



**UNIVERSITY OF
BIRMINGHAM**

**ATTENTION TO OBJECTS: EXPLORING REWARD ASSOCIATIONS,
NEUROPHYSIOLOGICAL INDICES AND CONCEPTUAL
REPRESENTATIONS IN THE HUMAN BRAIN THROUGH BEHAVIOUR,
NEUROIMAGING AND MACHINE LEARNING**

By

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Abstract

Object-based attention (OBA) refers to the preferential processing of information within an object. Despite extensive research, questions remain regarding how OBA interacts with reward systems, its neural basis, and its role in semantic processing. This thesis addresses these gaps through experiments investigating: (1) the interaction between reward and OBA; (2) neural indices reflecting OBA; and (3) how attention to objects relates to semantic processing. In **Chapter 2**, using modified two-rectangle paradigms, we found that OBA and reward associations coexist, with the latter enhancing the irrelevant-object capture of attention and effects persisting even after rewards were discontinued. **Chapter 3** used EEG to measure the effects of task-irrelevant objects on neural markers of attentional deployment—i.e. alpha oscillations and the anterior directing attention negativity (ADAN) component—. Results showed these indices reflect OBA independently of attentional anisotropies or perceptual clutter, indicating that OBA modulates neural attentional deployment even when not evident behaviourally. In **Chapter 4**, employing a novel analysis method involving machine learning on concurrent EEG-fMRI data, we investigated how attention influences semantic representations. We found that attention to objects modulates the enhancement and suppression of semantic information in specific brain regions with alpha oscillations correlating with target representations in the orbitofrontal cortex and distractor information in working memory network regions. Overall, the findings establish the object prioritisation as a robust attentional mechanism resistant to reward manipulations and tracked by alpha oscillations and ADAN ERP. Furthermore, this work advances the understanding of how attention modulates semantic information in the human brain.

*A Dario e Nina,
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About this thesis

Below is a list of papers included or related to this thesis.

Grignolio, D., Acunzo, D. J., & Hickey, C. (2024). Object-based attention is accentuated by object reward association. *Journal of Experimental Psychology: Human Perception and Performance*, 50(3), 280.

This paper is presented in **Chapter 2** as it was originally published in *Journal of Experimental Psychology: Human Perception and Performance*, with the exception of the section and figure numbering, which have been adjusted for ease of reference within the thesis. Author contributions: **Damiano Grignolio**: Investigation, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **David Acunzo**: Methodology, Writing – review & editing. **Clayton Hickey**: Visualization, Funding acquisition, Methodology, Supervision, Writing – original draft, Writing – review & editing.

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This preprint paper is fruit of the analysis of the same dataset used for the study presented in **Chapter 4**. Consequently, they share some content. For such shared content there was an equal contribution of the authors: David Acunzo, Damiano Grignolio, and Clayton Hickey. Author contributions to the whole paper: **David Acunzo**: Investigation, Data curation, Formal analysis, Visualization, Methodology, Writing – original draft, Writing – review & editing. **Damiano Grignolio**: Investigation, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Clayton Hickey**: Visualization, Funding acquisition, Methodology, Supervision, Writing – original draft, Writing – review & editing.

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List of abbreviations

ADAN – Anterior Directing Attention Negativity	IPL – Inferior Parietal Lobule
BOSS – Bank of Standardized Stimuli	ITG – Inferior Temporal Gyrus
CB – Cardioballistic	LDA – Linear Discriminant Analysis
CHBH – Centre for Human Brain Health	LOC – Lateral Occipital Cortex
DO – different object	MFG – Middle Frontal Gyrus
ECG – Electrocardiogram	MNI – Montreal Neurological Institute
EEG – Electroencephalography	MTG – Middle Temporal Gyrus
EOG – Electrooculogram	OBA – Object-Based Attention
EPI – Echo Planar Imaging	OFC – Orbitofrontal Cortex
ERP – Event-Related Potential	PPA – Parahippocampal Place Area
FA – Flip Angle	RT – Response Time
FEF – Frontal Eye Fields	SFG – Superior Frontal Gyrus
FFA – Fusiform Face Area	SO – same object
fMRI – Functional Magnetic Resonance Imaging	SPL – Superior Parietal Lobule
FOV – Field of View	TE – Echo Time
FWHM – Full Width at Half Maximum	TF – Time-frequency
GLM – General Linear Model	TPJ – Temporoparietal Junction
HEOG – Horizontal Electrooculogram	TR – Repetition Time
ICA – Independent Component Analysis	V1 – primary visual cortex
IFG – Inferior Frontal Gyrus	VCG – Vectorcardiogram
IFJ – Inferior Frontal Junction	VDAC – Value-Driven Attentional Capture
	VEOG – Vertical Electrooculogram

CHAPTER 1

GENERAL INTRODUCTION

Donald Broadbent's (1958) seminal theory described attention as a filter that selects incoming stimuli for further processing of their complex psychological properties. Broadbent's aim was to ground the nebulous concept of attention in a falsifiable theoretical framework, synthesising experimental findings into a cohesive model. The enduring influence of this theory is evident in its foundational role in the field of attention research—e.g., it is cited in the first sentence of most papers in the attention literature. However, over seven decades of investigation have revealed that attention is not a singular, monolithic function. Instead, it encompasses a range of phenomena (see Allport, 1992; Driver, 2001), with some researchers considering it as a "verbal phantom" (William James, 1890/1950) and advocating for a radical re-evaluation of approaches to the field (see Hommel, 2019; Anderson, 2011; Di Lollo, 2018; Hommel & Colzato, 2015; Krauzlis, Bollimunta, Arcizet, & Wang, 2014; Mole, 2011; Rosenholtz, 2024). As Driver (2001) noted, "Attention' now refers to a whole set of phenomena to be explained rather than to a single process which explains those phenomena". Nonetheless, the various psychological processes grouped under the umbrella of "attention" share a common thread: they all pertain to the selectivity of information and the neural mechanisms that prioritise it (Driver, 2001).

This thesis addresses key research questions concerning attentional processes: how different attentional mechanisms interact (Chapter 2), how these mechanisms relate to known physiological indices of information selection (Chapter 3), and how these indices are linked to the processing of abstract information in the brain (Chapter 4).

1.1 Attention through objects

In the early stages of attention research, auditory processing dominated the field, largely due to the pioneering work on selective auditory processing, such as Cherry's (1953) dichotic listening experiments. In the subsequent decades though, the focus shifted towards the study of visual attention.

Visual attention was long deemed to be spatial in nature. A prominent metaphor likened attention to a spotlight, capable of moving to different locations to selectively enhance the processing of stimuli, much like the movement of the eyes (Treisman & Gelade, 1980; see also Eriksen & Eriksen, 1974; Posner, 1980; Driver, 2001). This spatial perspective dominated early research on visual attention.

By the late 1960s, alternative views began to challenge this spatial framework. Ulric Neisser (1967) proposed that attention is not solely spatial but is also influenced by perceptual organisation. His work emphasised that visual attention can be guided by the grouping of elements into coherent perceptual units. Neisser's "selective looking" experiment (Neisser & Becklen, 1975) provided compelling evidence for this perspective. In the experiment, participants viewed superimposed videos of two distinct scenes—a basketball game and a hand-slapping game—and were instructed to attend to one while ignoring the other. Despite the spatial overlap of the scenes, participants were able to selectively attend to the target scene, showing that attention operates on perceptual objects, not solely on spatial locations.

Building on Neisser's insights, John Duncan (1984) reinforced the idea that attention is guided not only by spatial location but also by the structure of objects, proposing that object-based attention (OBA) functions independently of spatial

selection. In his seminal study, Duncan showed that the cost associated with searching for two different targets diminishes when both targets are attributes of the same object but re-emerges when the targets are perceived as belonging to different objects. These findings solidified the idea that OBA is not simply a byproduct of spatial attention but represents a distinct mechanism.

Subsequent research expanded on Duncan's work, with one of the most impactful contributions being the introduction of the two-rectangle paradigm by Egly, Driver, and Rafal (1994), which has since become a standard tool for studying object-based selection. The details of this paradigm are discussed in the next section.

1.2 The two-rectangle paradigm

In 1994, Egly, Driver, and Rafal introduced a paradigm designed to disentangle the effects of spatial location and object structure on attentional selection. Initially developed to investigate attentional deficits in patients with parietal lesions, the paradigm quickly became a standard method for exploring object-based attention in the typical brain.

The task involves presenting participants with two outlined, parallel rectangles on a screen. A cue briefly highlights one end of one rectangle, directing attention to that location. Following a brief interval, a target appears at one of three possible locations: (1) at the cued location (the valid condition), (2) at the opposite end of the same rectangle (the invalid same-object condition), or (3) at the end of the other rectangle, equidistant from the cue (the invalid different-object condition).

The results consistently reveal both spatial and object-based effects on attention. Reaction times are faster and accuracy is higher for targets appearing in the valid condition compared to the invalid conditions, reflecting the spatial prioritisation of the cued location. Critically, a same-object advantage emerges: participants respond more quickly and accurately to targets in the invalid same-object condition than to those in the invalid different-object condition, despite the cue-to-target distance being identical. These findings corroborate the hypothesis that attention is influenced not only by spatial proximity but also by how the visual system groups stimuli into objects.

1.3 Space- and object-based attention

As often occurs in science, these initial findings regarding the prioritisation of object-related information raised more questions than they answered. A key question that emerged is: Is the object-based selection mechanism still spatial in nature? While it is evident that stimuli can be selected based on their features or their association with objects, some evidence suggests that attention ultimately prioritises the spatial location that these objects occupy (Tsal & Lavie, 1993; Roelfsema et al., 1998; Ekman et al., 2020). For instance, Ekman et al. (2020) used functional MRI (fMRI) to show that when attention is directed to one end of an object, activity in the primary visual cortex (V1) propagates along the object's contours. This finding suggests that spatial propagation of attentional effects may play a critical role in object-based selection, linking it to spatial mechanisms in early visual processing.

Conversely, several arguments support the differentiation of selection mechanisms for spatial and object-based attention. First, homologous mechanisms

of the visual object-based effect on attention have been observed in the auditory modality (e.g., Marinato & Baldauf, 2019; see Shinn-Cunningham, 2008 for a discussion of OBA in the auditory domain), where objects are defined by auditory features rather than spatial configuration (see McDermott, 2009 for a description of selective attention and the sound segregation problem). This suggests that attention can operate in an object-centric manner even when spatial cues are minimal or absent. Additionally, the ability to select information from overlapping visual stimuli—such as focusing on a bird perched on a tree while ignoring the leaves partially obscuring its silhouette—further supports the existence of mechanisms that are not purely spatial. To investigate this relationship, paradigms using superimposed images as stimuli have become common in studies examining the interaction between spatial and object-based attention.

Baldauf and Desimone (2014) used MEG and fMRI to identify neural correlates of object-based attention, providing further evidence for the differentiation of spatial and object-based attentional mechanisms. Their findings showed that attention to faces activated the fusiform face area (FFA), whereas attention to houses activated the parahippocampal place area (PPA). Importantly, activity in the inferior frontal junction (IFJ) was linked to object-based attention, and connectivity analysis suggested that the IFJ directed activity in these specialised areas. Based on these results, Baldauf and Desimone proposed that the IFJ serves a role in object-based attention akin to the function of the frontal eye fields (FEF) in spatial attention, directing attention to objects rather than locations.

Adding to this understanding, Cohen and Tong (2015) conducted a study using overlapping face and house stimuli to investigate object-based attentional

mechanisms. Their results showed that attentional feedback to early visual areas (V1 to V4) selectively enhanced the low-level features corresponding to the attended object, even when stimuli were spatially overlapping. This suggests that object-based attention enhances the representation of attended objects through feedback mechanisms, complementing Baldauf and Desimone's findings on the role of higher-order control structures like the IFJ.

Together, the results considered so far indicate that while OBA appears to involve a spatial component, as suggested by Ekman et al.' findings of spatial spread in V1, it is also plausible that the underlying control mechanisms for object-based and space-based selection differ significantly. Baldauf and Desimone (2014) provide compelling evidence that object-based attention is directed by structures such as IFJ, much like the FEF control spatial selection. Meanwhile, Cohen and Tong (2015) shows that these higher-order controls ultimately converge on similar modulatory effects within early visual areas, selectively enhancing the features of attended objects. Thus, OBA and spatial attention may share common target regions for modulation (e.g., V1 to V4) but differ fundamentally in how these areas are instructed to prioritise information.

The question of whether these mechanisms are distinct or overlapping has also been extensively informed by neuropsychological evidence. The next section will delve into literature on clinical conditions that offer a complementary perspective on the relationship between these mechanisms.

1.4 Insights from Neuropsychology

When the brain suffers a lesion, cognitive functions may become impaired, leading to specific deficits that provide insights into the underlying neural mechanisms. Neuropsychology investigates these deficits, often using the method of dissociations to delineate distinct brain functions and their interrelationships. A dissociation occurs when damage to the brain impairs one cognitive function, A, while sparing another, B. Such cases suggest that A operates independently of B, though this independence is not absolute, as B may remain unaffected due to differences in task demands or the involvement of a compensatory process, C. A stronger inference of independence comes from observing a double dissociation, where a second patient exhibits the reverse pattern: impairment in B but not A. This provides robust evidence for the independence of these cognitive functions.

In the domain of attention, observations from neuropsychology seem to support the existence of an independent mechanism that prioritises object status. Two conditions exemplify the selective failure of object-based attentional processes: simultagnosia and object-centred neglect.

1.4.1 Neglect

As discussed earlier (Section 1.1.1), Egly, Driver, and Rafal (1994) introduced the two-rectangle paradigm to investigate object- and space-based attention in patients with parietal cortex lesions, a common lesion site associated with neglect.

Spatial neglect (or neglect) is an impairment in reporting, orienting, or responding to stimuli coming from the contralesional side, not attributable to low-level sensorimotor deficits (Heilman et al., 1984). Patients with neglect often fail to engage with stimuli in one half of their environment, ignoring food on one side of their plate, reading only one side of a newspaper, or shaving and applying makeup to just one side of their face. These patients often exhibit anosognosia (a lack of awareness of their deficit; Grattan et al., 2018), and when confronted about their behaviour, they may produce confabulations (absurd or inadequate explanations; Mijović, 1991; for a review of the semiology, see Rode et al., 2017). Other key features of the condition are a sub-normal level of arousal and a difficulty in initiating actions toward the contralesional side of the space, of objects or of their own body (Corbetta et al., 2012).

Neglect is a significant public health issue, given its prevalence following stroke. In the European Union, stroke is the leading cause of adult disability (Truelsen et al., 2006), and meta-analyses estimate that neglect affects approximately 30% of stroke survivors (Esposito et al., 2021; Prendes et al., 2024). These figures underscore the importance of understanding this condition and have driven extensive research efforts over the years.

As a result many explanations have been proposed to account for this condition, initially focusing on basic sensory deficits such as hemianopsia (Bay, 1953), impairments in ocular exploration (Schott et al., 1966), or the in the lack of awareness for such deficits due to anosognosia (Luria & Skorodumova, 1950, quoted by Luria, 1976). Later, more structured theories have emerged, framing neglect within various frameworks, including motor impairments—whether in

planning (e.g., Rizzolatti & Camarda, 1987), initiation, or execution of movements (Mattingley et al., 1992; Heilman et al., 1985)—arousal deficits (Robertson et al., 1998), attentional disengagement (Posner et al., 1984), or deficits in spatial representation (Bisiach & Luzzatti, 1978).

The abundance of theories in part sparks from the heterogeneity in the observed clinical manifestations of the condition (Williams et al., 2021) as well as the lesions causing it (Moore et al., 2023). The right parietal cortex is commonly implicated in neglect syndromes (De Renzi, 1982; Heilman et al., 1985). However, meta-analyses reveal more variable lesion sites, with the key regions within the right hemisphere encompassing the superior longitudinal fasciculus, as well as the supramarginal, postcentral, precentral and angular gyri. Lesions to the left hemisphere that cause neglect of the right side of space or body present with milder symptoms and are less frequent, accounting for approximately 10-40% of neglect cases (Beis et al., 2004). Left-sided lesions typically include the insula, Brodmann's area six, operculum, and angular gyrus (see Moore et al., 2023; Chechlacz et al., 2012; Molenberghs et al., 2012).

The taxonomy of the neglect variants is as complex as its neural substrate (see: Buxbaum et al., 2004; Vallar, 1998; Vallar and Bolognini, 2014; Williams et al., 2021; Aziz et al., 2024). Among the many manifestations is a double dissociation between a space-centred neglect, relative to the mid-sagittal plane of the head or body (also referred to as egocentric) and object-centred neglect, relative to the object's vertical axis (also known as allocentric; Vallar and Ronchi, 2021). For instance, the patients with space-centred neglect will fail to copy objects located on the contralesional side of space, whereas those with object-centred neglect will omit the contralesional side

of each object, drawing only half of it. On one hand, this double dissociation suggests the existence of differential mechanisms of selection of visual inputs. On the other hand, the nature of the object-centred neglect seems to remain spatial in nature, as it disrupts the selection of the contralesional side of the objects.

Many researchers have tried to investigate the anatomical side of this dissociation. It can be argued that the first researcher to suggest a distinct anatomical substrate for space and object centred neglect were indeed Egly, Driver & Rafal (1994) in the same study introducing the two-rectangle paradigm, as they showed a dissociation in the performance on the space and object component of the task for left- and right-lesion patients. More recently, some studies have specifically looked at patients showing a predominance of either space- or object-centred neglect and analysed the observed lesion patterns through modelling (Chechlacz et al., 2010) or lesion mapping (Moore et al., 2021a). These studies pointed at a more complex distinction than the one proposed by Egly and colleagues. Nonetheless, the distinction remains debated, with some studies supporting the existence of two separate patient groups (Ciaraffa and Gainotti, 2013) and others finding no clear separation (Karnath et al., 2011) or proposing alternative accounts (e.g., task demand in Leyland et al., 2017).

The double dissociation between space-centred and object-centred neglect suggests the existence of differential mechanisms for selecting visual inputs. However, the nature of object-centred neglect remains contested, as it appears to retain a spatial component, disrupting the selection of the contralesional side of objects. This ongoing debate has broader implications for understanding object-based attention. If object-centred neglect indeed relies on spatial

mechanisms, it challenges the notion that object-based attention operates as an independent process. Conversely, if distinct mechanisms underlie these phenomena, this would provide stronger support for the independence of object-based attention.

These unresolved questions are directly relevant to the research questions addressed in this thesis. Understanding whether object-based attention emerges from distinct neural mechanisms or reflects an extension of spatial selection is critical for interpreting its role in attentional prioritisation. In this context, the studies presented here (Chapters 2 and 3) investigate object selectivity under conditions that disentangle its spatial and object-specific components, providing new insights into the nature of object-based attention.

1.4.2 Simultagnosia

Look around. You can see an environment filled with stimuli: a desk, your phone, a cup of tea next to it. You can focus on the phone ringing, while remaining aware of the presence of the cup's presence nearby. Although they present to you as distinct perceptual units, they are seamlessly integrated into your visual experience and you can switch your focus from one to the other. Patients with simultagnosia instead live in a chaotic world, where only one object at the time is perceived—e.g., either the phone or the cup (Dalrymple et al., 2013; Rafal, 2001). Since there is no relative position as there is only one object, judging objects location in space becomes an insurmountable task for them. They can 'lock' on a detail, like the handle of the cup, unaware that it is part of a larger object (Rafal, 2003). As a general definition, we can

describe simultagnosia as the inability of attending or perceiving multiple objects at the same time (Bàlint 1909; Husain and Stein 1988).

In test batteries to assess perception, patients with simultagnosia fail in similar ways as patients with apperceptive agnosia. Patients struggle to process and distinguish objects presented in arrays and tend to focus on specific parts of an object trying to infer its identity based on local features. Unlike individuals with apperceptive agnosia though, patients with simultagnosia can utilise shape information to assist with object identification (Devinsky et al., 2008; Baugh et al., 2010).

Farah (1990) first organised simultagnosia into two main types differentiated by the symptoms displayed and the corresponding lesions in the dorsal and ventral visual processing pathways. The dorsal variant is often accompanied by ocular ataxia and visuomotor apraxia to form a rare syndrome called Bàlint's syndrome (Bàlint, 1909). This syndrome derives from an extensive bilateral occipito-parietal lesion often due to infarct of the posterior cerebral artery or less frequently by brain injury or neurodegenerative disease. Due to the low prevalence of the condition, identifying its precise neural substrate has been challenging. Nonetheless, studies of dorsal simultagnosia patients implicate the medial occipito-parietal junction, inferior intraparietal sulcus, cuneus, and adjacent white matter tracts (Chechacz et al., 2012a). Some researchers have also proposed a shared anatomical substrate between object-centred neglect and simultagnosia, linking these deficits to overlapping neural mechanisms (Medina et al., 2009; Chechacz et al., 2012a, Chechacz et al., 2012b; for review, see Dalrymple et al., 2013).

This particular disruption of the attentional network causes the restriction of visual focus and prevents more than one object to breach into patients' awareness (Dalrymple et al., 2013; Rizzo & Vecera, 2002; Moreaud, 2003; Rafal, 2003). Yet, whether this impairment reflects a failure in object-based or spatial attention remains debated. Some suggest that dorsal simultagnosia arises from compromised mechanisms responsible for selecting pre-attentively defined objects (Duncan, 1984; Driver & Baylis, 1989). Others argue that it reflects a restricted spatial focus, permitting only one object at a time to occupy the "spotlight" of attention (Dalrymple et al., 2013).

Despite the efforts in framing simultagnosia as a failure of spatial attention, some observations remain difficult to reconcile with a reduction of the spatial focus size. For instance, even within a narrowed attentional window, patients frequently show feature-binding errors (Robertson et al., 1997; Friedman-Hill et al., 1995) or struggle to perceive multiple overlapping objects (e.g., Poppelreuter-Ghent test, Luria, 1978; Rafal, 2001, 2003). Moreover, sometimes patients report objects being fixated to disappear spontaneously (Rizzo and Hurtig, 1987) and some can still show normal cueing effects during a Posner cueing paradigm (Egly et al., 1995).

The neuropsychological conditions discussed—neglect and simultagnosia—complement the neuroscientific findings reviewed earlier, reinforcing the evidence for object-based attention as a distinct mechanism. Understanding these mechanisms has implications not only for theoretical models but also for rehabilitation practices. To refine this understanding, this thesis investigates object selectivity using modified versions of the two-rectangle paradigm. Specifically, Chapter 2 explores whether object selectivity interacts with rewards, paralleling

known space-based effects. Chapter 3 examines whether established neurophysiological markers of spatial attention allocation also index attention to objects.

1.5 The role of reward

One of the most enduring frameworks in attention research distinguishes between goal-directed and stimulus-driven attentional control. However, evidence emerging over the past two decades suggests that the influence of reward on attention cannot be fully explained by this dichotomy (Della Libera & Chelazzi, 2006). While the idea that reward modulates attention is not new (see Maunsell, 2004), contemporary research highlights the autonomous and persistent effects of reward associations on attentional selection. These effects are independent of physical salience or volitional control and are now termed value-driven attention or value-driven attentional capture (VDAC; Anderson, 2013).

In 2010, Hickey and colleagues (2010a) sought to determine whether reward influence on visual processing could be reduced to a volitional control of attention. Participants engaged in a visual search task where they identified a target shape distinct from the distractors (e.g., a square among circles). During some trials, a salient singleton distractor with a unique colour (e.g., a brown shape among red shapes) was presented and participants received either high or low rewards for correctly identifying the target. Critically, target and distractor colours could remain constant or swap between trials, allowing the researchers to assess how previous rewards influenced attention. The results closely mirrored those found by Della

Libera and Chelazzi (2006), with strong priming following high rewards, whereas low rewards either diminished or reversed the priming effects. This study was pivotal in dissociating strategic and automatic influences of reward on attention.

The following year, Anderson and colleagues (2011) found that reward-associated stimuli could capture attention even when they were task-irrelevant, unrewarded, and non-salient. In their two-phase experiment, participants first learned to associate target colours with high or low reward probabilities during a training phase. In a subsequent test phase, these colours reappeared as distractors, disrupting participants' ability to focus on a task-relevant shape. Critically, both goal-directed and stimulus-driven accounts would predict no influence of the reward history on this second task. Instead, distractors with a history of high reward produced greater interference, illustrating the enduring and involuntary influence of reward on attentional capture.

Numerous studies have since expanded on these findings, showing that reward-associated stimuli consistently attract attention, even when the reward is no longer available (e.g., Le Pelley et al., 2015; Hickey & van Zoest, 2012, 2013; Anderson & Yantis, 2013). These effects have been observed over extended periods of time (Della Libera & Chelazzi, 2009), although they remain subject to extinction (Milner et al., 2023). Neuroimaging studies have shown that reward-associated objects elicit stronger representations in the object-selective visual cortex (Barbaro, Peelen, & Hickey, 2017; Hickey & Peelen, 2015). Furthermore, it has been shown that reward can bias action by undermining inhibitory control in the motor system (Anderson, 2016a, 2017; Kim & Anderson, 2019).

The implications of these findings extend to understanding psychopathological conditions such as addiction. Although the mechanism of reward-driven attention can prove adaptive as it allows to quickly and automatically prioritise useful stimuli without the need to purposely scan the environment for reward contingencies, in case of excessive or deficient bias toward reward-associated stimuli, it may become maladaptive. The maladaptive consequences of reward-driven attention have been linked to attentional biases toward drug-related stimuli (Field & Cox, 2008). Individual differences in value-driven attention have been associated with cognitive control and personality traits (Hickey et al., 2010b). Furthermore, abnormal value-driven attention mechanisms have been implicated in the development and maintenance of addiction (Anderson, 2016b, 2021). For example, the attentional bias toward drug related stimuli in addiction (Field & Cox, 2008) has been linked to an abnormal impact of value-driven attention (Anderson, 2016b), its neural mechanisms (Anderson et al., 2016; Anderson et al., 2017; Anderson, 2019) and associated behaviours (Kim & Anderson, 2019; Anderson et al., 2020; see also Anderson, 2021).

Understanding the mechanisms of attentional deployment on objects and the role of reward-driven processes is critical for elucidating how these systems contribute to adaptive and maladaptive behaviours. Chapter 2 of this thesis investigates how task-irrelevant rewards influence the object prioritisation bias observed in the two-rectangle paradigm and examines how this influence changes during extinction, when reward contingencies are withdrawn.

1.5.1 Reward and Object-Based Attention

To date, few studies have directly examined how reward influences OBA. Shomstein and Johnson (2013) conducted a notable experiment using the two-rectangle paradigm (described in Section 1.2). Participants received high or low rewards for correctly identifying a target. In Experiment 1b, high rewards were paired with the invalid different object (DO) condition, resulting in a reversed object-based effect: participants responded faster in the DO condition than in the same-object (SO) condition. However, it was unclear whether this reversal reflected a complete elimination of the OBA or whether reward effects masked a weaker OBA in the opposite direction. In a subsequent experiment, where rewards were randomly assigned to both conditions, the object-based effect disappeared entirely, leading the authors to suggest that OBA operates as a default strategy, abandoned when reward offers a more salient alternative. To foreshadow, in Chapter 2 (Experiment 1), we present a replication of Shomstein and Johnson's (2013) study, where a robust object-based effect unexpectedly emerged.

The original paradigm in these experiments, however, was not designed to disentangle the effects of OBA and reward. Reward was linked to the target's position relative to the cue rather than to the objects themselves, limiting comparisons between the effects of reward on OBA and space-based attention. Zhao et al. (2020) addressed this limitation by replacing the rectangles with banknotes of different value. They observed consistent object-based effects when both banknotes had equal value but found reduced effects when a lower-value banknote was cued, suggesting that higher-value objects can override object-based attentional prioritisation. However, the physical salience of the banknotes was

confounded with their value (e.g., 100-yuan notes are red, while 1-yuan notes are green) and carry complex cultural meaning, complicating interpretations.

To overcome these challenges, Diao et al. (2024) used coloured rectangles to isolate reward effects from physical salience, associating reward with colour and counterbalancing across participants. Their findings showed that reward enhanced both object-based and location-based effects, producing faster responses to targets on rewarded objects. This study replicates some findings from Chapter 2 while differing in key aspects. For instance, our design used high- and low-rewarded colours, avoiding the less informative comparison of reward versus no-reward (Rusz et al., 2020). Moreover, reward was task-irrelevant during both learning and testing phases, allowing us to examine interactions between OBA and reward over the course of association formation and extinction.

In Chapter 2, we used a novel version of the two-rectangle paradigm designed to assess the interaction between reward and OBA. We first assessed whether rewarding objects on screen would affect the OBA (Experiment 2). Then we extended the investigation to the extinction period, when reward contingencies were removed (Experiment 3). Finally, we disentangled the effects of practice and reward extinction on the modulation of OBA (Experiment 4). Together, these experiments represent a comprehensive evaluation of the value-driven attentional capture influence on object-based attention.

1.6 Challenges to Object-Based Attention.

At first glance, object-based effects appear to be a well-established phenomenon, extensively studied and consistently replicated over the years. For instance, in Chapter 2, we present evidence of the OBA effect's replication using the two-rectangle paradigm across four independent experiments involving a total of 200 participants. However, recent critiques have called into question the existence of OBA as a distinct mechanism based on object status (Al-Janabi & Greenberg, 2016; Chen & Cave, 2019; Francis & Thunnell, 2022; Pilz et al., 2012; Rosenholtz, 2024). These critiques have primarily focused on two alternative explanations: (1) anisotropy effects in attentional shifts and (2) visual clutter between cue and target. Below, I discuss these critiques and their implications, along with evidence addressing these challenges.

1.6.1 The Role of Anisotropy in Attentional Shifts

Anisotropy in attentional shifts refers to the observation that visual attention tends to shift more efficiently horizontally than vertically, a phenomenon supported by visual search tasks literature (Corballis & Roldan, 1975; Carrasco et al., 2004; Corbett & Carrasco, 2011; Carrasco & Chang, 1995; Carrasco et al., 2001; Mackeben, 1999; Montaser-Kouhsari & Carrasco, 2009; Rovamo & Virsu, 1979; Zénon et al., 2009; Tse et al., 2003). Some researchers have proposed that this horizontal facilitation, rather than object-based mechanisms, explains the differences observed in Egly and colleagues's two-rectangle paradigm (Barnas & Greenberg, 2024; Pilz et al., 2012; Francis & Thunnell, 2022). Specifically, when the rectangles

are oriented horizontally, attentional shifts along the same object align with the anisotropy effect, potentially driving the observed same-object advantage.

However, if anisotropy were the sole driver of the object-based effect, we would expect a same-object cost in the vertical condition. In other words, comparing the shifts of attention horizontally to a different object and vertically within the same object would produce an effect of opposite direction (same-object cost) but comparable magnitude. Yet, studies have shown that the magnitude of the same-object advantage in the horizontal condition is more consistently observed and bigger than the same-object cost in the vertical condition (Pilz et al., 2012; Francis & Thunnell, 2022; Barnas & Greenberg, 2024). Moreover, Pilz et al. (2016) showed that a weaker but significant object-based effect persists when controlling for meridian crossing in attentional shifts. Importantly, Barnas and Greenberg (2019) found that anisotropy effects disappear in the absence of an object. Taken together, these results suggest that horizontal facilitation and object-based effects are tightly linked but distinct phenomena that interact under certain conditions (Barnas & Greenberg, 2024; Francis & Thunnell, 2022).

1.6.2 The Visual Clutter Hypothesis

Another prominent critique posits that the object-based effect in the two-rectangle paradigm arises from differences in visual complexity rather than attentional mechanisms. Rosenholtz (2024) argued that shifts within the same object involve less visual clutter—fewer luminance edges and less complexity—than shifts between objects (Davis & Holmes, 2005; Chen et al., 2020). When the cue and

target are on the same rectangle, the intervening space is empty, whereas in the different-object condition, the edges of both rectangles increase visual complexity, potentially delaying target resolution.

Supporting this hypothesis, Chen et al. (2020) manipulated visual complexity in a single H-shaped object and found that reaction times increased when the cue and target were separated by more clutter (i.e., located on the "horns" of the H). However, these findings are also consistent with the spreading hypothesis (Jolicoeur, Ullman, & Mackey, 1991; Davis et al., 2000; Ekman et al., 2020; Jeurissen & Roelfsema, 2016; Roelfsema et al., 1998). For example, Ekman et al. (2020) showed that attentional signals spread along the contours of a cued object in early visual areas, with longer paths resulting in slower response times. Furthermore, Jeurissen et al. (2016) revealed that the speed of spreading decreases as the pathway narrows, as seen in the H-shaped object used by Chen et al. (2020).

While visual clutter may contribute to differences in reaction times, evidence from Ekman et al. (2020) and others suggests that attentional spreading along object contours plays a significant role, independent of cluttering effects. This distinction is critical for interpreting the OBA and underscores the need for direct measures of attentional deployment during the cue-to-target interval.

1.6.3 Addressing the Challenges: Looking at OBA Before Target Selection

In Chapter 3, we present a study examining two neurophysiological indices of attention to determine whether the OBA observed in the two-rectangle paradigm is solely driven by perceptual clutter. This was achieved by directly assessing

attentional deployment during the cue-to-target interval. If the presence of luminance edges or visual clutter between the cue and target were solely responsible for the attentional differences observed in the paradigm, no differences in attentional indices would be expected between horizontal and vertical rectangle orientations prior to target onset. In other words, any observed modulation of these indices based on rectangle orientation would indicate factors beyond target resolution difficulty.

Furthermore, investigating the neurophysiological indices during the cue-to-target period, allowed us to corroborate the independence of OBA and anisotropy in attentional shifts. The anisotropy effect alone would create the same lateralization of attention in both the horizontal and vertical condition. If the object orientation alone creates a difference in the lateralization of the attentional indices, it means that the object-status is having an effect on attention, independently from anisotropy effects.

1.7 Alpha Oscillations

Alpha oscillations, typically defined within the 8–13 Hz frequency range, are widely recognised as an index of covert spatial attention. While their role in attentional processes is well-established, the specific mechanisms they underpin remain a subject of debate. Initially, alpha oscillations were associated with resting states or mind-wandering, given their increase in the absence of task engagement. However, subsequent research revealed their persistence during working memory tasks (Klimesch et al., 1999) and their amplification with increasing memory load (Jensen et al., 2002), challenging the earlier "idle state" hypothesis (Pfurtscheller et

al., 1996). This shifted the paradigm towards interpreting alpha power increases as reflective of the inhibition of irrelevant information (Jensen & Mazaheri, 2010).

Further evidence of alpha's involvement in spatial attention came from studies showing its lateralisation with the direction of covert attention (Worden et al., 2000). Specifically, alpha power decreases contralaterally to the cued location and increases ipsilaterally to the uncued location, enabling precise spatial tracking of attention (e.g., Foster et al., 2017). These findings are often interpreted as indicative of a gating mechanism, where increased alpha suppresses distracting information (Jensen, 2024; Bonnefond & Jensen, 2024). However, others argue that decreased alpha power may instead reflect signal enhancement at the attended location (Foster & Awh, 2019). Although these interpretations appear distinct, they may coexist: alpha reduction contralateral to the attended site could enhance the target signal, while interhemispheric inhibition could concurrently increase ipsilateral alpha, suppressing distractors automatically (Schneider et al., 2021; see Jensen, 2024 for a possible implementation in the fronto-parietal network).

Schneider and colleagues (2021) emphasised that distinguishing between target enhancement and distractor suppression is critical for clarifying the attentional role(s) of alpha oscillations. They further noted that this distinction requires separating automatic and active mechanisms of distractor suppression. In traditional paradigms investigating alpha lateralisation, targets and distractors are typically presented in opposite hemifields to maximise lateralisation effects. However, this design conflates the contributions of target enhancement and distractor suppression. To address this issue, Wöstmann et al. (2019) employed a paradigm designed to disentangle these contributions, building on previous work showing its effectiveness for separating

target- and distractor-related mechanisms in lateralised neurophysiological indices (Hickey et al., 2009). In their paradigm, either the target or the distractor was presented centrally, while the other was lateralised. This ensured that any lateralisation observed in the EEG signal was attributable solely to the lateral stimulus.

Using this approach, Wöstmann and colleagues identified two distinct lateralised responses associated with target enhancement and distractor suppression. These responses were uncorrelated and originated from partially overlapping neural sources, strongly suggesting that alpha lateralisation to the distractor represents an independent active neural suppression mechanism rather than a mere consequence of the selection processes.

Notably, most of the studies discussed so far have focused on pre-stimulus alpha lateralisation. Pre-stimulus alpha has been linked to proactive gating mechanisms, whereas post-stimulus alpha lateralisation is thought to reflect reactive filtering processes (May et al., 2012; Geng, 2014). In everyday situations, proactive preparation for upcoming targets or distractors is often impossible, necessitating reactive responses. What role, then, does alpha oscillatory activity play in these reactive selection mechanisms?

Interestingly, Wöstmann et al. (2019) found no correlation between task performance and pre-stimulus alpha lateralisation to distractors. Instead, they observed a correlation between performance and post-stimulus alpha lateralisation, underscoring the behavioural relevance of the latter. However, because the cue used in their study predicted target position, the predictability of the stimulus and reactive mechanisms were not fully disentangled. This leaves open the possibility that

post-stimulus alpha might also be influenced by anticipatory mechanisms. Supporting this notion, van Diepen et al. (2016) showed that under certain conditions, post-stimulus alpha can be modulated by the predictability of stimulus position (e.g., informative vs uninformative cues).

In Chapter 4, we present a study designed to isolate target enhancement in post-stimulus alpha lateralisation from modulation attributable to active distractor suppression. By using cues that do not allow for preparatory modulation of spatial attention, we aim to investigate how the representation of semantic information in the brain is linked to reactive mechanisms of target selection.

1.7.2 Alpha in object-based attention

Although alpha oscillations are now well-recognized for their role in spatial attention modulation, their involvement in object-based attentional mechanisms remains unexplored. In Chapter 3, by examining pre-stimulus alpha activity during object-based attention, this work aims to extend current knowledge of how these oscillations may track or mediate object prioritisation.

Previous studies have explored the role of alpha oscillations in object-based attention within both visual and auditory domains. Findings suggest that alpha power correlates with the processing of selected objects in visual cortex (Zumer et al., 2014) and anticipates auditory object processing (de Vries et al., 2021). Interestingly, this is observed even with overlapping stimuli, where no spatial distinction exists between objects (Knakker et al., 2015; de Vries et al., 2021). For instance, Knakker and colleagues (2015) recorded anticipatory alpha power through EEG as

participants selectively attended to word or face stimuli, either presented alone or in overlapping word-face composites. Notably, attending to words led to increased alpha power in the right parieto-occipital cortex—typically associated with face processing—highlighting a potential role for alpha in object-based visual processing. However, these studies involved explicit task-driven focus on target objects, which may differ from automatic object-based effects seen in other paradigms, such as the two-rectangle paradigm (though for a review on attentional strategy versus automaticity, see Shomstein, 2012).

While the current literature largely investigates alpha's role in processing object-related information, it is still unclear whether alpha tracks object-based attention. For instance, when attention is directed to a spatial cue, alpha power decreases contralaterally and increases ipsilaterally to the cue. As discussed earlier, if this cue falls within an object, attention also selects the object, facilitating recognition of targets within it compared to targets falling outside the object. However, it remains to be seen whether this object-based attentional mechanism is reflected in alpha oscillations as it is for spatial attention. In Chapter 3, we present an EEG experiment employing the two-rectangle paradigm to test whether alpha lateralization is modulated by object prioritisation. Alongside alpha oscillations, we examine the role of another spatial attention index, an event-related potential (ERP) called anterior directing attention negativity (ADAN).

1.7.3 Anterior Directing Attention Negativity

The Anterior Directing Attention Negativity (ADAN) is an event-related potential (ERP) component recorded as a negative deflection in fronto-central electrodes typically between 300 and 500 milliseconds following an attention-directing cue (Jongen et al., 2007; Eimer et al., 2002; Nobre et al., 2000; Mangun, 1994; Hopfinger et al., 2000). ADAN presents as a greater negativity over scalp sites contralateral to the attended location when attention shifts laterally (Jongen et al., 2007; Eimer et al., 2002). This lateralization is thought to reflect the neural processes involved in initiating the attentional shift (Nobre et al., 2000; Gherri & Eimer, 2008) and has been linked to the activation of frontal brain structures involved in its control (Van der Lubbe et al., 2000; Corbetta et al., 1993; Posner & Petersen, 1990). Furthermore, ADAN has been shown to be supramodal, appearing across visual, auditory, and tactile modalities, suggesting that it reflects a general attentional mechanism rather than being specific to a single sensory domain (Eimer et al., 2002, Eimer et al., 2003).

In our study (Chapter 3), we measured ADAN as it is thought to reflect activation in frontal brain regions associated with voluntary attentional deployment. This makes it a suitable marker for assessing whether object-based attention influences the neural mechanisms underlying attentional control. Additionally, since our experimental paradigm redirects visual attention using auditory cues, the supramodal nature of ADAN ensures its relevance to our investigation.

Specifically, we hypothesised that ADAN would vary depending on the orientation of the irrelevant rectangles presented in a two-rectangle paradigm. When the rectangles are vertically oriented and confined within a single visual hemifield, we

anticipated that object-based attention would enhance the lateralization of ADAN, as the pull on attention by spatial cuing and the object-based effect would align on the same hemifield. Conversely, for horizontally oriented rectangles spanning both hemifields, we expected reduced ADAN lateralization due to the incongruent effects of spatial cuing and object-based effect. By examining ADAN, we aimed to determine whether object-based attention modulates attentional control mechanisms before the presentation of target stimuli, thereby providing evidence for object-dependent modulation of attention.

1.9 The influence of attention on conceptual information

Attention encompasses a set of mechanisms that selectively process incoming stimuli, allowing us to prioritise specific aspects of our environment over others. These stimuli may sometimes be simple flashes on a screen requiring detection — as in the case of a radar operator or participants in a detection experiment — or involve evaluating specific features of an object, such as matching the colour of one's shoes with a shirt. However, in many instances, our attention is directed toward objects to extract conceptual information — for example, when reading these words and comprehending their meaning.

Extensive research has focused on how semantic information influences attentional processes. As early as the 1970s, Broadbent's filter theory, which initially proposed that unattended information undergoes only low-level processing, faced significant challenges. Studies showed that the meaning of words presented in an unattended audio stream could indeed impact the interpretation of concurrent

messages in the attended stream (e.g., Lewis, 1970; Mackay, 1973). Many other studies have shown that conceptual information and categories can bias attention, thereby shaping perception and sensation. For example, priming effects have shown that pre-activated conceptual information can influence attention toward words (e.g., McNamara, 2005) or images (e.g., Warren & Morton, 1982; Dell'Acqua & Grainger, 1999).

While much has been uncovered about how semantic information shapes attentional processes, our understanding of the opposite influence—how attention modulates the activation of conceptual information in the brain—remains limited. We know that centres in frontal and temporal cortex represent semantic information abstracting from perceptual experiences (Freedman et al., 2001; Rigotti et al., 2013; Fairhall & Caramazza, 2013; Acunzo et al., 2022) and we hypothesise that attention plays a crucial role in activating and structuring conceptual representations to support higher-order cognitive processes. However, the neural mechanisms underlying this dynamic interaction are not fully understood.

Previous studies have shown that the behavioural relevance of stimuli modulates their representation in the ventral and dorsal visual streams (Jeong & Xu, 2016; Seidl et al., 2012; Hickey & Peelen, 2015; Barbaro et al., 2018). However, several studies have cast doubts on whether these effects are truly driven by semantic properties or merely by shared visual features within a category (Bracci & Op de Beeck, 2016; Watson et al., 2014; Rice et al., 2014). Bracci and Op de Beeck (2016) addressed this issue by employing a two-factor fMRI design that orthogonally manipulated a visual feature (i.e. shape) and category. Their results show that while there is a strong contribution of the shape in item representations, the relative contribution is

function of a posterior-to-anterior gradient, where more anterior regions appear to be more engaged in encoding semantic properties.

Another approach to this question has focused on stimuli with overlapping semantic content presented across different modalities (Rigotti et al., 2013; Binder et al., 2009; Fairhall & Caramazza, 2013; Devereux et al., 2013; Acunzo et al., 2022). For example, Fairhall and Caramazza (2013) presented participants with images and words representing the same object (e.g., an image of a cow and the word ‘cow’). They trained classifiers on brain data from one modality and tested the classifiers on data from the other modality, employing a searchlight approach. Their findings indicated that several regions, including the prefrontal, parietal, and temporal cortices, contained semantic information abstracted from sensory features. Thus, while much has been explored about how the semantic concepts are encoded in the brain (see Ralph et al., 2017, for a review of major theories; Popham et al., 2021, for a unifying perspective), we know little about how attention modulates the reactivation of these representations when needed.

In Chapter 4, we describe a study that investigates the role of attention in supporting post-perceptual cognition by modelling how and where abstracted information varies in the brain as a function of attentional engagement. In the experiment, participants viewed images of objects from different categories and were tasked with categorising a target image while ignoring distractors. Using EEG, we derived post-stimulus alpha lateralization as an index of attentional focus on the lateral object (Wöstmann et al. 2019; van Diepen et al., 2016), while concurrently using fMRI to measure semantic information via classifier accuracies. By leveraging trial-by-trial variance in these measures, we correlated the two, mapping brain

regions where attentional engagement with an object predicted its semantic representation.

In summary, by integrating behavioural paradigms and neuroimaging techniques such as EEG and concurrent EEG-fMRI, this work aims to address several questions both regarding how attention interacts with objects and how the representation of semantic information abstracted from objects relate to attention fluctuations. Through a series of experiments outlined in the following chapters, we address the following questions: (Chapter 2) how do OBA and reward interact? (Chapter 3) Is OBA reflected in the same neurophysiological markers as spatial attention? Is the object-based effect a byproduct of perceptual clutter or anisotropy in attentional shifts? (Chapter 4) Is the processing of an object's semantic representation correlated with attentional levels? Which brain regions carry this association?

1.10 References

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CHAPTER 2

OBJECT-BASED ATTENTION IS ACCENTUATED BY OBJECT REWARD ASSOCIATION¹

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2.1 Abstract

Humans use selective attention to prioritize visual features, like color or shape, as well as discrete spatial locations, and these effects are sensitive to the experience of reward. Reward-associated features and locations are accordingly prioritized from early in the visual hierarchy. Attention is also sensitive to the establishment of visual objects: selection of one constituent object part often leads to prioritization of other locations on that object. But very little is known about the influence of reward on this object-based control of attention. Here we show in 4 experiments that reward prioritization and object prioritization interact in visual cognition to guide selection. Experiment 1 establishes groundwork for this investigation, showing that reward feedback does not negate object prioritization. In Experiment 2, we find that reward prioritization and object prioritization emerge concurrently. In Experiment 3, reward prioritization and object prioritization sustain and interact in extinction, when reward feedback is discontinued. We verify this interaction in Experiment 4, linking it to task experience rather than the strategic utility of the reward association. Results suggest that information gathered from locations on reward-associated objects gains preferential access to cognition.

2.2 Public Significance Statement

Selective attention is biased to reward-associated stimuli and to locations on attended objects. Here, we show that these effects combine, such that locations on reward-associated objects are selected preferentially. Information from these locations will gain preferential access to downstream cognitive processes like decision-making and motor control.

2.3 Introduction

Visuo-spatial attention has traditionally been characterized as under the control of two concurrent influences, such that stimuli with high physical salience and stimuli that match strategic attentional templates are both prioritized (eg. Egeth & Yantis, 1997). However, in recent years there has been increasing awareness of additional influences on attentional control that do not conveniently fit this dichotomy. For example, attention is directly sensitive to associative learning (Le Pelley et al., 2016, for review). In particular, stimuli that have been associated with reward will draw selective attention in the future, even when this provides no strategic benefit (eg. Anderson et al., 2011; Hickey et al., 2010a; Hickey & van Zoest, 2012). At the same time, attention is sensitive to the definition of visual objects (Chen, 2012, for review). That is, when attention has been drawn to part of an object, locations containing other parts of that object also become prioritized. There is ongoing debate regarding the degree to which reward prioritization (Anderson, 2019; Awh et al., 2012) and object prioritization (Peters & Kriegeskorte, 2021; Shomstein, 2012) can be characterized as goal-driven or strategic and relatively little is known about how these influences on attention combine.

Here, we investigate the relationship between reward prioritization and object prioritization, with particular interest in the possibility that these influences combine and interact to prioritize information gathering from reward-associated visual objects. To this end, we had participants complete experiments based on a well-established object-based attention paradigm known as the 2-rectangle task (Egley et al., 1994). In the paradigm, a trial begins with the presentation of two rectangles designed so that their ends define 4 screen positions that are equidistant from fixation. An exogenous

cue - such as a flash of light - subsequently draws attention to one of these locations. A target then appears, but, critically, the target does not always appear at the cued location. When the target appears at an uncued location, this can either be on the same rectangle as the cue or on the other rectangle.

The key observation in the 2-rectangle task is that when the target does not appear at the cued location, but does appear on the same object as the cue, responses are quicker and more accurate than when the target appears at any other uncued location. That is, attention appears to engage with the cued object as a whole, benefitting processing of stimuli that happen to appear at uncued locations on that object. Early interpretation suggested this reflected a low-level and automatic role of object prioritization in visual segmentation during perception of visual environments (Driver et al., 2001; Egly et al., 1994; Wannig et al., 2011). In line with this, object prioritization emerges when task confines give sufficient opportunity and motivation for objects to be derived from visual input (Chen & Cave, 2006, 2008). However, subsequent results have shown that object prioritization disappears when cue validity is high (Shomstein & Yantis, 2004; Yeari & Goldsmith, 2010), when the target location is endogenously identified (Macquistan, 1997), and when the cue location provides indirect information about the target location (Drummond & Shomstein, 2010). This has motivated the alternative proposal that object prioritization might be a default strategy adopted during search that can be discarded when the target location is unambiguous (Shomstein, 2012).

If object prioritization is strategic, this raises the possibility that it may be sensitive to the concurrent establishment of other strategies, and this idea motivated Shomstein and Johnson (2013) to conduct a series of experiments combining

manipulation of reward outcome and object continuation in the 2-rectangle task. The experimental logic was that a strategy of attending to objects might be down-weighted, or even discarded, when task confines provided other, better ways to optimize performance. In Experiment 1, participants were consistently rewarded for accurately reporting targets that appeared on uncued objects. This reversed the pattern normally observed in the 2-rectangle task: responses became quicker when the target appeared on the uncued object rather than the cued object. By itself, this could simply mean that participants had learned to strategically deploy attention away from the cued object in order to optimize earnings, and that this strategic effect obscured any effect of object prioritization. However, the authors showed in a subsequent experiment that object prioritization also disappeared when reward was not linked to any specific object. In Experiment 2, reward feedback was randomly of either high- or low-magnitude whenever the target appeared at an uncued location. This removed the motivation to strategically attend to the uncued object, but the results again showed no evidence of object prioritization (see also, Lee & Shomstein, 2013).

This latter finding is puzzling. In line with the motivating hypothesis for the study, Shomstein and Johnson (2013) interpreted it as evidence of the strategic nature of object-based attention. That is, the authors suggested that participants discarded the strategy of attending to objects when another, better strategy was available. But it is unclear exactly what strategy participants might have adopted, or why they were motivated to make this strategic shift. Reward feedback in this experiment was random, so there was no opportunity to use outcome to optimize reward harvesting. As a result, there was no way to verify that participants actually changed strategy. Concerningly, this means that the interpretation offered by the

authors - that participants discarded one strategy and adopted another - rests on the null observation of no object-based effect.

There are alternative accounts for the data pattern. One possibility is that the effect of object-based attention did not emerge in analysis simply because that effect is small and noisy. This possibility is consistent with subsequent results from Zhao et al. (2020). These authors employed a variant of the two-rectangle paradigm where the 'rectangles' were images of high-denomination and low-denomination monetary notes and data was collected from a larger sample than was employed in Shomstein and Johnson (2013; 30 vs 10 individuals). Results show a robust object-based effect when the cued note was of higher value than the uncued note, with responses particularly slow when the high-denomination note was cued but the target ultimately appeared on the low-denomination note.

However, there are limitations to the design adopted by Zhao et al. (2020). In particular, the value of the high- and low-denomination notes employed in that study reflected real-world experience over a long time frame and the visual characteristics of the notes could not be controlled or counter-balanced. It happened that the higher-value note was bright red, while the lower-value note was dull green: if the salience of the red note was greater than the green note - and red stimuli are known to be of particular salience (eg. Pomerleau et al., 2014) - the putative impact of value on object-based attention observed in this study could actually reflect the influence of note color. Zhao et al. (2020) partially addressed this issue in a control experiment, showing that the interaction of value and object status did not reliably emerge when the rectangles had note color but no other defining features. But the behavioral

difference between experiments was small, and not statistically assessed, leaving ambiguity on the issue.

Another interpretation of the null result reported in Shomstein and Johnson (2013; Experiment 2) is that the object-based effect did not emerge in analysis because of conflicting sequential contingencies in the experimental design. In that experiment, reward was randomly determined to be of high- or low-magnitude in each invalidly cued trial, regardless of whether the target appeared on the same rectangle as the cue or on the other rectangle. This kind of random reward schedule is known to create inter-trial effects on behavior and brain activity that can be identified in sequential analysis (Hickey et al., 2010a, 2010b, 2015). The general observation is that when target selection in one trial results in high-magnitude reward, selective processing is biased toward similar stimuli in immediately subsequent task performance. When participants in Shomstein and Johnson (2013) successfully identified a target that appeared on the same object as the cue, and were rewarded for their performance, this may have created a bias toward cued objects in the next trial. This would create performance benefits when the relationship repeated between trials, but performance costs when this did not occur. Under these circumstances, mean results - collapsed over sequence - could show no evidence of object prioritization.

In light of these issues, the current study was designed to further investigate the relationship between reward prioritization and object prioritization in attentional control. We report results from 4 experiments using the 2-rectangle task. We begin in Experiment 1 by attempting to reproduce Shomstein and Johnson (2013; Experiment 2) in order to test the possibility that reward and object prioritization interact across

trial contingencies, as hypothesized above. To foreshadow, we find no evidence of this kind of sequential effect, but, in contrast to the original study, we do find evidence of object prioritization. In Experiment 2, we follow on from Zhao et al. (2020) to investigate how the association of reward to an object impacts object prioritization, importantly using a design that allows for counterbalancing of the association of reward to specific object features. In Experiment 3, we extend this design to measure the impact of reward on object prioritization during extinction, when reward contingencies are stopped. Finally, in Experiment 4, we directly compare results observed when reward associations are actively reinforced versus in extinction. Across experiments, the results show that reward prioritization and object prioritization guide attention concurrently. These effects initially appear as two independent influences on attention, but come to interact as participants gain task experience, regardless of the ongoing strategic utility of the reward association.

2.4 Transparency and openness

Sample sizes for each experiment are motivated from formal power analysis where possible and informal consideration of potential effect size otherwise; this is described in the 'Participants' section for each experiment. Power analyses were performed with G*Power software v3.1.9.6 with alpha of .05 (Faul et al., 2007, Erdfelder et al., 1996). All data exclusion parameters and data exclusions are described, as are all manipulations and measures. Age, sex, and nationality demographics are provided for each experiment; no other demographic information was considered. Results can be expected to generalize to the English-speaking, primarily high-income international population from which the sample was taken.

All data analysis was conducted using R 4.2.3 (R Core Team, 2020). Figures rely on output from the ggplot2 package for R 3.4.2 (Wickham, 2016) with subsequent adaptation in vector graphics software. None of the experiments were pre-registered. Data collection began in September, 2020, and completed in May, 2022. Data and research materials are available at [UBIRA eData repository - University of Birmingham institutional repository, link to be inserted at publication].

2.5 Experiment 1

2.5.1 Participants

Sixty-nine participants were recruited online through Prolific (www.prolific.co). All participants provided informed consent, reported normal or corrected-to-normal visual activity, fluency in English and were naïve to the purpose of the experiment. Participants were excluded from analysis based on interquartile range (IQR) of cross-conditional mean accuracy or cross-conditional median reaction time (excluded when median reaction time (RT) > 3Q +1.5*IQR, mean accuracy < 1Q-1.5*IQR). This led to the exclusion of 3 individuals for a final sample of 66 (30 male, 35 female, 1 other; mean age 34 years ± 11 years SD; nationality: AU 1 CA 3 GR 1 IE 1 NO 1 NZ 1 SA 2 UK 51 US 5). The sample size was guided by power analysis of the object-based effect identified in Shomstein et al. (2013, Experiment 1a, ANOVA $\eta_p^2 = .315$). This identified the need for 22 participants to reproduce, assuming power of .8. We approached data collection with the expectation that any sequential effect of reward on object prioritization - the a priori target of this

experiment - would have a substantially smaller effect than this. Accordingly, we increased our sample to triple this estimate in the hope this would provide sufficient power to detect a sequential effect of unknown size.

2.5.2 Design and procedure

The task was built in Python using Opensesame software (version 3.3.6), converted to Javascript using OSWeb (Mathôt et al., 2012), and further adapted in Javascript where necessary. The web application Jatos (Lange et al., 2015) was used to host the experiment on a computer server and participants completed the experiment in a web browser on a personal computer in their own environment. In order to standardize stimulus size across settings, participants were asked to maintain a distance of 60 cm from their computer screen and asked to adapt the web browser magnification such that an example rectangle on the screen fit the size of a standard bank card. The experiment began with detailed instructions that emphasized both speed and accuracy.

The experiment design is similar to Shomstein and Johnson (2013, Experiment 2). As illustrated in Figure 2.1a, in each experimental trial participants were asked to discriminate the identity of the target, which could either be a 'L' or 'T' ($1.2^\circ \times 0.9^\circ$ visual angle) and was presented at one of the four corners of the computer screen (4.4° visual angle from center). The other three locations contained non-targets, which were shapes created by superimposing the target letters and randomly orienting this image 90° , 180° , or 270° off vertical.

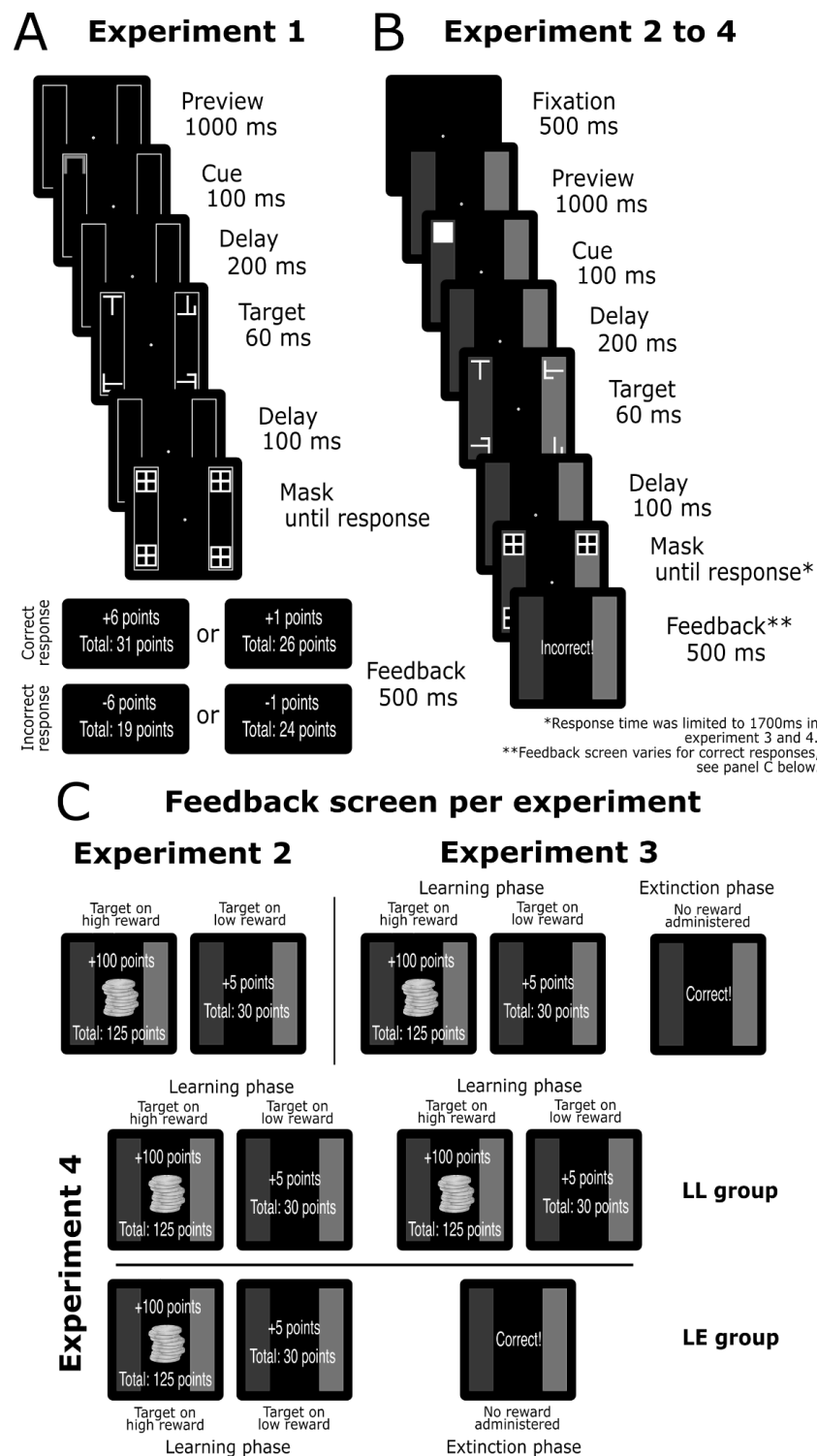


Figure 2.1 Task description. (A) In Experiment 1 the task starts with a 1 second preview screen containing only the two outline rectangles and a fixation dot, followed by the appearance of a red cue at the end of one of the rectangles. After a delay of 200ms, the target (an “L” or a “T”) appears at one of three locations at the end of a rectangle. At the same time the 3 other corners are filled with distractors. The target screen is followed by another 100ms delay screen and then all the 4 positions are masked until response. A feedback screen subsequently indicates the amount of points earned or lost in the current trial and the total points accumulated so far by the participant. (B) Experiments 2 through 4 differ from Experiment 1 in 5 ways: (1) A 500ms screen containing only a fixation point was inserted at the start of every trial; (2) The two rectangles had different colors, which randomly changed for each trial; (3) The cue was a box, rather than outline; (4) The colored rectangle sustained during the feedback screen, and the feedback included an image of coins that appeared only in high reward trials; (5) For incorrect responses a feedback screen with ‘Incorrect’ was showed, no point was deducted. Additionally, in Experiment 3 and 4, the mask screen was sustained until response or 1700ms. (C) Feedback conditions for correctly performed trials differed across Experiments 2 through 4. In Experiment 2, all trials resulted in either high-reward or low-reward feedback. In Experiment 3, this was initially the case, but reward was discontinued in a later experimental phase. In Experiment 4, the LL group completed a task very similar to that used in Experiment 2 and the LE group completed a task very similar to Experiment 3.

In order to link targets and non-targets to the same or different visual objects, each trial began with the presentation of two rectangles that each encompassed 2 of the 4 target and nontarget stimuli locations ($10^\circ \times 2.5^\circ$ visual angle). The rectangles were either oriented vertically, such that the two left stimuli locations and two right stimuli locations appeared on separate objects, or horizontally, such that the two top stimuli locations and the two bottom stimuli locations appeared on separate objects, and this was counterbalanced across participants. The rectangles were presented for 1 s before one of the target locations was cued. The cue took the form of a brightening and widening of the lines defining one end of the rectangle (200 ms; 2.4° visual angle). The cue appeared with equal likelihood at the location of the upcoming target, at the other location on the same rectangle, or at the equidistant location on the other rectangle. A pause of 200 ms followed, after which the target and nontargets appeared for 60 ms before a delay of 100 ms and subsequent onset of mask stimuli (crossed squares; $2.4^\circ \times 2.4^\circ$ visual angle). Mask stimuli sustained until response was registered, at which point a new trial began. Participants were instructed to report the target identity via key-press with the index finger on a standard keyboard. For all participants, left-hand response indicated that the target was a 'T' and right-hand response indicated that the target was an 'L'.

Each trial concluded with reward feedback. When the cue correctly identified the target location, correct performance earned 1 point, but when the cue was invalid, correct performance could randomly lead to either 1 or 6 points. Errors led to the loss of equivalent points (-1 point in valid trials and randomly -1 or -6 points in invalid trials). Participants were informed before taking part in the experiment that each 35 points led to payment of £0.10. Accuracy feedback was provided at the end of every experimental block, alongside information on points earned in that block and

points earned overall, and participants were paid at the end of the experiment based on the total points accumulated. Participants completed 24 practice trials followed by 9 blocks of 72 trials, the experiment took approximately 45 minutes to finish, and average pay was £4.10 (\pm £0.41 SD).

2.5.3 Results

Trials with RT greater than 1700 ms were excluded from the analysis (1.81% of trials, \pm 3.31% SD). This cutoff was applied to Experiments 1 and 2 in order to equate analytic parameters with Experiments 3 and 4, where there was no opportunity to respond beyond 1700 ms after stimulus onset (see the treatment of these experiments below for more detail).

The experimental design generated 3 equally-likely configurations between target and cue: the target either appeared on the same position of the cue (valid), on the other location on the same object (invalid same-object; SO), or at the nearest location on the other object (invalid different-object; DO). Figure 2.2A illustrates reaction times for these three conditions. Unexpectedly, given existing results from Shomstein and Johnson (2013; Experiment 2), we identified an object-based attentional effect, with faster RT in the SO condition than in the DO condition (683 ms vs 701 ms; $t(65) = 4.13$, $p < .001$, $d = 0.162$). A significant cueing effect was also evident in the difference between valid and invalid trials (collapsed across SO and DO conditions; 664 ms vs 692 ms; $t(65) = 2.91$, $p = .005$, $d = 0.285$). These effects were mirrored in accuracy: participants were significantly better in validly cued trials than invalidly cued trials (88.9% vs 85.7%; $t(65) = 2.70$, $p = .009$, $d = 0.304$) and were

better in the SO condition than the DO condition (86.2% vs. 85.1%; $t(65) = 2.10$, $p = .040$, $d = 0.104$). Statistical analysis of accuracy here and in subsequent experiments is based on data transformed to approximate normality (Box & Cox, 1964).

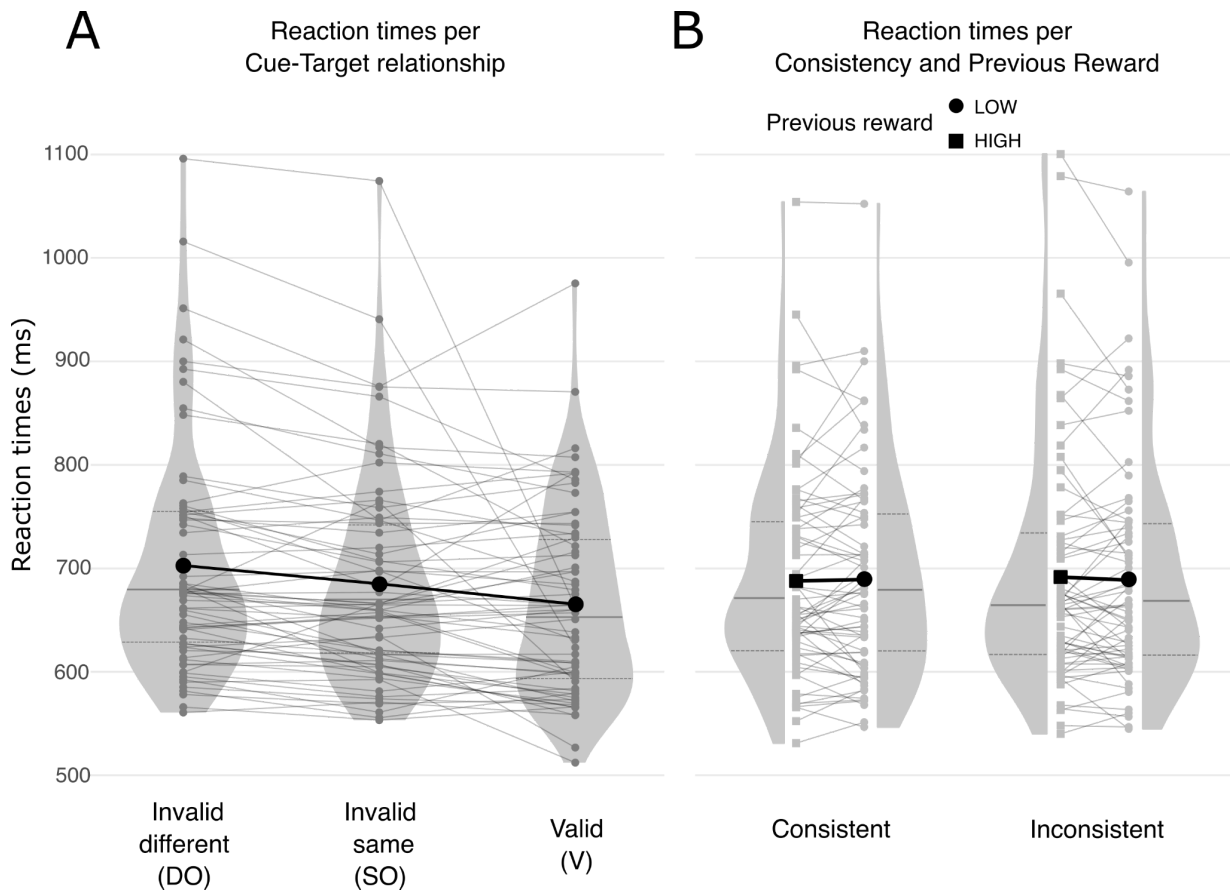


Figure 2.2 RT results from Experiment 1. Here and in subsequent figures, black circles and squares represent mean conditional reaction times. In gray, we illustrate the distribution of participant mean performance per condition and the conditional effect for each participant. The median, first, and third quartile are indicated for each distribution. Panel **A** illustrates results per cue-target relationship. An object prioritization effect is evident in the contrast of DO and SO conditions. Panel **B** illustrates results as a function of trial sequence (inconsistent: the target appeared on the cued object in the current trial, but appeared on the uncued object in the preceding trial, or, vice versa, the target appeared on the uncued object in the current trial but the cued object in the preceding trial; consistent: the target appeared on the cued object in two sequential trials, or the target appeared on the uncued object in two sequential trials) and the magnitude of reward received in the preceding trial (high or low).

As described above, we approached Experiment 1 with the idea that intertrial sequences might influence performance in this task, creating implicit expectations regarding the relationship between the cue and target locations. To assess this possibility, we divided invalidly-cued trials based on repeated cue-target relationship. Consistent trials were those where either the target appeared on the same object as the cue for consecutive invalidly cued trials, or the target appeared on the uncued object for consecutive invalidly cued trials. Inconsistent trials were invalidly cued trials where the target appeared on the same object as the cue in one trial but on the uncued object in the next trial, or vice versa. Our expectation was that consistency would interact with the magnitude of reward received for the preceding trial: when participants received high-magnitude reward in trial $n-1$, and the cue-target relationship from trial $n-1$ was repeated into trial n , participants should be faster to respond to the target. In contrast, when participants received high-magnitude reward in trial $n-1$, but the cue-target relationship was not repeated, participants would be slower. However, as illustrated in Figure 2.2B, no effect of trial sequence emerged in our results. A two-way repeated measures ANOVA (RANOVA) with factors for consistency and reward magnitude in the immediately preceding trial showed no significant effect of prior reward, consistency or interaction of these factors (all $F_s < 1$).

2.5.4 Discussion

Experiment 1 was motivated by the idea that object-based attention and reward-driven attention might co-exist in visual cognition, but that these influences were hidden in results from Shomstein and Johnson (2013; Experiment 2) by

inter-trial effects on performance. We expected to reproduce the null result observed by Shomstein and Johnson (2013; Experiment 2) in core analyses and add new perspective in analysis of trial sequence. Instead, we found a robust effect of object prioritization but no significant effect of sequence on object prioritization. As a null result, the non-significant effect of inter-trial sequence is, of course, ambiguous. However, the results suggest that if sequence has the impact on performance we expected, this effect is small and will require a very large sample to detect.

We have no clear account for the disparity between the current results and those from Shomstein and Johnson (2013; Experiment 2), other than that the null object prioritization effect observed in the earlier work was a type II error.

Results from Experiment 1 open the possibility that object prioritization and reward prioritization might co-exist. If this is the case, what influence do they have on one another? One possibility is that they interact, as would be the case if attention were to engage with objects with speed or strength that differs as a function of the object reward association. As noted in the Introduction, results from Zhao et al. (2020) suggest such an effect, but are arguably ambiguous due to low-level confounds in the design. To further test this idea while controlling for low-level visual properties of the stimuli we conducted a second experiment where the two rectangles each carried a unique color. For each participant, one color was associated with high-magnitude reward: correct response to a target appearing on the object characterized by this color garnered more points. If reward interacts with object-based attention, we expected the object-based effect to be accentuated when it was the reward-associated object that was cued.

2.6 Experiment 2

2.6.1 Participants

Experiment 2 was based on a new sample of 33 participants and used the same recruitment and exclusion procedures as for Experiment 1. Five participants were rejected from analysis due to outlier performance, leading to a final sample of 28 individuals (9 male, 19 female, 0 other; mean age 32 years \pm 10 years SD; nationality CA 2 SA 2 UK 22 US 2). The final sample size was determined by power analysis of the object-based effect observed in Experiment 1. Calculation of power was based on the effect size for the paired t-test contrasting SO and DO conditions ($d_z = 0.508$) with assumed power of .8.

2.6.2 Design and procedure

All data collection took place online and the procedure closely matched that of Experiment 1, except that each of the two rectangles had a filled color and the reward schedule was linked to these colors. Rectangle colors were pseudo-randomly selected for each trial so that the two rectangles never had the same color for a given trial and the colors were drawn from a set of five possibilities: red (RGB: 160,0,0), blue (34, 5, 255), purple (141, 21, 124), green (18, 90, 23), and brown (127, 58, 6). For each participant, one of the five colors was associated with high-magnitude reward: when the target appeared on the rectangle with this color, a correct response earned 100 points. If the target appeared on an object of any other color, correct performance earned 5 points. The association of reward outcome to

specific colors was described to participants before they began the experiment and was counterbalanced across participants. Participants earned £0.05 for every 95 points and no points were deducted for incorrect responses. The design otherwise differed from Experiment 1 in that rectangle onset was preceded by a shorter fixation duration (500 ms), the cue was defined by a white square ($2.4^\circ \times 2.4^\circ$ visual angle) that appeared at the end of one of the rectangles (see Figure 2.1B) and participants were presented with 10 blocks of 54 trials. The experiment took approximately 45 minutes to complete and average pay was £5.15 (\pm £0.38 SD).

2.6.3 Results

As in Experiment 1, trials with RT greater than 1700 ms were excluded from analysis (2.51% of trials, \pm 3.01% SD).

To assess a possible influence of reward on the object-based effect, we divided trials into conditions based on cue validity and reward association. High-reward trials (1/6 of trials) occurred when one of the two rectangles was characterized by the high-reward color and the target appeared on the high-reward object, whereas low-reward trials (1/6 of trials) occurred when one of the two rectangles was characterized by the high-reward color but the target appeared on the low-reward object. Finally, baseline trials (2/3 of trials) occurred when neither rectangle was characterized by the high-reward color.

Validly Cued Condition

Figure 2.3A illustrates the results for validly cued trials. A one-way RANOVA with a factor for reward (baseline, high and low reward conditions) identified a significant main effect (Greenhouse-Geisser correction; $F(1.26,34.12) = 82.65$, $p < .001$, $\eta_p^2 = .754$). Pairwise comparisons showed that RT was quicker in high-reward trials than in baseline ($t(27) = 2.59$, $p = .015$, $d = 0.251$) and slower in low-reward trials than in baseline ($t(27) = 9.81$, $p < .001$, $d = 1.223$). Analysis of accuracy also showed a significant main effect of reward (Greenhouse-Geisser correction; $F(1.30,35.03) = 30.94$, $p < .001$, $\eta_p^2 = .534$). Accuracy was improved for high-reward compared to low-reward trials (94.0% vs 79.6%, $t(27) = 5.72$, $p < .001$, $d = 1.328$), for baseline compared to low-reward trials (91.5% vs 79.6%, $t(27) = 6.30$, $p < .001$, $d = 0.850$), and approached corrected significance for baseline compared to high-reward trials (94.0% vs 91.5%, $t(27) = 2.24$, $p = .033$, $d = 0.457$).

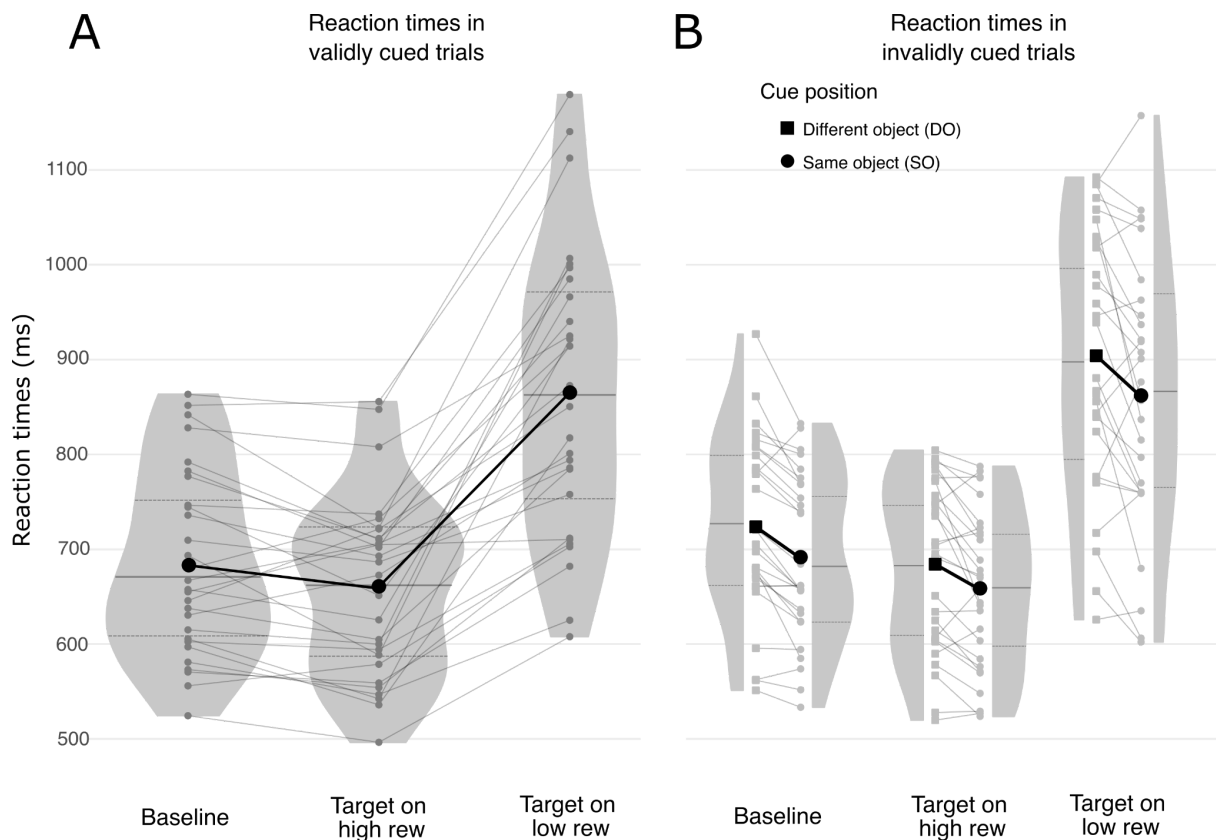


Figure 2.3 Results from Experiment 2. **Panel A** illustrates reaction times from the valid cue conditions. **Panel B** illustrates reaction times from the invalid cue conditions. Notably, the object prioritization effect emerges both when the target appears on the high-reward associated object and the low-reward associated object, with no appreciable distinction between these conditions.

Invalidly Cued Condition

As illustrated in Figure 2.3B, the pattern observed in validly cued conditions also appears in analysis of invalidly cued trials, with faster responses in high-reward trials than in baseline and slower responses in low-reward trials than in baseline. An additional effect of object prioritization emerged in these results, with faster responses when the target appeared on the cued object versus when it appeared on the uncued object. We began analysis by identifying a significant object prioritization effect in the baseline condition, when both rectangles were characterized by

low-reward color ($t(27) = 5.58, p < .001, d = 0.351$). The same effect of object prioritization emerged in analysis of accuracy in the baseline condition (91.9% vs 90.0%, $t(27) = 2.70, p = .011, d = 0.399$). We subsequently conducted a RANOVA of invalidly-cued data with factors for reward (target on high-reward colored object, target on low-reward colored object) and cue-target relationship (cue identified rectangle where target appeared, cue identified other rectangle). This identified a main effect of reward ($F(1,27) = 93.57, p < .001, \eta_p^2 = .776$) and a main effect of cue-target relationship ($F(1,27) = 13.73, p < .001, \eta_p^2 = .337$) but no significant interaction ($F(1,27) = 1.44, p = .240, \eta_p^2 = .051$). Results from the invalidly-cued trials thus show an effect of reward prioritization and an effect of object prioritization, but no significant relationship between these effects. Accuracy results show the same main effect of reward (93.6% high vs 78.3% low reward, $F(1,27) = 45.56, p < .001, \eta_p^2 = .628$), but no significant effect of cue-target relationship (86.9% same vs 84.9% different object, $F(1,27) = 2.46, p = .128, \eta_p^2 = .084$) or interaction ($F < 1$).

2.6.4 Discussion

Results from Experiment 2 suggest that while reward prioritization has a robust impact on performance, it does not substantively change the impact of object prioritization. There is the possibility that the absence of significant interaction reflects lack of statistical power or limitations to the sensitivity of ANOVA to interactions in the presence of main effects. Experiment 3 both addresses this ambiguity and tests new hypotheses.

In Experiment 2, participants were explicitly informed of the association between reward and color, and we expect this motivated them to establish a strategy to prioritize the reward-associated visual feature. This kind of strategic attentional control can have a strong impact on the prioritization and perception of features and objects (eg. Folk, Remington, & Johnston, 1992). However, as noted in the Introduction, reward can also have a more direct and automatic impact on perception and prioritization that sustains when it is no longer useful (Hickey, Chelazzi, & Theeuwes, 2010a, b; Anderson et al., 2011). It is unclear if the reward effect identified in Experiment 2 reflects the strategic effect of reward, associative learning, or both. Moreover, there is the possibility that a low-level, automatic effect of reward - driven by associative learning - might interact with object prioritization in ways that do not robustly emerge when reward is used to strategically guide selection.

Experiment 3 was designed to address these issues. In an initial phase of Experiment 3 - the learning phase - participants completed a task identical to that of Experiment 2, with color consistently predicting the reward outcome of correct performance. However, in a second stage of the experiment - the extinction phase - participants were informed that reward was no longer available, but they would have to complete the remainder of the task to receive the reward they had earned in the earlier stage. We approached this experiment with 3 key questions. First, will reward prioritization sustain in the extinction phase, when its strategic utility is removed? Second, does object prioritization also sustain in this phase of the experiment? And, finally, if both effects occur in extinction, do they show the additive relationship identified in Experiment 2?

2.7 Experiment 3

2.7.1 Participants

Experiment 3 was based on a new sample of 61 participants and used the same recruitment and exclusion procedures identified for Experiment 1. Three participants were rejected, leading to a final sample of 58 individuals (34 male, 24 female, 1 other; mean age 37 years \pm 12 years SD, one participant withheld report of age; nationality CA 2 HU 1 IN 1 IR 4 PL 2 SA 1 UK 40 US 4 ZW 1, one participant withheld report of nationality). The sample size was determined by consideration of the object-based effects observed in Experiments 1 ($d_z = 0.508$) and 2 ($\eta_p^2 = .337$). Our expectation was that the raw magnitude of this effect might reduce with the increased length of Experiment 3, as overall reaction times became faster, and thus that the effect size after training would be smaller than observed in Experiments 1 and 2. We therefore targeted a sample size twice that employed in Experiment 2. Fewer participants exhibited outlier performance than was predicted by results from Experiment 2, leading to slight over-recruitment (of 58 individuals rather than 56).

2.7.2 Design and procedure

In Experiments 1 and 2, we observed that participants occasionally failed to respond promptly to a trial, suggesting that they took impromptu breaks within an experimental block, and this introduced minor complications in analysis of results. To ensure that participants took breaks only within the block structure, we introduced a

response time limit. Participants were required to respond within 1700 ms of stimulus onset and a trial ended either when response was made or this interval had passed.

The learning phase of Experiment 3 was similar to the design of Experiment 2, with the rectangle colors predicting reward outcome (2 blocks of 72 trials). Reward was discontinued in the subsequent extinction phase (8 blocks of 72 trials; see Figure 2.1C). Participants were informed that they needed to maintain accuracy of 85% or greater in order for earnings from the learning phase to be paid out at the end of the experiment (or they would receive a lesser base rate payment of £5.85). During the learning phase, participants earned £0.26 for every 100 points accumulated, with no points lost for incorrect answers. Participants completed the experiment in approximately 70 minutes and average pay was £7.03 (\pm £0.3 SD).

2.7.3 Results

In 0.52% (\pm 0.92% SD) of trials participants did not respond within 1700 ms of stimulus onset. These trials were excluded from calculation of accuracy.

Validly Cued Conditions

For the sake of completeness, we analyzed the validly cued experimental conditions, though these results test no experimental hypotheses. A two-way RANOVA with factors for reward (baseline, high-reward and low-reward) and phase (learning and extinction) showed statistical significance of both main effects and the interaction (Greenhouse-Geisser correction; reward: 647 vs 646 vs 706 ms, $F(1.32,75.30) = 26.88$, $p < .001$., $\eta_p^2 = .320$; phase: 728 vs 604 ms, $F(1.00,57.00) =$

191.74, $p < .001$, $\eta_p^2 = .771$; phase x reward: (693 vs 691 vs 800) vs (601 vs 600 vs 611) ms, $F(1.37,78.37) = 20.80$, $p < .001$, $\eta_p^2 = .267$). Analysis of accuracy showed similar results (Greenhouse-Geisser correction; reward: 94.3% vs 95.2% vs 88.7%, $F(1.47,83.60) = 24.08$, $p < .001$, $\eta_p^2 = .297$; phase: 89.5% vs 96.0%, $F(1.00,57.00) = 74.73$, $p < .001$, $\eta_p^2 = .567$; phase x reward: (92.1% vs 94.2% vs 82.1%) vs (96.5% vs 96.2% vs 95.3%), $F(1.72,98.29) = 21.18$, $p < .001$, $\eta_p^2 = .271$). The interaction effects highlighted by the analysis could be due to floor and ceiling effects that affected the baseline and high reward condition more than the low reward condition, as the latter had more room for improvement over the course of the experiment.

We followed up on these results with separate analysis of validly cued conditions in each of the learning and extinction phases separately. Analysis of the learning phase constituted a reproduction of Experiment 2, and results were accordingly similar. A one-way RANOVA of RT from the learning phase identified a significant main effect of reward (Greenhouse-Geisser correction; $F(1.32,75.24) = 25.82$, $p < .001$, $\eta_p^2 = .312$). Pairwise comparisons identified quicker RT in both baseline and high-reward trials compared to low-reward trials (693 vs 800 ms, $t(57) = 5.82$, $p < .001$, $d = 0.714$; 691 vs 800 ms, $t(57) = 5.04$, $p < .001$, $d = 0.731$). Unlike Experiment 2, no significance difference was found between baseline and high-reward trials (693 vs 691 ms, $t(57) = 0.23$, $p = .816$, $d = 0.020$). Analysis of accuracy mirrored the RT results. A one-way RANOVA showed a significant main effect of reward (Greenhouse-Geisser correction; $F(1.58,90.31) = 26.19$, $p < .001$, $\eta_p^2 = .315$) with no significant difference between high-reward condition and baseline (94.2% vs 92.1%, $t(27) = 1.92$, $p = .060$, $d = .298$), but a significant difference between high-reward and low-reward conditions (94.2% vs 82.1%, $t(27) = 5.79$, $p < .001$, $d = 1.013$) and

between baseline and low-reward conditions (92.1% vs 82.1%, $t(27) = 5.25$, $p < .001$, $d = 0.795$).

In validly cued conditions of the extinction phase, reward did not have a significant effect on RT (601 vs 600 vs 611 ms, Greenhouse-Geisser correction; $F(1.56,88.87) = 2.84$, $p = .076$, $\eta_p^2 = .047$) or accuracy (96.5 vs 96.2 vs 95.3 ms, Greenhouse-Geisser correction; $F(1.66,94.72) = 1.74$, $p = .186$, $\eta_p^2 = .030$). Descriptive statistics for RT and accuracy are in line in the direction of a facilitation for baseline and high-reward over low-reward trials. For this reason we calculated and analyzed combined accuracy and RT scores (inverse efficiency; Townsend & Ashby, 1978, 1983). This identified a main effect of reward (624 vs 626 vs 645, Greenhouse-Geisser correction; $F(1.55,88.4) = 4.48$, $p = 0.022$, $\eta_p^2 = .073$). Pairwise comparisons showed a significance difference between baseline and low-reward conditions ($t(57) = 2.72$, $p = .009$, $d = 0.187$), but no other significant differences (high-reward vs low-reward: $t(57) = 2.01$, $p = .049$, $d = 0.170$; baseline vs high reward: $t(57) = 0.40$, $p = .69$, $d = 0.023$).

Invalidly Cued Conditions

Figure 2.4 presents RT results from invalidly cued conditions in Experiment 3. Analysis of these results tests core experimental hypotheses. As illustrated in Figure 2.4A, results from the learning phase replicated Experiment 2. A RANOVA with factors for reward (target at high-reward colored object, target at low-reward colored object) and cue-target relationship (same rectangle, different rectangle) identified main effects of reward ($F(1,57) = 75.90$, $p < .001$, $\eta_p^2 = .57$) and cue-target relationship ($F(1,27) = 9.03$, $p = .004$, $\eta_p^2 = .137$) with no significant interaction between these factors ($F < 1$). Similar analysis of accuracy revealed a main effect of

reward with improved performance with the target appearing on the rectangle with high-reward color (92% vs. 83.1%; $F(1,57) = 25.60, p < .001, \eta_p^2 = .310$). No other effects emerged (88.3% vs 86.8%, cue-target relationship: $F(1,57) = 1.29, p = .261, \eta_p^2 = .022$; interaction: $F < 1$).

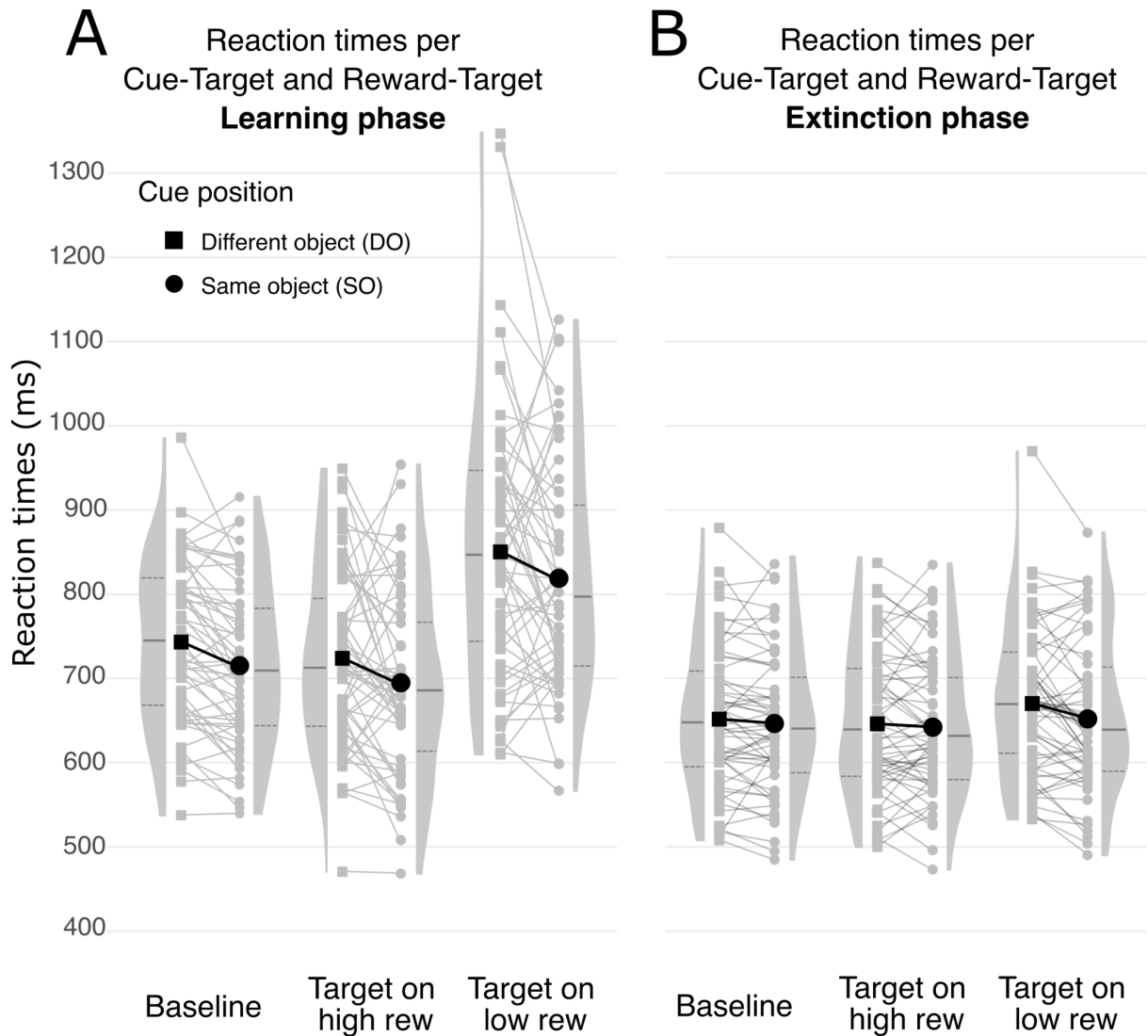


Figure 2.4 Results from Experiment 3. Reaction times from the learning phase are illustrated in **panel A**. The object prioritization effect emerges when the target appears on the high-reward associated object, and also when it appears on the low-reward associated object, with no appreciable difference in magnitude. Reaction times from the extinction phase are illustrated in **panel B**. The object prioritization effect appears larger when the target appears on the low-reward associated object.

Analysis of results from the extinction phase also identified main effects of reward ($F(1,57) = 13.01, p < .001, \eta_p^2 = .186$) and cue-target relationship ($F(1,57) =$

5.03, $p = .029$, $\eta_p^2 = .081$). However, a significant interaction between these factors also emerged ($F(1,57) = 5.32$, $p = .025$, $\eta_p^2 = .085$). A corresponding effect of reward emerged in analysis of accuracy (94.2% vs 92.6%; $F(1,57) = 4.02$, $p = .050$, $\eta_p^2 = .066$) but there was no evidence of the main effect of cue-target relationship (93.5% vs 93.2%, $F < 1$) or interaction ($F(1,57) = 2.40$, $p = .127$, $\eta_p^2 = .040$).

We conducted an omnibus RANOVA to determine if the interaction identified in the extinction phase was reliably different from the interaction identified in the learning phase. This was based on results from all invalidly-cued trials and had factors for experiment phase (learning, extinction) as well as reward and cue-target relationship. The 3-way interaction was not significant ($F < 1$). In line with group-wise results described above, this analysis otherwise identified 3 significant main effects (reward: $F(1,57) = 78.12$, $p < .001$, $\eta_p^2 = .578$; cue-target relationship: $F(1,57) = 13.78$, $p < .001$, $\eta_p^2 = 0.195$; phase: $F(1,57) = 186.22$, $p < .001$, $\eta_p^2 = 0.766$) and an interaction of reward and phase ($F(1,57) = 58.93$, $p < .001$, $\eta_p^2 = .508$), but no other effects (reward X cue-target relationship: $F < 1$; cue-target relationship X phase: $F(1,57) = 3.23$, $p = .078$, $\eta_p^2 = .054$). Analysis of accuracy identified a complementary pattern, with effects of reward (93.1% vs 87.8%; $F(1,57) = 23.66$, $p < .001$, $\eta_p^2 = .293$), experimental phase (87.5% vs 93.4%; $F(1,57) = 57.01$, $p < .001$, $\eta_p^2 = .500$) and an interaction of reward with phase ($F(1,57) = 57.01$, $p < .001$, $\eta_p^2 = .239$), but no other effects (90.9% vs 90.0%, cue-target relationship: $F(1,57) = 1.23$, $p = .272$, $\eta_p^2 = .021$; three-way interaction: $F(1,57) = 1.15$, $p = .288$, $\eta_p^2 = .020$; all other $Fs < 1$).

2.7.4 Discussion

Results from Experiment 3 indicate that reward prioritization sustains in the extinction phase, consistent with the idea of mechanism that is relatively insensitive to shifts in strategy (cf. Hickey, Chelazzi, & Theeuwes, 2010a, b; Anderson et al., 2011; Anderson & Yantis, 2013). Importantly, the effect of cue-target relationship - reflecting object prioritization - emerged in both the learning phase and the extinction phase.

Results from the learning phase reproduce results from Experiment 2. However, in contrast to Experiment 2 and the learning phase of Experiment 3, a statistical interaction of reward prioritization and object prioritization emerged in the extinction phase of Experiment 3. The object prioritization effect had greater strength when the target ultimately appeared on the low reward rectangle. This interaction is similar to that observed in Zhao et al. (2020; Experiment 2), where a nominal interaction of reward prioritization and object prioritization also emerged. As described above, visual objects in Zhao et al. (2020; Experiment 2) were images of monetary notes, which presumably had associations of value, but the presence of these objects did not signal actual receipt of reward. Similarly, in the extinction phase of the current experiment the visual objects had been associated with reward, but did not signal actual receipt of reward. In both studies, participants appear to have a particularly hard time orienting attention away from locations on the high-reward object when that object has been cued, but the target has appeared elsewhere.

Results from Experiments 2 and 3 tentatively suggest that when an object reward association is strategically useful - when it validly predicts monetary outcome - reward prioritization and object prioritization emerge as independent, additive

influence on attentional control. However, when a reward association is discontinued - in extinction - reward prioritization and object prioritization come to interact. But there are cogent reasons to delay this conclusion. First, the interaction of reward and cue-target relationship identified in the extinction period of Experiment 3 (which was significant) was not reliably different from the interaction identified in the learning phase (which was not significant). This highlights limitations in the experimental design. First, comparison of results from learning and extinction phases confounds the experimental manipulation of reward feedback with task sequence: the extinction phase necessarily follows the learning phase. This raises the possibility that the interaction emerges as a function of task familiarity and practice, rather than the manipulation of reward feedback. This is complicated by the fact that Experiment 3 was substantively longer than Experiment 2. Second, the extinction phase necessarily follows the learning phase, and performance is therefore more stable in the extinction phase. There is therefore more variance in behavior in the learning phase than in the extinction phase, which can render statistical estimates unreliable. This difference in variance is exacerbated by the difference in duration of the experimental phases: the short first phase of the experiment has fewer trials than the longer second phase, meaning that estimates of performance are noisier.

These shortcomings of Experiment 3 motivated the need for an additional experiment to explicitly determine if the interaction of object prioritization and reward prioritization observed in the extinction phase of Experiment 3 was caused by the manipulation of reward utility. In Experiment 4, two separate groups of participants each completed an independent version of our task. For one group - the learning-extinction (LE) group - the task was nearly identical to that of Experiment 3. That is, participants initially completed a learning phase, when points could be

earned, followed by an extinction phase, where there was no reward feedback. For the other group - the learning-learning (LL) group - the task was more similar to that of Experiment 2, with the learning phase sustaining until the end of the experiment. This design meant that in the second phase of the experiment LE participants had the same amount of practice as LL participants and that performance estimates in each group were based on an equivalent number of trials. If reward prioritization and object prioritization come to interact as a function of the manipulation of reward feedback, results in Experiment 4 should show an interaction of reward and cue-target relationship in the extinction phase of the experiment in the LE group, but not the LL group.

2.8 Experiment 4

2.8.1 Participants

Experiment 4 was based on a new sample of 53 participants and used the same recruitment and exclusion procedures identified for Experiment 1. Five participants were rejected, leading to a final sample of 48 individuals that were randomly assigned into two equal groups (LL group: 15 male, 9 female, 0 other; mean age 27 years \pm 5 years SD; nationality BD 1 BE 1 CA 1 GR 1 HU 1 IT 1 LV 1 MX 1 NG 1 PO 7 PT 1 SA 4 UK 3; LE group: 17 male, 7 female, 0 other; mean age 25 years \pm 7 years SD; nationality CZ 1 DK 1 GR 1 HU 1 IT 2 MX 1 PO 4 PT 5 SA 5 UK 2 US 1). The sample size was determined using the effect size of the interaction between factors for reward and cue-target in Experiment 3 ($\eta_p^2 = .085$). Power analysis suggested the need for 24 participants to detect an effect of reward on difference

scores derived from the effect of cue-target relationship on RT, based on assumed power of .8.

2.8.2 Design and procedure

Experiment 4 had two phases: a learning phase (2 blocks of 72 trials) that was closely modeled on the learning phase of Experiment 3, and a second phase (4 blocks of 72 trials) that differed between groups. For the LL group, the second phase was identical to the first. For the LE group, the second phase was an extinction phase, with no reward feedback. In order to equate the two conditions in terms of total reward incentive, participants in the LE group were informed that participation in the entire experiment would lead to earnings of 4 times the amount accumulated in the learning phase. The base pay rate adopted in Experiment 4 was £4. As more total points were accumulated by participants in Experiment 4 than in Experiment 3, points were associated with less cash value (£0.10 per 100 points). All other design characteristics were as in Experiment 3. The experiment took approximately 70 minutes and average pay was £8.38 (\pm £0.46 SD) for the LL group and £8.14 (\pm £0.61 SD) for the LE group.

2.8.3 Results

In 0.74% (\pm 1.49% SD) of trials participants did not respond within 1700 ms of stimulus onset. These trials were excluded from calculation of accuracy. Performance in the common learning phase was similar in both groups (mean RT

687 ms, \pm 76.8 SD; 682 ms, \pm 119 SD). As there was no a priori motivation to expect a difference between these groups, who completed the same task under the same task instructions, we collapse across groups in analysis of the learning phase of the experiment.

Validly Cued Conditions

First experimental phase

As in experiment 3, we report statistical analysis of validly cued conditions, though no critical hypotheses are tested. A one-way RANOVA on RT observed in the learning phase, collapsed across the LL and LE groups, identified a significant effect of reward (baseline with both rectangles characterized by low reward color, target on high reward rectangle, target on low reward rectangle; $F(1.38,65.08) = 24.15$, $p < .001$, $\eta_p^2 = .339$). A pairwise comparison identified significant differences between baseline and low reward conditions (641 vs 758, $t(47) = 5.50$, $p < .001$, $d = 0.783$) and high reward and low reward conditions (651 vs 758, $t(47) = 4.90$, $p < .001$, $d = 0.704$) but not between baseline and high reward conditions (641 vs 651, $t(47) = 0.93$, $p = 0.358$, $d = 0.090$). Accuracy results also showed a main effect of reward ($F(1.59,74.83) = 4.06$, $p = .029$, $\eta_p^2 = .080$). Pairwise comparison showed higher accuracy for high-reward trials compared to low-reward trials (93.0% vs 87.2%, $t(47) = 2.34$, $p = .024$, $d = 0.468$). No significant difference was identified for the remaining contrasts (baseline vs low reward: 91.1% vs 87.2%, $t(47) = 1.78$, $p = .082$, $d = 0.293$; high reward vs baseline: 93.0% vs 91.1%, $t(47) = 1.42$, $p = .161$, $d = 0.227$).

Second Experimental Phase

Analysis of the second experimental phase began with an omnibus RANOVA with between-participant factor group (LL, LE), and within-participant factor reward (a baseline with only low reward colored rectangles on the screen, target appears on rectangle with high-reward color, target appears on rectangle with low-reward color). A significant main effect of reward emerged (Greenhouse-Geisser correction; $F(1.29,59.45) = 27.55, p < .001, \eta_p^2 = .375$), as well as the interaction ($F(1.29,59.45) = 15.55, p < .001, \eta_p^2 = .253$), but the effect of group was not significant ($F(1.00,46.00) = 1.49, p = 0.229, \eta_p^2 = .031$). Further analysis showed that the interaction is driven by a prominent difference in RTs in the low reward condition for LL and LE groups (680 vs 586, Welch-Satterthwaite correction; $t(40.6) = 3.10, p = .004, d = 0.894$), in contrast to no significant difference in the baseline (566 vs 569, $t(45.6) = 0.11, p = .915, d = 0.031$) or high reward conditions (563 vs 570, $t(41.6) = 0.30, p = .768, d = 0.086$).

Analysis of accuracy also identified a significant main effect of reward (Greenhouse-Geisser correction; $F(1.57,72.06) = 5.16, p = .013, \eta_p^2 = .0101$) and interaction ($F(1.57,72.06) = 7.88, p = .002, \eta_p^2 = .0146$), but no significant effect of group ($F < 1$). Further analysis of accuracy mirrored the RT analysis with a significant difference between LL and LE group when the target appeared on the rectangle with the low-reward color (88.8% vs 95.1%, Welch-Satterthwaite correction; $t(31.3) = 2.33, p = .027, d = 0.672$), but no significant difference between groups for baseline (94.3% vs 96.0%, $t(39.9) = 1.02, p = .314, d = 0.294$) or high reward conditions (96.6% vs 93.8%, $t(42.1) = 1.59, p = .012, d = 0.459$).

Invalidly Cued Conditions

First Experimental Phase

Figure 2.5 illustrates results from invalidly cued trials. Analysis of these results tests core experimental hypotheses. Figure 2.5A presents RT results for the learning phase collapsed across the LL and LE groups. We conducted a RANOVA analysis of RT observed in invalidly cued trials when a high-reward object was present on the screen. This had factors for reward (target appears on high reward object, target appears on low reward object) and cue-target relationship (target appears on cued rectangle, target appears on other rectangle) and replicated results of Experiments 2 and 3, showing significant main effects of reward ($F(1,47) = 29.56, p < .001, \eta_p^2 = .386$) and cue-target relationship ($F(1,47) = 4.19, p = .046, \eta_p^2 = .082$) but no significant interaction ($F(1,47) = 1.50, p = .227, \eta_p^2 = .031$).

Corresponding analysis of accuracy identified a main effect of reward ($F(1,47) = 27.75, p < .001, \eta_p^2 = .371$) but no effect of cue-target relationship ($F(1,47) = 2.10, p = .154, \eta_p^2 = .094$). In contrast to RT, analysis of accuracy identified an interaction ($F(1,47) = 4.90, p = .032, \eta_p^2 = .094$). Accuracy was better when the target appeared on a cued low-reward object than when it appears on an uncued low-reward object (81.8% vs 75.5%). This did not emerge when the target appeared on a high-reward object (90.4% vs 90.9%). We expect that this is driven at least in part by a ceiling effect on results from the high-reward condition. Analysis of inverse efficiency was in line with RT results, with a significant effect of reward (751 vs 1072, $F(1,47) = 37.40, p < .001, \eta_p^2 = .443$) but no evidence of cue-target relationship (881 vs 942, $F(1,47) = 2.29, p = .137, \eta_p^2 = .046$) or interaction ($F < 1$).

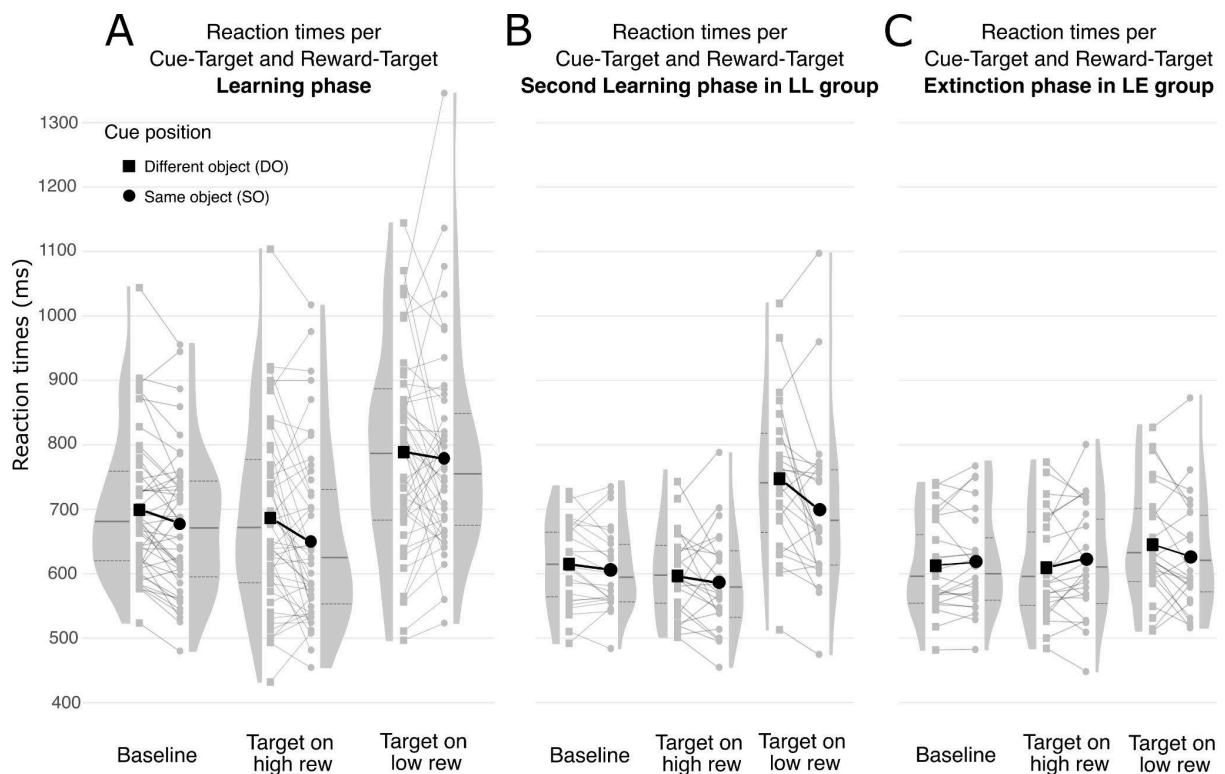


Figure 2.5 Results from Experiment 4. Reaction times from the first phase of the experiment are collapsed across LL and LE groups and illustrated in **panel A**. The object prioritization effect emerges both when the target appears on the high-reward associated object and the low-reward associated object; analysis identifies no reliable difference in these effects (see body of paper). Reaction times from the second phase of the experiment for the LL group are illustrated in **panel B**. The object prioritization effect appears to emerge more strongly when the target appears on the low-reward associated object. Reaction times from the second phase of the experiment for the LE group are illustrated in panel **C**. Again, the object prioritization effect appears to emerge more strongly when the target appears on the low-reward associated object.

Second Experimental Phase

Figures 5B and 5C present RT results from the second experimental phase for each of the LL and LE groups. Experiment 4 was conducted to test if the interaction of reward prioritization and object prioritization would emerge in each of the LL and LE groups, and analysis accordingly began with independent ANOVAs examining RT results in each group.

In the LE group, analysis identified a main effect of reward (614 vs 636, $F(1,23) = 8.78$, $p = .007$, $\eta_p^2 = .276$), no significant effect of cue-target relationship (622 vs 627, $F < 1$), but, critically, an interaction between these factors ($F(1,23) = 5.11$, $p = .034$, $\eta_p^2 = .182$). Analysis of accuracy garnered similar results (reward: 93.2 vs 90.5, $F(1,23) = 3.74$, $p = .066$, $\eta_p^2 = .140$; cue-target relationship: 92.1 vs 91.7, $F < 1$; interaction: $F < 1$). In the LL group, analysis identified a main effect of reward (591 vs 724, $F(1,23) = 28.12$, $p < .001$, $\eta_p^2 = .550$), a main effect of cue-target relationship (643 vs 672, $F(1,23) = 6.24$, $p = 0.02$, $\eta_p^2 = .213$), and an interaction that approached significance ($F(1,23) = 3.06$, $p = .093$, $\eta_p^2 = .117$). The broad similarity in statistical results for each of the groups was also evident in analysis of inverse efficiency scores (LE 2-way interaction: $F(1,23) = 4.21$, $p = 0.052$, $\eta_p^2 = .155$; LL 2-way interaction: $F(1,23) = 4.02$, $p = 0.057$, $\eta_p^2 = .149$).

The interaction effects identified in each of the two groups have the same direction and are of similar standardized effect size. In raw data, the RT interaction is in fact larger in the LL group. The 2-way interaction of object prioritization and reward prioritization therefore does not appear constrained to the LE group. In line with this, in a larger analysis of RT- with factors for group (LL, LE), reward, and cue-target relationship - the 2-way interaction was significant ($F(1,46) = 7.01$, $p = .011$, $\eta_p^2 = .132$) but the 3-way interaction was not ($F < 1$). This analysis otherwise paralleled the separate analyses of each group, identifying additional main effects of reward ($F(1,46) = 35.12$, $p < .001$, $\eta_p^2 = .433$) and cue-target relationship ($F(1,46) = 5.23$, $p = .027$, $\eta_p^2 = .102$), and interactions between group and reward ($F(1,46) = 17.99$, $p < .001$, $\eta_p^2 = .281$) - reflecting an accentuated reward effect in the LL group - and between cue-target relationship and reward ($F(1,46) = 7.01$, $p = 0.011$, $\eta_p^2 = .132$).

The only remaining effect in this analysis -the main effect of group - was not significant ($F(1,46) = 2.25, p = .140, \eta_p^2 = .047$).

Three-factor analysis of accuracy provided no substantive insight beyond that provided by analysis of the groups separately. A significant main effect of reward emerged, with participants more accurate when the cue appeared on the low reward rectangle (93.6% vs 87.5%, $F(1,46) = 21.66, p < .001, \eta_p^2 = .320$). This appears to reflect a speed accuracy tradeoff; participants were generally quicker when the cue appeared on the high reward rectangle, but slightly less accurate, regardless of the ultimate target location. A significant interaction of group and reward also emerged ($F(1,46) = 6.48, p = .014, \eta_p^2 = .123$): when the cue identified the high reward rectangle, this decreased accuracy more substantively in the LL group (93.9% vs 84.5%) than in the LE group (93.2% vs 90.5%). This appears to reflect an impact of the continuing strategic importance of reward association for the LL group. No other effects were significant (group: 89.2% vs 91.2%, $F(1,46) = 1.12, p = .296, \eta_p^2 = .024$; cue-target relationship: 91.2% vs 89.8%, $F(1,46) = 1.48, p = .230, \eta_p^2 = .031$; group X cue-target relationship: $F(1,46) = 1.13, p = .294, \eta_p^2 = .024$; all other effects $F_s < 1$).

2.8.4 Discussion

In Experiment 3, reward prioritization and object prioritization interacted in the extinction phase of the experiment, raising the possibility that this interaction was caused by manipulation of reward feedback. This idea predicts that the interaction should emerge in the LE group of Experiment 4, but not in the LL group. In contrast,

results show an interactive relationship in both groups. In RT, this effect is significant in the LE group and approaches significance in the LL group. These effects do not statistically differ between the groups, and the effect on raw RT is in fact nominally larger in the LL group than it is in the LE group. This pattern suggests that the interaction of reward prioritization and object prioritization emerges not as a product of the manipulation of reward feedback, but as a function of task practice. As in earlier experiments, the interaction of reward prioritization and object prioritization in Experiment 4 is driven in particular by a slowing of response when the cue has identified a high-reward object, but the target ultimately appears on the low-reward object.

2.9 General Discussion

Selective attention is sensitive to the prior experience of reward, causing reward-associated stimuli to draw attention even under circumstances where this has no immediate benefit. Similarly, attention is sensitive to the definition of visual objects, prioritizing locations on a cued object over locations elsewhere, often when this is not useful. Here we investigate the relationship between these effects. We focussed on the possibility of an interaction between reward prioritization and object prioritization: is attentional engagement of visual objects stronger when the object has been linked to reward in prior experience?

Our experiments relied on the 2-rectangle paradigm (Egley et al., 1994), in which participants search for a target that appears at one of 4 locations. These locations fall on two task-irrelevant rectangles, such that each rectangle contains two

possible target locations. When an exogenous cue identifies one location, participants are faster to detect the target at that location than when it appears elsewhere. More importantly, when a location is cued, but the target does not appear at this position, participants are faster to detect a target appearing on the same rectangle as the cue.

Our investigation began with a simple test of the impact of reward feedback on object prioritization in the 2-rectangle task. Existing experimental work from Shomstein and Johnson (2013) has suggested that the introduction of reward feedback to the 2-rectangle task causes object prioritization to disappear. We had the idea that this might reflect the influence of sequential contingencies on attentional deployment (eg. Hickey, Chelazzi, & Theeuwes, 2010a, 2010b), and Experiment 1 was designed as a replication of Shomstein and Johnson (2013, Experiment 2) in order that we might isolate intertrial effects in the results. Though we ultimately found no evidence of such intertrial contingencies, we did observe a robust effect of object prioritization. Experiment 1 thus re-opened a possibility that had been closed by Shomstein and Johnson (2013), namely that reward prioritization and object prioritization might coexist in visual cognition. This coexistence was corroborated and investigated in Experiments 2 through 4.

In critical conditions of Experiments 2 through 4, one rectangle in the display was characterized by a color that either validly predicted reward outcome (Experiment 2; learning stages of Experiments 3 and 4), or had predicted reward outcome in recent experience (extinction stage of Experiment 3; extinction stage of Experiment 4 for the LE group). Results from Experiment 2 suggested that, when the reward association had strategic utility and predicted feedback magnitude, reward

prioritization and object prioritization appeared as independent, additive effects on attentional selection. In Experiment 3, we tested if these effects would sustain when reward feedback was discontinued and the reward association entered into extinction. As in Experiment 2, reward prioritization and object prioritization emerged in the results of Experiment 3, but these effects now interacted: object prioritization emerged with greater strength when the target appeared on an object associated with low-magnitude reward, with RT particularly slowing when a high-reward objects was cued but the target appeared on a low-reward object.

A possible interpretation of results from Experiments 2 and 3 is that reward prioritization and object prioritization independently impacted performance when reward prioritization had strategic utility, but interacted when reward was discontinued, and this could have interesting implications for our understanding of these effects. That is, the emergence of additive effects on RT tentatively suggests an influence on different cognitive mechanisms, whereas interaction can be interpreted as reflecting an impact on the same processing stage (Sternberg, 1969). There was the possibility that a low-level, non-strategic impact of reward influenced the same cognitive stage as object prioritization, but a high-level, strategic impact of reward expressed elsewhere.

However, the design of Experiment 3 confounded the discontinuation of reward feedback with task practice. That is, the extinction phase necessarily came at the end of the experiment, raising the possibility that it was not the manipulation of strategic utility that caused the interaction of effects, but task practice. This was exacerbated by the fact that Experiment 3 was substantially longer than Experiment 2. With this in mind, Experiment 4 compared two groups of participants. The LE

group completed a task very similar to that employed in Experiment 3, with discontinuation of reward feedback in an extinction period. The LL group completed a task very similar to that employed in Experiment 2, with reward feedback sustaining throughout the experiment. Each group had the same amount of task experience, and this design provided the opportunity to identify whether it was the strategic utility of the reward association that impacted the relationship between object prioritization and reward prioritization, or task experience. Results suggest that it was task experience that was important, with the interaction of object prioritization and reward prioritization emerging in both LL and LE groups with roughly equal strength.

We approached the current study with the broad idea that there may be evolutionary utility to the gathering of information from locations on reward-associated visual objects, and therefore that reward prioritization and object prioritization might interact in visual cognition to benefit processing of stimuli appearing at these locations (Toates, 1990; Hickey, Chelazzi, & Theeuwes, 2010). Our results are consistent with this idea, but they do not actually demonstrate a benefit to the processing of target stimuli on the high-reward object. The interaction of reward prioritization and object prioritization identified in Experiments 3 and 4 appears rather to be driven by a slowing of RT when attention was drawn to a location on an object associated with high-magnitude reward, but participants had to subsequently reorient to a location on an object associated with low-magnitude reward (see also Zhao et al, 2020). That is, when the target appeared on a high-reward object, it did not much matter if that object had been cued, suggesting that locations on the high-reward object were prioritized regardless of cue location. However, when cue location and reward status combined, it became difficult for

participants to orient attention elsewhere. It appears that all locations on a high-reward object are constantly monitored, and that it is particularly difficult to disengage attention from this kind of high-reward object in order to resolve a target that unexpectedly appears on a low-reward object.

Participants in Experiments 3 and 4 show a lingering influence of reward association during extinction, when an ideal observer would not. At first blush, the insensitivity of the interaction of object prioritization and reward prioritization to the utility of the reward association is surprising. However, reward prioritization is well known in the broader literature to be relatively impervious to countermanding strategy (eg. Hickey, Chelazzi, & Theeuwes, 2010a, b; Hickey & van Zoest, 2012) and to extinguish slowly over the course of many trials (eg. Anderson et al., 2011; Stankevitch & Geng, 2015). In the extreme case, Anderson and Yantis (2013) found that a reward-associated object drew attention 9 months after training. This is in contrast to the broader motivational impact of reward prospect, which disappears quickly when the strategic utility of the reward association is removed. The motivational impact of reward is evident in the current results in the substantive main effect of reward in analysis of Experiments 3 and 4; when the utility of the reward signal is discontinued, the presence of the reward-associated object at the beginning of each trial no longer triggers the same broad arousal and investment of resources. However, the reward-associated object still draws selective attention, and this reward prioritization continues to interact with object prioritization in selective control.

The current results add to a developing literature investigating the impact of reinforcement learning on the deployment of visuospatial attention. This literature has been influenced by empirical and theoretical work on animal associative

learning, and specifically by the idea that mesencephalic dopamine may play a core role in cognition through an impact on selective control (eg. Ikemoto & Panksepp, 1999; Redgrave, Prescott, & Gurney, 1999; Jeong et al., 2022). For example, the incentive salience hypothesis of Berridge and Robinson (1998) suggests that reward-related dopamine acts to prime the perceptual and attentive representation of reward-associated stimuli, making it more likely that animals will notice similar stimuli in the future and ensuring that information from reward-associated stimuli gains preferential access to downstream cognitive operations like decision making and motor control. Pathological misattribution of incentive salience has been linked to a variety of clinical disorders, including eating disorders, depression, paranoia, obsessive compulsive behaviour, and - prominently - addiction (Robinson & Berridge, 1993; Olney, Warlow, Naffziger, & Berridge, 2018). In addiction, direct drug stimulation of dopaminergic circuitry is thought to drive the attribution of incentive salience to drug-related stimuli. As a result, drug-related paraphernalia become salient and attention-drawing, and, once noticed, trigger craving and drug-seeking behaviour (ie. the 'drug trigger' phenomenon; Dackis & O'Brien, 2005). As discussed in the Introduction, the study of human incentive salience to date has largely focussed on the association of reward to low-level visual features, like color (Hickey, Chelazzi, & Theeuwes, 2010; Anderson, Laurent, & Yantis, 2011), or to categories of real-world objects (Hickey & Peelen, 2015; Donohue, Hopf, Bartsch, Schoenfeld, Heinze, & Woldorff, 2016; Hickey, Acunzo, & Dell, under review). The current results provide the basis for further investigation of the interaction of raw visual salience, reward, and object status in the core phenomenon of incentive salience, as well as in disorders reflecting the misattribution of incentive salience.

As noted in the introduction, recent theoretical interpretation of object prioritization has suggested the effect may be strategic in nature and contingent on goal-driven attentional control settings (Shomstein & Johnson, 2013; Lee & Shomstein, 2013; Taylor et al., 2016). For example, Taylor and colleagues (2016) have shown that object prioritization manifests when the object matches the top-down perceptual filters strategically adopted by participants, but does not emerge otherwise. Results from the current study do not directly speak to this issue, but do support the idea that object prioritization can emerge when the environment offers other strategic opportunities for the optimization of performance (cf. Shomstein & Johnson, 2013, [Lee & Shomstein, 2013](#)). This could reflect the adoption of multiple concurrent strategic approaches to visual search (Wolfe, 2021).

In conclusion, we find that reward prioritization and object prioritization have concurrent influence on the deployment of selective attention. These effects appear to combine and interact such that attention is particularly engaged with locations on visual objects that have been associated with reward.

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CHAPTER 3

NEURAL MECHANISMS OF OBJECT PRIORITISATION IN VISION

3.1 Abstract

Selective attention is widely thought to be sensitive to visual objects. This is commonly shown in cueing studies, which reveal that when attention is deployed to a known target location that happens to fall on a visual object, responses to targets that unexpectedly appear at other locations on that object are faster and more accurate, as if the object in its entirety has been visually prioritized. However, this notion has recently been challenged by results suggesting that putative object-based effects may reflect the influence of hemifield anisotropies in attentional deployment, or of unacknowledged influences of perceptual complexity and visual clutter. Studies employing measures of behaviour provide limited opportunity to address these challenges. Here, we used EEG to directly measure the influence of task-irrelevant objects on the deployment of visual attention. We had participants complete a simple visual cueing task involving identification of a target that appeared at either a cued location or elsewhere. Throughout each experimental trial, displays contained task-irrelevant rectangle stimuli that could be oriented horizontally or vertically. We derived two cue-elicited indices of attentional deployment—lateralized alpha oscillations and the ADAN component of the event-related potential—and found that these were sensitive to the otherwise irrelevant orientation of the rectangles. Our results revealed that the allocation of visual attention is influenced by objects boundaries, supporting models of object-based attentional prioritisation.

3.2 Introduction

Adaptive behaviour relies on identifying useful objects in our environment. Accordingly, sensory and cognitive systems, including visual attention, express object-based organization (Scholl, 2001; Duncan, 1984). This appears both in studies of patients and healthy participants. In patients, parietal lesions degrade the ability to attend multiple objects simultaneously (i.e., simultagnosia; Luria, 1959; Coslett, & Saffran, 1991), or bias attention to the ipsi-lesional side of objects, regardless of their position in retinotopic space (i.e., object-centered or allocentric neglect; Walker, 1995). In healthy participants, attention is more efficiently deployed to stimuli that fall on a cued object rather than outside that object (Chen et al., 2012).

This latter instantiation of object prioritisation is commonly studied using the two-rectangle task (see Figure 3.2; Egly, Driver, & Rafal, 1994; Moore, Yantis, & Vaughan, 1998). In this paradigm, attention is cued - either by an exogenous cue such as luminance onset (eg. Egly, Driver, & Rafal, 1994) or by an endogenous cue such as a central arrow (eg. Abrams & Law, 2000, Exp. 2; Chen & Cave, 2008) - to an endpoint of one of two rectangles rendered on the computer screen. Responses are faster and more accurate when attention is invalidly cued to an endpoint that happens to fall within the same rectangle as the cued location, as compared to when the target appears at any other uncued position.

This has been interpreted as reflecting the automatic spreading of spatial attention along the contours of the cued object, reflecting a role for attention in object completion and other Gestalt principles of visual perception (Davis & Driver, 1997;

Cohen et al., 2015; Watson & Kramer, 1999). However, recent studies have raised challenges to this idea (Reppa, Schmidt, & Leek, 2012; Francis & Thunnell, 2022).

First, object prioritisation appears to be contingent on cognitive strategy. For example, Shomstein and Yantis (2002) found that non-targets on the same object as targets had no impact on performance unless there was uncertainty about target location. This and other results are difficult to reconcile with the notion that object prioritisation is closely involved in low-level perception, which should not be sensitive to task set (for a review see Shomstein, 2012).

Second, object effects in the two-rectangle task are worryingly sensitive to rectangle orientation, emerging with more strength when the rectangles are horizontal (Al-Janabi & Greenberg, 2016; Chen & Cave, 2019; Francis & Thunnell, 2022; Pilz et al., 2012). Performance of many visual tasks is known to be better when stimuli appear across the horizontal meridian (Corballis & Roldan, 1975; Carrasco et al., 2004; Corbett & Carrasco, 2011), raising the possibility that putative object prioritisation might instead reflect an influence of hemifield anisotropy (Pilz et al., 2012; Barnas & Greenberg, 2024).

Third, interpretation of object-based effects is complicated by reporting bias. A meta-analysis of 37 behavioural studies found that 19 were unlikely to replicate with the original sample size (Francis & Thunnell, 2022) and a large-sample study suggest that the object-based attention effect is much smaller than commonly assumed: i.e., only a minority of individuals showed an object-based effect, and this effect only emerged when rectangles were oriented horizontally but was reversed when they were oriented vertically, resulting in a overall small impact on behaviour (6.5 ms) and not statistically significant (Pilz et al., 2012, Exp. 2).

Motivated by these and other findings, Rosenholtz (2024) has recently challenged the notion that behavioural measures of object prioritisation reflect attention at all, noting that when cue and target appear on different objects, the edges of both objects intervene. This could generate a small cost to target resolution through visual crowding, and this could be exacerbated if participants move their eyes to bring the visual clutter closer to foveal vision - which is likely, given that studies of object prioritisation commonly employ cue validity of >70% without monitoring fixation. In line with this, the effect of object prioritisation reverses when visual complexity is introduced into the space between same-object locations (Chen et al., 2020).

It is therefore unclear if attention is necessarily sensitive to the presence of visual objects at all. This uncertainty is caused in part by a reliance in the literature on inference from behaviour. On one hand, issues like stimulus crowding, complexity, and hemifield anisotropies can create costs in the behavioural response to targets that are difficult to distinguish from effects of object prioritisation. On the other hand, object prioritisation may simply degrade over time (Lou et al., 2023), such that small, absent, or even reversed effects at the time of target onset do not mean that earlier deployment of attention was unaffected. Here, we resolve this ambiguity by deriving indices of attention from human EEG, allowing us to directly measure the impact of task-irrelevant objects on the deployment of attention. We had participants complete a variant of the two-rectangle paradigm where target location was endogenously cued by a spoken word identifying a screen location (Goldsmith & Yeari, 2003). We recorded EEG while participants completed this task and derived two indices of attentional deployment from this signal: lateralized posterior EEG alpha power

(Worden et al., 2000), and an ERP component known as the anterior directing-attention negativity (ADAN: Eimer et al., 2002; Van der Lubbe et al., 2000).

Occipital alpha oscillations are known to be modulated by the deployment of attention in retinotopic space (Popov et al., 2019; Foster et al., 2017). In particular, when attention is directed to a lateral position, alpha oscillations originating from contralateral posterior cortex exhibit lower amplitude compared to those originating ipsilaterally. This is thought to reflect the preparatory downregulation of ongoing inhibitory activity, such that visual cortex contralateral to the cued location becomes broadly more responsive to stimulus inputs (Klimesch et al., 2007; Jensen and Mazaheri, 2010; Foxe and Snyder, 2011; Jensen, 2024).

In contrast, the ADAN emerges over lateral frontal brain areas. It is evoked by endogenous attention-directing cues and is associated with activation of cortical areas involved in the control and voluntary deployment of spatial attention (Praamstra 2005, Eimer et al. 2002; Hopf and Mangun, 2000). It typically emerges 300-500 ms after cue onset and is characterized by a negative deflection in the ERP waveform that is more pronounced over frontal and central scalp regions contralateral to the focus of attention (see Zani et al., 2023; Holmes et al., 2010; Seiss et al., 2007; Eimer et al., 2002; Hopf & Mangun, 2000; Nobre et al., 2000; van Velzen, Forster, & Eimer, 2002; Yamaguchi et al., 1995b).

As depicted in Figure 3.1, we hypothesized that lateralized alpha activity and the ADAN would differ based on the orientation of the irrelevant rectangles used in our task. When the rectangles are oriented vertically, each lies entirely within a single visual hemifield. If object-based attention causes selection of the cued object in this circumstance, attention will be strongly lateralized because the effects of spatial

cuing and object-based attention will align. This should accordingly create strong lateralization of occipital EEG alpha activity and the ADAN. Conversely, when the rectangles are oriented horizontally, each rectangle appears in both visual hemifields. If object-based attention causes selection of the cued object in this circumstance, attention will be less lateralized because the effects of spatial cuing and object-based attention will be incongruent. This should create weaker lateralization of occipital alpha and the ADAN.

Unlike behavioural studies of object-based attention, which compare reaction times for validly versus invalidly cued targets on the same versus different objects, our critical comparison focuses solely on the vertical versus horizontal rectangle conditions. The dependent measures are the post-cue/pre-target EEG alpha activity and ADAN, which reflect the strength of anticipatory lateralization of spatial attention before the target appears.

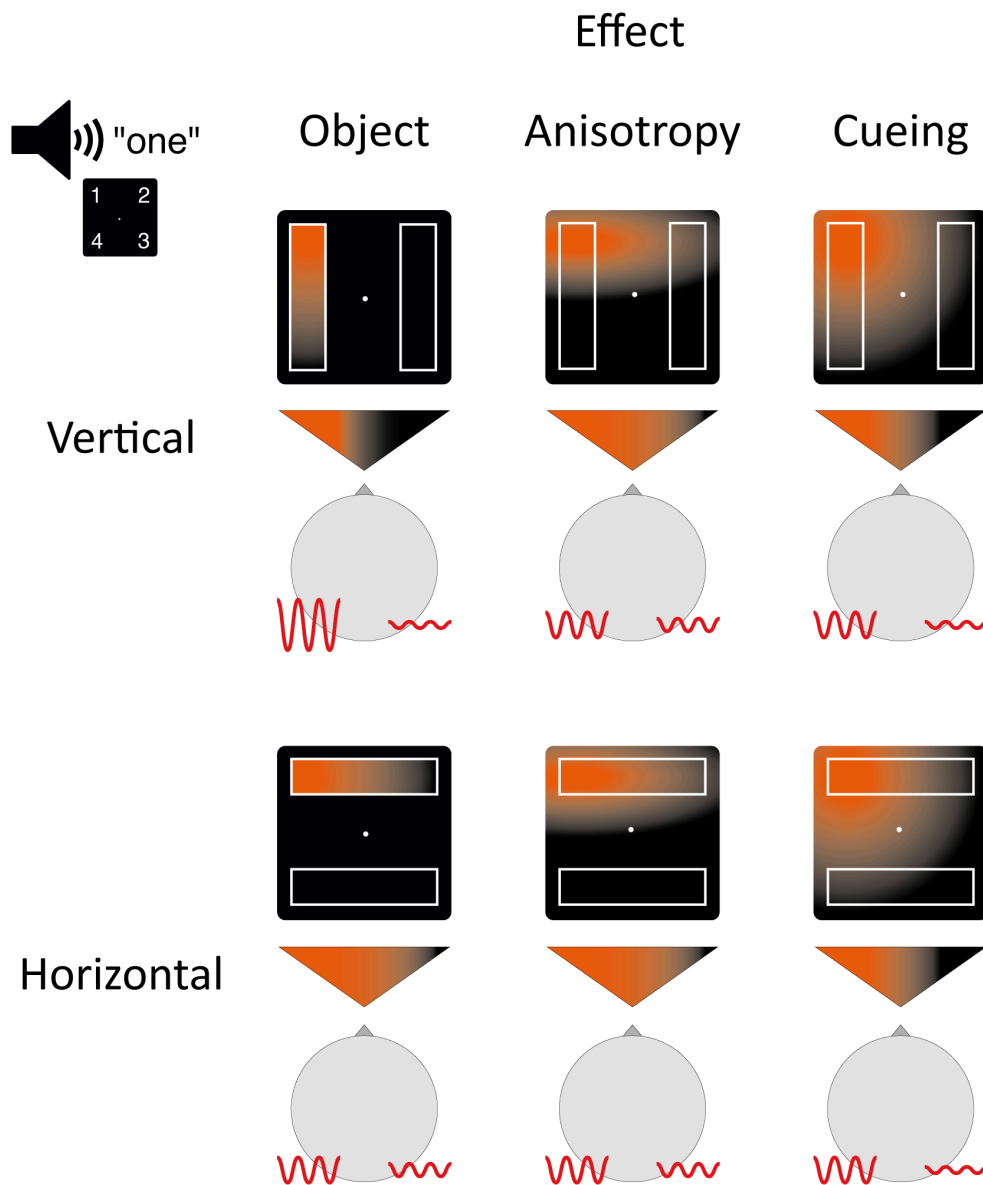


Figure 3.1 Attention deployment in horizontal and vertical conditions under the influence of three effects: OBA (object), attentional anisotropy (anisotropy) and space-based effect (cueing). An auditory cue indicates position one (upper-left corner). The orange gradient represents the distribution of attention across the screen following the cue, while the gradient within the triangles illustrates the direction or lateralization of attention. The red lines depict alpha oscillations ipsilateral and contralateral to the cued position, as well as their power. The contributions to the attention distribution from attentional anisotropy and cueing effects do not result in differences in alpha lateralization between horizontal and vertical conditions. In contrast, the object-based effect is the only factor that induces a difference in alpha lateralization between horizontal and vertical trials. A similar rationale was applied in hypothesising a conditional difference for the ADAN. It is important to note that this does not preclude the possibility of multiple influences on attention operating simultaneously.

3.3 Methods

3.3.4 Participants

Thirty participants (6 males, 24 females; mean age 23.13 years \pm 4.12 years SD; 6 left-handed) were recruited from the University of California, Davis, community. All had normal or corrected-to-normal vision and received compensation for their participation (mean compensation \$45). All participants gave informed written consent, and the study procedure was approved by the local institutional review board of the University of California, Davis.

3.3.5 Stimuli, Experimental Task, and Apparatus

Figure 3.2 depicts the stimuli and timing of an experimental trial. Each trial began with an auditory cue that indicated one of 4 screen locations where a subsequent target might appear, each located 4.4° visual angle from the screen center. The cue constituted a male voice with a standard British accent pronouncing one of four numbers: 'one', 'two', 'three', or 'four'. Each number took 300 ms to pronounce and corresponded to a specific corner on the screen of an LCD computer monitor (57 cm x 39 cm; 120 Hz refresh rate), with 'one' designating the upper left corner and proceeding clockwise. The mapping between numbers and screen locations remained consistent across all participants and the cues were generated using Audacity (v3.2.4, Audacity Team, 2021).

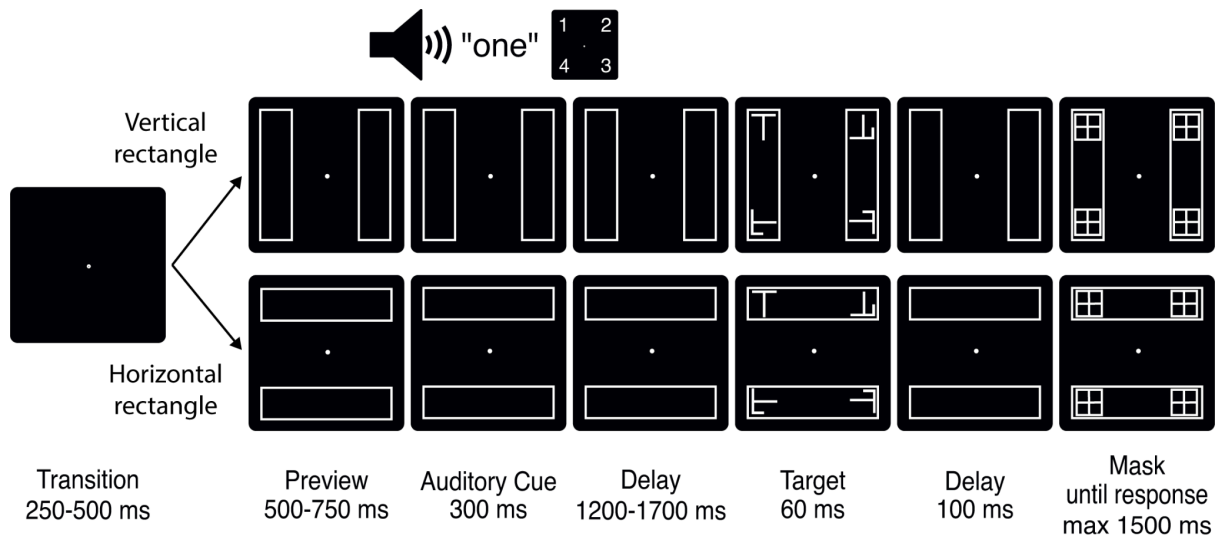


Figure 3.2 Task description: A fixation dot was presented for a variable duration of 250 to 500 ms, followed by a preview screen displaying the two rectangles for a variable duration of 500 to 750 ms. A 300-ms auditory cue then identified one of the four rectangle endpoints where the target was 70% likely to appear. The target and nontargets subsequently appeared after a delay of 1500 to 2000 ms. The target remained on the screen for 60 ms, followed by a 100 ms interval before the four potential target locations were masked. The mask sustained for 1500 ms or until response. Left index finger response indicated that the target was an 'L' and right index finger response indicated that the target was a 'T'.

The target was either the character 'L' or 'T', and participants were required to report the identity of this stimulus by pressing the corresponding 'L' or 'T' key on a standard QWERTY computer keyboard with the left or right index finger. Nontargets appeared at the 3 screen locations where the target did not appear, and these were generated by superimposing the two target letters and applying a random rotation of 90°, 180°, or 270°. The target and nontarget stimuli subtended a visual angle of 1.2° x 0.9°, and appeared for 60 ms before being masked 100 ms later (Figure 3.2). The mask remained present until either the participant made a response or 1500 ms had passed, at which time the trial concluded.

In two-thirds of trials, the target appeared at the cued location. In the remaining trials, the target appeared with equal probability at the uncued end of the cued rectangle or at the nearest end of the uncued rectangle. For example, if position

“one” (upper-left) was cued, the target had two-thirds probability of appearing in position “one”, and otherwise appeared at either position “two” or “four” with equal probability.

Throughout each experimental trial, two rectangle stimuli were present on the screen ($10^\circ \times 2.5^\circ$ visual angle). The rectangles were created such that each of the four potential target locations lay at a rectangle endpoint. The orientation of these rectangles varied randomly from trial to trial, and was either vertical (such that left and right hemifield stimulus locations appeared on the same rectangle objects) or horizontal (such that top and bottom stimulus locations appeared on the same rectangle objects).

The experiment was programmed using Python and JavaScript in conjunction with the Opensesame software package (v3.3.6, Mathôt et al., 2012). The first participant in the experiment completed 720 trials, while the remaining participants completed 960 trials each. Detailed instructions emphasizing the importance of both speed and accuracy were provided to participants at the beginning of the experiment. Participants underwent a practice phase to familiarize themselves with the cue-location association. This phase involved a point-and-click task in which participants identified the location indicated by the auditory cue. Practice continued until participants achieved an average reaction time below 1300 ms and at least 80% accuracy. At the beginning of each practice trial, the mouse pointer was positioned at the center of the screen.

3.3.6 EEG Recording and Pre-processing

EEG data were continuously sampled at a rate of at 1 kHz using a Neuroscan SynAmps 2 amplifier and sintered Ag/AgCl ActiCap Snap active electrodes (Brain Products GmbH). Electrodes were placed at 64 scalp locations according to a 10-10 montage (Oostenveld & Praamstra, 2001). Two additional electrodes were placed one centimeter lateral to the external canthi of each eye to measure the horizontal electrooculogram (HEOG), and two further electrodes were placed 1 cm above and below the center of the left eye to measure the vertical electrooculogram (VEOG) and blink potentials. Signals were referenced to FCz during recording.

The data were digitally downsampled to 500 Hz. A high-pass filter with a cutoff frequency of 0.01 Hz was applied to remove low-frequency drift (Acunzo, MacKenzie, & van Rossum, 2012). The "pop_cleanline" function from the EEGLAB toolbox (Delorme & Makeig, 2004) for MATLAB was used to eliminate interference from line noise (60 Hz). The EEG signal was subsequently re-referenced to the average signal of all scalp electrodes, leaving the EOG channels unaffected. To identify and remove artifacts, independent component analysis (ICA; Bell & Sejnowski, 1995) was conducted on a copy of the EEG dataset that had been high-pass filtered at 1 Hz, with ICA weights then copied and associated with the original dataset.

Artifact rejection was performed using a combination of automatic and manual procedures. Muscle activity, electrical noise, eye blinks, and other noise-associated components were first automatically labeled using the ICLabel classifier (Pion-Tonachini, 2019), with labels subsequently confirmed via visual inspection. Trials with eye movements were marked for rejection based on two measures. First,

we applied an absolute signal deviation threshold of 20 μV to the horizontal electrooculogram (HEOG) in the interval 0 to 800 ms after the cue. Second, we visually identified the ICA component reflecting horizontal eye movements, applying a subject-tailored absolute threshold to this signal to identify contaminated trials. The results from both approaches largely overlapped and trials identified as containing eye movements via either criteria were first individually inspected and then rejected from further analysis (2.28% of trials \pm 1.8% SD were discarded from either time window). Variance associated with artifactual and noise-associated ICA components, including residual variance stemming from eye movements, was subsequently removed from the data.

3.3.7 Time-frequency Analysis

Time-frequency representations were calculated using the `newtimef` function in the EEGLAB toolbox (Delorme & Makeig, 2004). This involved convolution of the EEG signal with a series of complex Morlet wavelets estimating 40 linear-spaced frequencies from 5.9 Hz to 40.0 Hz, with wavelets sampling from 3 cycles at the lowest frequency to 10.24 at the highest and increasing linearly across this range. We extracted the event-related power spectrum changes of two-hundred points across a time range beginning 714 ms before cue onset and ending 1714 ms after the cue. As we were interested in power differences between ipsilateral and contralateral hemifields, we initially calculated raw power values with no baseline correction.

To track the deployment of attention, we calculated the difference between contralateral and ipsilateral alpha power as observed at a set of symmetrically located channels (O1/O2, PO3/PO4, PO7/PO8), subsequently computing the difference in alpha power lateralization between horizontal and vertical rectangle conditions. The specific channels used were chosen based on previous research investigating alpha oscillations in the context of attentional selection (Kelly et al., 2006; Wang et al., 2019; Redding & Fiebelkorn, 2024). T-values were generated for each time-frequency point against a null hypothesis of zero and results were cluster-corrected to control family-wise error. Each point with t-value greater than 1.699 (df = 29, $p < 0.05$, one-sided) became part of a cluster with the neighboring values that also met this criterion. Cluster mass was used as the permutation statistic (Maris & Oostenveld, 2007). Cluster correction was applied to data observed from 300 ms (end of auditory cue) to 800 ms and from 5.9 to 40 Hz.

3.3.8 ERP Analysis

ERPs were calculated with a precue baseline of 100 ms. We isolated the ADAN by calculating the difference in ipsilateral and contralateral cue-elicited ERPs as observed at two sets of four frontal channels - F3/F4, F5/F6, FC3/FC4, FC5/FC6 (Störmer, Green, & McDonald, 2009; Seiss et al., 2007). The ADAN was defined as the mean difference between these clusters in a 300 - 500 ms time window after cue onset.

3.4 Results

3.4.1 Alpha Oscillations

If attention automatically spreads along object contours, or if attention has the effect of enhancing the entirety of an attended object, we reasoned that cue-elicited alpha laterality should emerge more strongly in the vertical rectangle condition than in the horizontal rectangle condition. The results supported this hypothesis. As illustrated in Figure 3.3, cluster-corrected contralateral-minus-ipsilateral alpha power at clusters of posterior channels was greater in the vertical rectangle condition than in the horizontal rectangle condition (one-tailed H_0 : true mean higher than 0, $p_{\text{cluster}} = 0.038$). This effect emerged around 500-600 ms after the onset of the audio spatial cue. Though we approached the experiment with an expectation of results in the alpha band, the cluster identified spanned alpha (8-14 Hz) and low beta bands (14 - 20 Hz; Sassenhagen & Draschkow, 2019). To test the specific involvement of alpha in object-based attention, we conducted an additional analysis, in which we band-pass filtered the experimental results to isolate the 8-14 Hz frequency band and repeated the analysis described above. This identified a significant cluster in the alpha frequency range that had much the same temporal characteristics of the alpha/beta cluster described above.

As can be noted in the last row of Figure 3.3A, there is a prominent conditional difference in lateralization that begins soon after onset of the auditory cue in the beta frequency band (~12 - 30 Hz). The analyses described above were limited to the interval following offset of the auditory cue, but in separate analysis of the 0 - 300 ms interval where the auditory cue occurred, we found a significant cluster in the beta

band. This effect emerges before the semantic content of the cue could be available, and its latency suggests it may reflect auditory sensory activity, and thus we do not consider it further (Gourévitch et al., 2020).

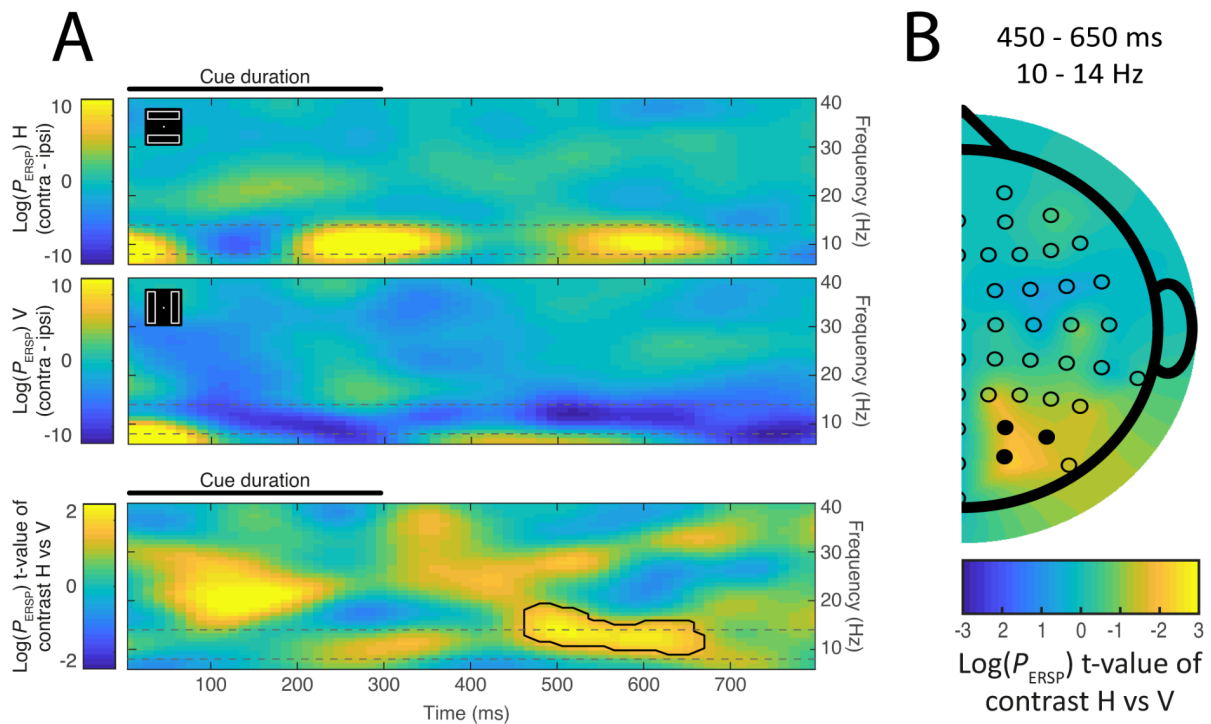


Figure 3.3 The effect of rectangle orientation on lateralized alpha amplitude. The first two rows of **Panel A** show the contralateral-minus-ipsilateral difference in time-frequency space during horizontal and vertical rectangle conditions respectively. Cool colors (blue) reflect reduced power contralateral to the cued location, while warm colors reflect greater power contralateral to the cued location. The third row illustrates the statistical contrast of data illustrated in the first two panels (horizontal-minus-vertical). Warm colors in this third row identify a combination of the relative increase in alpha laterality when the bars are vertical, with lower alpha power contralateral rather than ipsilateral to the cue location, and the relative decrease or reversal of this effect when the bars are horizontal. Results from cluster-level statistical analysis are identified; the emergence of a significant cluster (solid line) at approximately 500 - 600 ms captures this effect. This is consistent with the idea that task-irrelevant rectangle is attentionally selected, and thus that attention is more strongly lateralized when the rectangle is vertical rather than horizontal. Alpha was measured as mean signal at a set of lateral occipital electrodes (O1 / PO3 / PO7, O2 / PO4 / PO8). Time zero represents the onset of the auditory cue, which had duration of 300 ms. The alpha range (8-12 Hz) is identified by broken lines. For this illustration, but not statistical analyses, the time-frequency matrix was smoothed with a 2D Gaussian filter ($\sigma = 1$; filter size = 10x10). **Panel B** illustrates the scalp topography of the lateralized alpha effect illustrated in the bottom row of Panel A. This topographic map reflects the emergence of this contralateral-minus-ipsilateral difference as calculated at 8 - 12 Hz for symmetric pairs of electrodes across the scalp, with values for electrodes on the vertical midline set to zero (Hickey, Di Lollo, & McDonald, 2009). Topography reflects mean signal from 450 - 650 ms after cue onset. The MATLAB function *plot_topography* was used (Martínez-Cagigal 2024).

3.4.2 ADAN

The cue-elicited ERPs at anterior electrode locations for horizontal rectangle and vertical rectangle conditions are illustrated in Figure 3.4. The difference between ipsilateral and contralateral channels in the 300 - 500 ms latency range is significant from zero for vertical rectangle trials ($\mu = 0.308$, bootstrapped 95%, CI = [0.054 0.635], $d = 0.374$), but not for horizontal rectangle trials ($\mu = -0.075$, bootstrapped 95%, CI = [-0.293 0.160], $d = 0.117$). Notably, the contrast between contralateral and ipsilateral channels exhibits a pronounced increase for vertical rather than horizontal rectangles ($\mu = 0.383$, bootstrapped 95% CI = [0.004 0.854], $d = 0.315$). This difference is highlighted in the contralateral-minus-ipsilateral difference waves illustrated in Figure 3.4C.

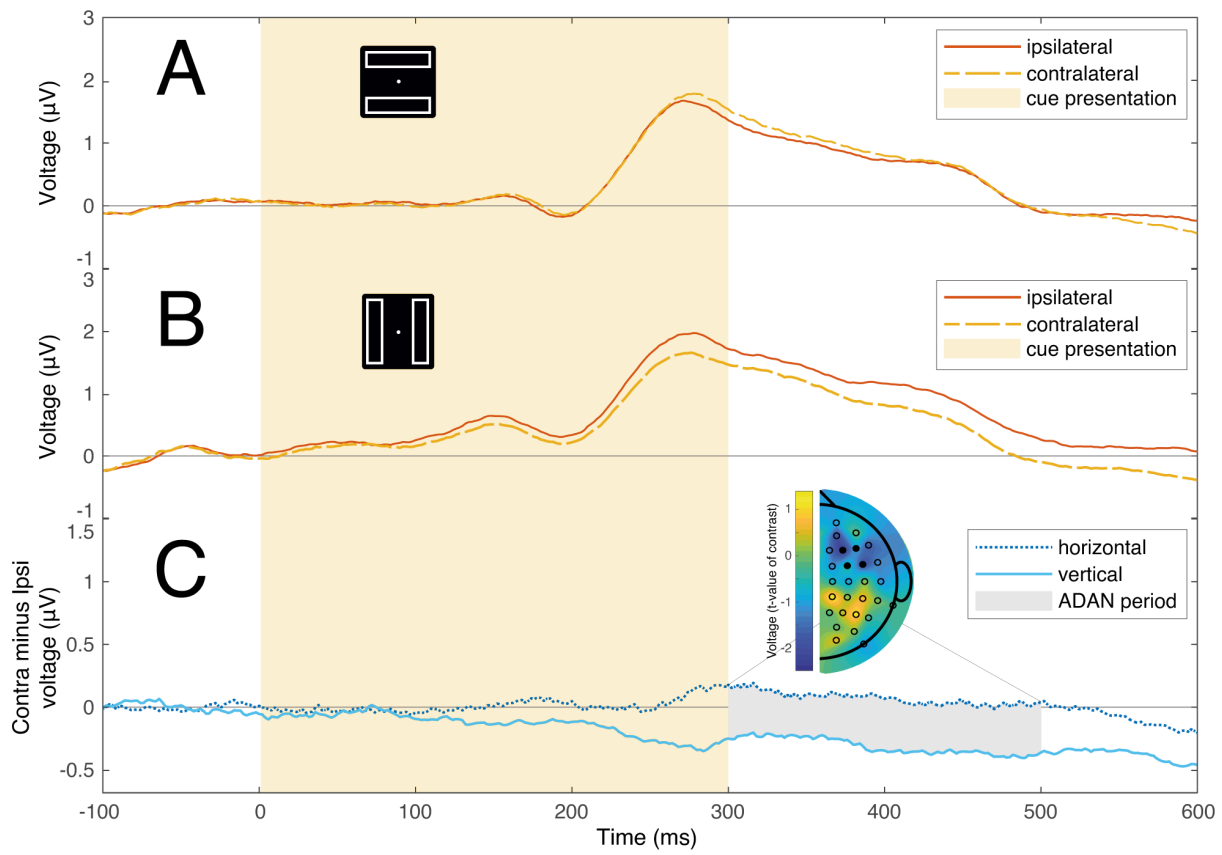


Figure 3.4 Anterior ERPs elicited by the cue stimulus. Time 0 represents the start of the auditory cue, which lasted for 300 ms (light yellow background). Panels A and B show ERPs measured at channels contralateral (yellow dashed line) and ipsilateral (red solid line) to the cue when the rectangles were horizontal or vertical. Panel C shows the difference waves between ipsilateral and contralateral ERPs in horizontal rectangle (dark blue dotted line) and vertical rectangle conditions (light blue solid line). Gray shading identified the typical interval of the ADAN (300-500ms). The topographical map shows the scalp distribution of t-values resulting from a test of the difference in lateralized signals illustrated in panels A and B (df = 29). As in Experiment 1, this topographic map reflects the contralateral-minus-ipsilateral difference as calculated for symmetric pairs of electrodes across the scalp, with values for electrodes on the vertical midline set to zero (Hickey, Di Lollo, & McDonald, 2009). The ERPs reflect mean signal at electrode clusters in the left (F3, F5, FC3, FC5) and right hemispheres (F4, F6, FC4, FC6), and the lateral location of these electrodes is identified in the topographical plot with filled black markers.

3.4.3 Behaviour

Target responses were reliably faster when the target location was validly cued, as compared to when the target appeared at any uncued location (591 vs. 731 ms, $t(29) = 8.99$, $p < .001$, $d = 1.344$). However, we did not find a significant difference in reaction time for invalidly cued targets when on the same-object versus a different-object (730 vs. 731 ms, $t(29) = 0.36$, $p = .721$, $d = 0.013$). Accuracy closely matched the reaction times results with reliably higher accuracies following valid trials compared to invalidly cued ones (96.8% vs 86.6%, $t(29) = 5.38$, $p < .001$, $d = 1.249$) and no significant difference between same- and different-object conditions (86.5% vs. 86.7%, $t(29) = 0.25$, $p = .807$, $d = 0.018$). This is in contrast to earlier results from Goldsmith and Yeari (2003), where similar endogenous auditory cues were also employed. Note, however, that characteristics of our design differed substantially from this earlier work. In line with Abrams and Law (2000), we employed longer cue-target intervals to give participants sufficient opportunity to interpret the endogenous cues and to deploy attention. Moreover, the cue-to-target delay varied across trials to allow for the deconvolution of cue-elicited and target-elicited brain activity. The long and uncertain cue-target interval (1200-1700 ms) may have reduced the participants' ability to maintain prioritisation of the entire cued object, which was manifest in the behavioural results (Lou, Lorist, & Pilz, 2023).

As described in the Introduction, recent results have shown that behavioural effects associated with object-based attention in the two-rectangle paradigm may be strongest for horizontally-oriented rectangles, sometimes only emerging in this condition (Al-Janabi & Greenberg, 2016; Chen & Cave, 2019). To test this in the current data, we separated invalidly cued trials as a function of rectangle orientation.

As illustrated in Figure 3.5, rectangle orientation had a dramatic effect on the behavioural results. A 2-way ANOVA with factors for rectangle orientation (horizontal vs. vertical) and cue-target relationship (same-object vs. different-object) identified an interaction between rectangle orientation and cue-target relationship ($F(1,29) = 35.350$, $p < .001$, $\eta_p^2 = .549$). Further analysis showed that while there was a speeding of invalid target reaction time in same-object trials in the horizontal-rectangle condition (horizontal-same vs. horizontal-different: 709 vs 759 ms, $t(29) = 5.04$, Bonferroni-corrected $p < .001$, $d = 0.340$), but that the reverse pattern emerged in the vertical-rectangle condition (vertical-same vs. vertical-different: 757 vs 709 ms, $t(29) = 5.71$, Bonferroni-corrected $p < .001$, $d = 0.305$). Separate analysis of validly cued trials identified no effect of rectangle orientation (632 vs. 630 ms, $t(29) = 0.745$, $p = .462$, $d = 0.020$). Accuracy showed a similar pattern. A 2-way ANOVA with factors for rectangle orientation and cue-target relationship identified only a significant interaction effect ($F(1,29) = 31.394$, $p < .001$, $\eta_p^2 = 0.520$). Pairwise comparison highlighted a significant difference in opposite directions: in the horizontal condition, accuracy was greater for same-objects trials are associated with higher accuracy than different-object trials (horizontal-same vs. horizontal-different: 92.0% vs 81.5%, $t(29) = 5.029$, Bonferroni-corrected $p < .001$, $d = 0.798$), but this effect reversed in the vertical condition (vertical-same vs. vertical-different: 80.6% vs 91.5% , $t(29) = -5.303$, Bonferroni-corrected $p < .001$, $d = 0.892$).

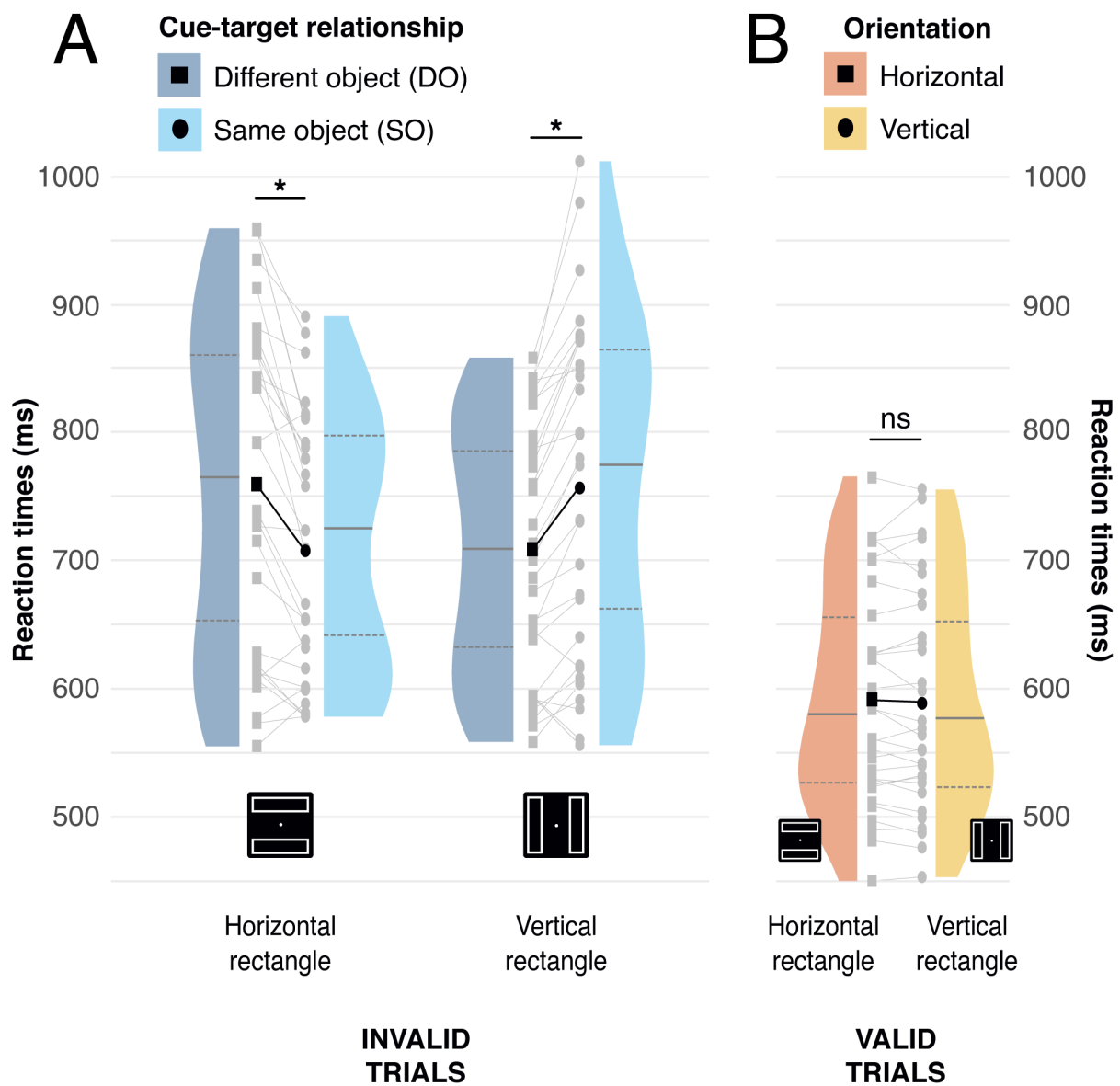


Figure 3.5 Reaction times (RT) from the behavioural task. Panel A shows Invalid Same and Different-object conditions as a function of rectangle orientation. Black squares and circles represent mean conditional reaction times for Invalid Same- and Different-object conditions, respectively. Darker and lighter blue represent invalid same- and different-object conditions, respectively. Panel B shows the valid cue condition. Black squares and circles represent mean conditional reaction times for Horizontal and Vertical conditions, respectively. Darker and lighter orange represent invalid Horizontal and Vertical conditions, respectively. In both panels, the distribution of participant mean performance is indicated for each condition, and per-participant results are illustrated in grey. The median, first, and third quartile are indicated for each distribution, and * indicate statistical significance ($\alpha = .05$).

3.5 Discussion

A substantial body of research suggests that selective attention is influenced by the presence of visual objects. Specifically, when attention is deployed to one location on an object, other locations on the same item appear to be prioritized. However, recent years have seen an accumulation of findings and ideas that are inconsistent or hard to reconcile with this framework. First, behavioural evidence of object prioritisation is stronger when objects span the visual hemifields (eg. horizontal rectangle conditions), and in some cases only emerges in this scenario (Al-Janabi & Greenberg, 2016; Chen & Cave, 2019; Francis & Thunnell, 2022; Pilz et al., 2012). This has led to the suggestion that putative object-based attention may in fact result from the presence of independent pools of attention resources in each cerebral hemisphere (Luck et al., 1989), which facilitates shifts of attention across the vertical meridian (Barnas & Greenberg, 2016, 2024). By this, evidence of object prioritisation may be confounded with effects on the deployment of attention linked to the independence of cerebral hemispheres.

Second, manipulations of object status have concomitant and often unacknowledged effects on low-level stimuli characteristics in paradigms commonly employed to investigate object-based attention (Rosenholtz, 2024). When the cue and target appear on different objects in the two-rectangle task, for example, the space between these locations contain contours and other visual clutter that is not present when cue and target appear on the same object. This may create a small cost in perceptual resolution of the target, much as is observed in studies of visual

crowding (Whitney & Levi, 2011; Chen, Cave, Basu, Suresh, & Wiltshire, 2020). By this, evidence of object prioritisation may be confounded with effects of perceptual clutter and crowding on target resolution.

In this context, the current study used EEG to identify if task-irrelevant objects impact the deployment of attention in the interval immediately following a directional cue. Though EEG has been used to study object-based attention before, existing studies have tended to concentrate on how object status modulates the sensory processing of targets. This type of work has shown that invalidly-cued targets that appear on cued objects elicit a larger posterior N1 ERP component (Martínez et al., 2006), much as is observed when targets are validly cued (Mangun & Hillyard, 1991; Hopfinger & Mangun, 2001), though the effect created by object prioritisation appears to have a more posterior source (He, Fan, Zhou, & Chen, 2004; He, Humphreys, Fan, Chen, & Han, 2008).

In contrast to this literature, here we focus on EEG effects in the interval prior to appearance of the target. There are two prominent patterns in our results. First, we see that participants use our endogenous cue to deploy spatial attention. This is evident in the cue-elicited emergence of posterior EEG alpha lateralization and in emergence of the anterior ADAN ERP component, and in a significant effect of cue validity on behavioural responses to the target. Second, and most importantly, we see that manipulation of the orientation of visual objects in our task led to significant changes in the hemispheric pattern of alpha and ADAN. We found greater lateralization of both alpha and the ADAN when a cued rectangle was oriented vertically, and thus appeared entirely within one visual hemifield. In contrast, we found a reduction in the laterality of alpha and the ADAN when the cued rectangle

was oriented horizontally, and therefore spanned the vertical meridian of the visual field. This pattern is in line with the notion that attention is more strongly lateralized when the cued object appears entirely in one visual hemifield.

Because we investigate the deployment of attention in the anticipatory period between cued and targets, our results allow us to conclude that object-based attention is a real psychological and neurological phenomenon. However, this does not mean that concerns regarding the confounding impact of hemifield anisotropies or visual crowding on behavioural indices of object-based attention are misplaced. First, it is not clear that the effect of irrelevant objects on attention identified here is the cause of behavioural effects reported in earlier literature. It is possible that cue-elicited deployment of attention is sensitive to the definition of irrelevant objects, but that this has minimal subsequent impact on behavioural responses to target stimuli, with putative behavioural evidence of object-based attention entirely a product of confounds like hemifield anisotropy and visual crowding. Second, our behavioural results do not show the same-object benefit that is the hallmark of object-based attention. Instead, we find strong evidence of hemifield anisotropy: when the rectangles are oriented horizontally, participants are quicker to respond to targets appearing on the cued object, but when the rectangles are oriented vertically, they are quicker to respond to targets appearing on the uncued object. The deployment of attention across the vertical meridian appears to be facilitated, reproducing an effect observed by Pilz, Roggeveen, Creighton, Bennett, and Sekuler (2012, Exp 2).

Why do our EEG results show that objects guide attention, but our behavioural results show no evidence of this influence? One possibility is that our experimental

design introduces too much time between cue and target. Our design builds from that employed by Goldsmith and Yeari (2003), where an auditory cue created object prioritisation effects in behaviour, but with a longer cue-target delay. This allowed us to isolate the electrophysiological response to the cue without a confounding influence of the response to the target, but long cue-target intervals are known to reduce or eliminate effects of object-based attention on behaviour (Lou, Lorist, & Pilz, 2023). However, this explanation requires an important caveat. Behavioural results from Pilz et al (2012, Exp. 2) are very similar those reported here - with no evidence of object prioritisation, but strong hemifield anisotropy - though that study employed a two-rectangle task with standard, short-duration cue-target intervals.

If long cue-target duration plays a role in reducing the effect of object prioritisation on behaviour, this suggests that participants may have strategically disengaged from the cued rectangle when they were given sufficient time to do so, and this raises a broader issue regarding the role of strategy in object prioritisation. The notion that object prioritisation is necessary and automatic has been challenged by results suggesting a strategic basis for the effect (Shomstein, 2012; Shomstein & Yantis, 2002; Shomstein et al., 2013). For example, object prioritisation in the two-rectangle paradigm disappears when the target location is known in advance (Drummond & Shomstein, 2010) or when other strategies have greater economic utility (Shomstein & Johnson, 2013; though see Grignolio, Acunzo, & Hickey, 2024 and Diao et al., 2024). Our results from the ADAN ERP component are relevant in this context. In contrast to lateral alpha, which is thought to reflect low-level, mechanistic effects of inhibitory gating or gain in sensory cortex (Jensen & Mazaheri, 2010; Jensen, 2024), the ADAN appears to reflect anterior brain structures - likely including the lateral frontal eye fields - that are involved in the strategic control of

attention (Eimer, van Velzen, & Forster, 2003; Hopf & Mangun, 2000). We find that object prioritisation is expressed in ADAN lateralization, and this suggests that such prioritisation is represented in high-level, anterior cortical structures responsible for the strategic control of selection. While far from conclusive, the emergence of object prioritisation in the ADAN adds to accumulating evidence suggesting that object-based attention may not be an automatic, low-level effect instantiated in sensory cortex, but instead reflect a strategic approach to task completion (Shomstein, 2012).

Our results are consistent with two potential models of object-based attention. One possibility is that participants deploy attention to the cued spatial location to find that this location contains object contours. Attention then spreads along these contours, possibly to support the definition of the visual object (Duncan, 1994; Ekman, Roelfsema, & De Lange, 2022). The alternative is that objects play a more fundamental role in attentional prioritisation. By this, objects are defined in the visual system prior to the deployment of attention, and attention is deployed in this representational space (Scholl, 2001). Though the current results do not allow us to differentiate between these possibilities, recent results from fMRI provide compelling evidence of attentional spreading. Ekman, Roelfsema, and de Lange (2020) have used advanced techniques to map the effect of a spatial cue on the representation of an underlying object in V1, showing a spread of activity from populations of neurons representing the initially selected region of the object to others representing the rest of the object. Similarly, Cohen and Tong (2015) have used multivariate pattern analysis to show that the neural signal carried more information about characteristics of an irrelevant object when attention was cued to a location on that object.

To conclude, we revealed here that selective attention is sensitive to the definition of task-irrelevant visual objects. We directly index this effect of objects on attention using EEG, finding that lateralized alpha and the ADAN component of the ERP vary as a function of the orientation of irrelevant rectangle stimuli. As we index the deployment of attention in response to the cue, before the target appears, our results are insensitive to potential confounds impacting the interpretation of behavioural studies of object-based attention.

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CHAPTER 4

ATTENTIONAL MODULATION OF OBJECTS' SEMANTIC CATEGORISATION IN THE HUMAN BRAIN

4.1 Abstract

Humans face the complexity of the world around them by selecting the sources of relevant information. It is assumed that selective attention has the ultimate goal of allowing the abstraction and manipulation of conceptual information from the percepts to support cognition. However, neuroscientific research has largely concentrated on understanding the mechanisms that govern attentional control or the ways attention modulates sensory and perceptual processes. In contrast, much less attention has been given to its role in shaping the extraction of higher-order information. This study employs machine learning techniques on simultaneous EEG and MRI recordings to identify the neural networks involved in processing conceptual information influenced by attention. The results show that trial-specific alpha oscillation lateralisation—a neural signature of selective attention—predicts the encoding of target category information in the orbitofrontal cortex (OFC). These findings suggest that the mapping of choices in the OFC is linked to the attention levels. Furthermore, alpha lateralisation towards the target correlates with category information in frontal and temporal regions associated with working memory network. Here we interpret this association as a signature of an efficient suppression of distractor-related information when attention levels to the target are higher.

4.2 Introduction

The ability to select the stimuli in our environment is fundamental for adaptive behaviour, yet the scope of this process extends beyond sensory processing. Humans often need to extract and manipulate conceptual representations from objects and attention is assumed to play a fundamental role in the activation and maintenance of such representations. While research has focused on the sensory and perceptual changes following spatial or feature prioritisation of stimuli, emerging literature suggests that attention influences activation of conceptual representations (Jeong & Xu, 2016; Seidl et al., 2012; Hickey & Peelen, 2015; Barbaro et al., 2018).

Research has shown that semantic information can guide attentional selection, with priming effects revealing how activated conceptual knowledge can bias perception (e.g., McNamara, 2005; Warren & Morton, 1982; Dell'Acqua & Grainger, 1999). However, less is known about the reverse relationship—how attentional engagement affects the processing of conceptual information. The neural basis of this process remains poorly understood, particularly in terms of how attentional levels influence conceptual representations in the brain.

Previous research has linked the behavioural relevance of a visual stimuli to the strength of their encoding in ventral and dorsal visual stream areas (Jeong & Xu, 2016; Seidl et al., 2012; Hickey & Peelen, 2015; Barbaro et al., 2018), but it remains debated whether these effects are driven by semantic properties or by low-level perceptual features (Bracci & Op de Beeck, 2016; Watson et al., 2014; Rice et al., 2014). The evidence for cross-modal semantic abstraction—where shared semantic representations emerge across visual and verbal inputs—suggests that this abstraction occurs in higher-order regions of the temporal, parietal, and frontal

cortices (Fairhall & Caramazza, 2013; Devereux et al., 2013; Acunzo et al., 2022). These areas may be a target for investigating how attention levels may relate to the strength of objects' semantic representations. Here we present a study that uses a novel methodological approach to address this question.

Using a combination of electroencephalography (EEG) and functional magnetic resonance imaging (fMRI), we measure attentional engagement via alpha lateralisation while simultaneously tracking semantic representations through multivariate pattern analysis (MVPA) of fMRI activity. By correlating trial-by-trial levels of alpha lateralisation with the fidelity of semantic representations, this approach enables a direct examination of how attention correlates with the activation of conceptual information in the brain. Moreover, by using a searchlight approach to identify the neural regions where the link between the two measures is stronger, this work sheds light on the specific areas that bridge attention and semantic cognition.

Central to this study is the role of alpha oscillations, which are well established as a neural marker of attentional selection (Foster et al., 2017; Worden et al., 2000; Jensen & Mazaheri, 2010). Pre- and post-stimulus alpha oscillations lateralise following the lateralization of attention, with increased power ipsilateral to the attended target and decreased power contralateral to it (Diepen et al., 2016). While it is currently debated whether this lateralisation reflects the suppression of distractors (Jensen, 2024; Bonnefond & Jensen, 2024) or the enhancement of the target signal (Foster & Awh, 2019), specific designs have been developed to distinguish target selection and active mechanisms of distractor suppression (Wöstmann et al., 2019; Hickey et al., 2009). Using such a design, we assessed how attention to target objects modulates their conceptual representations. Furthermore, we were able to

investigate the specific effect of attention to the target objects on the representation of the distractor stimuli.

In summary, this study reveals that attentional engagement modulates the neural representation of both target and distractor, with fluctuations in attention to target predicting the strength of semantic encoding for each. By integrating EEG and fMRI, we identified brain regions where attention and conceptual processing converge, highlighting how attention not only enhances target representations while also influencing distractor processing. This work provides both a methodological and theoretical foundation for understanding how attention shapes the dynamic balance between target prioritisation and distractor suppression in higher-order cognition.

4.3 Methods

4.3.1 Participants

Thirty-nine individuals from the University of Birmingham community participated in this study. All participants provided written informed consent, confirmed having normal or corrected-to-normal vision, and reported no history of neurological or psychiatric conditions. Of these, eight participants were excluded for the following reasons: two due to excessive eye movement artefacts in the EEG (>40% of trials), four due to incomplete datasets caused by technical issues or equipment failure, and two due to low task accuracy (below 70%). The final sample consisted of 31 participants (mean age = 23.2, SD = 3.8; 19 female; 3 left-handed). The study lasted approximately four hours, encompassing EEG preparation, MRI screening, task

practice, experimental trials, breaks, and debriefing. Participants received monetary compensation of £15 per hour for their time. Ethical approval was obtained from the University of Birmingham STEM ethics committee and the CHBH Health and Safety committee.

4.3.2 Experimental task

Participants engaged in a visual search task and a repetition detection task presented in alternating blocks, totalling four blocks of 128 trials each. The order of blocks was counterbalanced (task illustrated in Figure 4.1B). The visual search task, which accounted for approximately 75% of the total experiment time, is the central focus of this paper.

In each trial, participants identified the semantic category of a target object displayed in a cued location while disregarding a distractor presented in an uncued location. Trials commenced with a black fixation cross on a white background, presented for 1550–1850 ms, along with four grey circles (4.2° visual angle) arranged on the horizontal and vertical midlines, each positioned 5.2° from the centre. The fixation cross was then briefly replaced by the letter ‘G’ or ‘R’ for 1350–1650 ms, serving as a cue for the red or green circle that would subsequently contain the target object in the search display. The search array, displayed for 600 ms, featured two intact object images appearing within the green and red circles, alongside two scrambled images located within the two grey circles. The intact objects belonged to one of four categories (food, tools, vehicles, or animals), with images drawn from a pool of 30 exemplars per category sourced from the BOSS

database (Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010) or other publicly accessible online repositories. Each image was randomly selected 30 times without replacement before the selection process was reset. The scrambled images within the grey circles were unrecognisable versions of the 120 objects in the image set, created using the distortion method outlined by Stojanoski and Cusack (2014) (maximum distortion: 160, nsteps: 4, iterations: 9) and selected through a similar procedure (examples of intact and scrambled stimuli are provided in Figure 4.1A). The next trial began either immediately after the participant's response or after a fixed interval of 1800 ms.

During the experiment, participants were required to classify the object category displayed within the cued circle using their right hand. Two of the four object categories were linked to a response using the index finger, while the other two were associated with a response using the middle finger. The specific category-to-finger assignments were counterbalanced across participants. Responses were recorded using an MRI-compatible button box. To ensure task integrity, target and distractor objects were always mapped to opposing responses.

Before scanning, participants received verbal instructions and completed a practice session until they achieved a performance level of approximately 80% accuracy, which was typically achieved within a single training block. Each experimental block contained 128 trials with varying combinations of cue colour, target and distractor categories, and their spatial arrangement. Visual stimuli were projected via a ProPiXX projector operating at 100 Hz and viewed through a mirror attached to the scanner head coil. The experimental tasks were executed using the PsychToolbox 3 (Brainard, 1997) within Matlab 2017a.

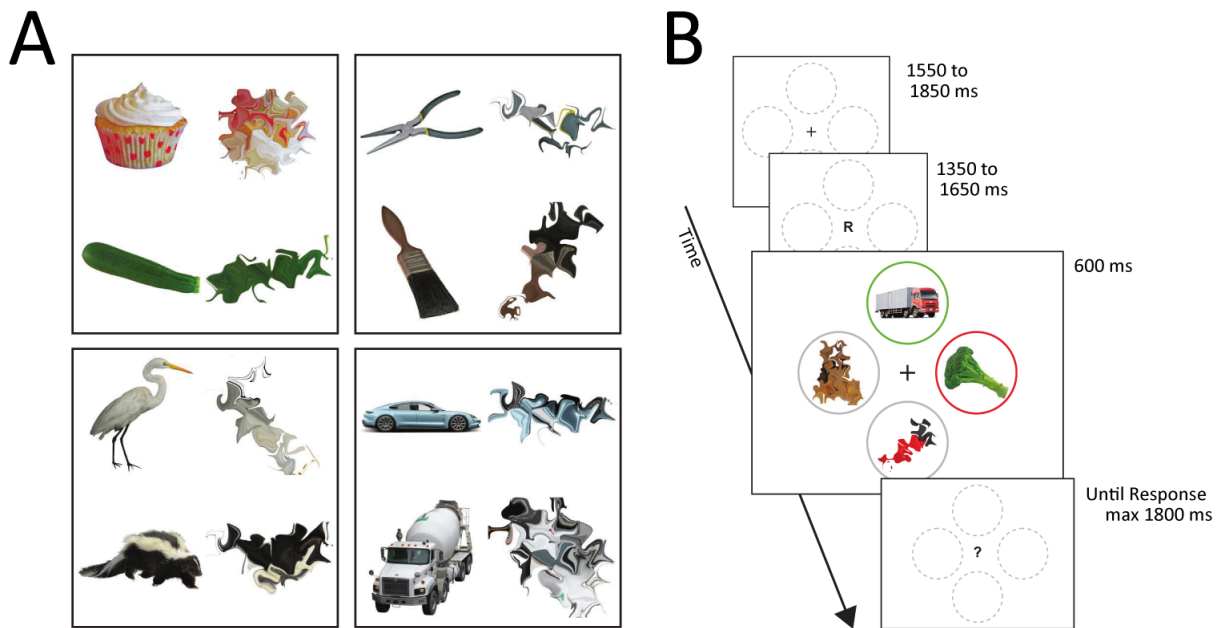


Figure 4.1 Experimental task. **Panel A** shows complete, recognizable examples of object categories and morphed, unrecognisable versions of the same images. The stimuli set was composed of 40 complete images in each of the 4 categories. **Panel B** shows the experimental procedure. The target was cued by a central letter, either 'R' or 'G' to denote red or green. Participants had to report which category appeared in the cued circle via right hand button response. Two categories were associated with index finger response and two with middle finger response, with response mapping counterbalanced across participants.

4.3.3 Data acquisition and preprocessing

MRI

Whole-brain imaging was conducted using a 3T Siemens Prisma MRI scanner fitted with a 64-channel head coil. Functional images were acquired using an echo planar imaging (EPI) sequence, capturing 57 axial slices with a voxel resolution of 84 x 84, a field-of-view (FOV) of 210 mm x 210 mm, and a slice thickness of 2.5 mm without any inter-slice gap. Imaging parameters included a repetition time (TR) of 1.5 seconds, an echo time (TE) of 35 ms, a flip angle (FA) of 71°, and a multi-band acceleration factor of 3. Structural images were collected using a T1-weighted

MPRAGE sequence, which produced 208 axial slices at a voxel resolution of 257 x 257, an FOV of 256 mm x 256 mm, and a slice thickness of 1 mm with no gap. The T1-weighted sequence had a TR of 2 seconds, a TE of 2.03 ms, and an FA of 8°. To correct for image distortions, a field map was obtained via a double-echo sequence. This field map included 36 axial slices at a voxel resolution of 64 x 64, an FOV of 192 mm x 192 mm, a slice thickness of 3.75 mm without gaps, a TR of 400 ms, and two echo times (TE1 = 4.92 ms, TE2 = 7.38 ms) with an FA of 45°. Additionally, a four-lead vectorcardiogram (VCG) was recorded inside the scanner using standard chest electrodes. The VCG was synchronised with the MRI signal and sampled at 5 kHz.

Preprocessing of MRI images included corrections for head motion, field map inhomogeneities, and slice acquisition timing (referenced to the middle slice). Following these corrections, the images were normalised to Montreal Neurological Institute (MNI) space, resampled to an isotropic voxel size of 2 mm, and smoothed using an isotropic Gaussian kernel with a full width at half maximum (FWHM) of 6 mm. The fMRI time-series data were processed using the GLMsingle toolbox (Prince, Charest, Kurzawski, Pyle, Tarr, & Kay, 2022), which estimates single-trial voxel-wise beta values. The toolbox achieves this by fitting hemodynamic kernel functions, generating nuisance regressors, and optimising a ridge regularisation shrinkage factor for each voxel. To ensure precise alignment of the EPI volumes with visual stimulus onset, the EPI time series was up-sampled to 6.7 Hz (150 ms per image) prior to linear modelling. This interpolation was implemented using a shape-preserving piecewise cubic method via the `tseriesinterp.m` function from the `knkutils` toolbox (<https://github.com/cvnlab/knkutils>). The analysis was limited to voxels outside the brainstem, ventricles, and cerebellum.

EEG

EEG data were recorded within the scanner using sintered Ag/AgCl electrodes connected to a Brain Products BrainAmp MR amplifier. The EEG signal was captured from 63 electrodes positioned on a BrainCap MRI-compatible elastic cap, arranged according to the extended 10/20 system. Additionally, a single-lead electrocardiogram (ECG) was recorded using an electrode placed on the participant's back, approximately 10 cm below the top of the shoulder and 5 cm to the left of the spine. All data were acquired at a sampling rate of 5 kHz, synchronised with the MRI clock signal.

EEG preprocessing started with the removal of gradient artefacts using BrainVision Analyzer 2 (v2.2). Gradient triggers from the scanner served as temporal markers for the artefact waveforms, and artefacts were corrected via template subtraction. This subtraction employed a sliding average of 21 repetition time (TR) intervals, followed by baseline correction. The EEG data were subsequently downsampled to 250 Hz and subjected to correction for cardioballistic (CB) artefacts. The CB correction process involved semi-automatic detection of heartbeat peaks, using the available heartbeat signals. For the 124 experimental blocks analysed (4 blocks for each of the 31 participants), the source of heartbeat signals varied due to differences in signal quality and availability. Specifically, VCG data were used for correction in 52 blocks, ECG signals in 48 blocks, and, for the remaining 24 blocks, a heartbeat component was extracted directly from the EEG signal using independent component analysis (ICA). A running average of 21 heartbeat intervals was

employed to generate a correction template, while the delay between the heartbeat and the resulting artefact was estimated automatically over a 40-second window.

The EEG signal was digitally filtered using symmetric Hamming windowed finite-impulse response (FIR) filters. High-pass filtering was applied at 0.05 Hz (-6 dB at 0.025 Hz), while low-pass filtering was set at 45 Hz (-6 dB at 50.6 Hz). The signal was re-referenced to the average of all encephalic channels and baseline-corrected using the 200 ms period preceding stimulus onset. Noisy channels were visually inspected and corrected through spherical spline interpolation.

Independent component analysis (ICA) was conducted on combined EEG and electrooculogram (EOG) data to identify components associated with eye movement artefacts. Trials containing eye movements within the 500 ms window following stimulus onset were excluded from further analysis, and the ICA components corresponding to ocular artefacts were subsequently removed from the EEG data.

On average, 0.29 EEG channels were interpolated, and 2.0 independent components were removed per participant. On average, 27 trials (SD = 26) were excluded from analysis due to excessive noise or ocular artefacts, and 52 incorrect trials (SD = 36) were also discarded. This left approximately 433 clean trials (SD = 41) per participant available for further analysis.

4.3.4 Analyses

EEG alpha lateralization

To obtain a single representative value for each trial, it was essential to maximise the signal-to-noise ratio (SNR). Given our aim to correlate the EEG data with fMRI data, which has inherently low temporal resolution, high temporal precision in the EEG data was not a priority. Therefore, we chose the multitaper method over the Morlet wavelet approach, as the former provides a better SNR at the cost of temporal resolution (Cohen, 2014), a trade-off that was acceptable for our purposes.

Time-frequency representations (TFRs) were then calculated using the `tfr_multitaper` function in the MNE-Python library. This approach involved applying the multitaper spectral estimation method to the EEG signal, estimating 30 linear-spaced frequencies from 2 Hz to 31 Hz. The number of cycles for each frequency was set to half the frequency value, ranging from 1 cycle at the lowest frequency to 15.5 cycles at the highest, thereby balancing temporal and spectral resolution. The analysis covered 750 time points, spanning from 1000 ms before stimulus onset to 1996 ms after. The TFRs were computed on a trial-by-trial basis without averaging, and the raw power values were used, with no baseline correction applied.

Time-frequency analysis was conducted to quantify alpha lateralization. Specifically, we calculated the difference in power between ipsilateral and contralateral hemispheres at a set of symmetrically located electrodes (O2/O1, PO4/PO3, PO8/PO7). To minimise the impact of the single images presented on the overall alpha level, we normalised these difference values by the sum of ipsilateral

and contralateral power observed at the corresponding channels, obtaining a lateralization index. This normalisation helps ensure that the our index reflects the lateralization of alpha power rather than fluctuations in overall alpha levels induced by other variables like a general state (e.g. arousal) or the perceptual differences in individual stimuli. The specific electrode sites were selected based on their established relevance in previous studies that have explored alpha oscillations in the context of attentional selection (e.g., Redding & Fiebelkorn, 2024; Kelly et al., 2006; Flevaris et al., 2011).

To identify reliable clusters of lateralization in the alpha band, we applied a cluster-based permutation test (Maris & Oostenveld, 2007) to the trial-averaged data. The analysis was constrained to the frequency range of 8 to 12 Hz and the time window of 0 to 800 ms. For each time-frequency point, a t-value was calculated based on the corresponding power value using a one-sample t-test, where the alternative hypothesis was that the average power value was greater than 0. T-values exceeding 1.697 ($df = 30$, $p < 0.05$, one-sided) were grouped into clusters with neighbouring t-values that met the same criterion. Cluster mass was used as the measure in the cluster permutation procedure to control for family-wise error.

The identified cluster was then used to define the time-frequency window from which the alpha lateralization index was extracted for each trial. This index was subsequently used for correlation with the information index derived from the fMRI data.

Measure of semantic category information from fMRI classification

MRI data were classified using machine-learning methods to label the target or distractor category for each trial, employing linear discriminant analysis (LDA) with cross-validation. Trial-wise classification was performed without prior averaging of trials. Each feature in the training set was z-scored across observations to standardise the data. Approximately 2.1×10^5 searchlight spheres were defined, with sphere boundaries adjusted according to brain space constraints, resulting in an average sphere volume of 111.8 voxels.

Two cross-validation schemes were implemented for classification. The first used a 4-fold cross-validation procedure to produce the results depicted in Figure 4.3. The second scheme employed a 1140-fold cross-validation approach to examine the relationship between MRI classification performance and alpha lateralisation. Consistent classification results were observed across both validation approaches.

Statistical analysis of MRI classification accuracy was conducted using t-tests to determine whether the classification performance within each searchlight sphere exceeded chance levels. To control for multiple comparisons, a cluster-based correction was applied using a cluster-defining threshold of $p < 0.005$, with cluster significance set at $p < 0.05$ (Maris & Oostenveld, 2007). Differences in classification accuracy for target and distractor categories were assessed using a similar approach, with t-tests directly contrasting the classification performance of the two categories.

Coupling Variance in Alpha Lateralization to MRI-Derived Semantic Category Information

As outlined in Results Section 4.4.3 and illustrated in Figure 4.2, the relationship between alpha lateralisation and MRI-derived target category information was assessed using an iterative resampling procedure. This approach yielded 1140 value pairs for each participant, each pair consisting of mean alpha lateralisation and mean classification accuracy. The analysis was then extended to every voxel in the brain using a searchlight procedure.

Statistical evaluation of the correlation values was performed using one-tailed t-tests, testing against a null hypothesis of zero correlation. To control for multiple comparisons, a cluster-based correction was applied with a cluster-defining threshold of $p < 0.005$ and cluster significance set at $p < 0.05$. Additionally, Bonferroni correction was applied to account for the testing of both positive and negative clusters.

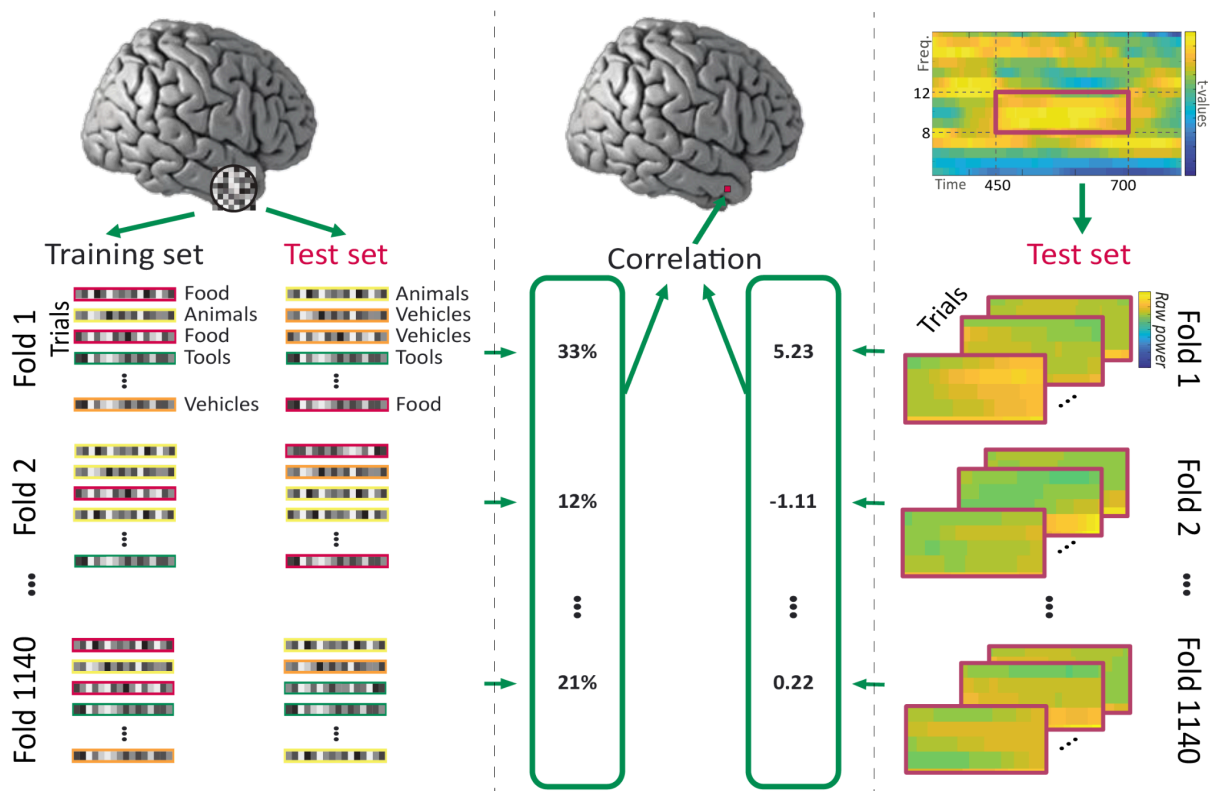


Figure 4.2 Trials were repeatedly divided into training and test sets, ensuring that the same trials were present in both the fMRI and EEG test sets. This alignment allowed for the concurrent examination of brain activity across the two imaging modalities. For each test set, two dependent measures were calculated: classification accuracy from fMRI data and the alpha lateralisation index from EEG data (as illustrated at the centre of the figure). The alpha lateralisation index was computed within the time-frequency window defined in the EEG analysis (see Section 4.4.2 for details). To establish a link between the EEG and fMRI results, we computed the correlation between fMRI classification accuracy and the alpha lateralisation index across 1140 sampling iterations. This correlation was calculated separately for each searchlight sphere, enabling the identification of spatially localised correspondences between neural oscillatory activity and stimulus-specific information in the brain.

4.4 Results

Participants ($n = 44$, $n = 31$) were instructed to complete the task while maintaining stable eye position. Their objective was to identify the category of a target object (Figure 4.1A) that appeared at a cued location (Figure 4.1B) and report it via button press, while disregarding non-target items, which included a set of visually degraded objects and a single recognisable distractor. The objects were

drawn from a pool of images that exhibited visual heterogeneity within each category. Participants performed the task with high speed (mean response time = 1088 ms, SD = 240 ms) and accuracy (mean = 89.9%, SD = 7.0%).

To evaluate the quality of attentional engagement, we examined the lateralisation of alpha oscillations, a widely recognised neural marker of attentional allocation (Kelly, Lalor, Reilly, & Foxe, 2006; Thut, Nietzel, Brandt, & Pascual-Leone, 2006). Alpha lateralisation is characterised by a reduction in alpha power over the hemisphere contralateral to the attended location, reflecting either the inhibition of unattended regions (Worden, Foxe, Wang, & Simpson, 2000; Klimesch, 2012) or the facilitation of processing in attended areas (Foster & Awh, 2019; Wöstmann et al., 2019). This lateralisation effect becomes more pronounced as attentional demands increase, making it a robust indicator of the intensity and spatial specificity of attentional processing (Sauseng et al., 2005; Rihs, Michel, & Thut, 2007). Notably, post-stimulus alpha oscillations have been linked to reactive attentional selection mechanisms (van Diepen et al., 2016).

To track the emergence of category-specific information in the brain, we used linear discriminant analysis (LDA) to classify neuroimaging data. Classification models were trained to predict the category of the target or distractor based on normalised patterns of post-stimulus brain activity. The models were tested on held-out data to compute classification accuracy, providing an index of how well brain activity patterns reflected the categorical information of the visual stimuli.

4.4.1 Measuring category information in unimodal fMRI

Participants performed the task while EEG and fMRI data were simultaneously recorded (Figure 4.2). The analysis began by examining category-specific information in the unimodal fMRI signal. Single-trial fMRI responses were estimated using the GLMsingle toolbox (Prince et al., 2022), and spatial searchlight analysis combined with linear discriminant analysis (LDA) classification was used to identify category information in brain space. In this approach, a spherical region is defined around each voxel, and classification is performed using the activity patterns of the voxels within that sphere (Kriegeskorte et al., 2006). Searchlight spheres had a diameter of 7 voxels (14 mm), and classification was conducted using a 4-fold cross-validation procedure.

This analysis revealed a set of overlapping brain regions containing information about both the target and the distractor, as well as a smaller set of regions containing information specific to only one of the two objects (Figure 4.3A). Brain areas encoding information for both target and distractor included the ventral visual cortex, inferior and superior parietal lobules (IPL/SPL), as well as premotor, motor, and somatosensory cortices. Information specific to the target was also observed in the left inferior frontal gyrus (IFG), bilateral orbitofrontal cortex (OFC), and the precuneus/cingulate cortex. Distractor information extended from the IPL into the left temporal-parietal junction (TPJ). Statistical analysis revealed that bilateral lateral occipital cortex (LOC), IPL/SPL, left IFG, left OFC, posterior cingulate cortex, and the left basal ganglia (BG) consistently contained more information about the target than the distractor (Figure 4.3B). No brain region was found to contain significantly more information about the distractor than the target.

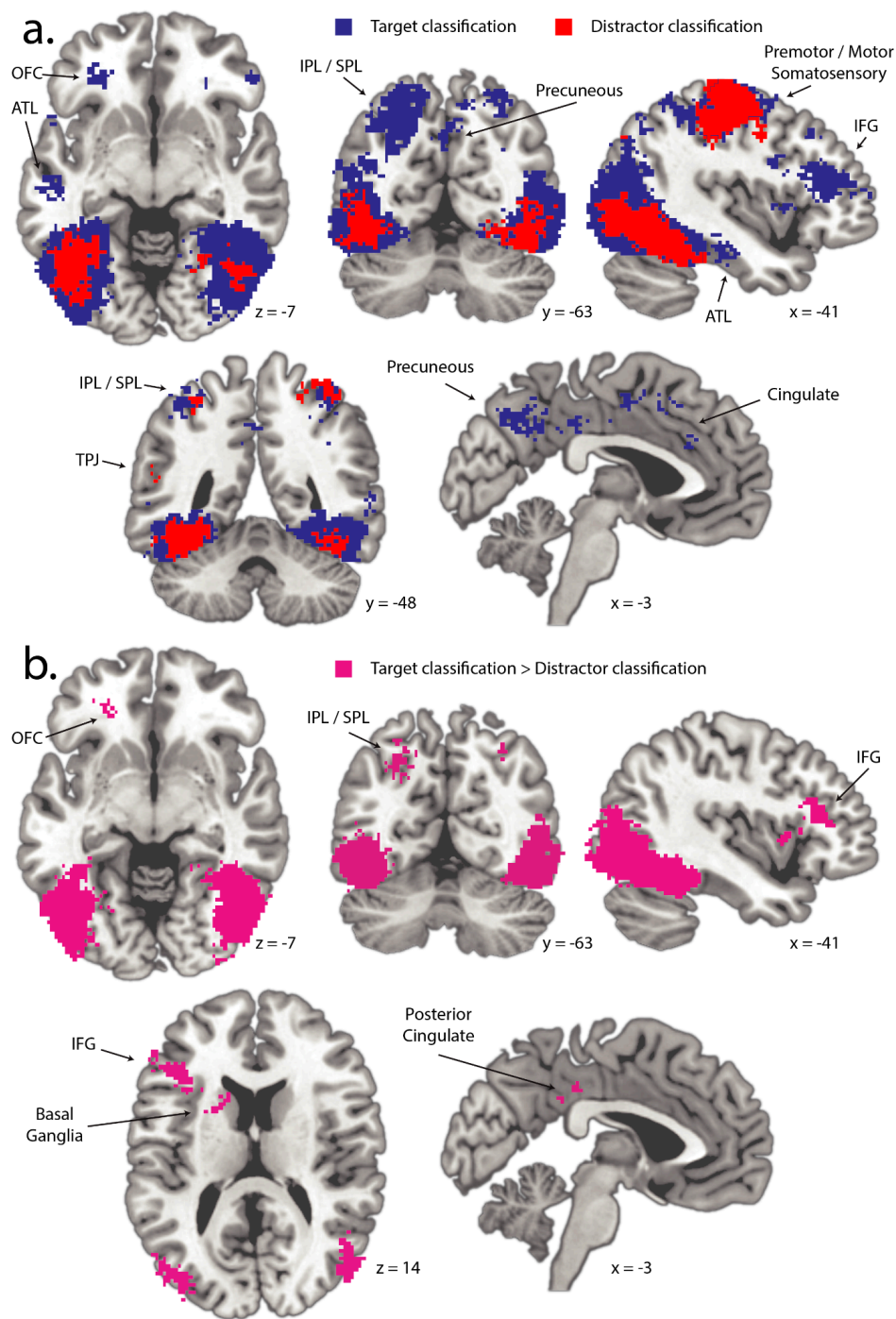


Figure 4.3 – MRI Classification Results. (Panel A) The searchlight analysis reveals the spatial distribution of target and distractor information, with distinct activation patterns observed in the occipital and posterior temporal lobes, which are integral to the ventral visual stream. Panel B shows the voxels part of clusters that convey more information about the target relative to the distractor. Notably, the most prominent clusters are situated in the ventral visual cortex, with additional clusters indicated at other locations. Abbreviations used are OFC – orbitofrontal cortex; IPL – inferior parietal lobe; SPL – superior parietal lobe; IFG – inferior frontal gyrus; TPJ – temporoparietal junction. The left hemisphere is shown on the left side of this figure and in all subsequent figures.

4.4.2 Measuring visuo-spatial attentional index from unimodal EEG

As shown in Figure 4.4, consistently with previous research on alpha lateralization associated with attentional mechanisms following stimulus presentation, a significant cluster of brain activity lateralization in the alpha band was identified between 450 and 700 ms after stimulus onset ($p_{\text{cluster}} = .0473$) consistently with previous findings (Diepen et al, 2016). An alpha lateralization index was therefore computed for each trial by averaging the lateralization index within the defined time-frequency window (450-700 ms; 8-12 Hz). This index constitutes the attentional index used in the subsequent correlation analysis with the information measure derived from the fMRI data.

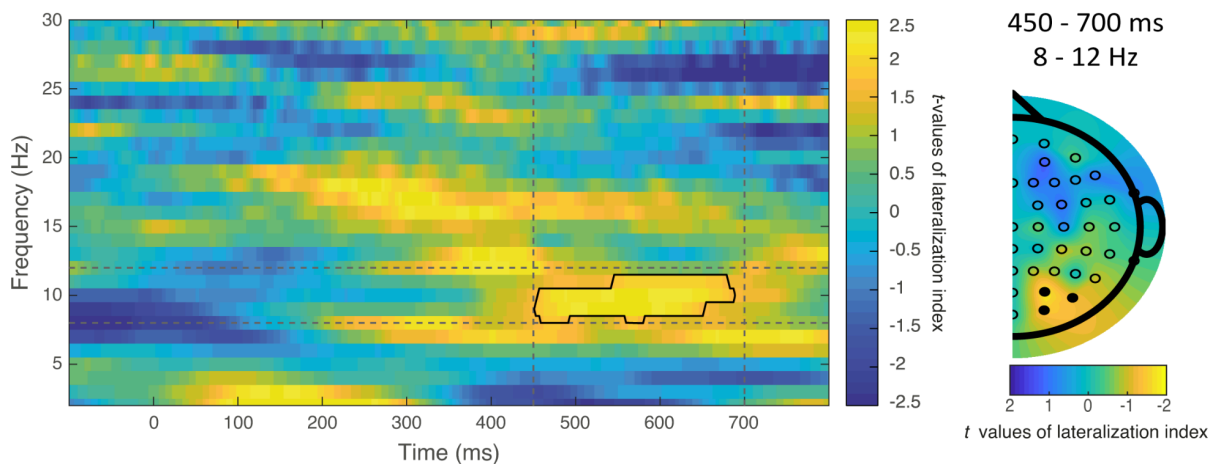


Figure 4.4. The alpha lateralization index peaks after the target presentation on a lateral side of the screen. **On the left**, the time-frequency plot of the lateralization signal (contralateral minus ipsilateral divided by ipsilateral plus contralateral) after the stimulus presentation (0 ms). Colour represent the t-values derived from testing the lateralization index values across participants with a one-sample t-test against a true μ of 0. Higher than zero t-values then represents an increased lateralization, with lower alpha power contralateral to the target. The illustrated positive t-values in the alpha frequency band thus reflects a higher focus of the attention on the hemifield containing the target image compared to the contralateral hemifield. The lateralization index was measured as a mean signal at a set of lateral occipital electrodes (O2 / PO4 / PO8, O1 / PO3 / PO7). Time zero represents the onset of the images, and solid line identifies results in the alpha frequency range surviving cluster-based correction for family-wise error. **On the right**, the scalp distribution of the mean lateralization index in the alpha frequency range over the approximate time window where the observed significant cluster emerges (450-700 ms), again the colours represent t-values, this time one value for every pair of contralateral and ipsilateral channel.

4.4.3 Coupling Variance in Alpha Lateralization to MRI-Derived Semantic Category Information

The primary objective of this study was to investigate whether, and in which brain regions, the level of attention directed at a stimulus relates to the flow of semantic information about that stimulus. To achieve this, we calculated two key metrics: classification accuracy for the target image (representing semantic information) and the alpha lateralisation index (representing the degree of attentional focus). A trial-by-trial correlation analysis was then conducted to link these two modalities.

To reduce noise inherent in single-trial measurements, a resampling approach was adopted (Figure 4.2). For each participant, trials were split into 20 chunks of equal size, with 17 chunks assigned to the training set and 3 to the test set. This process was repeated 1,140 times for each of the $\sim 2.1 \times 10^5$ searchlight spheres. For each iteration, the alpha lateralisation index was calculated as the mean lateralisation value within a time-frequency window of 450–700 ms and 8–12 Hz, as determined by the unimodal EEG analysis. This approach produced 1,140 paired values of alpha lateralisation and classification accuracy for each searchlight sphere. Fisher-transformed Pearson correlations were then computed for each of these value pairs, and the resulting correlation coefficients were mapped onto a brain volume at the corresponding searchlight centre.

The results, shown in Figure 4.5, revealed a single significant cluster where alpha lateralisation related to the target was positively associated with MRI-derived target category information. This cluster spanned several brain regions, including the left and right superior orbitofrontal gyrus (363 and 31 voxels, respectively), the left and right middle orbitofrontal gyrus (343 and 84 voxels, respectively), and the left

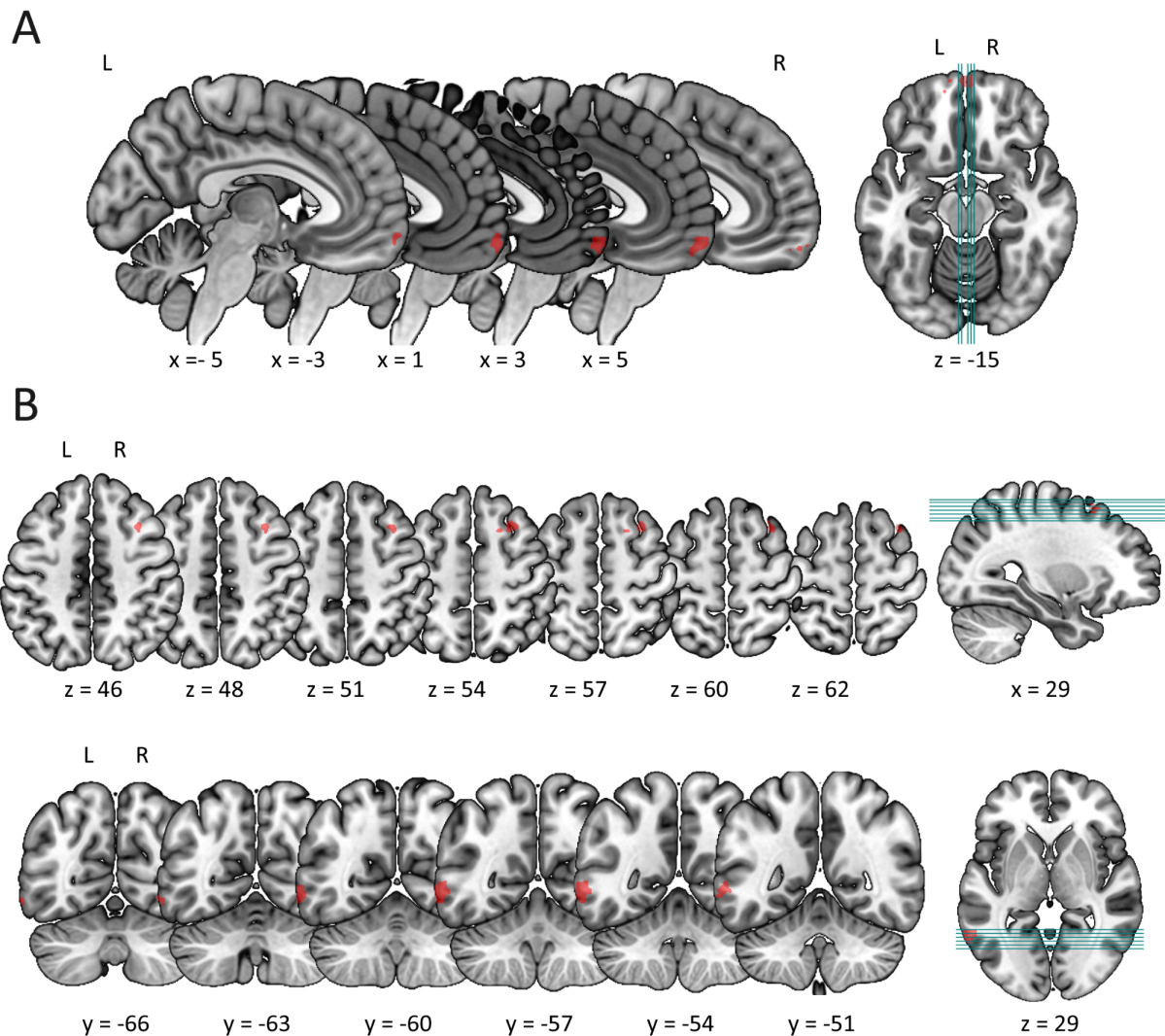


Figure 4.5 Alpha and fMRI category information. Results show brain regions where target-elicited alpha lateralization index covaries with target (**Panel A**) and distractor (**Panel B**) category information. Panel A shows a single cluster of positive correlations spanning bilateral OFG and rectus gyrus. Panel B illustrates 2 distinct clusters. One in the right middle frontal gyrus, reaching the right superior frontal gyrus. The second spans left middle and inferior temporal gyrus. Visualization was performed through MRICron software (Rorden, 2007), applying the default interpolation settings for display.

and right rectus gyrus² (117 and 179 voxels, respectively). Additionally, a small number of voxels (5 voxels) were located in the left anterior cingulum. No significant negative correlations were observed.

² The rectus gyrus is considered part of the orbitofrontal gyrus (OFG; Rudebeck & Rich, 2018). Therefore, from this point forward, the term OFC will encompass the rectus gyrus portion of the cluster.

These findings suggest that enhanced attentional selection of the target, as indexed by alpha lateralisation over occipital regions, drives the representation of conceptual information in the aforementioned brain regions. However, an alternative explanation is that alpha lateralisation and category information may covary more generally due to other factors, such as fluctuations in participant arousal. If this were the case, target information would be expected to correlate equally with alpha lateralisation linked to the target and the distractor. To test this possibility, a control analysis was conducted by correlating alpha lateralisation to the distractor (rather than the target) with target-related category information in a predefined region of interest (ROI) based on the significant cluster identified in Figure 4.5, Panel A. For each participant and condition (target-related lateralisation and distractor-related lateralisation), the correlation values within the ROI were averaged. A paired t-test comparing these two correlation values revealed that, within the ROI, the relationship between alpha lateralisation linked to the target and target category information was significantly stronger than the relationship between alpha lateralisation linked to the distractor and target category information ($t(30) = 4.3281, p < .001, d = 0.777$). This finding supports the interpretation that alpha lateralisation specific to the target is linked to target-specific semantic processing, rather than being a generalised effect driven by arousal or task state.

A similar analysis was conducted to investigate whether, and in which brain regions, trial-by-trial variance in distractor-related information is linked to attention to the target. Specifically, the analysis examined whether focusing attention on a target also enhances the brain's processing of semantic information related to the distractor. As shown in Figure 4.5, Panel B, two significant clusters were identified where alpha lateralisation towards the target positively covary with distractor

category information. The first cluster primarily encompassed the right middle frontal gyrus (613 voxels) and extended into the right superior frontal gyrus (47 voxels). The second cluster was located in the left middle temporal gyrus (589 voxels) and the left inferior temporal gyrus (131 voxels). No significant clusters of negative correlations were detected.

To further evaluate the specificity of these effects, two separate control analyses were conducted using ROIs defined from the two significant clusters. For each ROI, a paired t-test compared the correlation between distractor classification accuracy and target-related alpha lateralisation with the correlation between distractor classification accuracy and distractor-related alpha lateralisation. In both the right frontal ROI and the left temporal ROI, the correlation between distractor classification and alpha lateralisation to the target was significantly stronger than the correlation between distractor classification and alpha lateralisation to the distractor. Both in the left temporal ROI ($t(30) = 2.48$, $p_{\text{corr}} = .038$, $d = 0.445$) and the right frontal ROI ($t(30) = 3.86$, $p_{\text{corr}} = .001$, $d = 0.694$) the correlation was significantly higher for alpha lateralization to the distractor. The p-values were Bonferroni-corrected for the two comparisons. These findings indicate that the processing of distractor-related information in these areas is strongly linked to attentional allocation to the target, suggesting that attention to the target may have a spillover effect on distractor processing in the brain.

4.5 Discussion

This investigation explored how inherent fluctuations in attentional selection affect the transmission of conceptual information throughout the human brain, providing an anatomical delineation of this effect. By employing a searchlight method, we linked EEG-measured posterior post-stimulus alpha oscillations with fMRI-derived classification accuracies of stimulus categories. The results reveal how attentional mechanisms shape the representation of semantic information for both task-relevant and irrelevant stimuli, underscoring the significance of alpha oscillations in selective attention.

4.5.1 Target-Distractor Representations in Unimodal fMRI

Analysis of unimodal fMRI revealed a network of brain regions where category-specific information was more prominent for targets compared to distractors (Figure 4.3B). This network included extensive bilateral activation in the ventral visual cortex, along with smaller clusters in bilateral inferior parietal lobule/sulcus (IPL/SPL), left inferior frontal gyrus (IFG), left orbitofrontal cortex (OFC), left basal ganglia, and bilateral posterior cingulate gyrus (PC). These findings highlight the involvement of occipital and posterior parietal cortices, which are strongly linked to the encoding of visual features and the transformation of visual input into motor responses (Konen & Kastner, 2008; Freud, Plaut, & Behrmann, 2016). Additionally, engagement of the basal ganglia suggests a potential role in visual perceptual processes (Ding, 2023).

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Notably, the analysis also identified a set of left-lateralized regions, including the IFG and ventromedial prefrontal/orbitofrontal cortex (VMPFC/OFC), as well as bilateral PC, which are not traditionally regarded as visual processing areas. These regions have, however, been implicated in previous research as supporting abstract semantic representations (Binder et al., 2009; Acunzo et al., 2022; Ralph et al., 2017). No regions exhibited significantly greater classification accuracy for distractors than for targets, indicating the absence of brain areas significantly more engaged in encoding distractor-related information than target-related information.

Nonetheless, distractor information was still represented, with several visual processing regions and higher-order areas implicated in semantic processing (such as the left IFG, left VMPFC/OFC, and bilateral PC) displaying stronger classification accuracy for targets than for distractors. These findings align with perceptual load theory (Lavie, 1995, 2005; Lavie et al., 2014), which posits that both target and distractor information are initially processed. According to this view, the selection of

the target occurs at a later stage of processing, by which point some degree of distractor information has already been extracted.

4.5.2 Attentional Modulation of Target Semantic Information

Further analysis revealed a significant positive correlation between alpha lateralization and the accuracy of fMRI-based classification of target category information, particularly within the orbitofrontal cortex (OFC). The OFC is traditionally linked to neuroeconomic functions, specifically its role in encoding the subjective value of stimuli during decision-making (Bechara et al., 1994; Padoa-Schioppa & Assad, 2006; Padoa-Schioppa & Cai, 2011). However, recent research broadens this understanding, suggesting that the OFC constructs a cognitive map of all the available options, with heightened activity for the selected choice (Rustichini & Padoa-Schioppa, 2015; Hunt et al., 2012). Thus, within the context of our task, enhanced attention to the target might enhance the representation of the correct semantic category within the OFC, ultimately correlating attention with the selected choice.

As our analysis is based on a correlation, it could be argued that the direction of this influence is unknown. Consequently, the attention to the target might result in an enhancement of the correct choice's representation in the OFC. Or, alternatively, more confidence in the resolution of the chosen category might bring more attention to the target. Though, this second option seems less likely as in our task what distinguishes target and distractor is the colour of the circle that is orthogonal to the

image categories. Thus, it is unlikely for the target selection to be initiated by the category choice. Instead, a form of reciprocal influence might be more likely.

4.5.3 Attentional Modulation of Distractor Semantic Information

Greater alpha lateralization toward target stimuli has been associated with the selection of target information (Wöstmann et al., 2019; Foster & Awh, 2019), as well as in suppressing distractor information (Jensen, 2024; Diepen, 2016; May et al., 2012; Wöstmann et al., 2019). This relationship makes it somewhat counterintuitive that increased alpha lateralization to the target correlates positively with the classifier's ability to categorise information about the distractor. One possible explanation is that attentional control operates through a "search and destroy" mechanism (Moher & Egeth, 2012; Geng, 2014). This strategy involves initially selecting the distractor to effectively suppress it in later stages of processing, pairing heightened attention to the target with enhanced distractor information flow. This sequence may explain the observed positive correlation between alpha lateralisation to the target and distractor classification accuracy that may be the fruit of an initial selection of the distractor.

Another explanation is that increased alpha lateralization to the target reflects a more efficient suppression of distractor-related information, and this suppression effectively trains the classifier to recognize the absence of distractor-related activity. Notably, the correlation is statistically significant in clusters within the working memory network, including the left middle temporal gyrus (MTG: Sato et al, 2018; ITG: Hamame, 2012), associated with semantic working memory, and the right

superior and middle frontal gyri (SFG: Alagapan et al, 2018; MFG: McCarthy et al, 1996; Hampson et al, 2006), known for attentional control over working memory and working memory resistance to distractor interference (Sakai et al. 2002). A plausible interpretation is then that stronger attention directed to the target is associated with greater suppression of the distractor's semantic category in working memory. Crucially, this suppression leaves a "fingerprint" of the distractor's semantic information—essentially the residual neural activity patterns reflecting the combined representation of the other three categories—for the classifier to use as a training signal. Participants needed to keep all four categories in mind to respond correctly. After the stimulus array presentation, distractor categories were processed and then selectively inhibited in working memory. This inhibition generates a recognizable pattern for the classifier to detect.

When examining the testing set, greater suppression of the distractor's semantic representation in working memory is associated with increased alpha lateralization to the target. This enhanced suppression makes the distractor's "fingerprint" more distinct and easier for the classifier to identify, leading to the observed positive correlation between alpha lateralization to the target and classifier accuracy for the distractor category.

In summary, this study provides new insights into the connection between attention levels and semantic category representations in the human brain. By integrating EEG and fMRI data, we identified specific brain areas in which the representation of target and distractor information is linked to attentional selection. Our results reveal new relationships between prioritisation processes and the modulation of higher order regions involved in the representation of task-dependent

cognitive maps. At the same time, these results suggest the modulation of distractor semantic representation held in working memory-related brain regions. Future work should investigate both the causality and the direction of the relationship highlighted in this study. The present work gives novel insights into our understanding of how attention shapes the processing of semantic information in the brain, offering a framework for future investigations into the interplay between attention, memory, and conceptual knowledge.

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CHAPTER 5

GENERAL DISCUSSION

Imagine you are driving and feeling hungry. Your attention is captured by the image of a succulent hamburger displayed on a billboard. The advertiser who designed the commercial likely relied on the assumption that, before refocusing on the road, you would also process the name of the fast-food company printed on that billboard, while neglecting the car company name on the adjacent billboard. This selective processing involves object-based attention. Despite seven decades of research on this topic, several intriguing questions remain unresolved and the very existence of such a mechanism in question. What happens to the OBA when a reward object is present in the scene (e.g. a hamburger vs a car)? What are the neural indices reflecting OBA? How does the attention to an object relate with the semantic information that we process about that object and the surrounding ones?

5.1 Object-Based Attention Is Accentuated By Object Reward Association

The first question for which this thesis offers an answer is: does reward interact with OBA? In Chapter 2, results from Experiments 3 and 4 indicate that reward prioritisation and object prioritisation interact during selective attention, with this interaction emerging as a function of task practice rather than the strategic utility of reward feedback. In Experiment 3, reward feedback was discontinued during the extinction phase, and an interaction between reward and object prioritisation was observed. This raised the question of whether the interaction arose from the reward feedback manipulation or from task practice. Experiment 4 clarified this by showing that the interaction occurred in both groups—one with reward feedback sustained

and the other with reward feedback discontinued—and was not statistically different between them, suggesting that task experience plays a critical role.

A key finding across both experiments is that the interaction between reward and object prioritisation was driven by a slowing of responses when attention was drawn to a high-reward object, but the target required reorienting to a low-reward object. This effect highlights the challenge of disengaging from high-reward objects and suggests that all locations on such objects are closely monitored, creating a resistance to reorienting attention elsewhere.

Notably, the lingering influence of reward associations during extinction further reveals that reward prioritisation is robust and persists even when the strategic utility of the reward signal is removed (Hickey et al., 2010b; MacLean et al., 2016; Anderson & Yantis, 2013). This contrasts with the broader motivational effects of reward, which dissipate more rapidly. These findings align with the literature on reinforcement learning and incentive salience, where reward-associated stimuli continue to draw attention despite a lack of immediate benefit. This persistent attentional capture by reward-associated objects underscores their impact on visual cognition, potentially through mechanisms such as the priming of perceptual and attentional representations by mesencephalic dopamine (Berridge & Robinson, 1998; Ikemoto & Panksepp, 1999; Redgrave, Prescott, & Gurney, 1999; Jeong et al., 2022).

The results also support the coexistence of reward prioritisation and object prioritisation, initially suggested in Experiment 1 and corroborated in Experiments 2 through 4. While earlier studies posited that reward feedback could suppress object prioritisation (Shomstein & Johnson, 2013; Lee & Shomstein, 2013), the current

experiments show that these effects can operate simultaneously, with reward associations enhancing attentional engagement with specific objects.

Overall, the findings highlight the enduring influence of reward associations on attentional deployment, even when these associations no longer carry strategic value (Hickey et al., 2010b; MacLean et al., 2016; Anderson & Yantis, 2013). This persistence reflects the broader impact of reinforcement learning on selective attention and offers insights into the mechanisms of incentive salience and its potential misattributions in clinical contexts, such as addiction and other disorders involving maladaptive attentional biases (Anderson, 2016b, 2021; Berridge & Robinson, 1998).

5.1 Addressing the Challenges To the Object-Based Attention

The classic findings of object-based attention (OBA) have faced significant challenges in recent years, with critiques questioning both the robustness of the effect and its underlying mechanisms (Francis & Thunnell, 2022; Rosenholtz, 2024; Barnas & Greenberg, 2024; Li et al., 2024). In this thesis, we provide key evidence addressing these concerns. Specifically, we show that the object-based effect is replicable, robust to manipulations such as reward (Chapter 2) and that the attentional prioritisation of objects cannot be fully explained by alternative accounts such as perceptual clutter or anisotropy in attentional shifts (Chapter 3).

Our findings strengthen the supporting evidence for the OBA, showing that while certain factors may interact with or modulate the phenomenon, the underlying mechanisms of OBA remain distinct and measurable. Furthermore, by leveraging

neurophysiological measures, we provide novel insights into how attentional processes operate in relation to objects, independent of confounds related to attentional shifts to target or target resolution processes.

5.1.1 Anisotropy and Object-Based Attention Mechanisms

A key challenge to OBA arises from studies showing anisotropy in attentional shifts, with horizontal shifts often favoured over vertical ones (Francis & Thunnell, 2022; Barnas & Greenberg, 2024). In Chapter 3, we observed a similar pattern in our behavioural results, where an anisotropy favouring horizontal shifts guided the reaction times with no main effect of object-based attention. Despite this behavioural outcome, neurophysiological evidence from EEG recordings during the cue-to-target period provided clear support for task-irrelevant object prioritisation. Specifically, both alpha oscillation lateralization and the ADAN ERP component exhibited enhanced lateralization for vertically oriented objects compared to horizontally oriented ones, directly indexing the prioritisation of objects independent of later-intervening anisotropy effects.

We also addressed the hypothesis that perceptual clutter could explain the same-object advantage observed in the two-rectangle paradigm (Rosenholtz, 2024). Our findings showed that differences in perceptual clutter between same- and different-object conditions cannot fully account for the object-based effect. Crucially, we revealed that object prioritization occurs during the cue-to-target interval, before the target resolution process begins, indicating that OBA operates independently of the perceptual demands associated with target identification.

While the behavioural results of Chapter 3 did not reveal a significant overall object-based effect in reaction times, they strongly highlighted the influence of anisotropy, favouring horizontal shifts of attention. These findings align with broader evidence suggesting that anisotropy interacts with underlying object-based mechanisms to shape the behavioural effects observed in paradigms like the two-rectangle task (Chapter 2; Barnas & Greenberg, 2024; Francis & Thunnell, 2022).

Notably, our study introduces the first evidence of leveraging neurophysiological indices, such as alpha oscillations and the ADAN component, to directly index OBA mechanisms. These measures provide a means to isolate object-based attentional processes from other confounding factors, such as perceptual clutter or anisotropic biases in attentional shifts, offering a new avenue for understanding OBA's underlying mechanisms. To achieve that, future work should take the opposite route and assess the behavioural relevance of such physiological measures in contributing to the object-based effect.

5.2 Is Object-Based Attention A Strategic Mechanism?

The present thesis contributes to the ongoing debate regarding whether object-based attention (OBA) operates as an automatic or a strategic mechanism. Supporting the strategic account, Shomstein and Johnson (2013) argued against the automaticity of OBA, showing that OBA can be abandoned when competing strategies are present. However, findings from this thesis offer a more nuanced perspective.

In Chapter 2, we investigated the influence of reward schedules on OBA and found that introducing a reward schedule did not negate the object-based effect. This outcome fails to falsify, and instead supports, the automaticity hypothesis. Even under conditions where participants could potentially adopt a reward-driven strategy, OBA persisted, suggesting a degree of resilience and independence from strategic manipulations.

Potentially contrasting the above results, findings in Chapter 3 revealed evidence that may suggest strategic mechanisms also play a role in OBA. Specifically, we observed lateralization of the ADAN event-related potential (ERP) component, which is thought to be associated with frontal brain regions involved in voluntary attentional control. This lateralization tracked object prioritisation following an endogenous cue, raising the possibility that voluntary shifts of attention accommodate for the object status. However, it is important to note that the interpretation of ADAN as a marker of voluntary mechanisms is not conclusively established (Green et al., 2005; Green & McDonald, 2006; Green et al., 2008). While our findings provide a novel association, they do not speak conclusively about its underlying causes. Thus, while intriguing, the link between ADAN lateralization and strategic attentional processes in OBA warrants further investigation.

Together, these results suggest that the mechanisms underlying object prioritisation are complex, potentially reflecting an interaction between automatic and voluntary processes. While OBA appears to manifest as a robust mechanism operating independently of reward-based strategies, it may also be influenced by strategic, high-level attentional control, particularly during endogenous redirection of attention. These findings contribute to the broader debate about the mechanisms

driving object-based attention, challenging a strictly dichotomous classification as either automatic or strategic and instead supporting a more integrative perspective (Shomstein, 2012).

5.2 Models of object-based attention

Our findings align with two prevailing models of how object-based attention (OBA) might be implemented in the visual cortex. These models provide complementary perspectives on the interaction between low-level visual processing and attentional mechanisms.

One model suggests that objects are pre-attentively formed through low-level segmentation processes, resulting in the creation of proto-objects—rudimentary object representations based on visual features (Rensink, 2000a; Rensink, 2000b; Scholl, 2001). Within this framework, physiological measures such as those described in Chapter 3 might reflect the attentional selection of these predefined proto-objects, guiding the reallocation of attention toward the cued location. This view implies that object definitions are established prior to attentional engagement, with attentional mechanisms subsequently acting on these representations to prioritize specific objects or locations.

The second model posits that attention is initially deployed to the cued spatial location, where object contours are detected by early visual cortex neurons tuned to boundaries (e.g., V1-V4 neurons; Poort et al., 2012). Following this initial engagement, attention spreads along the contours of the object, potentially enhancing the perception or facilitating the definition of the object (Duncan, 1994;

Ekman et al., 2022). In this view, the physiological measures reported in Chapter 3, such as alpha lateralization and the ADAN component, could be linked to the spreading of attentional selection across the object's boundaries. This interpretation resonates with findings from Ekman and colleagues, who showed in fMRI that attentional selection in early visual cortex propagates along the structure of an attended object.

Our findings contribute to this discussion by providing evidence that may reflect both the pre-attentive definition of proto-objects and the subsequent attentional spreading along object contours. Further investigation will be necessary to delineate the specific contributions of these mechanisms to the observed physiological patterns.

5.3 Attention and Objects' Semantic Information

How does the attentional selection of the object correlate with its semantic representation in the brain? Literature investigating the behavioural relevance of the objects' representation found that target categories were more represented than distractor information in the object-selective cortex (Seidl et al., 2012; Hickey & Peelen, 2015). In Chapter 4, we expanded those results by showing that multiple brain regions encode both target- and distractor-related semantic information. Critically, several of these regions show a stronger representation of targets compared to distractors, spanning areas associated with both perceptual and semantic processing.

Furthermore, by integrating EEG and fMRI data, we observed that alpha oscillations correlate with the modulation of target- and distractor-related semantic representations. Specifically, we found that post-stimulus alpha lateralisation correlates with the classification accuracy of target categories in the OFC and distractor categories in working memory-related regions, such as the left MTG/ITG and right SFG/MFG.

The OFC's involvement in target representation aligns with its role in constructing cognitive maps and decision-making processes. Stronger alpha lateralisation towards targets was associated with improved semantic representation in this region, suggesting that attention enhances task-relevant information. In contrast, the positive correlation between alpha lateralisation and distractor-related semantic representations in working memory regions could reflect a reactive suppression mechanism. Specifically, these activity patterns may represent residual encoding traces resulting from effective suppression of distractor information. These findings contribute to the growing body of literature investigating the functional role of alpha oscillations in attentional processes. Our study provides novel evidence supporting the dual role of alpha oscillations in enhancing target representations and suppressing distractor information, thereby supporting object categorization.

5.4 Limitations and Future Directions

This thesis has advanced understanding of the mechanisms underlying selective attention, yet certain limitations warrant further exploration. The interaction between reward and object prioritisation raises critical questions about the processes that

support attentional selection. In Chapter 3, additive effects observed in Experiments 1 and 2 suggest distinct cognitive processes, while the interaction in Experiments 3 and 4 implies a shared modulator, likely task practice. Future studies should investigate the influence of extended practice on object-based attention (OBA) by employing longer experimental designs, where practice can be systematically manipulated as a continuous variable.

As outlined in Section 5.1.1, our results suggest an interaction between OBA and anisotropy effects, particularly when horizontally oriented objects are present. However, our findings cannot exclude the possibility that anisotropy enhances attentional spreading along horizontal objects more than vertical ones. Evidence from previous studies (e.g., Barnas & Greenberg, 2024) supports this notion. To disentangle these effects, future research should measure alpha oscillations and anterior directing attention negativity (ADAN) in paradigms that independently manipulate expected OBA effects and object orientation. Moreover, the neural correlates and functional role of ADAN also remain open to further inquiry. While our findings suggest that ADAN indexes the object status, additional evidence is required to establish its specific role in voluntary attentional control within OBA mechanisms.

Another limitation concerns the definition of semantic information in the study presented in Chapter 5. As highlighted in the Introduction, experiments using categorisation tasks within a single modality may inadvertently allow participants to rely on shared visual features to solve the task (Bracci & Op de Beeck, 2016; Watson et al., 2014; Rice et al., 2014). Although this does not compromise the novel findings presented here, it does leave open the possibility that attention may modulate amodal processing in additional brain regions, such as the anterior

temporal lobe (Ralph et al., 2017). Interestingly, the OFC has extensive anatomical (Binney et al., 2012) and functional (Pascual et al., 2013) connectivity with the anterior temporal lobe, suggesting that it may be part of a broader network supporting amodal semantic representations.

To address these limitations, future research should employ diverse stimulus modalities, such as both images and words, to test whether attention modulates conceptual representations in the anterior temporal cortex. Additionally, investigating the functional connectivity between the OFC and anterior temporal lobe during tasks involving amodal semantic information will provide critical insights into the broader networks underlying attentional modulation of conceptual processing.

5.5 Concluding Remarks

This thesis provides critical insights into the mechanisms of attention, focusing on its role in object-based selection, its interaction with reward systems, and its influence on conceptual representations in the brain. By integrating novel behavioural paradigms and advanced neuroimaging techniques, the findings re-establish object-based attention (OBA) as a distinct mechanism of attentional selection and reveal its modulation of semantic information in the human brain.

The findings reveal that reward associations significantly enhance object prioritisation, with effects persisting even during extinction phases. This highlights the enduring influence of value-driven biases on attentional selection. At the same time it shows that OBA is an independent mechanism that cannot be strategically suppressed. Additionally, neurophysiological evidence indicates that oscillatory

frequencies and event-related potentials traditionally associated with spatial attention also index object-based mechanisms. These results reinforce OBA as separable from attentional anisotropies and perceptual clutter effects.

Finally, the concurrent use of EEG and fMRI revealed that attention to objects modulates the enhancement and suppression of semantic-related information across specific brain regions. These findings underscore the role of attention not only in selecting relevant objects in the environment but also in supporting their semantic processing.

In summary, this work contributes to the understanding of attentional mechanisms by revealing the modulation of object-based attention through reward, identifying neurophysiological correlates of object prioritisation, and uncovering how attention correlates with the representation of conceptual information in the human brain. These findings pave the way for future investigations into attentional mechanisms related to object selection, reward association, and semantic representation, offering a building block towards the development of an integrative model of attention.

5.6 References

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