & Kim, 2018 a/b).

2.2. Experiment 1

2.2.1. Methods

2.2.1.1. Participants

Forty participants (18–35 years of age, M = 22.2 years; 25 females, 15 males) were recruited from the Texas A&M Community. Participants were compensated with money earned in the experimental task. All reported normal or corrected-to-normal visual acuity and normal color vision. The data from one participant were dropped and replaced with data from a new participant due to an inability to reliably track eye position (resulting in a failure to register a

target fixation on over 30% of trials); thus, 41 individuals in total were consented and participated. All procedures were approved by the Texas A&M University Institutional Review Board and conformed with the principles outlined in the Declaration of Helsinki. The sample size of n=40 was determined a priori and would yield $\beta > 0.80$ to detect an effect as small as $dz = 0.46$ (computed using G*Power 3.1), which was smaller than the effect size for reward learning on eye movements evident in Anderson and Kim (2018a/b).

2.2.1.2. Apparatus

A Dell OptiPlex equipped with Matlab software 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. Eye position was monitored using an EyeLink 1000-plus desktop-mount eyetracker (SR Research, Ottawa, Ontario, Canada). Head position was maintained using an adjustable chin rest (SR Research).

2.2.1.3. Design

2.2.1.3.1. Training Phase

Each trial consisted of a fixation display, a secondary fixation display, a choice array, and a reward feedback display (see Fig. 1A). The fixation cross (1.3° visual angle) remained on the screen until eye position had been registered within 1.8°of the fixation cross for a continuous period of 500ms. After a 200ms blank screen, a circle would then appear in one of four cardinal directions at 5.8° eccentricity and remain until eye position had been registered within 3.4° of the center of the circle for a continuous period of 250ms. A choice array consisting of four grey circles jittered (randomly up to 20° of arc in either direction from the cardinal positions) on an imaginary circle with a radius of 8.2° was then presented until fixation on a target was registered for a continuous period of 150ms. The grey circles were approximately 1.0° in radius, and a

region extending 2.5° beyond the boundary of the circle was used as an area of interest for determining target fixations. Once a fixation on a target was registered, the chosen circle would turn green for 500ms before a 200ms blank screen. After which, the reward feedback display was presented for 1,500ms, and consisted of the money earned on the current trial along with the updated total earnings. Each trial concluded with a 1,500ms blank interval.

Participants were instructed to fixate ("look directly at") the cross to begin each trial, then to fixate on the first circle, and then choose the best one out of four circles to look at. The first circle appeared randomly in the four cardinal directions, with the constraint that a circle appeared in each position equally-often in each block of the task. Fixating on a circle appearing in one direction (up, right, down, or left, counterbalanced across participants) in the display with four peripheral circles was associated with an 80% probability of a high reward of 10¢, and a 20% probability of a low reward of 2¢, while for the other directions these percentages were reversed. Each block consisted of 60 trials, the order of which was randomized.

2.2.1.3.2. Test Phase

Each trial consisted of a fixation display (until fixation was acquired for a continuous period of 500ms), a search array until target was found, and a 1,500ms feedback screen (see Fig. 1B). The search array consisted of 10 circles (two in two quadrants and three in two quadrants, counterbalanced across trials), with each circle 0.9° in radius. On each trial the circles were at least 2.9° away from the edge of the screen, 6.4° away from any other circle and 7.4° away from the center of the screen.

A region extending 2.5° beyond the boundary of the circle was used as an area of interest for determining stimulus fixations. Participants were instructed to look directly at different circles until the target was found. There was no explicit time pressure, and participants could not

time out. Selection of a circle was registered after 100ms of continuous fixation on that circle, after which the circle would disappear if it was not the target or turn green for 500ms to indicate that the target had been found. The feedback display consisted of the words "Trial Complete!" presented at the center of the screen. The target appeared equally-often in each quadrant. Each block consisted of 48 trials (with each combination of 3 and 2 stimuli per quadrant presented eight times), the order of which was randomized.

2.2.1.4. Procedure

Participants completed 4 blocks of trials of the training phase, followed by 3 blocks of trials of the test phase. Both the training and test phases were preceded by interactive instructions that included practice trials (4 for the training phase and 6 for the test phase). Participants were paid the amount of money earned in the training phase at the completion of the experiment (mean = $16.81, range = $8.96 - $20.08).

2.2.1.5. Measurement of Eye Position

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 different runs of the task, during which they were allowed to reposition their head to maintain comfort. Eye position was calibrated prior to each block of trials using a 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 had been registered within 1.8° visual angle 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).

2.2.1.6. Analysis of Saccades

I calculated the direction of saccade in the test phase via the coordinates of the circle fixated. If the distance from the prior fixation to the next circle fixated was greater in the x than y dimension, then the direction of saccade was either to the left or right as opposed to up or down. The direction of saccades was summed up, separately for each saccade made in the trial (first, second, third, etc.), and the proportion of high-value choices was calculated. The resulting proportions were then corrected for training-independent biases to look in a particular direction by subtracting the proportion of choices in that high-value direction computed across participants in the other training conditions, and tested against zero using a one-sample t-test. A parallel analysis was performed on the number of saccades required to find the target by the quadrant within which the target was located.

2.2.2. Results

2.2.2.1. Training Phase

Participants were able to learn the reward association, with 70.5% of all saccades going in the high-value direction (as opposed to 25% if participants made saccades in random directions), $t(39) = 11.765$, $p < 0.001$, $d = 1.860$. Saccades made in the high-value direction increased over the course of the task, from 52.7% in the first block to 81.3% in the last block, $t(39) = 7.419$, $p < 0.001$, $d = 1.173$. To determine whether the learning was robust to the direction of the initial (first-step) saccade, as would be predicted from a directional bias rather than a bias to orient to a particular region of space, I ran a paired samples t-test comparing the percentage of high-value target choice between first-step saccades in the rewarded direction and in the opposite direction and found no difference between them in any block (ps > 0.120).

2.2.2.2. Test Phase

Rewarding directional saccades during training produced an 8.1% increase in the frequency of initial saccades made in the high-value direction, which was significant, $t(39) = 2.99$, $p = 0.005$, $d = 0.472$ (visual depiction of this effect is shown in Fig. 2 and 3). The magnitude of this bias did not significantly differ across the four training conditions, $F(3,36) = 0.82$, $p = 0.491$. This bias was also robust to extinction, being individually significant in the first (7.9%) and last (6.9%) block of the test phase, ts > 2.49, ps < 0.018, ds > 0.39, with the difference between blocks being non-significant, $t(39) = 0.45$, $p = 0.658$. For completeness, I also investigated the second and third saccades relative to the center and to the prior circle fixated. Only the second saccade relative to the first circle fixated was significant, $t(39) = -2.39$, $p = 0.022$, $d = -0.379$ (other ps > 0.17), reflecting a bias to look in a different direction.

Analysis of the number of saccades required to find the target mirrored the bias in the direction of the initial saccade, with fewer overall saccades observed when the target was in the high-value quadrant (mean = 5.19) compared to a low-value quadrant (mean = 5.50), $t(39) = 2.20$, $p = 0.034$, $d = 0.35$.

2.2.3. Discussion

Previous studies have investigated direction and speed of saccades towards a previously reward-associated object as an index of value-driven attentional capture (Anderson & Yantis, 2012; Bucker et al., 2015; Kim & Anderson, 2020b; Kim & Anderson, 2019a; Le Pelley et al., 2015; Milstein & Dorris, 2007; Milstein & Dorris, 2011; Theeuwes & Belopolsky, 2012), but the reward association is never assigned to the eye movement itself. In the present study, through a combination of reinforcement-guided selection history and reward feedback, participants were encouraged to repeatedly make saccades towards a target in a particular direction. The training contingencies had a robust influence on eye movements, with 70% of all choice saccades

occurring in the reward-associated direction. This saccade preference was driven by a bias to orient in a particular direction rather than to stimuli appearing within a particular region of space, as participants were equally likely to look in the high-value direction regardless of the direction of the initial saccade. This suggests that the high-value direction had greater attentional priority than low-value directions. Because participants were not explicitly informed of the reward structure of the task, this attentional bias was the result of learning from experience.

Despite the irrelevance of reward associations in the test phase, participants were still biased to make initial saccades in the direction previously associated with high reward, but the bias to saccade in the previously-rewarded direction did not persist past the first saccade. That the bias was restricted to the first saccade is not surprising given that there are more potential targets remaining in the directions other than that of the prior choice given the structure of the stimulus displays used (and possibly no stimuli further in the initially-saccaded direction that could be fixated next on some trials, which may explain the tendency to saccade in a direction different from the previously-rewarded direction following the initial saccade).

The unguided visual search task employed in the test phase assessed the influence of prior learning without competing influences of goal-directed attentional priority, analogous to the free-viewing task of Anderson and Kim (2018a/b). No one element in the display was distinct from the others, providing no basis for feature-based guidance. The resulting search patterns provide direct support for an influence of reward history on the oculomotor system when searching through a display.

2.3. Experiment 2

Experiment 1 demonstrated a bias to direct an initial saccade in the direction previously associated with high reward during unguided visual search (foraging). In Experiment 2, I sought

to determine whether a similar bias would be evident in the context of goal-directed visual search. To this end, following the same training procedure, participants completed a test phase in which the task was to saccade to a shape-defined target. Of interest was whether eye movements would be facilitated on trials in which the target appeared in the previously reward-associated direction, consistent with a bias to execute a saccade in that direction. It cannot be assumed that the oculomotor bias evident in the test phase of Experiment 1 would be sufficiently strong to exert an influence over-and-above goal-directed influences on oculomotor priority in a goal-directed search task, as attentional biases for regions of space do not translate from unguided (free viewing) to guided search when the scenes do not contain objects that could themselves guide attention (Anderson & Kim, 2018a/b).

2.3.1. Methods

2.3.1.1. Participants

Forty new participants (18–35 years of age, M = 22.5 years; 27 females, 12 males, 1 no response) were recruited from the Texas A&M Community. Participants were compensated with money earned in the experimental task (mean = $16.15, range = $10.80 - $20.16). All 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 conformed with the principles outlined in the Declaration of Helsinki.

2.3.1.2. Apparatus

The apparatus was identical to that used in Experiment 1.

2.3.1.3. Design

2.3.1.3.1. Training Phase

The training phase was identical to that used in Experiment 1, with the exception that a cross was used instead of a circle for the first-step saccade before the directional choice display, to more closely match the appearance of the stimulus displays used in the test phase.

2.3.1.3.2. Test Phase

Similar to the training phase, each trial consisted of a fixation display, a secondary fixation display, and a search array (see Fig. 4). The fixation display (cross 1.3°) remained on the screen until 500ms of continuous fixation within 1.8° of the fixation cross had been registered. After a 200ms blank screen, the same cross (with the same fixation window) would appear in one of four cardinal directions at 5.8° eccentricity and remain until eye position had been registered within the fixation window for a continuous period of 250ms. A search array consisting of four grey shapes jittered (randomly up to 20° of arc in either direction from the cardinal positions) on an imaginary circle with a radius of 7.9° was then presented for 1000ms or until fixation on a target was registered for a minimum of 150ms. The nontarget shapes were always a square (2.3°), a diamond (2.2°), and a triangle (3.0°), and the target shape was always a circle (2.85°). A region extending 3.9° beyond the center of each shape was used as an area of interest for determining stimulus fixations.

The shapes appeared randomly in each cardinal direction, with the constraint that the target circle appeared in each cardinal position equally-often in each block. Participants were instructed to "look at the circle as fast as possible." If the target was the first shape fixated, it would turn green; otherwise, the non-target shape the participant looked at first would turn red. Correct and incorrect feedback (color change) were presented for 500ms, while timeout feedback with the words "Too Slow!" at the center of the screen was presented for 1000ms. Each block consisted of 80 trials, the order of which was randomized.

2.3.1.4. Procedure

The procedure was identical to that of Experiment 1.

2.3.1.5. Analysis of Fixations and Response Times

For the test phase, a trial was considered valid if the target appeared in the previously high-value direction, and invalid if it appeared in any of the other three directions. Only correct responses were included in the mean RT for each participant, and RTs exceeding 2.5 standard deviations (SDs) of the mean for each condition for each participant were trimmed. The RT trimming procedure resulted in the exclusion of 2.6% of trials. The validity effect was calculated by subtracting valid target RTs from invalid target RTs, which were normalized in the same manner as Experiment 1 to account for training-independent biases to more rapidly saccade to a target in a particular direction.

2.3.2. Results

2.3.2.1. Training Phase

Participants were able to learn the reward association, with 64.1% of all saccades going in the high-value direction (as opposed to 25% if participants made saccades in random directions), $t(39) = 11.565$, $p < 0.001$, $d = 1.829$. Saccades made in the high-value direction increased over the course of the task, from 43.1% in the first block to 76.1% in the last block, $t(39) = 8.385$, $p < 0.001$, $d = 1.326$. Learning rates were overall similar to Experiment 1, as the percent of saccades in the high-value direction did not differ between experiments either in total or in the last block of trials (ps > 0.21). To determine whether the learning was robust to the direction of the initial (first-step) saccade, as would be predicted from a directional bias rather than a bias to orient to a particular region of space, I ran a paired samples t-test comparing the percentage of high-value target choice between first-step saccades in the rewarded direction and

in the opposite direction and found no difference between them in any block (ps > 0.131). The results from the training phase closely replicate the findings from Experiment 1.

2.3.2.2. Test Phase

Rewarding directional saccades during training produced a 9ms increase in the validity effect, which was significant, $t(39) = 2.47$, $p = 0.018$, $d = 0.389$ (see Fig. 5). No corresponding bias was evident in accuracy, $t(39) = 0.041$, $p = 0.967$, which was overall high (mean accuracy = 99.3%), indicating that the RT data were not contaminated by a speed-accuracy tradeoff.

The cuing effects observed in RT differed by training condition, $F(3,36) = 4.07$, $p = 0.014$, $\eta_p^2 = 0.253$, being particularly pronounced for the participants for whom the bottom location was associated with high-value ($p = 0.12$ for the same ANOVA with this condition removed). It was also the case that participants were generally slower to saccade to the bottom location collapsed across training conditions: 471 ms vs. 417, 413, and 419 ms (top, right, and left, respectively), ts > 8.75, ps < 0.001, ds > 1.38. Although the reason for the differential effectiveness of the different training conditions is unclear, given the generally slower RTs when saccading in the bottom direction it may be the case that participants simply had more room for improvement in this condition as a result of reward bias. To determine if the observed cueing effects were driven by a general bias towards a particular region in space rather than a directional bias, I ran a 2x2 analysis of variance (ANOVA) with first-step saccade (high-value/opposite direction) and validity (valid/invalid) as factors, which revealed no significant interaction between the two, $F(3,156) = 1.08$, $p = 0.359$. The results from the test phase of Experiment 2 therefore replicate a bias in directional saccades arising from reward history, in this case extending to a context in which eye movements were also guided by feature-based task goals.

2.4. Summary and General Discussion

The findings of this chapter extend our understanding of the effects of prior reward learning on attention to the direction of eye movements. I provide clear evidence for reward learning modulating saccadic behavior on choices during learning (training phase) and on the execution of directional eye movements during extinction (unrewarded test phase).

In the rewarded training phase, participants made more saccades in the high-value direction and the magnitude of this bias did not differ across first-step saccade direction (i.e., the starting point around which the stimuli were presented on the screen). This suggests that participants learned a directional association instead of associating reward with a particular region of space. This learning had a broad and persistent influence on the execution of future eye movements, transferring to both unguided search (a different oculomotor choice task) and guided search (forced-choice orienting). This latter result suggests that the consequence of reward learning on saccades extends beyond the choices participants made and is not specific to a decision-making context. My results provide clear evidence that, at least under certain circumstances (see Dunne et al., 2015; 2019; Jiang et al., 2013; Jiang et al., 2015; Won & Leber, 2016), it is possible to shape oculomotor behavior with rewards.

3. NEURAL CORRELATES OF VALUE-DRIVEN SPATIAL ORIENTING

3.1. Introduction

The neural correlates of value-driven attention for features are well established (see Anderson, 2019 for a review), but the neural mechanisms that support reward history effects on spatial attention are less understood (Anderson & Kim, 2018a, 2018b; Chelazzi et al., 2014; see also Liao & Anderson, 2020). Bourgeois et al. (2022) modified the test phase of the VDAC paradigm to include an exogenous spatial cue and found that FEF, parietal cortex, SC, and striatum were involved in both goal-directed and reward-related shifts of attention. Evidence from both behavior and neuroimaging (Bourgeois et al., 2022; see also Anderson, 2019 for review) suggests that a common system underlying value-driven attentional orienting that integrates sources of feature- and space-based guidance.

A unique element of value-driven spatial orienting in the paradigm of Anderson and Kim (2018a, b) is the reliance on object-rich scenes that can provide contextual information about where to guide overt attention (Brockmole & Henderson, 2006a, 2006b). With the inclusion of complex objects and spatial layout that collectively serve as a cue for a high-value region, I expect parts of the medial temporal lobe like the hippocampus and parahippocampal gyrus—not previously implicated in value-driven feature-based attention (see Anderson, 2019)—to play an important role in signaling scene-specific spatial biases. The caudate tail receives input via the ventral visual stream and in particular the visual cortico-striatal loop (Anderson, 2019; Seger, 2013); the ventral visual cortex is robustly activated by complex scenes in a manner modulated by reward (Barbaro et al., 2017; Hickey & Peelen, 2015, 2017), and the caudate tail runs adjacent to the hippocampus and surrounding parahippocampal gyrus, which play a well-defined role in spatial memory (Epstein & Kanwisher, 1998; Maguire et al., 1996; O'keefe & Nadel,

*Parts of this chapter are adapted with permission from Liao et al., 2020a

1978). Value-driven attention for low-level features are sensitive to specific scene contexts (Anderson, 2015a, 2015b; see also Gregoire et al., 2021) which, along with the caudate tail's proximity to the medial temporal lobe (Seger, 2013) and its connections with the superior colliculus (Yamamoto et al., 2012), raise the possibility that this network of brain regions is collectively involved in representing value-driven spatial orienting.

Using human fMRI, I employed a whole-brain approach to investigate the representation of task-irrelevant, value-driven spatial orienting biases using the paradigm established by Anderson and Kim (2018a). In this task, valid trials necessitate an eye movement to the region of a scene previously associated with high value, while on invalid trials I expected less robust processing of the previously reward-associated region. Given the aforementioned considerations, I hypothesized that, when controlling for the position of the target, valid trials would be associated with more robust activation (biased competition driven by the reward history of the target quadrant) in oculomotor regions of the brain previously implicated in value-driven feature-based attention (caudate tail, superior colliculus, frontal eye field) in addition to the hippocampus and parahippocampal gyrus given the reliance on scene context. It is important to note that this paradigm focuses on spatial biases as measured by overt attentional orienting, which may yield different findings compared to covert spatial attention (Hunt & Kingstone, 2003a; 200b).

3.2. Methods

3.2.1. Participants

Forty-seven participants (18-35 years of age, M = 22.83 years, SD = 4.55; 24 females, 23 males) were recruited from the Texas A&M Community. The demographic information for one participant was lost due to experimenter error. Participants were compensated with money earned in the experimental task. All 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 conformed with the principles outlined in the Declaration of Helsinki. All participants provided written informed consent. Of the 47 recruited participants, 12 did not meet the required task performance to continue in the scanner (failed to robustly learn the pairings between locations in scenes and reward or could not perform that test phase task with sufficient accuracy), and one withdrew partway through the scan. The final sample consisted of 34 participants who completed the entire experiment, for which 33 of their demographic data is available (M = 22.33 years, SD = 4.36; 15 females, 18 males). The obtained sample size provided power (1-β) > 0.9 to replicate an effect of reward learning on eye movements in the test phase of Anderson and Kim (2018a, b) (computed using G*Power 3.1), and was similar to (and in most cases exceeded) the sample sizes used in prior studies of the neural correlates of value-driven attention (Anderson et al., 2014; Anderson, 2017; Itthipuripat et al., 2019; Barbaro et al., 2017; Hickey & Peelen, 2015; Kim & Anderson, 2020a, 2020b; Kim & Anderson, 2019b, 2019c).

3.2.2. Apparatus & Stimuli

In-lab tasks were completed on a Dell OptiPlex equipped with Matlab software and Psychophysics Toolbox extensions (Brainard, 1997). Stimuli were presented on a Dell P2717H Monitor. Participants viewed the monitor from a distance of approximately 70cm in a dimly lit room. Manual responses were entered using a standard keyboard. Eye-tracking was conducted using the EyeLink 1000 Plus system while head position was maintained using a manufacturer-provided chin rest (SR Research Ltd). Stimulus presentation during the fMRI portion was controlled by an Invivo SensaVue display system. The eye-to-screen distance was approximately

125cm. Responses were entered using Cedrus Lumina two-button response pads. An EyeLink 1000 Plus system was again used to track eye position.

3.2.3. Design

3.2.3.1. Training Phase

Each trial began with a fixation cross (1.1º visual angle) that remained at the center of the screen until eye position had been registered within 1.8º of the fixation cross for a continuous period of 500ms (Fig. 6). After which, a scene image was displayed that filled the entire computer screen. Four grey rectangular outlines (9.1º x 6.9º) were also displayed at the center of each quadrant, the center of which were 11.4º away from the center of the screen. The scene and rectangles remained on the screen until eye position had been registered within the boundary of one of the rectangles for a continuous period of 1000ms. After a 500ms blank screen, the reward feedback display was presented for 1500ms and consisted of the money earned on the current trial along with the updated total earnings.

Participants were instructed to fixate ("look directly at") the cross to begin each trial, then to "pick a box and look directly at it". Participants were also informed that they would earn money on each trial, and the amount earned would depend on which box they looked in. Participants were encouraged to maximize their earnings by picking good boxes but were otherwise not provided any explicit information about which boxes were good. There were four 80-trial runs of the training phase during the in-lab visit, and two runs of abridged training phases that only had 40 trials while in the scanner. There were eight practice trials before the in-lab training phases where participants earned 5¢ on each trial but were informed that money earned was for demonstration purposes only. Eight different scenes were used in the experiment, totaling 50 presentations of each scene over 400 trials. The scenes were taken from the CB

Database (Sareen et al., 2016) and were used in previous studies of value-driven spatial orienting (Anderson & Kim, 2018a, b). For each scene, one quadrant (and the box it contained) was designated the high-value quadrant and yielded a 10¢ reward while picking any other boxes yielded a 2¢ reward.

Participants were assigned to one of four training conditions in alternating fashion, with each quadrant of each scene serving as the high-value quadrant in one of the four conditions. The order in which the scenes were presented to each participant was randomized. If eye-tracking was unable to be conducted in the scanner, participants instead used two two-button response pads to indicate their selection on each trial (one button per quadrant) and received some initial practice trials to learn the button mapping. To be eligible for the scanning session, participants needed to earn at least $10.00 during the training phase runs conducted in the lab, which was taken to indicate sufficiently robust learning of the scene-reward contingencies.

3.2.3.2. Test Phase

Each trial began with the presentation of one of the scenes from training along with the 4 rectangular boxes for 1200ms, followed by the presentation of a 1.1º "T" stimulus in white against a black background centered within each of the boxes. One "T" was tilted either 90º to the left or right and served as the target, while the other three "T"s were either upright or upside down (randomly determined with the constraint that all three non-target "T"s could not be oriented in the same direction). The display remained on screen for 2400ms during which participants could enter their response. That is, the duration of the display was fixed for all participants regardless of RT. For a subset of participants, eye-tracking data was also collected during this time and eye-positions within a region extending 4.6 º x 3.4 º beyond the boundary of the rectangle for a continuous period of 100ms were counted as fixations. Unlike the training

phase, eye movements in the test phase were neither encouraged nor discouraged, although the size and position of the "T" stimuli were such that the identity of the target would be very difficult to resolve using peripheral version. Each trial ended with a blank inter-trial-interval (ITI) which lasted 1200, 1800, 2400, 3000, or 3600ms (equally-often). The fixation cross reappeared 200ms for the last 200ms of the ITI to indicate to the participant that the next trial was about to begin. The test phase consisted of six runs of 80 trials each for a total of 480 trials, with each scene being presented a total of 60 times. During each run there were 16 trials where the "T" displays never appeared and the scene continued to stay on the screen for 2400ms (non-search trials). During the 64 search trials (containing "T" display) in each run, the target appeared in each box/quadrant of each scene equally-often (and thus target position was unbiased with respect to which quadrant previously served as the high-value quadrant). The target was titled 90º to the left and right equally-often for each scene. Trials were presented in a random order. At the end of each run, the accuracy on the 64 target present trials was displayed for six seconds to provide performance feedback.

During the in-lab visit, participants were instructed to press the "m" key with their right-hand index finger if the vertical line of the sideways "T" was on the left, denoting an arrow pointing to the right. If the vertical line of the sideways "T" was on the right, participants were instructed to press the "z" key with their left-hand index finger. To become familiar with the mapping, participants had 8 practice trials that included feedback displays that said "Correct!" or "Incorrect!" depending on their response, after which participants had four runs of 80 trials to reach 85% accuracy and be eligible for scanning. If participants reached 85% accuracy in one of these runs, they became eligible and moved on to the next task. During the scan-center visit,

participants were instructed to indicate the orientation of the target with their right-hand index and middle finger on the button response pad.

3.2.4. Procedure

The experiment consisted of a lab visit for 1hr followed by a scan-center visit on the following day. During the initial appointment, participants provided their consent, completed the MRI safety screening, and were screened for adequate performance on the behavioral task. The majority of scene-reward training took place during the lab visit. Each eligible participant underwent fMRI in a single 1.25hrs session that took place the following day. Participants completed one run of the training phase, three runs of the test phase, an anatomical scan, another run of the training phase, and lastly completed three more runs of the test phase. The abridged training phases were completed to re-instantiate the space-outcome associations to protect against possible extinction (e.g., Lee & Shomstein, 2014).

3.2.5. Measurement of Eye Position

During the lab visit, head position was maintained using an adjustable chin rest including a bar upon which to rest the forehead (SR Research). Participants were given a short break between different runs of the task, during which they were allowed to reposition their head to maintain comfort. 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. Participants were given short breaks in between runs where they were allowed to close their eyes but otherwise were encouraged to remain still. Eye position was calibrated prior to each run of trials using a 9-point calibration (Liao & Anderson, 2020a, 2020b; Liao et al., 2020) and was manually drift-corrected by the experimenter during the initial fixation

display as necessary. Due to the difficulty of measuring eye position in the scanner environment, eye data could only be acquired for a subset of participants (n = 19) during the scan session.

3.2.6. MRI Data Acquisition

MRI data was acquired with a Siemens 3-Tesla MAGNETOM Verio scanner and a 32-channel head coil at the Texas A&M Translational Imaging Center (TIC), College Station, TX. An anatomical scan was acquired using a T1- weighted magnetization prepared rapid gradient echo (MPRAGE) sequence (150 coronal slices, voxel size = 1mm isotropic, repetition time (TR) = 7.9ms, echo time (TE) = 3.65ms, flip angle = 8º). Whole-brain functional images were acquired using a T2*-weighted echo planar imaging (EPI) sequence (56 axial slices, TR = 600ms, TE = 29ms, flip angle = 52º, image matrix = 96 x 96, field of view = 240mm, slice thickness = 2.5mm with no gap), using the same parameters as Kim and Anderson (2019c, 2020a, 2020b). 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 of the 6 runs of the test phase lasted 8.1 mins during which 810 volumes were acquired.

3.2.7. Behavioral Data Analyses

In the training phase, performance was categorized in terms of how many times the high-value quadrant was chosen per run, averaged over the scenes. A one-way analysis of variance (ANOVA) was conducted on the proportion of high-value choice for each run, followed by pair-wise comparison between the first and last run of the training phase. Only training phase data collected in-lab were analyzed. In the test phase, RT was recorded from the onset of the four items comprising the search array, and RTs exceeding 2.5 SD of the mean of their respective condition or faster than 150ms were trimmed (2.78%). If eye-tracking data were available, the proportion of first saccade towards the high-value quadrant was compared to chance (25%); in

addition, on no-target trials (which amounted to a free-viewing situation), total fixation duration was also computed for each quadrant and the mean for the high-value quadrant was compared to the mean of a given low-value quadrant (mean across low-value quadrants divided by three, paralleling Anderson & Kim, 2018a, 2018b). Only correct responses were analyzed. The effect sizes *d* were also computed, but the data were not otherwise transformed. Data were analyzed using SPSS and MATLAB, and figures were generated in Python using the seaborn package (Waskom, 2021).

3.2.8. MRI Data Analyses

3.2.8.1. Preprocessing

All preprocessing was conducted using the AFNI software package (Cox, 1996). Each EPI run for each participant was motion corrected using the last image prior to the anatomical scan as a reference. EPI images were then coregistered to the corresponding anatomical image for each participant. The images were then non-linearly warped to the Talairach brain (Talairach & Tournoux, 1998) using 3dQwarp, and masks of activation locations were created for each participant using 3dAutoMask and combined using 3dmask_tool. Additionally, the cerebrospinal fluid mask was generated using 3dSeg and subtracted from the combined mask for all participants. Finally, the EPI images were converted to percent signal change normalized to the mean of each run, and then spatially smoothed to a resulting 5mm full-width half-maximum using 3dBlurToFWHM.

3.2.8.2. Statistical Analyses

All statistical analyses were performed using the AFNI software package. A general linear model (GLM) was performed on the test phase data and included the following regressors of interest: (1) valid trial, reward/target quadrant on the left, (2) valid trial, reward/target location

on the right, (3) invalid trial, both reward and target location on the left, (4) invalid trial, both reward and target location on the right, (5) invalid trial, target location on the left and reward location on the right, (6) invalid trial, target location on the right and reward location on the left, and no-target trials with (7) reward location on the left and (8) reward location on the right. Each regressor of interest was modeled using sixteen finite impulse response functions (e.g., Kim & Anderson, 2019c, 2020a, 2020b) beginning at the onset of stimulus presentation, and drift in the scanner signal was modeled using nuisance regressors.

To compare the peak of the haemodynamic response, the peak β value from the 3-6s range (i.e., 3, 3.6, 4.2, … 6) post scene display onset for each task-based regressor was extracted (Kim & Anderson, 2020a, 2020b) and submitted to a priori paired samples *t*-tests (two-tailed). Three paired samples *t*-tests were conducted on the peak beta weight estimates using the '-Clustsim' option under 3dttest++ (voxelwise $p < 0.005$, clusterwise $\alpha < 0.05$), a more conservative and non-parametric method for determining cluster-level threshold values (Cox et al., 2017). I compared trials where the target appeared in the previously high-value quadrant (valid) versus where the target appeared contralateral to the previously high-value quadrant (invalid), separately for each of the two hemifields (i.e., the peak of regressor 1 vs. 5 and 2 vs. 6) (as in Anderson et al., 2014; Anderson, 2017; Kim & Anderson, 2020a, 2020b). I focused on invalid trials in which the target was in the opposite hemifield as the previously reward-associated quadrant in order to isolate trials of maximal spatial competition between the target and reward history. The third paired samples *t*-test was conducted comparing no-target trials in which the previously reward-associated quadrant was on the left and right (i.e.., the peak for regressor 7 vs. 8). A post-hoc contrast using 3dANOVA3 was conducted to compare activations with respect to target hemifield (left vs right, collapsed across reward condition). This contrast

was 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 $p < 0.005$).

3.3. Results

3.3.1. Behavior

During the training phase, participants were able to learn the reward association. The proportion of trials on which the high-value quadrant was selected in the final run was high (0.962; see Fig. 7A) and averaged across all runs (0.784) was well above chance, $t(33) = 19.35$, $p < 0.001$, $d = 3.32$. Pairwise comparisons show that participants on average made more high-value choices on the last run compared to the first, $t(33) = 15.1$, $p < 0.001$, $d = 2.59$. During the test phase, accuracy was high (97.5%) and participants were faster to respond to valid trials compared to invalid trials, $t(33) = 7.99$, $p < 0.001$, $d = 1.37$ (see Fig. 7B). For the 19 participants I had eye tracking data for, initial fixations over all trials were significantly biased towards the high-value quadrant (33.6%), $t(18) = 7.68$, $p < 0.001$, $d = 1.76$. On trials where the targets and distractors were presented, initial fixations were significantly biased towards the high-value quadrant (33.5%), $t = 7.88$, $p < 0.001$, $d = 1.81$, and towards the target quadrant (29.0%), $t(18) = 2.70$, $p = 0.015$, $d = 0.62$. On trials where the target and distractors were not presented, total fixation duration was higher on high-value quadrants (2992 ms) compared to low-value quadrants (2012 ms), $t(18) = 4.33$, $p < 0.001$, $d = 0.99$ and initial fixations were significantly biased towards the high-value quadrant (38.4%), $t(18) = 3.84$, $p = 0.001$, $d = 0.88$. The behavioral data on both target-present and no-target trials fully replicate Anderson and Kim (2018a, 2018b).

3.3.2. Neuroimaging

I compared valid trials on which the target appears in the same quadrant that was previously associated with reward against invalid trials in which the previously reward-associated quadrant is in the opposite hemifield (see Fig. 8). Valid trials evoked elevated responses in oculomotor areas of the value-driven attention network (Anderson, 2017, 2019; Kim & Anderson, 2020a, 2020b) including the caudate tail, superior colliculus, and frontal eye field. I also observed increased activation on valid trials in the medial temporal lobes, particularly in regions associated with scene, space, and object processing like the hippocampus (O'keefe & Nadel, 1978), parahippocampal gyrus (Epstein & Kanwisher, 1998; Maguire et al., 1996), and the lateral occipital cortex (Grill-Spector et al., 2001). These are not regions typically associated with the value-driven attention network but may have been recruited to represent additional reward-related information in object-rich scenes. I also observed an increase in activity for the insula and anterior cingulate cortex (ACC), which have been previously implicated in reward-modulated attentional control (Hickey et al., 2010; Wang et al., 2015).

Probing no-target trials where only the scenes were presented revealed no significant activations as a function of whether the previously reward-associated quadrant was on the left or right. To examine target-related activation, I compared activity on trials where the target appeared on the left versus the right hemifield (see Fig. 9) and observed increased activity in the left extrastriate visual cortex and decreased activity in the right extrastriate visual cortex, indicating more elevated activation ipsilateral to the target. A complete list of all regions activated across all contrasts is provided in Supplemental Table 1.

3.4. Discussion

I used object-rich scenes in this experiment to provide contextual information about the location of high-value quadrants and observed increased activation on valid trials in regions of the brain known to play an important role in representing spatial layout, including the hippocampus, parahippocampal gyrus, and occipito-temporal cortex (Epstein & Kanwisher, 1998; Maguire et al., 1996; O'keefe & Nadel, 1978). In using scenes with distinct arrangement of objects, I also observed elevated activity in regions traditionally associated with object processing like the lateral occipital cortex (Grill-Spector et al., 2001). Such regions have not been previously implicated in value-driven attention and may be particular to reward's modulatory influence on spatial orienting in scenes. The caudate tail is particularly suited in playing a more central role in integrating value-based attentional priority across feature and space, given its role in the control of eye movements (Yamamoto et al., 2012, 2013) and proximity to both the hippocampus and parahippocampal gyrus on the one hand and its connections with the ventral visual stream on the other hand (Seger, 2013).

Another interesting finding is that when examining target-evoked activation as a function of hemifield collapsed across reward condition, there was greater activity in the visual cortex ipsilateral to the target. This seems to be a product of my experimental paradigm where participants were to some degree suppressing the background scene to better respond to the superimposed target. This interpretation is consistent with a prior finding where the multivoxel information content of objects in real-world scenes was suppressed for reward-associated distractors and the strength of this suppression was associated with the degree of distractor-related impairment (Barbaro et al., 2017; Hickey & Peelen, 2015; Seidl et al., 2012; van Zoest et al., 2021; see also Payne et al., 2008).

In summary, my findings lend support to the dual mechanism of value-driven attention proposed by Anderson (2019), as I found biased representation in the caudate tail but not the posterior parietal cortex. My task incorporated object-rich scenes into the signaling of value, with scene-space reward contingencies, which may have resulted in scene and object-specific regions to be recruited into the value-driven attention network, highlighting a greater flexibility in the neural computation of value-based attentional priority than previously assumed (Anderson, 2019).

4. THE INFLUENCE OF REWARD HISTORY ON NEURAL REPRESENTATIONS FOR MULTIFEATURE OBJECTS

4.1. Introduction

Our environment consists of multiple complex objects that are combinations of many simple features, but how representations of multiple individual features are integrated in the expression of value-driven attention remains unknown. The influence of reward history on attention has typically been demonstrated using simple features like color (e.g., Anderson et al., 2011a, Le Pelley et al., 2015; Pearson et al., 2015), but also extends to complex objects (Clement et al., in press; Donohue et al., 2016). Participants searched for a target color with objects overlaid on top of it, receiving extra rewards if the object was in a rewarded category. Although there were no significant differences in behavioral measures, when the target contained the rewarded object category and the distractor did not, the amplitude of the N2pc was larger and also earlier, indicating a stronger and more rapid shift of attention.

This is potentially the same mechanism that drives attentional capture towards drug cues amongst populations with substance use disorders (Field & Cox, 2008), as drug cues are often complex objects rather than simple colors and shapes. We know how the brain represents the elevated priority of an object as a whole, but what happens to the other features within the object that are not themselves associated with reward? Here we designed a neuroimaging study where participants searched for a square target and learned to associate a color with high-value reward, and two colors with low-value rewards. Critically, the targets also contain Gabor-like stripes tilted 45° to the left or to the right, that is not relevant to the task. In the test phase, participants

performed a visual search task for a circle while ignoring the square. Both objects contained a color and orientation from the training phase.

The biased competition model (Desimone & Duncan, 1995) and guided search 6.0 (Wolfe, 2021) would predict greater weight afforded to the representation of the high-value color but offer no predictions towards the presentation of the orientation of the high-value object. On the other hand, stimulus sampling theory would predict that all visual elements associated with reward to be sampled, leading to an elevated representation for the entire object, regardless of what feature was predictive of reward (Estes, 1950). I predict that reward-associations for multi-feature objects will permeate features not associated with reward such that multi voxel pattern analysis (MVPA) will decode orientations of high-value objects with greater accuracy over orientations of low-value objects.

4.2. Methods

4.2.1. Participants

Twelve healthy participants were recruited from the Texas A&M University community. Participants were compensated with money earned in the experimental task. All 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 conformed with the principles outline din the Declaration of Helsinki. All participants provided written informed consent. The obtained sample size was the same as an MVPA study investigating representation of conjunction features across the ventral visual pathway (Taylor & Xu, 2022). Due to problems calibrating the eye tracker, eye tracking data were collected for only 10 out of 12 participants. Due to experimenter error, the test phase RT data for the two participants that did not have their eyes tracked were lost.

4.2.2. Apparatus

In-lab tasks were completed on a Dell OptiPlex equipped with Matlab software and Psychophysics Toolbox extensions (Brainard, 1997). Stimuli were presented on a Dell P2717H Monitor. Participants viewed the monitor from a distance of approximately 70cm in a dimly lit room. Manual responses were entered using a standard keyboard. Eye-tracking was conducted using the EyeLink 1000 Plus system while head position was maintained using a manufacturer-provided chin rest (SR Research Ltd). Stimulus presentation during the fMRI portion was controlled by an Invivo SensaVue display system. The eye-to-screen distance was approximately 125cm. Responses were entered using Cedrus Lumina two-button response pads. An EyeLink 1000 Plus system was again used to track eye position.

4.2.3. Stimulus and Design

4.2.3.1. Training Phase

Each trial began with a fixation display for 1200ms, followed by a stimulus display for 1200ms, an ISI with the fixation display for 500 to 1700ms, feedback for 1400ms, and an ITI with the fixation display for 2400 to 4800ms (Fig. 10A). A blank screen was also inserted before the feedback display and the ITI for 100ms, and at the end of the trial for 200ms. During the in-lab version of the training phase, the trial would begin after a 500ms fixation, and the stimulus display would end after a correct response was made, but the rest of the timing remained the same. The fixation display contained a fixation cross (1.1º x 1.1º) at the center. The stimulus display contained a square (3.7º x 3.7º), presented 9.2º to the left or right of the center, and participants were instructed to look directly at it. On each trial, the color of the square could be one of three colors (red, green, or blue, RGB: [255,74,18], [22,159,0], [0,131,255], respectively) of which one served as the high-value color while the other two served as low-value colors

(counterbalanced across participants). Participants earned money on correct trials (40c for high-value colors and 5c for low-value colors), and the feedback display would consist of the money earned on the current trial along with the updated total earnings. The square also contained Gabor-like patches tilted 45° to the left or right. The location, color, and orientation of the square was fully counterbalanced within each run.

4.2.3.2. Test Phase

Each trial began with a fixation display for 1200ms, followed by a stimulus display for 1200ms, and an ITI with the fixation display for 6000 to 7800ms (Fig. 10B). A 200ms blank was inserted before the beginning of the next trial to prepare participants. The fixation display was the same as in the training phase. The stimulus display consisted of a circle (3.7º in diameter) and a square (3.7º x 3.7º), presented 9.2º to the left and right of the center of the screen. Participants were instructed to look directly at the circle while ignoring the square. The circle and square were presented in the colors and orientations presented during the training phase, but in unique combinations (the colors and orientation of the circle and square were never the same). The location, color, and orientation of the two shapes in the stimulus display was fully counterbalanced. During the in-lab version of the training phase, the trial would begin after a 500ms fixation, but the rest of the timing remained the same.

4.2.4. Procedure

The study required a laboratory visit on the first day and an fMRI scan on the following day. During the laboratory visit, participants completed four untimed and four timed practice trials for the test phase followed by a full run of test phase trials. The shapes for the practice trials were all presented in grey (RGB: [136,136,138]). Afterwards, participants completed four untimed and four timed practice trials for the training phase followed by five runs of the training

phase. Each run began with a 5-point eye position calibration. During the scan visit, participants completed a total of 10 brain scans which began with the acquisition of a pair of gradient echo scans with opposite phase encoding direction while they performed a run of the training phase. This was followed by a run of the training phase, three runs of the test phase, an anatomical scan, another run of the training phase, and three more runs of the test phase. Therefore, participants performed a total of eight training phase runs (five in lab, three in the scanner but only two were scanned) and seven test phase runs (the first of which was practice and so will not be analyzed).

4.2.5. MRI Data Acquisition

MRI data were acquired with a Siemens 3-Tesla MAGNETOM Verio scanner and a 32-channel head coil at the Texas A&M Translational Imaging Center (TIC), College Station, TX. An anatomical scan was acquired using a T1- weighted magnetization prepared rapid gradient echo (MPRAGE) sequence (150 coronal slices, voxel size = 1mm isotropic, repetition time (TR) = 7.9ms, echo time (TE) = 3.65ms, flip angle = 8º). Whole-brain functional images were acquired using a T2*-weighted echo planar imaging (EPI) sequence (56 axial slices, TR = 600ms, TE = 29ms, flip angle = 52º, image matrix = 96 x 96, field of view = 240mm, slice thickness = 2.5mm with no gap), using the same parameters as Kim and Anderson (2020a, 2020b). 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 of the two runs of the training phase lasted 7.06 mins during which 706 volumes were acquired. Each of the six runs of the test phase lasted 7.54 mins during which 754 volumes were acquired.

4.2.6. Behavioral Data Analysis

Data for the training phase of the experiment were binned by value (high vs low) and RTs trimmed if they were faster than 150ms (anticipatory) or exceed three SD of the conditional

mean. The resulting conditional mean RTs were analyzed with a pairwise t-test. Data for the test phase were binned by trial type (HV target-LV distractor, LV target-HV distractor, and LV-target-LV distractor), and the RTs trimmed and averaged. The conditional mean RTs were analyzed with a one-way ANOVA and pairwise comparisons.

4.2.7. fMRI MVPA Preprocessing

FMRI data were analyzed using FreeSurfer (surfer.nmr.mgh.harvard.edu) and AFNI (Cox, 1996), partly with the high-performance research computing resources provided by Texas A&M University. Nonbrain removal was conducted using BET (Smith, 2002), and anatomical and functional data were warped to the 2mm 152 MNI standard space using FreeSurfer for both wholebrain contrasts and MVPA. Visual cortex ROIs for the left and right visual field were created by combining the regions for V1-V4 from the MNI_Glasser_HCP_v1.0 atlas, using AFNI.

No additional preprocessing was conducted before a GLM was performed on the data along with six motion regressors (reflecting the translation and rotation parameters in three dimensions) using AFNI's 3ddeconvolve to extract trial-level beta maps within each ROI (LVF mask for RVF stimulus, and vice versa). The beta maps were then subjected to an MVPA using the linear support vector machine classifier (*3dsvm*) in AFNI. The classifier was trained to distinguish the orientation of the distractor using the leave-one-(pair of)-trial-out approach and tested on the left-out pair of trials, resulting in 24 classification accuracies for each of the 12 conditions (3 colors, 2 orientations, 2 locations).

These accuracies were averaged to generate the mean classification accuracy per participant, which were then averaged across participants to compute a grand mean for high-value, and the two low-value colors. The resulting decoding accuracies were compared against

chance (one sample non-parametric randomization test, one-tailed), and to each other (paired-samples non-parametric randomization tests, two-tailed, corrected for multiple comparisons). I repeated the same process to investigate decoding accuracy for HV and LV colored distractors.

4.3. Results

4.3.1. Behavioral Data

There were no difference in RT or error rates between HV and LV color conditions in the training phase, $t(9) = -1.03$, $p = 0.331$, $d = 0.32$, and $t(11) = 0.49$, $p = 0.636$, $d = 0.15$, respectively (see Fig. 11). There was no overall difference in the test phase for RT and error rates, $F(2,27) = 0.44$, $p = 0.649$, and $F(2, 33) = 0.012$, $p = 0.988$, respectively (see Fig. 12). However, RT was slower for HV distractors compared to LV distractors, $t(9) = 2.03$, $p = 0.073$, $d = 0.64$, and a randomization test with resampling produced comparable results. The comparisons between the other conditions for RT, and for error rates were not statistically significant, ps > 0.1.

There was no overall difference in the test phase for oculomotor capture and dwell time, $F(2, 2.27) = 1.54$, $p = 0.232$, and $F(2, 2.27) = 1.27$, $p = 0.297$ (see Fig. 13). However, there was significantly more oculomotor capture on trials with a HV distractor compared to trials with a HV target and LV distractor, $t(9) = 2.47$, $p = 0.035$, $d = 0.78$, and trials with both a LV target and LV distractor, $t(9) = 2.32$, $p = 0.045$, $d = 0.73$. Although numerically, distractor dwell times were lower for trials with both a LV target and LV distractor, the comparisons were not statistically significant, ps > 0.1.

4.3.2. MVPA

The MVPA revealed that orientation decoding was more accurate for distractors with LV colors, compared to distractors with HV colors, $t(11) = 2.47$, $p = 0.031$, $d = 0.71$ (see Fig. 14A).

Orientation decoding for stimuli with high-value colors was not greater than chance, $t(11) = 1.16$, $p = 0.0270$, $d = 0.33$, but was marginally significant for stimuli with low-value colors, $t(11) = 1.98$, $p = 0.074$, $d = 0.57$. Although this was not significant, there was a medium negative correlation between the difference in orientation decoding between HV and LV distractors, and the difference in oculomotor capture between HV distractor and HV target-LV distractor trials, $r(8) = -0.41$, $p = 0.238$ (Fig. 15A). Even with 10,000 bootstrapped samples, however, the correlation did not become significant, [-0.81, 0.23] (Fig. 15B). The second MVPA revealed that color decoding for distractors with HV colors and LV colors were not significantly different, $t(11) = 0.50$, $p = 0.626$, $d = 0.16$ (see Fig. 14B). Color decoding for HV distractors was significantly greater than chance, $t(11) = 5.54$, $p < 0.001$, $d = 1.75$, and marginally significant for LV distractors, $t(11) = 2.07$, $p = 0.062$, $d = 0.65$.

4.4. Discussion

Although many studies have demonstrated that no longer task-relevant reward-associated stimuli are afforded elevated representation in the brain (e.g., Anderson et al., 2014; Anderson et al., 2016, 2017; see Anderson, 2019 for a comprehensive review), studies have not investigated how features not predictive of reward within the stimulus are represented. In the present study, participants learned to associate a particular color with high-value reward and two colors with low-value rewards, while ignoring the orientation of the Gabor-like stripes within the same stimuli. The proportion of oculomotor capture was higher on HV distractor trials, suggesting that participants learned the reward associations as the behavior matches with that of prior studies employing a similar paradigm (e.g., Kim et al., 2021).

Decoding accuracy of the Gabor-like stripes was revealed to be higher when it appeared on the stimuli rendered in the low-value colors, compared to stimuli rendered in the high-value

color. Additionally, this decoding accuracy was marginally greater than chance for the low-value colors only. On the other hand, although the decoding accuracy for color did not differ between high- and low-value colors, only the high-value color trials had decoding accuracy greater than chance. Taken together, this suggests that attentional priority is more evenly split between uninformative features and reward-associated features in a low-value context, but greater representation is distributed to the reward-associated feature in a high-value context. Although contemporary theories of attention would have predicted something similar for single-feature objects (Desimone & Duncan, 1995; Wolfe, 1994; Wolfe, 2021), they do not provide any insight into how different features of a multi-feature object are represented. Further investigation into how color and orientation of the target stimuli are represented would grant a more holistic understanding of how attentional priority is distributed within and between objects.

However, it is important to note that my results reflect only how areas V1-V4 represents the Gabor-like stripes of the stimuli. The visual system of the brain is organized hierarchically, with activity for simple stimuli (e.g., orientations) being localized to the lower levels which are used to construct higher level activity to represent more complex stimuli (van Essen & Gallant, 1994). There is some evidence that visual information is represented disjointedly within V1-V4 such that orientation is represented more strongly in V1, color more strongly in V4, and shapes more strongly in V8 (e.g., Kozlovskiy & Rogachev, 2021; van Essen & Gallant, 1994). Therefore, orientation decoding may be generally more accurate if conducted over V1, and color over V4, as opposed to being over V1-V4.

In summary, my findings suggest that the biased-competition model of attention works not just between objects, but also within objects and stimuli. The specificity of value-driven

attention may contribute to its persistence, as overcoming its allure by suppression or new learning does not happen spontaneously.

5. OVERCOMING VALUE-DRIVEN ATTENTION

5.1. Introduction

VDAC has been shown to persist without additional reinforcement for well over one hundred trials (e.g., Anderson et al., 2011b, 2014; Anderson & Yantis, 2012) and for up to nine months post-learning (Anderson & Yantis, 2013), but eventually extinguishes with a sufficient number of non-reinforced trials (e.g., Anderson et al., 2011a, 2016). The persistence of VDAC is inconsistent with what might be predicted from classical conditioning, where the previously reward-predictive stimulus would cease to evoke a conditioned response more quickly with non-reinforcement (Pavlov, 1927). Milner et al. (2023) found that VDAC is markedly slow to extinguish in a non-reinforced test phase, although it can eventually extinguish over many unrewarded trials, especially when the previously reward-associated feature appears more frequently. What remains to be understood are the dynamics by which value-based attentional priorities update when stimulus-reward contingencies change.

The present study investigated how a change in the relative value of different stimuli is reflected in the updating of attentional bias. Participants started with a training phase where they learn to associate one color with high-value reward, one color with low-value reward, and another color with no reward. This is later followed by a second training phase that devalues the previously-learned reward association: the former high-value color is now unrewarded and the previously unrewarded color is now predictive of high-value reward (reversal learning). Immediately following each of the two training phases is a test phase measuring attentional bias for the different colors. Humans can rapidly adapt to new reward structures and even to frequently-changing reward contingencies (e.g., Behrens et al., 2007; Ghahremani et al., 2010; Lee & Keramati, 2017). I hypothesized that, although attentional capture by an originally high-

*Parts of this chapter are adapted with permission from Liao and Anderson, 2020b

value color may persist following such reversal learning, the bias should be markedly reduced, being overshadowed by the bias towards a newly-learned high-value color (Fig. 16A). It is also possible that signal suppression occurs, whereby the original high-value color continues to generate a salience signal but is subsequently suppressed (Gaspelin et al., 2015; Sawaki & Luck, 2010; Fig. 16B). Finally, to the degree that value-based attentional priority is computed over long periods of time and tracks total associated reward, the old and new high-value color would be expected to be similarly prioritized (Fig. 16C).

5.2. Methods

5.2.1. Participants

Forty participants were recruited from the Texas A&M University community. All reported normal or corrected-to-normal visual acuity, normal color vision, and provided written informed consent. Five participants did not complete the study (two because of experimenter error, two because of inability to reliably track the eyes, and one withdrew). The data for three participants were excluded from analyses due to low accuracy (either training or test phase < 2.5 SD of the group mean). The final sample included 32 participants (17 females), with a mean age of 21.00 years (SD = 2.90), which indicated power (1-β) = 0.82 using the oculomotor RT-based measures of VDAC in a prior eye tracking study (Anderson & Kim, 2019b). Participants were compensated with their earnings from the task. All procedures were approved by the Texas A&M University Institutional Review Board and conformed with the principles outlined in the Declaration of Helsinki.

5.2.2. Apparatus & Stimuli

Stimuli were generated using MATLAB and Psychophysics Toolbox extensions (Brainard, 1997), then presented on a Dell P2717H monitor linked to a Dell OptiPlex 7040. Participants

viewed the monitor from a distance of approximately 70 cm in a dimly-lit room. An EyeLink 1000 Plus desktop-mount eye tracker (SR Research) monitored participants' right eye position. Head position was maintained throughout the experiment using an adjustable chin and forehead rest (SR Research). Eye position was calibrated prior to each block of trials using 9-point calibration (Anderson & Yantis, 2012; Liao & Anderson, 2020) and was manually drift-corrected by the experimenter as needed (each trial could only begin once a valid fixation had been registered within 1.2° of the center of the screen). During the presentation of the search array, the X and Y position of the eyes were continuously monitored in real time with respect to the six stimulus positions, such that fixations were coded online (Anderson & Kim, 2019a, 2019b).

Three colors were associated with monetary reward throughout various periods during the experiment. These critical colors were red (RGB: 255, 0, 0), green (0, 255, 0), and blue (0, 127, 255), and served as the first or old high-value color, low-value color, and the second or new high-value color (randomly assigned for each participant). There were four other colors, grey (190, 190, 190), pink (255, 0, 255), yellow (240, 240, 0) and brown (180, 90, 0), that served as neutral colors.

5.2.3. Design & Procedure

Each trial in the first training phase consisted of a fixation display, a search array, and a reward feedback display (Fig. 17A). The fixation cross (1.1° visual angle) remained on the screen until eye position had been registered within 1.2° of it for a continuous period of 500ms. The search array consisted of four squares (3.0° x 3.0°) on an imaginary circle with a radius of 8.3°. A region extending 1.1° beyond the boundary of each square was used to determine fixations. The reward feedback display consisted of the money earned on the current trial along with the updated total earnings.

Participants were instructed to fixate ("look directly at") either the red, green, or blue square on each trial and that different colors would be worth different amounts of money on average. One critical color (red, green, or blue) was associated with an 80% probability of a high reward of 8¢ and a 20% probability of a low reward of 2¢ (old high-value color), while for another color these percentages were reversed (low-value color), and the last color always resulted in 0¢. Only one of the critical colors was displayed on each trial, along with three neutral colors (randomly chosen without replacement). The position of each target color was counterbalanced across trials, the order of which was randomized. At no point in the experiment was any relationship between color and reward mentioned to participants. There were 8 practice trials without a time limit, after which participants completed two blocks of 96 trials each (192 trials total).

Similar to the training phase, each trial in the first test phase consisted of a gaze-contingent fixation display and a search array in which the task was to fixate a target (Fig. 17B). The search array now consisted of either three circles (1.7° radius) and a diamond (2.7° x 2.7°) or three diamonds and a circle, which were positioned on an imaginary circle with a radius of 9.8°. Regions extending 3.4° beyond the center of the circle and 3.0° beyond the center of the diamond were used as areas for determining stimulus fixations.

Participants were instructed to "pick the unique shape by looking directly at it," and to "try to be as fast as possible while still being accurate." On neutral trials, the shapes appeared in the four neutral colors. On distractor-present trials, a non-target shape would appear in one of the critical colors (red, green, or blue). The position of the distractor and the target shape was counterbalanced, while the neutral colors were selected randomly without replacement on each

trial, and the order of trials was randomized. There was a 10-trial practice block with no time limit, after which there were two blocks of 96 trials (192 trials in total).

The second training phase was exactly the same as the first training phase, but the old high-value color was now never rewarded (always followed by 0¢) and the previously unrewarded color was now associated with an 80% probability of a high reward of 8¢ and a 20% probability of a low reward of 2¢ (new high-value color). There were also no more practice trials. The second test phase was exactly the same as the first test phase, with the exception that there were no more practice trials.

5.2.4. Data Analysis

RT was measured from the onset of the search array to the moment eye position entered into the fixation window surrounding the target, and only correct responses were included in the mean RT for each participant (82.5% and 90.3% of trials in training and test respectively). RTs exceeding 3 *SD* of the mean for each condition for each participant were trimmed (1.75% of trials in the training phase and 1.5% in the test phase). RTs in the test phase were normalized to the neutral condition (i.e., mean RT for the neutral condition was subtracted; see, e.g., Krebs et al., 2010; Liao et al., 2020) and RT for the critical colors in each phase were compared using 3 (target/distractor color) x 2 (block) repeated-measures analysis of variance (ANOVA).

5.3. Results

5.3.1. Training Phase

In the first training phase, there was a significant main effect of target color, $F(2,62) = 6.98$, $p = 0.002$, $\eta_p^2 = 0.184$, a significant main effect of block, $F(1,31) = 14.40$, $p = 0.001$, $\eta_p^2 = 0.317$, and no interaction, $F(2,62) = 2.28$, $p = 0.111$ (Fig. 18A). Post-hoc contrasts revealed that RT to the

high-value target was significantly faster than to the other two targets (collapsed), $t(31) = 3.78$, $p < 0.001$, $d = 0.67$, which did not significantly differ from each other, $t < 1$.

In the second training phase, there was again a significant main effect of target color, $F(2,62) = 11.67$, $p < 0.001$, $\eta_p^2 = 0.274$, but no main effect of block, $F < 1$, and a marginally-significant interaction, $F(2,62) = 2.42$, $p = 0.097$, $\eta_p^2 = 0.072$. Post-hoc contrasts revealed that, in the first block (block 3), RT was faster for both old high-value and new high-value targets compared to low-value targets, ts > 3.07, $p < 0.005$, ds > 0.54, and was similar for old high-value and new high-value targets, $t < 1$. In the second block (block 4), new high-value targets were still reported faster than low-value targets, $t(31) = 4.83$, $p < 0.001$, $d = 0.85$, whereas the difference between old high-value targets and low-value targets was now marginally-significant, $t(31) = 1.80$, $p = 0.081$. Importantly, new high-value targets were now reported faster than old high-value targets, $t(31) = 2.60$, $p = 0.014$, $d = 0.46$.

5.3.2. Test Phase

In the first test phase, there was no main effect of distractor condition, $F(2,62) = 1.34$, $p = 0.268$, nor a main effect of block or interaction, Fs < 1. Numerically, RT was slowest for the old high-value condition (Fig. 18B).

In the second test phase, the was no main effect of distractor condition, $F(2,62) = 1.98$, $p = 0.146$, or block, $F < 1$, but there was a significant interaction, $F(2,62) = 3.46$, $p = 0.038$, $\eta_p^2 = 0.100$. Post-hoc contrasts revealed that in the first block (block 3), RT was slower in the old high-value distractor condition than in the other two conditions (collapsed), $t(31) = 2.75$, $p = 0.010$, $d = 0.48$, which did not significantly differ from each other, $t < 1$. In the second block (block 4), there were no significant differences, although RT was now numerically slower in the

new high-value condition. Distractor fixations were very infrequent (< 3%) and there were no main effects or interactions in the frequency of distractor fixations in either test phase, *p*s > 0.08.

5.4. Discussion

My reversal learning manipulation was not immediately effective in modulating attentional bias in either the training or test phase. Although participants successfully adapted to the new reward contingency, more quickly reporting the new high-value target by the end of training, this learning did not immediately generalize to the test phase. It is possible that attentional biases are not as flexible and malleable as learning and decision making, which have been shown to be sensitive to rapidly changing environments (Behrens et al., 2007; Ghahremani et al., 2010; Lee & Keramati, 2017). It is also possible that participants were learning to suppress inputs for the old high-value color in the second test phase and did not become proficient at doing so until later trials. Signal suppression is known to occur after capture under certain circumstances (Gaspelin et al., 2015; Gaspelin & Luck, 2018; Sawaki & Luck, 2010). It is also possible that automatic value-based attentional priority does not recalibrate unless such attending is explicitly counterproductive for some number of trials, as when previously reward-associated stimuli appear as task-irrelevant distractors (see Milner et al., 2023).

Either way, my findings shed light on an important distinction between adjusting attentional priorities based on ongoing reward learning and the corresponding updating of involuntary attentional biases, with the former being more rapid and flexible, and the latter being slower and less malleable. My findings also provide compelling evidence that VDAC does not reflect a mere spill-over of motivated attention from the training phase but rather involves a persistent and habitual bias (see Anderson, 2016a) that cannot be quickly recalibrated with new learning. The inflexibility of VDAC is what makes it a useful model for investigating clinical

syndromes where valuable but undesirable stimuli conflict with behavioral goals (e.g., addiction and obesity; Anderson, 2016b). When an individual becomes addicted to a substance, related stimuli automatically capture attention similar to reward-associated distractors (see Field & Cox, 2008; Rook et al., 2008 for reviews), and continue to bias attention even within successfully recovered patients (Field & Cox, 2008; Field et al., 2013; Marissen et al., 2006; Stormark et al., 1997). In this respect, my findings offer compelling evidence that VDAC does not reflect a mere spill-over of motivated attention from the training phase but rather involves a persistent and habitual bias (see Anderson, 2016a) that cannot be quickly recalibrated with new learning.

6. CONCLUSIONS

In this dissertation, I presented a series of experiments that explored the scope of reward history effects on attention. Reward history effects on attention has only recently become an independent phenomenon, and although some studies have investigated its effects beyond basic visual features to complex objects (e.g., Donohue et al., 2016) and regions in space (Anderson & Kim, 2018a, b), the extent of its effects remain unclear. Reward history effects are persistent and resistant to extinction, similar to maladaptive behaviors in patients with clinical disorders. There has been some interest in taking elements of reward history to inform clinical interventions (e.g., Anderson, 2020b), but the magnitude of attentional capture does not always predict relapse of substance abuse disorder treatment (Field et al., 2013; Waters et al., 2003). Although reward history effects on attention as measured through VDAC can be a useful model for failures in cognitive control where attention is captured by stimuli or cues that conflict with behavioral goals, more research is necessary to understand the scope of this phenomenon and to identify potential implications in clinical disorders and everyday behavior.

In my second chapter, I provide evidence in contrast to prior studies that reward history can bias oculomotor behavior; but it seems that separating abstract directions and regions in space during both learning and test phases are important (Dunne et al., 2015; 2019; Jiang et al., 2013, 2015; Won & Leber, 2016; but see also Chen et al., 2014; Sohn & Lee, 2006). This is not entirely surprising given that a region in space is allocentric while directions are egocentric, so the two sources of information are inherently distinct from each other. Findings from neuroimaging and neurophysiology studies support this distinction in subcortical regions like the hippocampus (representing allocentric information) and the striatum (representing egocentric information; Cook & Kesner, 1988; McDonald & White, 1994; Morris et al., 1982; Packard &

McGaugh, 1992, 1996). However, allocentric and egocentric information are eventually integrated to improve the accuracy of motor behavior (Byrne & Crawford, 2010; Chen et al., 2011; Li et al., 2017).

Eye movements seldom get executed to abstract points in space without regard for objects within the environment, so the smaller effect sizes I observed are not surprising. The utility of these findings for clinical interventions are dubious as participants trained to make antisaccades from the reward-associated feature actually exhibit attentional biases towards that feature during the test phase when rewards were no longer available (Kim & Anderson, 2019a). However, my findings demonstrate the feasibility of using reward history to train sequences of saccades that may be important for systematic search during search and rescue drone piloting or cancer screening. Although the viability of this idea has not been explicitly tested, it has been shown to be successful with another component of experience-driven attention – aversive conditioning (Anderson, 2021d), as patterns of eye movements during naturalistic scene viewing were shaped near-real-time using electric shocks. Although spatial attention has been studied extensively, most studies restrict eye movements to focus on covert attention (Hunt & Kingstone, 2003a, b) even though overt attention is more ecologically valid.

My third chapter investigated how the brain support spatial orienting and reorienting away from previously reward-associated regions in space. Along with brain regions typically associated with VDAC such as the caudate tail, frontal eye field, and superior colliculus (e.g., Anderson, 2017; Anderson et al., 2014; Anderson et al., 2016; Anderson et al., 2017; Bourgeois et al., 2022), we also observed activity in regions that represent reward-modulated attentional control such as the anterior cingulate cortex and the insula (Hickey et al., 2010; Wang et al., 2015), and in ventral regions that represent scene and spatial information such as the

hippocampus, parahippocampal gyrus, and temporo-occipital cortex (Epstein & Kanwisher, 1998; Maguire et al., 1996; O'keefe & Nadel, 1978). Interestingly, my data reflects elevated visual cortex activity ipsilateral to the target hemifield. We all have the ability to choose between foreground and background information for further processing and it appears that our brains adapt in a similar manner. Participants were suppressing the background to better identify foreground targets. Flexible adaptation seems to be the theme as our brains also recruit different brain regions accordingly, as the task involved spatial information as well as object-rich scenes as stimuli instead of just simple colors and shapes.

My findings demonstrate that we have the ability to prioritize a particular region in space for preferential processing while simultaneously applying local prioritization and suppression. Further investigations into the mechanisms behind this phenomenon could prove useful for any situation that requires cognitive control to maintain attention on task-relevant stimuli. Under the biased competition framework, participants automatically attend to stimuli that have a stronger priority signal (Desimone & Duncan, 1995). If a diagnostic feature of this stimuli is known ahead of time (e.g., bottom left quadrant), participants can apply a top-down suppression signal for that particular location (Arita et al., 2012; Moher & Egeth, 2012; Reeder et al., 2017). How this suppression is applied within my experiment is unclear, but future investigations can apply dynamic causal modeling to uncover the direction of connectivity between active brain region. The origin of the suppression could be through scene, space, and object representative regions (e.g., hippocampus, parahippocampal gyrus, and lateral occipital complex) that feedback into the visual cortex, or it could be through oculomotor regions of the brain (e.g., superior colliculus and frontal eye field). Insights from these studies could uncover potentially useful information that can inform clinical interventions – as we could maybe train participants to be able to attend to

objects in the environment as they normally would while simultaneously ignoring irrelevant and potentially maladaptive or dangerous objects.

I observed a similar result in my fourth chapter which used multivariate analyses to investigate how attentional priority is distributed amongst features of objects containing multiple features – color and orientation. Prior experiments (e.g., Anderson et al., 2011a; Le Pelley et al., 2015) as well as contemporary models of attention (Desimone & Duncan, 1995; Wolfe, 2021) offer predictions and theories on inter-object competition, without conjecture on how intra-object competition gets resolved. I found that reward history effects within an object was specific to the feature that predicted reward, as our model decoded high-value colors greater than chance, but decoded the orientations of objects with high-value colors with less accuracy compared to objects with low-value colors. Since colors were the diagnostic feature that predicted reward, it is likely that the colors of distractors were suppressed to allow participants to focus their attention onto the targets. My analyses were limited to that of the distractor to investigate the effect of reward history, but additional analyses applied to the targets will provide a more holistic interpretation of the results.

The stimuli participants viewed were multifeatured objects so it is possible that they are represented differently across brain regions. My findings are restricted to the early visual cortex which represent simple features, while regions closer to the temporo-occipital cortex such as the LOC that represent object information (Grill-Spector et al., 2001) may be more suited to understanding how features of the object as a whole are represented. It is possible that the LOC is one such area where models can decode orientations of high-value objects with greater fidelity compared to low-value objects. This would imply that how we view parts of an object may not necessarily translate to how we view the whole object and the suppression signal may originate

from a region that is disconnected from the temporo-occipital cortex. Although we have a general idea of how signal suppression works through EEG studies (see Gaspelin & Luck, 2018 for a review), more fMRI studies are required to fully understand how signal suppression works. The findings of this chapter reinforce the need for further studies into how the brain flexibly supports the prioritization and suppression of specific information to undertake a task, as well as motivating a new avenue of research into intra-object competition for attention. Although still a step down from realistic objects, multifeatured objects are a more ecologically valid stimuli than simple feature objects, and is the necessary next step in attention research that aspires to be more applicable to every day scenarios. Another rather unrealistic component of prior research into reward history effects on attention is the single learning phase, while learning about our environment is an endless activity.

My fifth chapter thus, investigated how reward history effects are exhibited after reversal learning of color-reward associations. Reward history effects on attention have been shown to be persistent, as VDAC can persists for up to nine months post-learning (Anderson & Yantis, 2013; but see Anderson et al., 2011a and Milner et al., 2023). Despite learning the new color-reward contingency in this experiment, participants continued to have their attention captured by the old high-value color, at least initially. Not only does this inflexibility emphasize the similarities between VDAC and substance-abuse disorder and support its use as an investigative model, it suggests a temporal delay in the updating or recalibrating of value-based attentional priority. VDAC studies often incorporate a single contiguous training or learning session followed by the test session (e.g., Anderson et al., 2011a), so it is difficult to see how attentional biases unfold. Although Le Pelley et al. (2015) demonstrated a relatively stable acquisition of value-based attentional priority, they do not incorporate a context shift where the reward history effect

transfers. Alternatively, my results could imply that the learning of cue-reward associations and the expression of attentional biases in a different context are two related, but different processes, such that exposures to test phase events are required to calibrate attention. Future studies can uncover the mechanism of how reward history effects on attention update following reversal learning by incorporating a temporal delay or some practice test phase trials.

It is important to note that although the manipulation for this study is inspired by reversal learning, it has been slightly modified. Traditionally, the participant initially learns to discriminate between two stimuli where one is preferentially rewarded. After which, the outcomes of the two stimuli are reversed (Izquierdo et al., 2017). Critically, the participant views the two stimuli on every trial during reversal learning, whereas the participant only views one at a time in this study. It is likely that on top of learning that one stimulus is rewarding and the other is not, participants were also learning to actively suppress processing of the irrelevant stimuli. A possible follow-up study could be to replicate my experiment but replace the learning phase with a more traditional two alternative forced choice task.

Reversal learning has been shown to involve a different set of brain regions such as the prefrontal cortex and the amygdala (Schoenbaum et al., 2000). The results of chapter three suggests that both brain and behavior adapt to differences in tasks, so it is likely that these additional regions would be recruited. A neurophysiological study on macaques found elevated activity in the orbitofrontal cortex and the anterior cingulate cortex to cocaine-associated distractors, but not in striatal regions (Baeg et al., 2019). These findings deviated from the expected in human studies (see Anderson, 2019 for a review), but additional investigations into the neural mechanisms behind this experiment could provide insight into how these diverging studies are linked.

My investigations have been broad, but the common thread appears to be the specificity of the reward history effects. Moving away from objects with diagnostic colors and shapes led to seemingly surprising results that make sense given that reward history effects differ depending on the context during both the learning and the test phase. The brain has a tendency for parsimony, which could explain why an orientation can be learned but only after it has been dissociated from space, or how a sub-region of a particular region is prioritized while others are simultaneously suppressed, or that only the most relevant feature of an object was presented with greater fidelity. The VDAC paradigm is interesting in that a learned association continues to bias behavior even with a shift in context and relevance, which makes it much more ecologically valid. However, it appears that some aspects of the learning and test phases are still distinct from each other, reflecting the effort required to overcome maladaptive attention. Scientific advancement is incremental, and I hope that my findings and themes presented in this dissertation provide the first few steps towards novel investigations that can be of use in the future within any setting, clinical, or otherwise.

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LIST OF FIGURES

Experimental Paradigm for Associating Reward with Eye Movements to A Particular Direction

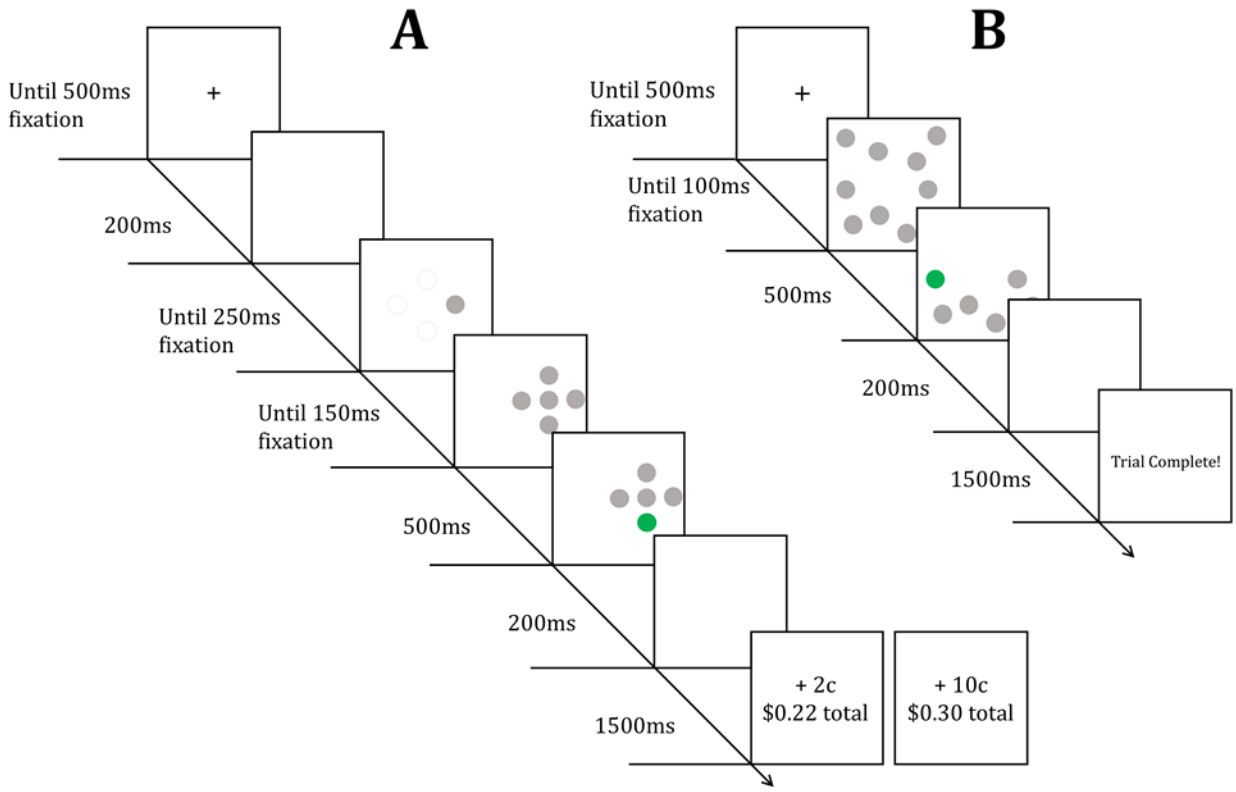

Figure 1 - Time course of trial events during the training and test phase of Experiment 1. (A) Participants fixated on the first circle before choosing one of four circles to fixate on. Note that the dotted-line circles indicate the other locations where the first circle could also appear and are for illustration purposes only (i.e., did not appear in the actual task). The reward was contingent upon the direction of their choice. In this example, the bottom direction is the high-value direction, and fixating on the bottom target yielded the highest possible reward. The same procedure was used for Experiment 2 albeit with a minor modification – the first circle fixated was a fixation cross instead of another circle. (B) Participants fixated on the cross before choosing a circle by fixating on it. The chosen circle will disappear or turn green to indicate that the target has been found. Reprinted from Liao and Anderson, 2020a.

Proportion of Choices During Unguided Visual Search Following Reward Learning of Eye Movements to Particular Directions

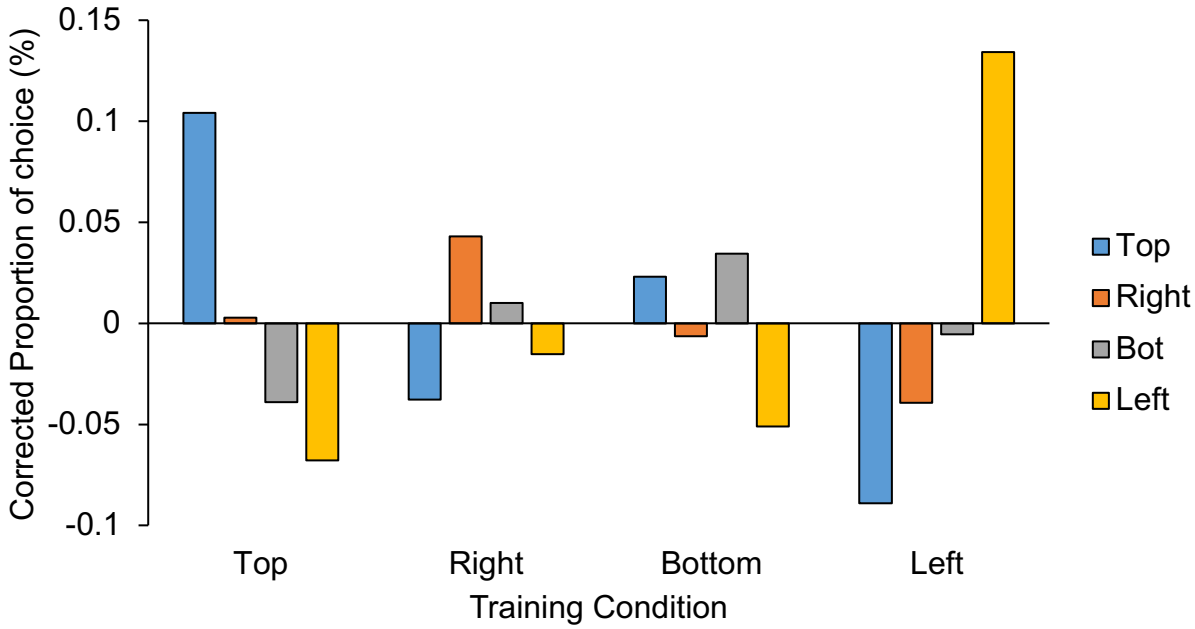

Figure 2 – The distribution of proportion of choices per training condition, for each cardinal direction. The y-axis is the proportion of choice corrected for training-independent bias (see Methods). Reprinted from Liao and Anderson, 2020a.

Heatmap of Saccades Towards Previously High-Value Direction During Unguided Visual Search Following Reward Learning of Eye Movements to Particular Directions

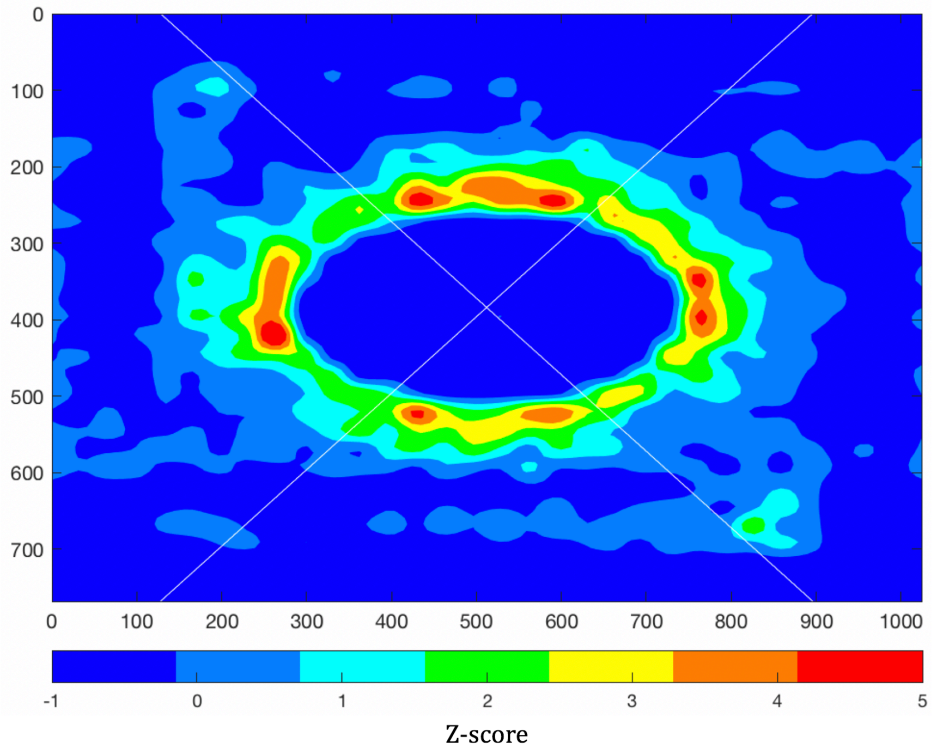

Figure 3 – A visualization of saccades towards the high-value direction, with direction rotated such that the high-value direction is always to the right for each condition. The X and Y axes reflect pixels on the monitor, and z-scores are computed over the number of fixations to the corresponding pixel (with the resulting z-score map smoothed for visualization). Reprinted from Liao and Anderson, 2020a.

Experimental Paradigm for Guided Visual Search Following Reward Learning of Eye Movements to Particular Directions

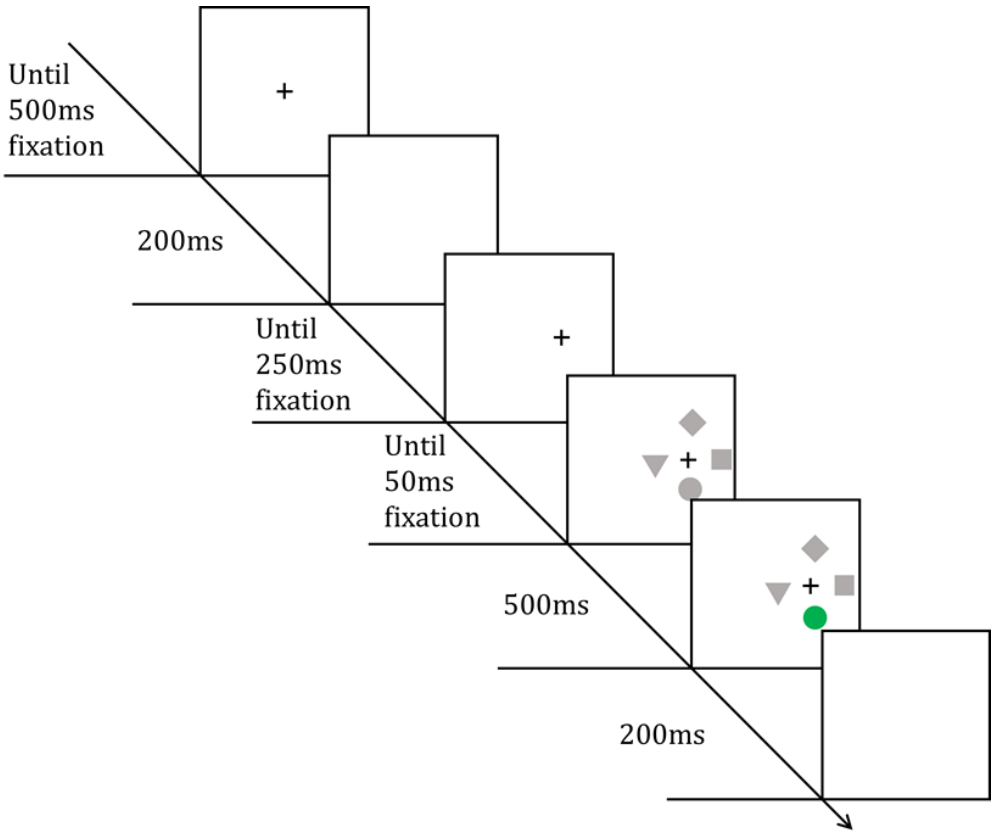

Figure 4 - Time course of trial events during the test phase of Experiment 2. Participants fixated on the cross before finding the circular target and fixating on it. The chosen shape would turn red if incorrect, green if correct, or the words "Too Slow!" would appear if no shape was fixated before the timeout limit. Reprinted from Liao and Anderson, 2020a.

Response Times for Guided Visual Search Following Reward Learning of Eye Movements to Particular Directions

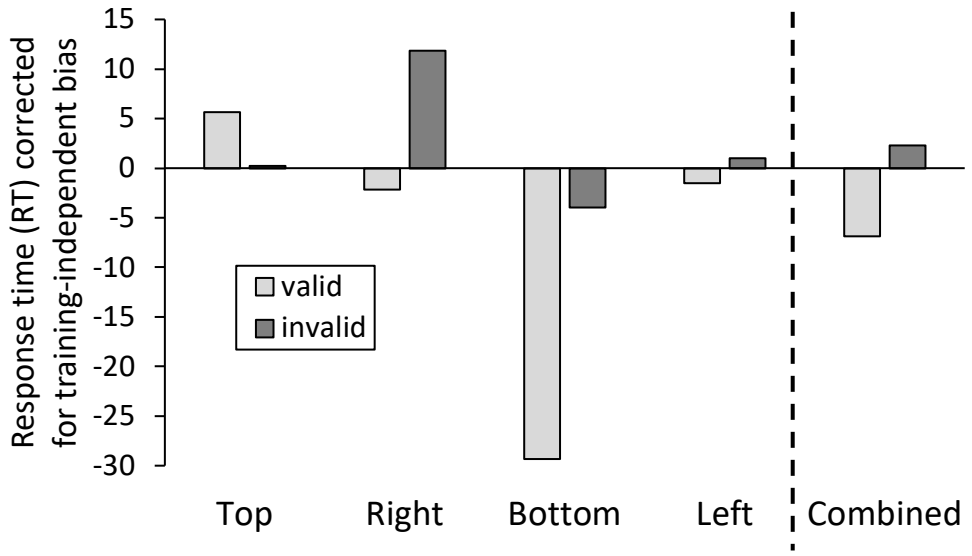

Figure 5 – Response time for valid and invalid trials Experiment 2, corrected for training-independent bias (see Methods), broken down by the different training conditions (high-value direction). Reprinted from Liao and Anderson, 2020a.

Experimental Paradigm for Investigating the Neural Correlates of Value-Driven Attentional Orienting in Space

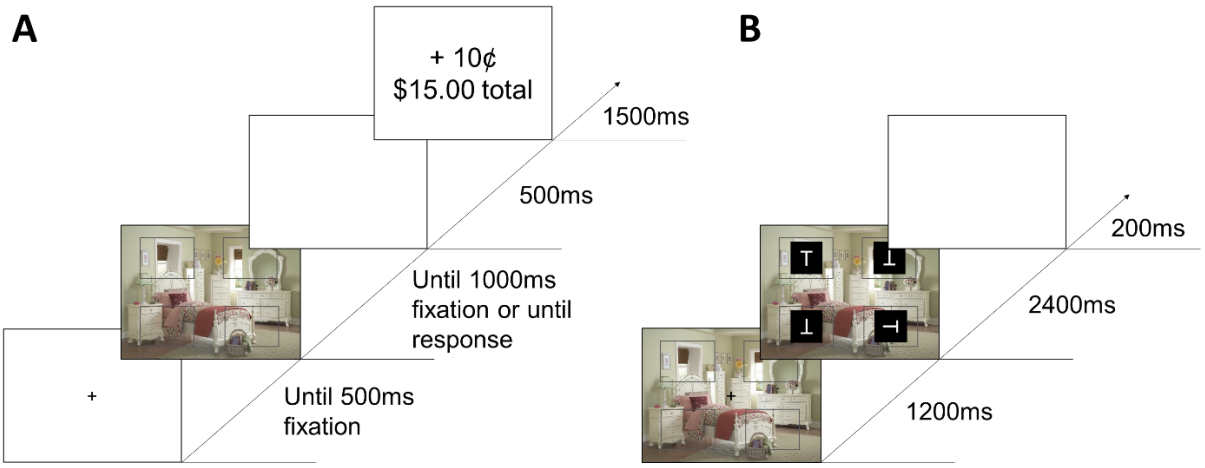

Figure 6 – Time course of trial events during the training and test phases of the experiment. During the training phase (A) participants were presented with scenes with an empty box in each quadrant and instructed to pick a box by looking directly at it. Depending on their choice, participants earn either 10c or 2c on every trial. During the test phase (B) participants were tasked with searching for a side-ways "T" among upright and upside down "T" distractors. Scenes previously experienced during the training phase were used as the background and were irrelevant to the task. Note that the stimuli are not drawn to scale in the figure, and the background has been changed from black to white for display purposes. Reprinted from Liao et al., 2020a.

Analysis of Behavioral Responses During Value-Driven Attentional Orienting in Space

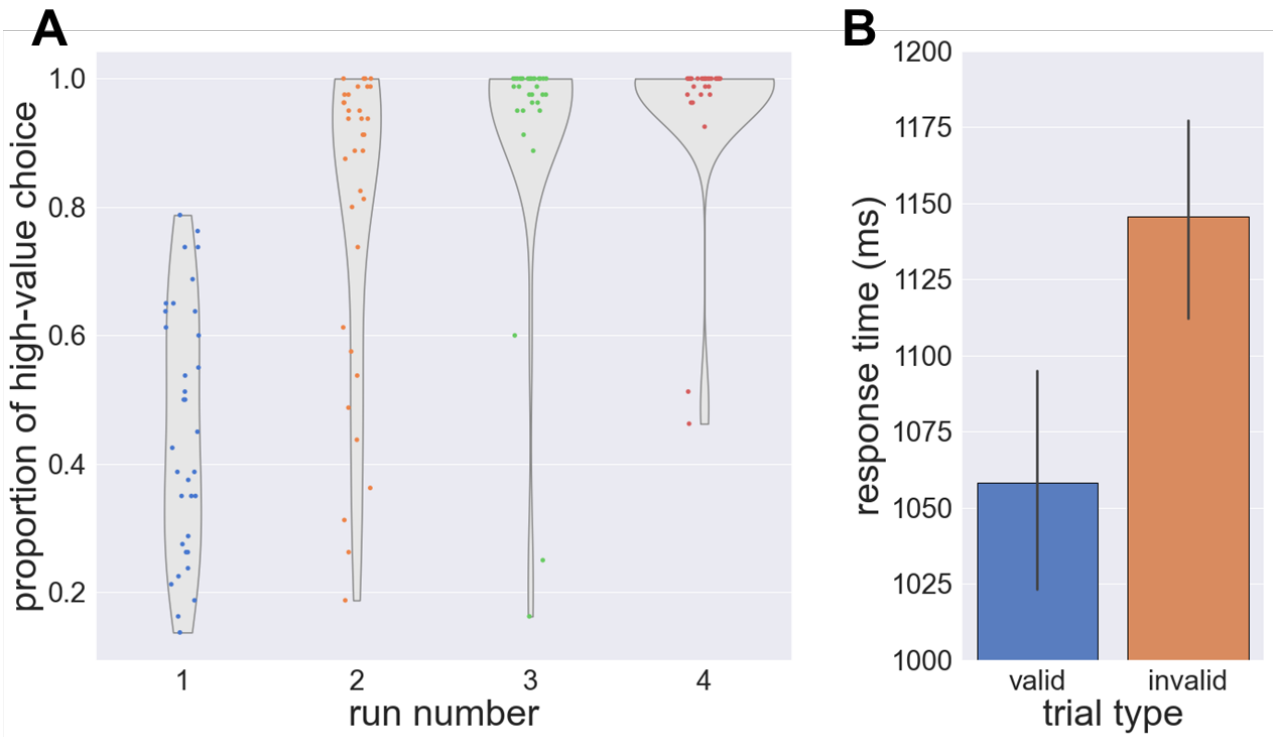

Figure 7 – Behavioral results in the training and test phase. (A) Proportion of high-value choice by run during the training phase (B) Response time in the test phase by trial type. Error bars reflect standard error of the means. Reprinted from Liao et al., 2020a.

Brain Regions Reflecting Value-Driven Attentional Orienting During Visual Search in Object-Rich Scenes Following Reward Learning

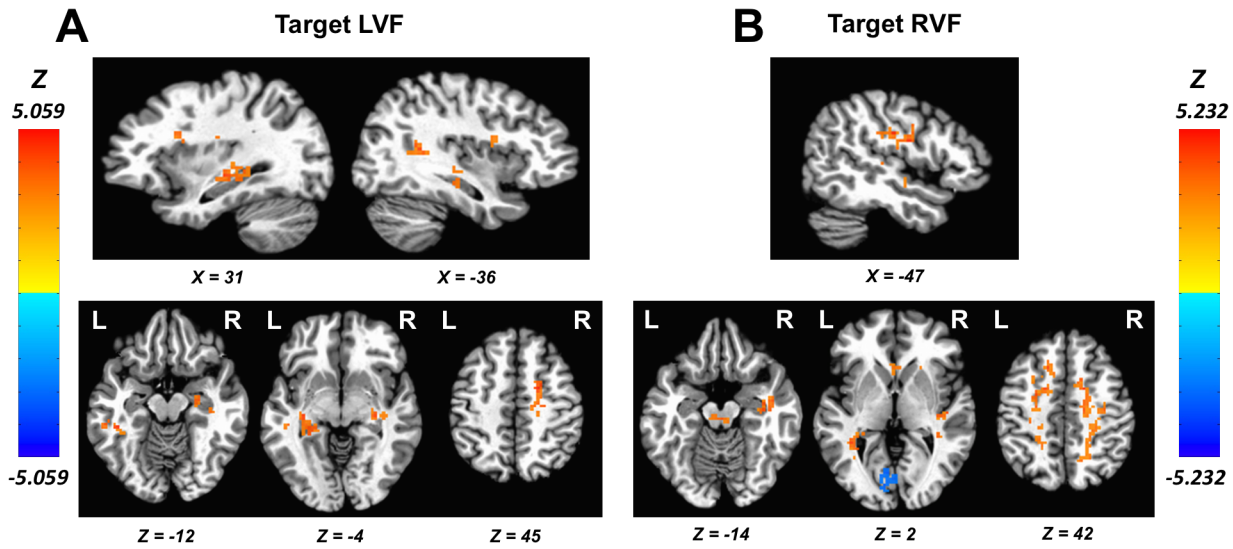

Figure 8 – Regions in which activation differed between valid compared to invalid (high-value quadrant in opposite hemifield) trials during the test phase for targets appearing in the A) left visual field (LVF) and B) right visual field (RVF). The contrast is set up such that warmer colors indicate greater activation on value trials. Activations are overlaid on an image of the Talairach brain. A complete list of all regions showing significant activation is provided in Supplemental Table 1. Reprinted from Liao et al., 2020a.

Brain Regions Reflecting Target Presence During Visual Search in Object-Rich Scenes Following Reward Learning

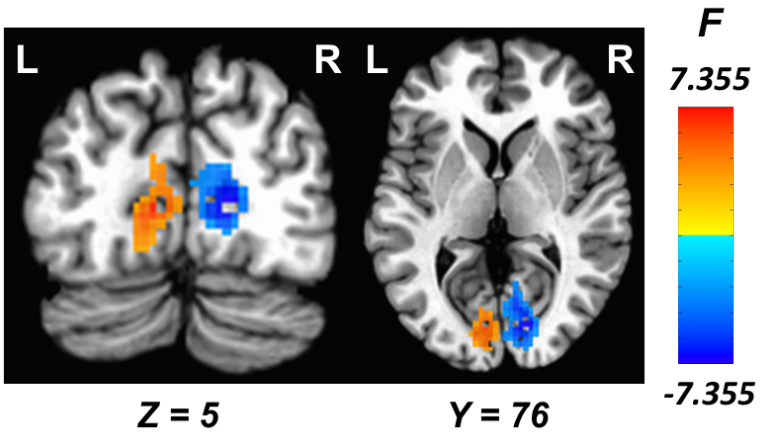

Figure 9 – Regions that were significantly more active in response to the presentation of targets in the left vs right hemifield. The contrast depicted is the difference between left and right (left-right) such that cooler colors correspond to stronger activations in response to targets on the right and warmer colors to targets on the left. Reprinted from Liao et al., 2020a.

Experimental Paradigm for Investigating the Neural Representation of a Value-Driven Feature in a Multifeature Object

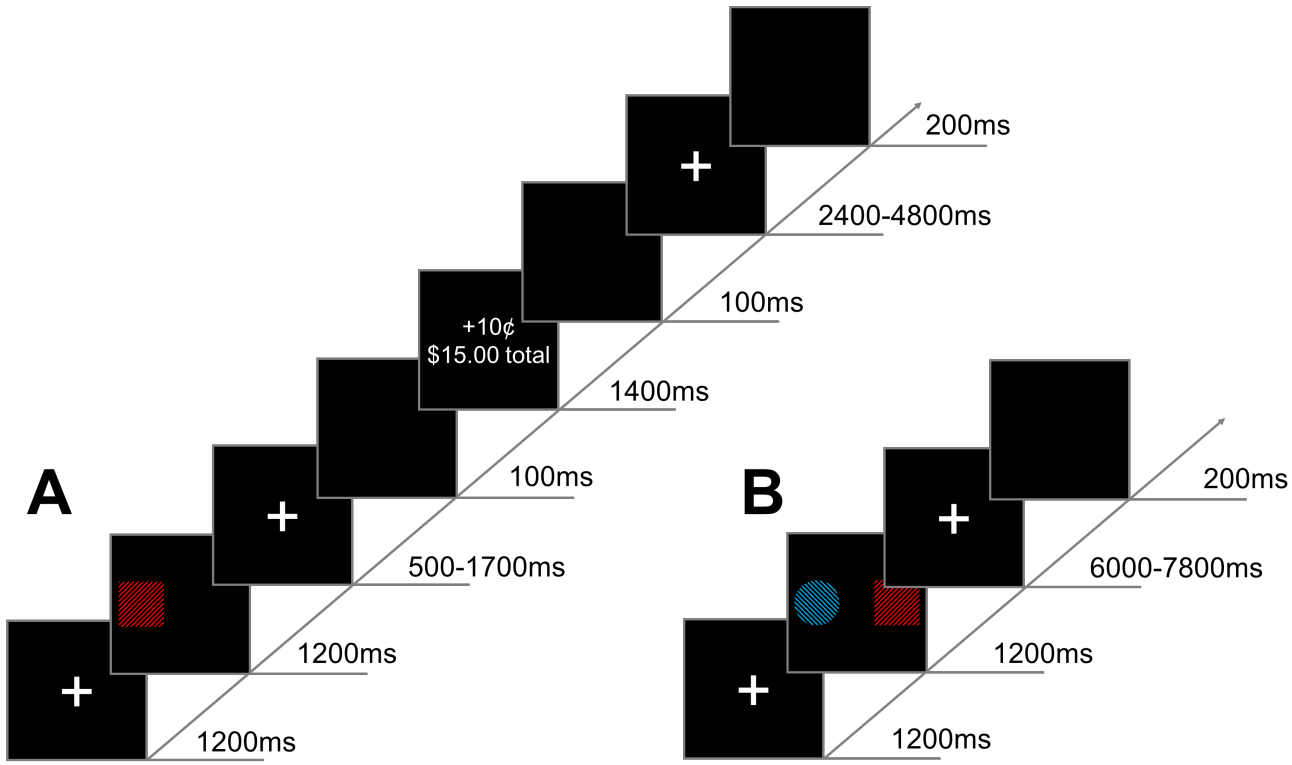

Figure 10 – Time course of trial events during the training and test phases in Experiment 2. (A) Training phase. A fixation display was presented for 1200ms, followed by the stimulus display for 1200ms. Participants were instructed to report which side on the screen the shape appeared on. A 500-700ms inter-stimulus-interval was followed by a 100ms blank, then the monetary feedback for 1400ms, followed by another 100ms blank. The trial concluded with the fixation display for 2400-4800ms and a 200ms blank to alert participants for the next trial. (B). Test phase. A fixation display was presented for 1200ms, followed by the stimulus display for 1200ms. Participants were instructed to report which side on the screen the circle appeared on. This was followed by a fixation display for 6000-7800ms and a 200ms blank to alert participants for the next trial.

Behavioral Responses During Reward Learning with Multifeature Objects

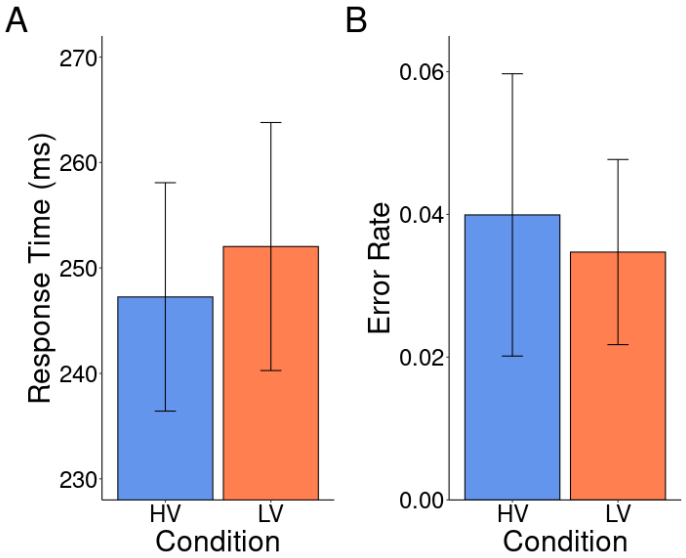

Figure 11– A) RT and B) error rate in the training phase for the high-value (HV) and low-value (LV) colors. Error bars represent the standard error of the mean.

Response Times During Attentional Orienting Towards Multifeature Objects

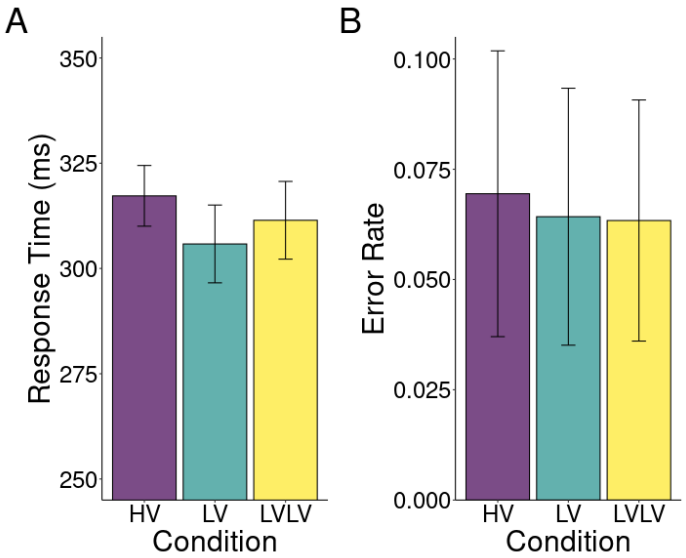

Figure 12 – A) RT and B) error rate in the test phase for the high-value distractor and low-value target condition (HV), the low-value distractor and high-value target condition (LV), and the low-value distractor and low-value target condition (LVLV). Error bars represent the standard error of the mean.

Oculomotor Capture During Attentional Orienting Towards Multifeature Objects

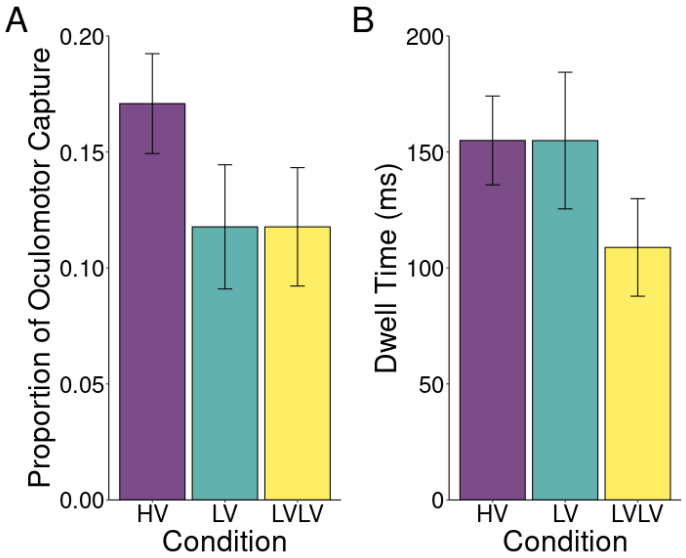

Figure 13 – A) Proportion of oculomotor capture and B) dwell time in the test phase for the three conditions. Error bars represent the standard error of the mean.

Accuracy of Feature Decoding from Multifeature Distractors

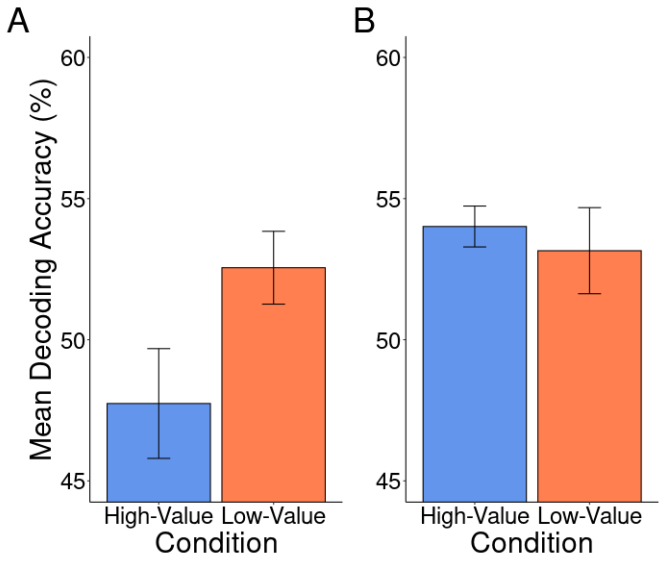

Figure 14 – Mean classifier decoding accuracy in the test phase for A) orientations and B) color. Error bars represent the standard error of the mean.

Alternate Performance Metric of Classifier Decoding Feature of Multifeature Distractors

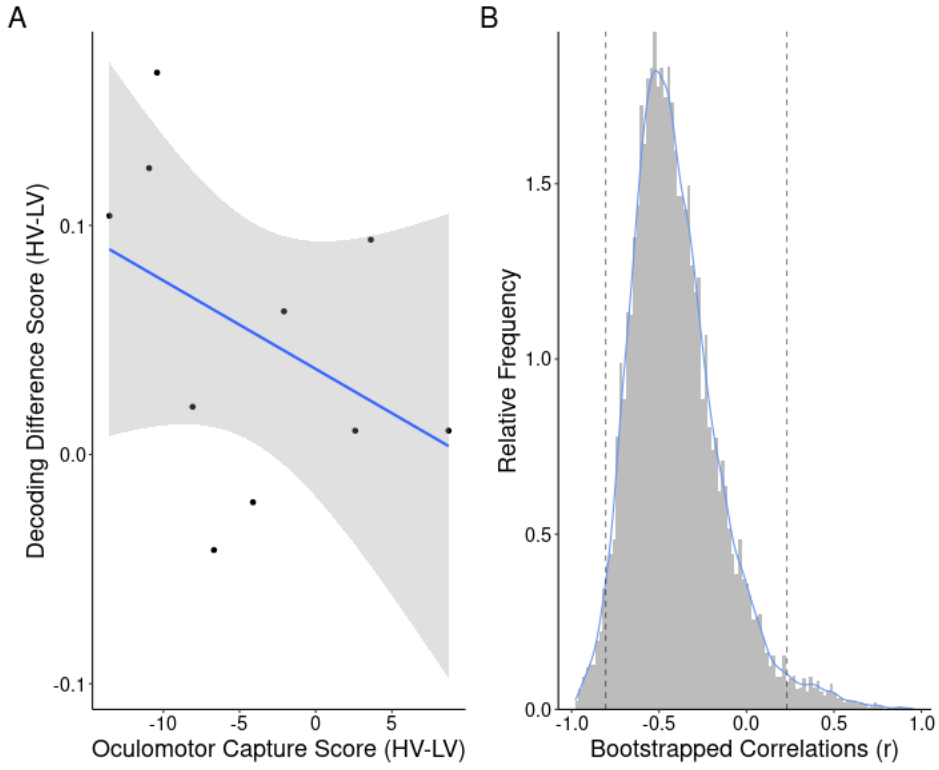

Figure 15 – A) Correlation between the difference in orientation decoding accuracy (HV-LV) and the difference in oculomotor capture rates (HV-LV), and B) the 10,000 bootstrapped samples of the correlation.

Simulation of Attentional Priority Map Following Reversal Learning Procedure

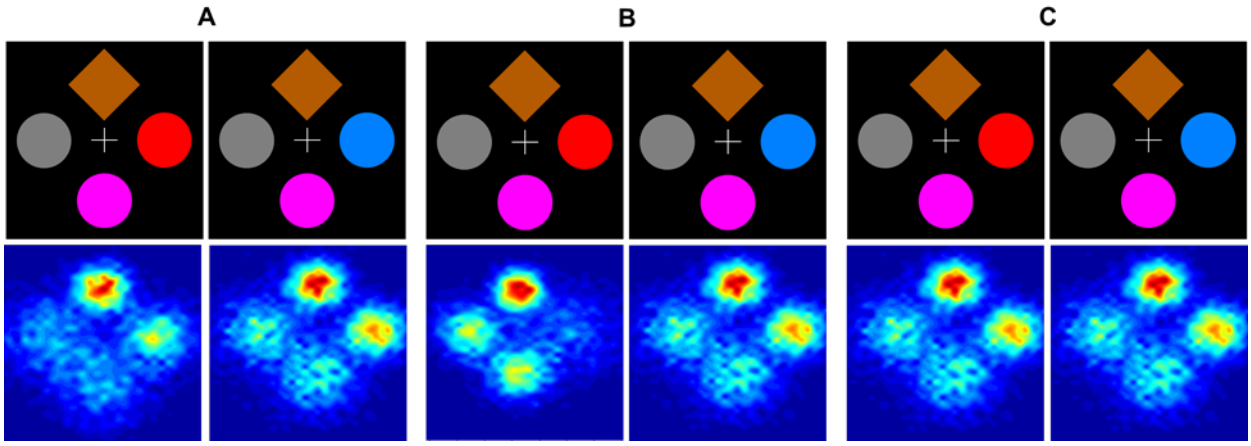

Figure 16 – Schematic of experiment stimuli (top) and simulated priority map representation (bottom) for our hypotheses where A) old high-value color (red) loses its priority, B) the old high-value color is inhibited, and C) new (blue) and old high-value colors remain equally prioritized. The target is the shape singleton (diamond). More intense colors in the priority map reflect stronger attentional priority associated with the corresponding stimulus. The simulation is for illustrative purposes only, and the exact intensity values are arbitrary. Reprinted from Liao and Anderson, 2020b.

Experimental Paradigm Investigating Reversal Learning to Overcome Value-Driven Attentional Capture

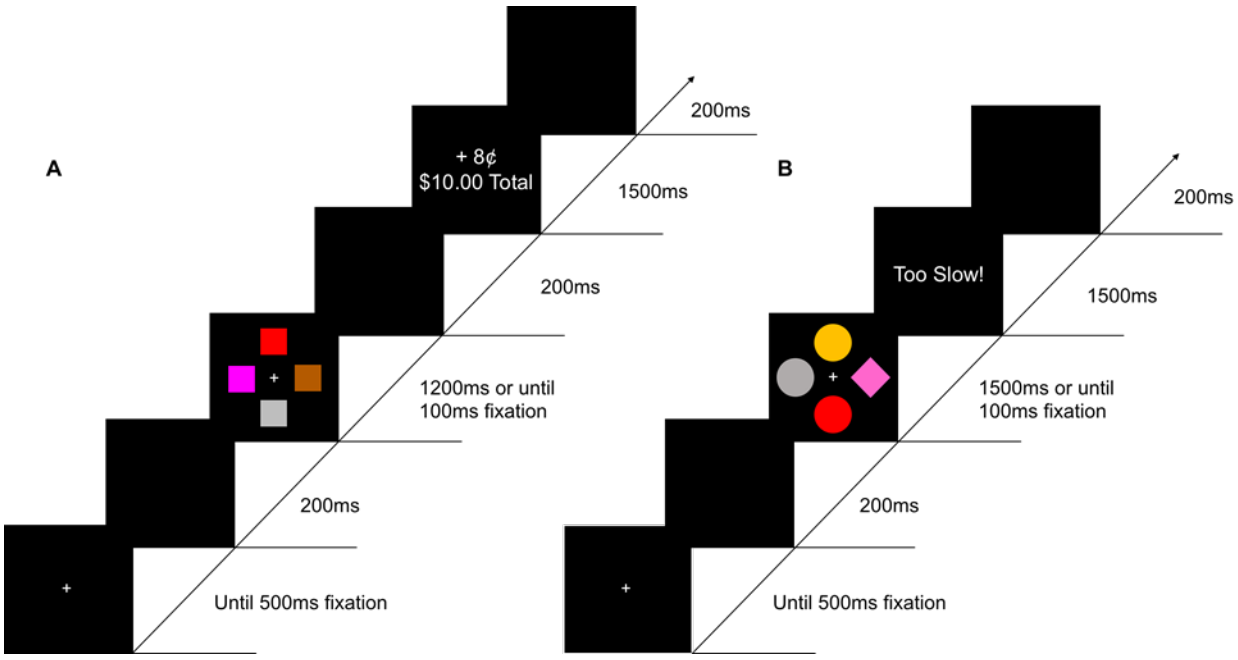

Figure 17 – Time course of trial events during the training and test phases. (A) Training phase. Participants were tasked to fixate on the target color (red, green, or blue) on every trial. Participants had a 1200ms time limit to fixate on the target for a continuous period of 100ms before a blank was presented, followed by a feedback display showing the amount earned on the current trial along with total earnings. There was only one target color present on each trial; one was associated with a high-value reward when fixated, another with low-value reward, and the third with no reward. In the second training phase, the high-value color and the no reward color switched contingencies. (B) Test phase. Participants had 1500ms to fixate on the unique shape (singleton) for a continuous period of 100ms, while sometimes ignoring a critical color distractor from the training phase. If participants were successful in fixating the target within the time limit, the search array would be replaced with a blank screen for 500ms, otherwise they would see the words "Too Slow!" for 1500ms, followed by a 200ms blank to end the trial. The second test phase was identical to the first. Reprinted from Liao and Anderson, 2020b.

Response Time Data from Investigating Reversal Learning to Overcome Value-Driven Attentional Capture

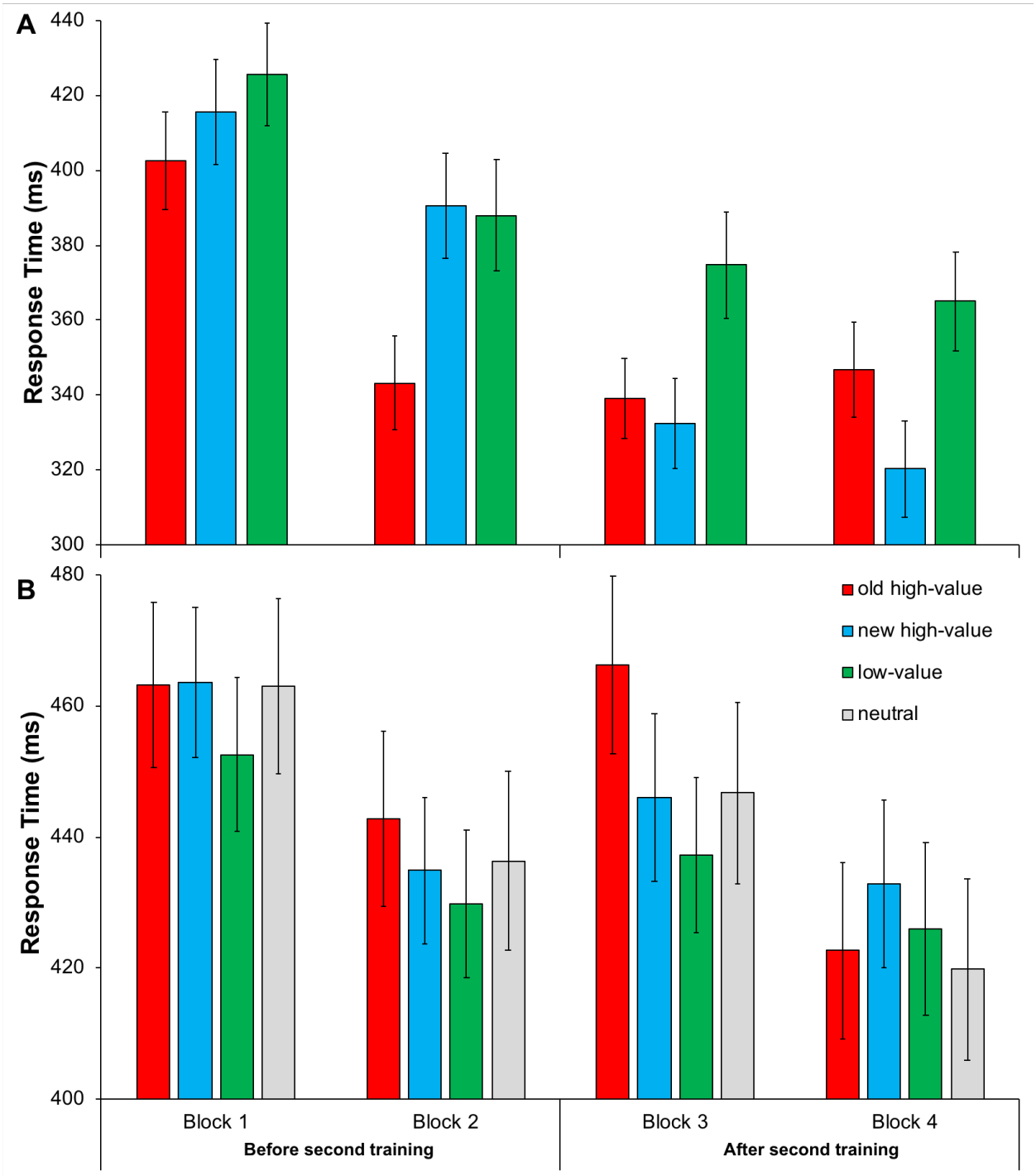

Figure 18 – A) RT in the training phase for each target color and B) in the test phase for each distractor color, for each block. Error bars represent standard error of the mean. Reprinted from Liao and Anderson, 2020b.

LIST OF TABLES

Regions of the Brain Active During Value-Driven Attentional Orienting in Space

A. Validity Effect in LVF

Region	x, y, z	Volume (ml)
Left Caudate Tail	31, 33, -1	1.188
Left Hipocampus	26, 35, -3	1.188
Left Parahippocampal Gyrus	24, 33, -4	1.188
Left Insula	28, 15, 21	1.047
Left Caudate	21, -6, 21	1.047
Right Brain Stem	-16, 31, -46	1.016
Right Frontal Eye Field	-19, 4, 46	1.000
Right Cingulate Gyrus	-15, 44, 29	0.875
Right Parahippocampal Gyrus	-26, 16, -10	0.797
Left Parahippocampal Gyrus	41, 36, -11	0.719
Left Cingulate Gyrus	11, 29, 24	0.688
Right Insula	-32, -4, 16	0.672
Right Middle Temporal Gyrus	-36, 46, 11	0.531
Right Precuneus	-21, 49, 34	0.516

B. Validity Effect in RVF

Region	x, y, z	Volume (ml)
Right Frontal Eye Field	-16, 14, 44	4.859
Right Postcentral Gyrus	-26, 32, 44	4.859
Right Precentral Gyrus	-29, 6, 29	3.781
Left Cingulate Gyrus	16, -9, 34	3.578
Left Frontal Eye Field	23, 23, 42	3.578
Right Superior Temporal Gyrus	-34, 49, 19	3.406
Superior Colliculus	1, 29, -21	2.297
Left Postcentral Gyrus	29, 26, 46	2.000
Left Paracentral Lobule	11, 26, 49	2.000
Left Posterior Cingulate	11, 46, 16	1.672
Left Cingulate Gyrus	11, 36, 30	1.672
Left Cuneus	9, 79, 9	1.656
Left Precentral Gyrus	41, 9, 24	1.469
Left Lateral Occipital Cortex	31, 59, 6	1.203
Right Caudate Tail	-36, 14, -11	0.922
Rght Anterior Cingulate	-1, -21, 16	0.781

Left Anterior Cingulate	0, -25, 6	0.781
Right Middle Frontal Gryus	-30, -40, 12	0.703
Right Inferior Frontal Gyrus	-34, -30, 14	0.703
Right Insula	-44, 19, 1	0.672
Left Parahippocampal Gyrus	36, 44, 1	0.672
Left Inferior Parietal Lobule	41, 39, 24	0.672
Right Precentral Gyrus	-46, 6, 21	0.625
Right Lentiform Nucleus	-21, -19, -4	0.594
Right Superior Temporal Gyrus	-31, 41, 14	0.594

C. Target LVF-RVF Contrast

Region	**x, y, z**	**Volume (ml)**
Right Primary Visual Cortex	-11, 69, 4	8.875
Left Primary Visual Cortex	11, 66, -6	4.484

Table 1 – All regions of the brain demonstrating significantly greater activations across all our contrasts. 1A and 1B contain the list of regions that had greater activation in response to valid compared to invalid trials. Valid trials were those where the target appeared in the previously high-value quadrant for that specific scene, while invalid trials were those where the target appeared in the opposite hemifield to the previously high-value quadrant for that specific scene. 1C contains regions that were more activated on targets appearing in the LVF compared to the RVF, collapsed across reward conditions. LVF = right visual field; LVF = left visual field. x, y, z refers to the Talairach coordinates of the peak voxel of the cluster. Regions with the same volume of activation formed one contiguous cluster. Reprinted from Liao et al., 2020a.