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On the Relationship between Visual Attention and Perceptual Awareness

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Abstract

Selectively attending to what is important in the environment while ignoring less important information is strongly correlated with what is experienced subjectively. Despite this seemingly obvious relationship between what is attended and what is perceived, there is a long-standing debate regarding whether attention and awareness are functionally related. While some have suggested that the two processes are identical, others have argued that they can be dissociated, either singularly (i.e., one process depends on the other) or doubly (i.e., the two processes can act independently). The overarching aim of my thesis was to investigate the relationship between visual attention and awareness, by combining behavioral methods, electroencephalography (EEG) and computational modeling.

The thesis is divided into five chapters. In **Chapter 1**, I review previous literature related to the debate in relation to the no dissociation, single dissociation, and double dissociation views. In doing so, I highlight that the conclusions made about the way attention and awareness relate depend on the task or physical stimulation differences between conditions.

In **Chapter 2**, I endeavored to replicate a study by van Boxtel, Tsuchiya, and Koch (2010a), who reported a double dissociation between attention and awareness using a perceptual adaptation task in which participants' perceptual awareness and visual attention were manipulated independently. van Boxtel et al. (2010a) found that participants' awareness of an adapting stimulus increased afterimage duration, whereas attending to the adaptor decreased it. Consistent with van Boxtel et al. (2010a), I found that afterimage duration was reliably increased when participants were aware of the adapting stimulus. In contrast to van Boxtel et al., however, I found that attention to the adaptor also increased afterimage duration, suggesting that attention and awareness had the same – rather than opposing – effects on afterimage duration. This failure to replicate suggests caution in using this specific approach to support the argument that attention and awareness are dissociable processes.

In **Chapter 3**, across three experiments, I investigated behavioral and EEG responses to examine whether enhancement of goal-relevant stimuli and suppression of goal-irrelevant stimuli arise even when stimuli are masked from awareness. I used a feature-based spatial cueing paradigm in which participants searched four-item arrays for a target in a specific color. Immediately before the target array, a non-predictive cue display was presented in which a cue matched or mismatched the searched-for target color, and appeared either at the target location (valid) or another location (invalid). Cue displays were masked using continuous flash suppression, so that participants were unaware of them on roughly half the trials. The EEG data revealed that target-colored cues produced robust signatures of spatial orienting and distractor-colored cues produced a signature of suppression. Critically, these signatures occurred for both aware and unaware cues. The signatures

of enhancement were larger in the aware than in the unaware cue condition, but the signature of suppression was roughly equivalent in magnitude across the two conditions, suggesting that conscious perception modulates selective enhancement of visual features, but suppression of those features is largely independent of awareness.

In **Chapter 4**, I investigated the brain events associated with reports of awareness when visual stimulation remains invariant across trials. When an observer reports that he or she is aware of a stimulus, there are several processing stages that contribute to the final decision: sensory evidence accumulation, decision formation, motor preparation, and response execution. I used EEG to measure brain responses to oriented gratings that were progressively incremented in contrast, using a method known as "breaking flash suppression". Participants performed a simple orientation discrimination task. I analyzed the centroparietal-positivity (CPP), which is thought to track evidence accumulation for determining a subsequent action. I also employed forward encoding modeling to analyze brain activity specific to grating orientation, and generated tuning functions for orientation information across the entire trial. I found a robust CPP that occurred earlier and at a faster rate when participants responded earlier, relative to later, in the trial. Furthermore, I found evidence for orientation tuning to the presented grating which increased over the duration of the trial, beginning earlier and reaching a larger magnitude when participants responded earlier versus later in the trial. These results suggest that variation in stimulus-specific encoding during unaware states can predict awareness.

In **Chapter 5**, I summarize the findings from the empirical work presented in the preceding chapters, and conclude that the findings overall are most consistent with the single dissociation view, in which attention is the critical antecedent to awareness. I also posit that attentional mechanisms of enhancement and suppression are independent mechanisms that relate to awareness differently and at different processing stages. Furthermore, I emphasize that the relationship between attention and perceptual awareness may be different depending on the dependent measures used during experimentation. Future work investigating the relationship between attention and awareness should focus on how different types of attentional tasks and dependent measures interact at different processing stages.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

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Publications during candidature

Published Manuscripts:

Harris, Anthony M., Jacoby, Oscar, Remington, Roger W., Travis, Susan L. & Mattingley, Jason B. (2019). Taking a closer look at visual search: just how feature-agnostic is singleton detection mode? *Attention, Perception, & Psychophysics, 81* 3: 654-665. doi:10.3758/s13414-018-01642-y

Travis, Susan L., Dux, Paul E. & Mattingley, Jason B. (2018). Neural correlates of goal-directed enhancement and suppression of visual stimuli in the absence of conscious perception. *Attention, Perception, and Psychophysics*. doi:10.3758/s13414-018-1615-7

Travis, S.L., Dux, P.E., & Mattingley, J.B. (2017). Re-examining the influence of attention and consciousness on visual afterimage duration. *Journal of Experimental Psychology: Human Perception and Performance, 43 (12)*,1944- 1949.

Painter, D.R., Dux, P.E., Travis, S.L., & Mattingley, J.B. (2014). Neural responses to target features outside a search array are enhanced during conjunction but not unique-feature search. *Journal of Neuroscience, 34(9),* 3390–3401.

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Contributor	Statement of contribution
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Contributions by others to the thesis

Jason Mattingley and Paul Dux (advisors) contributed to the conception and design of the studies described in this thesis and reviewed all written content.

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Research Involving Human or Animal Subjects

This research was approved by the University of Queensland Medical Research Ethics Committee (ethics approval number: 2015001198). A copy of the ethics approval letter is included in **Appendix A**.

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List of Abbreviations used in the thesis

ANOVA	Analysis of variance
bCFS	breaking continuous flash suppression
BF	Bayes factor
cd/m^2	Candela per square meter
CFS	Continuous flash suppression
CI	Confidence interval
CIE	Tristimulus color model
CPP	Centroparietal positivity
EEG	Electroencephalography
EOG	Electro-oculography
ERP	Event-related potential
fMRI	Functional magnetic resonance imaging
Hz	Hertz
LCD	Liquid-crystal display
M	Mean
ms	Milliseconds
N2pc	Negativity in the ERP around 200ms at posterior contralateral electrodes
NT	Negative ERP component associated with target enhancement
OSM	Object substitution masking
PC	Personal computer
PD	Positive ERP component associated with distractor suppression
RGB	Red-green-blue colour value
ROI	Region of interest
RSVP	Rapid serial visual presentation
RT	Reaction time
SD	Standard deviation
SEM	Standard error of the mean
SSVEP	Steady state visual evoked potential
V1	Primary visual cortex
V4	Monkey visual area 4

Chapter 1 : General Introduction

1.1 General Introduction

Our visual experience suggests a rich and stable representation of the external world. On waking, all this visual information seems to become an integral part of ongoing conscious experience, from the flashing alarm clock to the sunlight streaming through the window. The process of seeing, however, is not as simple as it appears. The sheer quantity of light reflected off the various objects and surfaces in the world onto the retina is vast. To respond in an adaptive manner some sources of visual information must be prioritized over others, so that relevant information is enhanced and irrelevant information is ignored or even suppressed. Front-end bottlenecks, such as the cells in the retina that respond selectively to particular wavelengths within the visible spectrum, help reduce the deluge; however, the ability to selectively attend to some objects and events and to ignore others appears to be directly related to what is subjectively experienced when "seeing" something. When reading a book, for example, attention is given to specific words on the page, isolating those words from others. Attended words become the subject of experience, while unattended words are scarcely noticed. Everyday examples such as this illustrate the seemingly strong relationship between attention and perceptual awareness: objects and events that are attended constitute the content of the subjective experience of the external world, whereas those that are ignored generally elude awareness entirely. The work presented in this thesis deals with the nature of the relationship between attention and conscious perception.

1.2 The debate: A brief overview

Despite the intuitive idea that attention and awareness are inherently linked, there is much debate in the literature as to whether this everyday notion captures the true relationship between attention and perceptual awareness. For now, I will define 'attention' as the process of selecting relevant information while ignoring irrelevant information, and 'awareness' as the content of subjective experience. Later I will explore the meanings of these concepts in more depth. The intuitive idea suggests that attention and awareness are virtually synonymous, such that everything that is attended is equivalent to everything of which we are aware. Some researchers and philosophers, however, have suggested that there is a dissociation between attention and awareness, arguing that the two should be considered separate processes. Some have argued for a single dissociation in which attention is necessary, but not sufficient for awareness (e.g., Cohen, Cavanagh, Chun & Nakayama, 2012). Others have argued that attention and perceptual awareness can be doubly dissociated, such that attention is neither necessary nor sufficient for awareness (e.g., van Boxtel, Tsuchiya, & Koch, 2010b). The literature on the relationship between attention and awareness can be divided into three broad perspectives: the intuitive *no dissociation view,* the *single dissociation* view, and the *double dissociation* view (see Figure 1.1). The overarching aim of this

introductory chapter is to review the evidence in support of these three views. In subsequent chapters, I will present the empirical findings of the thesis and discuss their implications for the relationship between visual attention and perceptual awareness.

The 'No dissociation' view

Proponents of *'No dissociation'* view argue that attention and perceptual awareness are so intrinsically linked that one cannot occur without the other, i.e., attending to something invariably results in awareness of that thing, and without attention awareness cannot occur (Chun & Wolfe, 2000; De Brigard & Prinz, 2010; Mole, 2008; O'Regan & Noe, 2001; Posner, 1994; Prinz, 2011, 2012; Wolfe, 1999). Driving while distracted provides a useful everyday example of this view in action. While driving, it may seem possible to attend to the road ahead while simultaneously checking a phone, but without attending to the road ahead, the driver likely fails to see the brake lights of a car directly in front. Such *inattentional blindness* is thought to be a common cause of rear-end collisions (Strayer & Drews, 2004).

The 'Single dissociation' view

Proponents of the single dissociation view argue that attention and perceptual awareness are distinct, but that one is critical for the other (Cohen, Cavanagh, Chun & Nakayama, 2012). The most popular conception of this relationship is that attention is the critical antecedent for perceptual awareness: directing attention to something does not necessarily lead to awareness of that thing, but being aware of something requires attention. Some of the strongest evidence for the single dissociation view comes from masked priming studies, in which visible targets are preceded by a word or object prime that has been rendered invisible by masking. For example, Naccache et al. (2002) found that even though observers were unaware of masked word-primes, when attention was directed toward the prime-target pair, the word-primes influenced responses to subsequent targets (a *priming effect*), whereas without attention, the word-primes had no such effect.

The 'Double dissociation' view

Proponents of the double dissociation view suggest that attention and awareness are fundamentally different processes: attending to something does not necessarily lead to awareness of it, and awareness of something does not require attention (Koch & Tsuchiya, 2007; Tsuchiya & Koch, 2016). Much of the evidence for a double dissociation between attention and awareness comes from studies of the concept known as the *gist*. Even with brief presentations of a scene, the meaning – or *gist* – of the image depicted is available for conscious report (Oliva & Schyns, 1997; Parker et al., 1992; 1996; Schyns & Oliva, 1994). Indeed, even when attention is diverted to a demanding task, the gist of a scene can be exempt from inattentional blindness (Mack & Rock,

1998). Proponents of the double dissociation view suggest that awareness of the gist of a scene can occur without attention (Biederman, 1972; Biederman, Rabinowitz, Glass, & Stacy, 1974; Potter, 1975, 1976; but see below for a critical review of this literature).

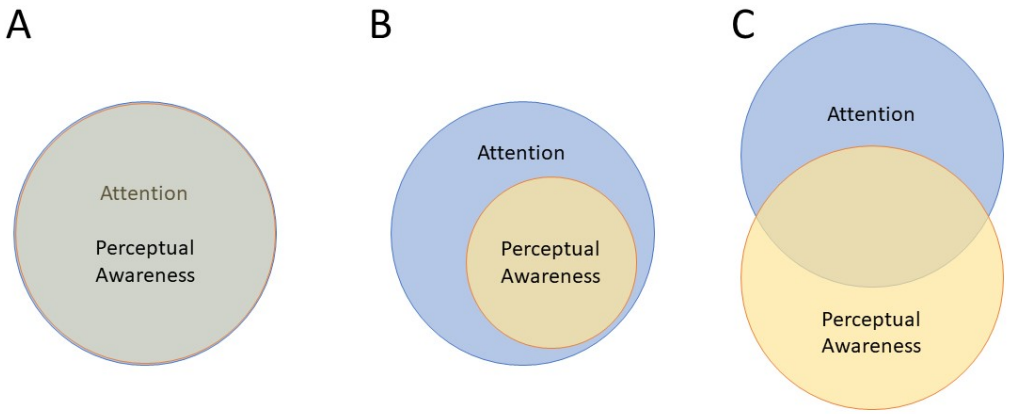

Figure 1.1. Venn diagrams representing the three main views on the relationship between attention and perceptual awareness. (A) The no dissociation view – attention and awareness completely overlap such that one cannot occur without the other. (B) The single dissociation view. Attending to something does not necessarily lead to awareness of it, but all perceptual awareness requires attention. (C) The double dissociation view. Attention and awareness overlap, but attending to something does not necessarily lead to awareness of it, and awareness of something does not require attention.

Before reviewing further evidence in support of each view, it is important to delve deeper into the definitions of attention and perceptual awareness. Many attempts have been made to define these concepts (e.g. Baddeley & Weiskrantz, 1993; Broadbent, 1958; Carrasco, 2011; Cherry, 1953; Chun & Wolfe, 2001; Driver, 2000; Helmholtz, 1896; James, 1890; Lamme, 2004; Lavie & Tsal, 1994; Overgaard, 2017; Parasuraman & Davis, 1984; Posner, 1988; Zeman, 2005). Indeed, much research on attention and perceptual awareness has been centrally motivated either by a desire to distinguish them from other potentially related concepts (e.g., attention vs. motivation, perceptual awareness vs. verbal report, etc.), or to identify differences between presumed subtypes of each (e.g., overt vs. covert attention, pre-conscious vs. sub-conscious perception, etc. For a review see Hommel et al., 2019).

1.3 What is Attention?

James (1890) provided the quintessential definition of attention, a favorite of professors first introducing the topic to undergraduates in cognitive psychology courses:

"*Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others…*" (pages 403-404).

In his definition, James highlights the central problem that attention aims to solve – the world is rich and vastly detailed, but what is subjectively experienced via the senses is comparatively limited due to a capacity limitation in the processes that make the content of the sensory world available for the control of action and higher cognition.

From an evolutionary perspective, it is curious that the brain, which has evolved to survive and navigate in the environment, is limited in its capacity to process sensory information. Surely a larger capacity for experience would allow for higher detection rates, affording an evolutionary advantage? There are, however, two important advantages to a limited-capacity system. First, a limited capacity system requires less metabolic resources than a larger-capacity system (Barlow, 1972). Second, by limiting the capacity of the system, prioritization becomes an important feature for navigating and surviving in the environment. Without such prioritization, an organism would find features irrelevant to its survival as important as highly relevant features. The concept of prioritization is central to James' (1890) definition of attention, in which he states that attention "*implies withdrawal from some things in order to deal effectively with others.*" The main function of attention, according to James, is to prioritize important and relevant information and to filter out or suppress irrelevant information.

Given the debate as to how attention and awareness are related, an astute reader may notice a problem with James' definition, which describes attention in a way that makes it seem almost synonymous with awareness. "Taking possession by the mind, in clear and vivid form," is a description many would give to perceptual awareness. Thus, James' definition fits with the no dissociation view and seemingly excludes situations in which attention does not lead to subjective experience (the single dissociation view) as well as situations in which experience does not require attention (double dissociation view). If the debate about how attention and awareness are related is to be resolved, the definition of attention should not embed the concept of awareness within it. Thus, in this thesis, I use the term attention to denote those processes that prioritize some sensory inputs over others, without making any claims as to whether these selective processes are required for, or inevitably lead to, subjective awareness.

Selective attention

Taking the two basic observations that define attention – a limited capacity for processing sensory inputs and selectivity – it becomes apparent that sensory inputs must compete for neural

resources such that some inputs are selected for further processing while others are ignored (Desimone & Duncan, 1995). The precise point at which selection occurs has been the focus of an intense debate over many years. During the 1950s, Cherry (1953) and Broadbent (1958) conducted seminal work using the so-called dichotic listening paradigm, in which participants monitor two auditory streams simultaneously, one played to each ear. In a typical dichotic listening experiment, participants are asked to attend to a stream of numbers, such as "7 – 2 – 1 – 9 – 4 – 5" in which successive numbers alternate between the two ears. According to Broadbent's Filter theory, attention is controlled by two components, a buffer that temporarily stores both auditory streams followed by a filter, at an early stage of processing, that processes one auditory stream at a time (see Figure 1.2).

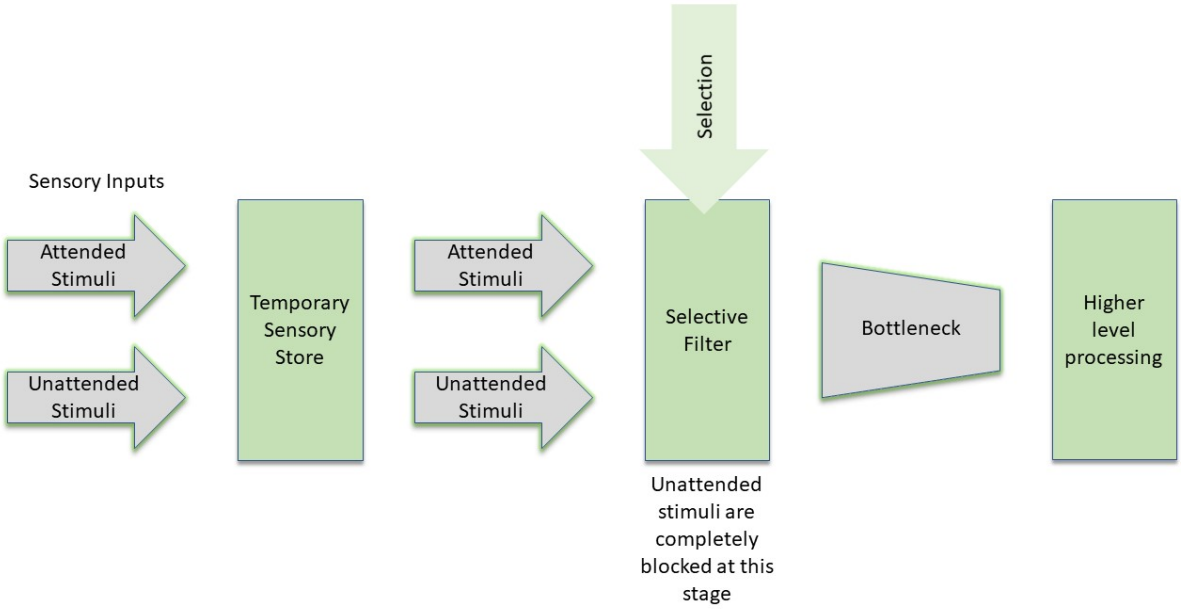

Figure 1.2. Broadbent's Filter Model of attention. Based on the concept of a limited-capacity bottleneck, this early selection model claims that attention acts as a filter at an early stage of sensory processing. According to this model, sensory inputs enter a temporary sensory store and are then processed through a selective filter based on basic stimulus features (e.g., color, orientation, direction). Attended inputs proceed to higher-level analysis, whereas unattended inputs are filtered out. Figure adapted from Broadbent (1958).

Initially, all basic features, such as color, orientation, and direction, are processed in a temporary sensory buffer (Broadbent, 1958; Friedenberg & Silverman, 2012). More complex features, such as semantic information, are thought to be processed after selective filtering and are thus subject to the limited capacity of high-level processing. This model has since become known as the *early-selection* model. In the above-mentioned study, instead of repeating the numbers in the order heard, participants tend to repeat the numbers presented to one ear followed by the numbers

presented to the other ear, providing support for the idea that the information that is to be further processed is selected early when basic features, such as sound location, are processed.

Not long after Broadbent proposed his early-selection model, Deutsch and Deutsch (1963) and Norman (1968) highlighted evidence that seemed counter to the early selection model. For example, again using the dichotic listening paradigm, participants heard a string of numbers and words in one ear, such as "Dear – 9 – Joe" and a different string of words and numbers in the other ear, such as "7 – Uncle – 3" (Gray & Wedderburn, 1960). Early selection theory would predict that all items presented to one ear should be reported before those presented to the other ear, based on the elementary stimulus feature of sound location. Contrary to this prediction, however, participants reported "Dear – Uncle – Joe" followed by "7 – 9 – 3". From these findings, it was argued that semantic features can determine the order in which stimulus information is selected. This model became known as the *late-selection model* (see Figure 1.3).

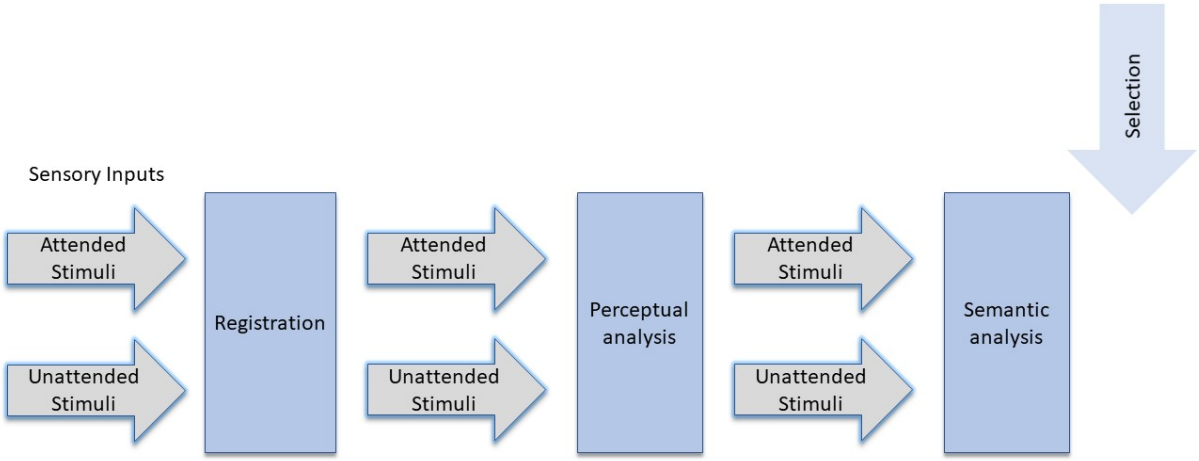

Figure 1.3. Late selection models hypothesize that stimulus selection arises after initial sensory registration and perceptual analysis. According to late selection models, all sensory inputs are processed, and information is filtered based on semantic analysis. Attended inputs proceed to higher-level analysis, and unattended inputs are attenuated, rather than completely filtered out. Figure adapted from Treisman (1964).

Perceptual load theory

During the mid-1990s, Lavie and her colleagues conducted a series of seminal experiments aimed at resolving the early- versus late-selection debate (Lavie & Tsal, 1994; Lavie, 1995; Lavie & Cox, 1997; Lavie et al., 2014; Rees et al., 1997). They introduced the concept of *perceptual load* and suggested that whether selection occurs early or late in processing depends on the perceptual complexity (or "load") of the target task. Their idea is based on two underlying assumptions: first, that attentional resources are limited, so the degree to which a stimulus is processed will be determined by the attentional resources available; and second, that all stimuli are processed automatically until attentional capacity limits are reached. Thus, goal-relevant stimuli will be

preferentially processed, and the degree to which goal-irrelevant stimuli are processed will depend on the attentional demands of the task. During an easy target task, when attentional demands are low, spare resources will automatically "spill over" to goal-irrelevant stimuli, thus yielding distractor interference consistent with late selection theories. By contrast, during a difficult target task, when attentional demands are high, resources are exhausted leaving no spare capacity for processing of irrelevant stimuli, and yielding performance suggestive of early selection (Lavie, 1995; 2006).

A distinction has been made between different types of information processing under Lavie's load theory. *Perceptual load* refers to the relative complexity of stimulus discrimination in the target task (Lavie, 2005). For example, during a perceptual-load task (see Figure 1.4), a circle of letters is presented centrally, and a distractor letter is presented in the periphery. According to load theory, under low-load excess resources will be available to "spill over" to the distractor letter, but under high-load fewer resources will be available to process the distractor. Therefore, load theory predicts that distractor interference will be greater under low-load than under high-load conditions.

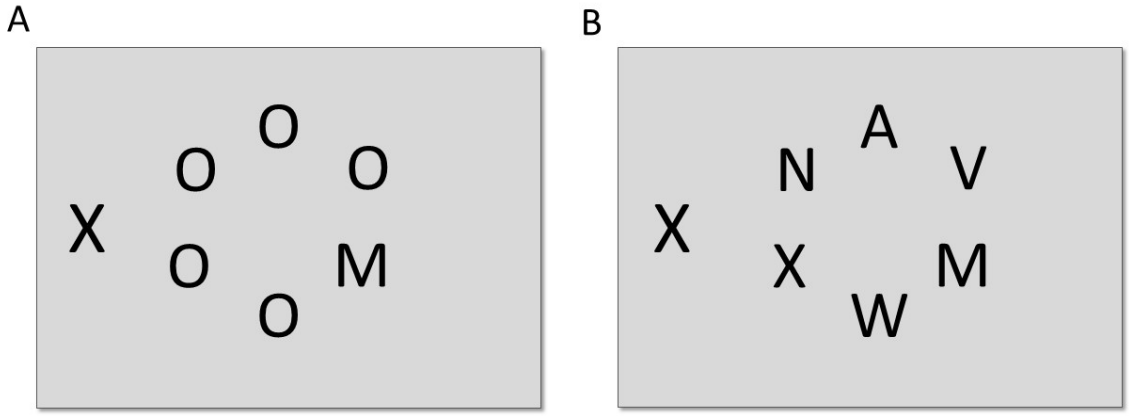

Figure 1.4. Example of a low (A) and a high (B) perceptual load task. The task is to identify a target "M" or "X" presented in the circle, while ignoring the peripheral distractor letter that could be congruent or incongruent with the target (in this example both distractors are incongruent). (A) A low-load task, in which the target (M) is surrounded by identical O-shaped distractors. (B) A high-load task, in which the target (M) is surrounded by a mixture of different letters.

In a variant of this approach, sometimes called "attentional load", participants are asked to perform an easy or difficult discrimination on a target stimulus that is identical across load manipulations. For example, participants might be presented with a stream of upright and inverted crosses in different colors (Figure 1.5). In the low-load condition, participants are asked to count the number of upright and inverted red stimuli (a single unique feature), whereas in the high-load condition they are asked to count the number of upright green and inverted yellow T-shapes

(conjunctions of features; see Figure 1.5). Typically, performance on a peripheral secondary task is better under the easy task condition than the difficult task condition.

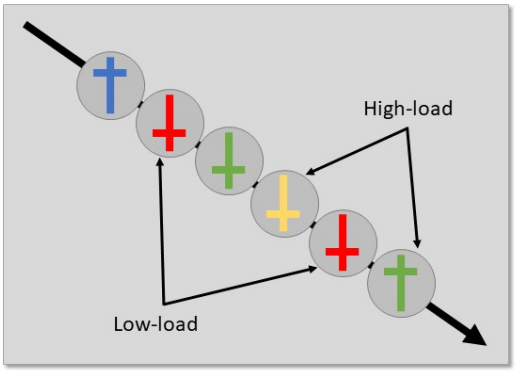

Figure 1.5. Schematic of a task involving a manipulation of attentional load. A stream of upright and inverted crosses in various colors is presented. In the low-load task, participants are asked to count the number of upright and inverted red crosses. In the high load task, participants are asked to count the number of upright green and inverted yellow crosses. Adapted from Bahrami, Carmel, Walsh, & Rees (2008).

A distinction has been made between perceptual load, which uses perceptual resources to process visual information presented in a display, and *cognitive load*, which uses executive resources to process task difficulty (Lavie, 2005). It is important to note that some findings have shown that high-cognitive load tasks (e.g., those that tax working memory) can have the effect of increasing, rather than decreasing, the processing of peripheral stimuli (de Fockert et al., 2001; Lavie, 2006; Lavie, 2005). For example, irrelevant peripheral face stimuli evoked an increase in brain activity under high-cognitive load compared with low-cognitive load (de Fockert et al., 2001). It has been argued that in tasks that require executive resources, such as working memory, the high-load condition can attenuate the filtering of irrelevant stimuli as the demands of the high-load task reduce the participant's ability to actively maintain selective priorities that distinguish between task-relevant and task-irrelevant information (Burnham, 2010; de Fockert et al., 2001; Kelley & Lavie, 2001; Lavie et al., 2004; Lavie & de Fockert, 2005; Rissman et al., 2009).

Feedforward and feedback mechanisms

Contemporary understanding from neuroscience is that attentional selection can involve both feedback and feedforward processes, which may occur concurrently and often rely on the same neural mechanisms within the same brain areas (Hillyard & Anllo-Vento,1998; Luck & Hillyard, 2014; Posner & DiGirolamo, 1998; see Khorsand, Moore, & Soltani, 2015 for a review). Classic views hypothesized that the initial feedforward processing of stimulus input is independent of the influence of top-down feedback projections (Nakayama & Mackeben, 1989; Treisman & Gelade,

1980; Treisman & Gormican, 1988), and that feedback processes derived from task goals intervene after initial visual processing (Itti & Koch, 2001; Koch & Ullman, 1985; Wolfe, 1994). Recent evidence, however, has suggested that feedback signals from higher cortical areas can change behavioral performance (Einhauser et al., 2008; Joseph et al., 1997; Krummenacher et al., 2001) as well as neural signatures associated with feedforward processing (Burrows & Moore, 2009). Such findings have led to the idea that feedforward and feedback processes operate in parallel in the same brain areas and at similar times using the same neural mechanisms (see Khorsand, Moore, & Soltani, 2015 for a comprehensive review).

Goal-based attention

As mentioned above, attention is assumed to operate by selecting relevant information for further processing while filtering out or attenuating irrelevant information. Thus, task goals play an important role in determining which stimuli are relevant and, thus, which stimuli will be selected for further processing (Wolfe & Horowitz, 2017). Depending on the task, prioritization of visual information can be restricted to a specific object, time, location, or feature within the visual field. Object-based attention and temporal attention are not directly relevant to this thesis, so they are not discussed in detail here. For completeness, however, *object-based attention* refers to the selection of stimuli based on their identity (e.g., shape, category, etc.) regardless of other features such as their spatial location (Egly, Driver, & Rafel, 1994, Roelfsema, Lamme, Spekreijse, 1998; see Chen, 2012 for a review). *Temporal attention*, on the other hand, refers to selection based on the relative timing of a stimulus event or events (Coull & Nobre, 1998; see Nobre & Rohenkohl, 2014 for a review).

Spatial Attention

When a task requires monitoring of a specific location in space, stimuli appearing in this location are prioritized over those appearing at irrelevant locations (Colby, 1991; Eriksen & Hoffman, 1973; Posner et al., 1980; Posner & Petersen, 1990; Sperling, 1960). This can either occur overtly, via shifts in gaze direction or covertly while gaze remains fixed on a specific location (Posner, 1980). Thus, when an observer has prior knowledge of a target's likely spatial location, attention is devoted to that location and processing of stimuli at irrelevant locations only occurs if spare resources are available. Much evidence suggests that neural responses are enhanced for stimuli presented at an attended location relative to those at unattended locations (Desimone & Duncan, 1995; Hillyard et al., 1998; Kastner et al., 1998; Luck et al., 1997; Mangun & Hillyard, 1988; Martinez et al., 1999; McAdams & Munsell, 1999; Morgan et al., 1996; Muller et al., 1998; Muller & Hillyard, 2000; Reynolds et al., 2000; Spitzer et al., 1988; Tootel et al., 1998). In human electroencephalography (EEG) studies, for example, the stimuli that fall within an attended spatial location evoke larger amplitude event-related potential (ERP) responses than those presented in

unattended locations (see Figure 1.6; for a comprehensive review, see Hillyard & Anllo-Vento, 1998).

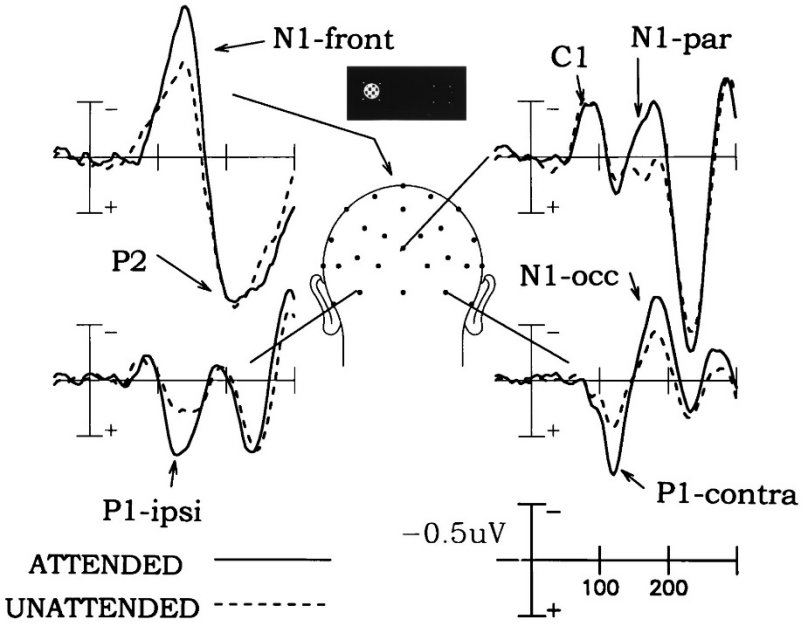

Figure 1.6. Stimulus-evoked neural responses (ERPs) recorded using EEG. Two early ERP components (the N1 and P1) are increased in amplitude for attended stimuli (solid lines) compared with unattended stimuli (dashed lines). Figure from Clark and Hillyard (1996), with permission.

A popular concept advanced in the 1980s holds that covert spatial attention acts as a *spotlight* or *zoom lens* (Eriksen & James, 1986; Posner et al., 1980). Stimuli that fall within the spotlight are prioritized, whereas those that fall elsewhere receive little or no processing. According to this conception, the spotlight of attention can be allocated voluntarily (top-down or *endogenous* attention; Nakayama & Mackeben, 1989; Posner, 1980), such as when an observer monitors a specific location, or involuntarily (bottom-up or *exogenous* attention; Posner, 1980), such as when a stimulus in peripheral vision moves suddenly and the spotlight of attention is "*captured*" by the moving object. Under the traditional view, attention is applied spatially to one location at a time; however, subsequent evidence has shown that attention can be applied to multiple locations simultaneously, and that stimuli outside the current spotlight are also processed to some degree (McMains & Somers, 2004; Treue & Martinez-Trujillo, 2007).

Feature-based attention

While spatial attention enhances stimuli at a given location in the visual field, *feature-based attention* enhances responses to a specific feature (e.g., color, orientation, direction of motion) regardless of its position within visual field (Maunsell & Treue, 2006; Serences & Boynton, 2007; Treue & Martinez-Trujillo, 1999). For example, when observers are required to search for any red

item, priority will be given to red over other colored items (Treue & Martinez-Trujillo, 1999). During task performance, if a red item appears it will capture attention to its location, a phenomenon called *contingent attentional capture*. Contingent attentional capture was first demonstrated by Folk, Remington, & Johnston (1992), using a spatial cueing paradigm (see Figure 1.7). I will describe this work in detail, as the experiments presented in **Chapter 3** of this thesis employ a similar methodology. In the study of Folk et al. (1992), participants were required to report the identity of a visual target. Prior to the presentation of the target display, a cue display was presented. The cue display consisted of a central fixation square with four peripheral squares. Four small distractor dots appeared surrounding each of the four peripheral squares. The dots surrounding three of the peripheral squares were white, and those around the remaining square were red (the cue). The target display contained either one target (an "X" or an "=") in one square (onset target condition), or one red target in one square and three white distractors in the other peripheral squares (color target condition). Participants made a speeded forced-choice response indicating whether the target was an "X" or a "=". The authors hypothesized that attention would be captured to the location of the red-colored cue, but only when participants were cued to respond to red targets and not when they were cued to respond to onset targets. Specifically, they reasoned that when the cue appeared in the same location as the target (valid trial), response times should be faster than when the cue appeared in a different location to the target (invalid trial). Alternatively, if attention was not captured to the location of the cue, then response times should be similar for valid and invalid trials. Using this method, Folk et al. (1992) found that when participants searched for a colored target, a cueing effect was found for color-cue trials, but no cueing effect was found for onset-cue trials. In contrast, when participants searched for onset targets, a cueing effect was found for onset-cue trials, but no cueing effect was found for color-cue trials. These results demonstrate that whether attention is captured to the location of a stimulus is contingent on the observer's current goals.

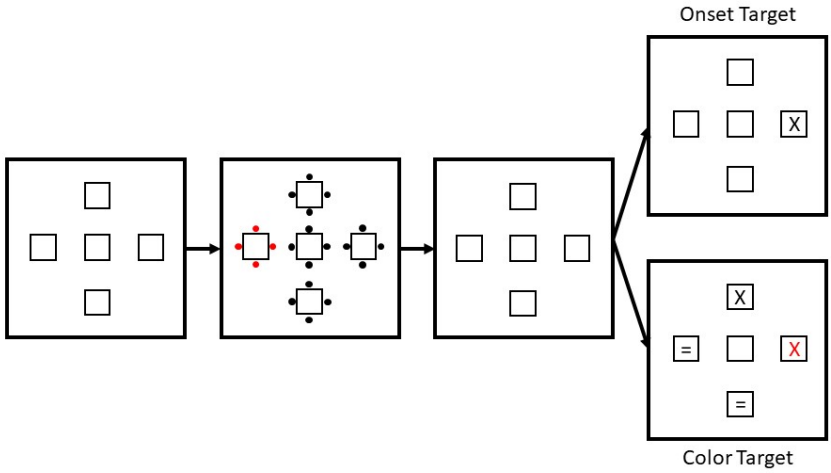

Figure 1.7. Schematic of the sequence of events during the contingent attentional capture paradigm. The sequence consisted of a fixation display, a cue display (50 ms), an interstimulus interval (100 ms), and a target display. The fixation display consisted of one central fixation square and four peripheral cue placeholder squares. During the cue display, four small dots were placed around each square. One set of dots was colored red and acted as the cue, while the other distractor dots were colored white (black dots in the example). The target display was either an onset target display or a color target display. On onset-target displays, a target (X or =) was presented in one of the peripheral squares that either matched the location of the cue (valid trial) or was presented in a different location (invalid trial). On color target displays, all peripheral squares were filled with an item (X or =). One item was colored red and acted as the target (red X in the example). The remaining distractor items were colored white (black items in the example). Figure adapted from Folk, Remington, & Johnson (1992).

At the neural level, contingent attentional capture can be explained by modulation of activity across populations of sensory neurons that represent task-relevant visual features. Specifically, when participants have a goal to find a target defined by a specific feature, neurons that represent that feature increase their firing rate, such that when relevant items are presented, they are more likely to respond than when other features are presented (Martinez-Trujillo & Treue, 2004). When searching the visual world for an item that is defined by a specific feature without knowing its location, it would be beneficial to enhance the relevant feature wherever it appears across the visual field (Herrmann, Heeger, & Carrasco, 2012; Wolfe, 1994). Recent neurophysiological recordings in non-human primates supports this view, providing evidence that feature-based facilitation occurs globally across the visual field (Treue & Martinez-Trujillo, 1999). Similar global enhancements have also been shown in EEG studies of human brain activity (Andersen, Muller, & Hillyard, 2011; Hopf, Boelmans, Schoenfeld, Luck, & Heinze, 2004; Zhang & Luck, 2009).

Enhancement and suppression

A great deal of research has assumed that attention *enhances* representations of relevant stimuli, with little emphasis on the potential role of *suppression* of distracting or task-irrelevant

stimuli. As a reminder, James (1890) defined attention as "*withdrawal from some things in order to deal effectively with others",* implying that attention works to enhance relevant information and suppress irrelevant information. Until recently, little work has addressed the question of whether suppression of irrelevant stimuli is an inevitable consequence of enhancement of relevant inputs, as implied in James' definition, or arises as a separate attentional mechanism independent of facilitation. Evidence from feature-based attention studies has yielded mixed findings.

While some studies have shown both enhancement of relevant features and suppression of irrelevant features (e.g., Stormer & Alvarez, 2014), others have found only a suppression effect (Moher, Lakhmanan, Egeth, & Ewen, 2014) or only an enhancement effect (Painter, Dux, Travis, & Mattingley, 2014). A prominent model of feature-based attention – *the feature similarity gain model* (Treue & Martinez-Trujillo, 1999) – makes no assumptions about the role of suppression in feature-based attention, except to argue that as with feature-based enhancement, if feature-based suppression were to modulate processing it would do so across the visual field. Others, however, have argued that while enhancement acts on stimuli across the entire visual field, suppression acts locally at the attended location (Desimone & Duncan, 1995; Forschack, Andersen, & Muller, 2017; Reynolds & Heeger, 2009). Evidence that enhancement of relevant features acts alone, or is otherwise distinct from suppression of irrelevant features, suggests that enhancement and suppression are two mechanisms that can act independently. As outlined in later chapters of this thesis, whether attention involves independent mechanisms of enhancement and suppression, or enhancement and suppression are different outcomes of a common underlying mechanism, is crucial for the interpretation of studies investigating the relationship between attention and awareness.

Neural mechanisms of visual attention

According to the *biased competition model* enhancement and suppression occur because information must compete for cortical processing (Desimone & Duncan, 1995). This competition is resolved at the neural level by differentially weighting sensory information based on task demands. This bias in the weighting of sensory information affords enhancement of relevant information and filtering out of irrelevant information. Current goals play an important role in biasing the system; stimuli that are currently relevant to an observer's goals receive higher weights and, thus, are more likely to be processed, while irrelevant stimuli receive lower weights and are less likely to be processed (or possibly go unprocessed).

The biasing process of enhancement and suppression can be seen in the firing rate of neurons, which respond preferentially to external stimuli with a specific attribute (e.g., orientation, color, wavelength, or frequency; DiCarlo, Zoccolan, & Rust, 2012; Grill-Spector & Malach, 2004;

Kobatake & Tanaka, 1994; Riesenhuber & Poggio, 1999). For example, neurons in the primary visual cortex are broadly tuned to the specific orientation of an edge or grating (Hubel & Wiesel, 1968), such that they fire maximally to their "preferred" orientation and gradually reduce their responses as stimuli depart further from this orientation. The responses of orientation-selective neurons can be plotted as a *tuning curve* (see Figure 1.8B), in which firing rates are plotted as a function of orientation. The tuning function has a peak, which corresponds to the preferred orientation, a width corresponding to the degree of selectivity of the neuron, and a height, which is a measure of the amplitude of the response.

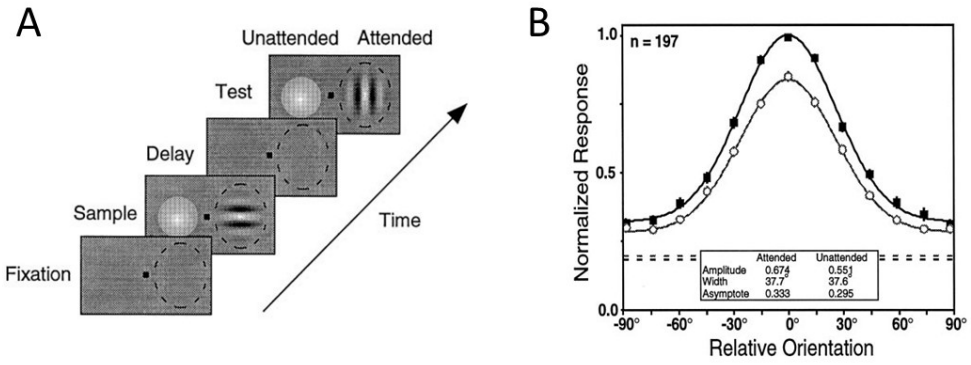

Figure 1.8. Schematic of task sequence from the study by McAdams and Maunsell (1999). (A). The trial sequence consisted of a fixation display, sample display, followed by a delay period and then a test display. During the fixation display, the monkey was required to fixate on a central fixation dot. During the sample display, an oriented grating was presented in the recorded cell's receptive field (dashed oval), and a colored patch was presented in the opposite location. In the attend condition, the monkey was required to attend to the grating (presented in the receptive field), and in the unattended condition, the monkey was required to attend to the color patch (outside the receptive field). Following a delay period, a test display was presented. The monkey was required to report whether the test stimulus at the attended location matched the sample stimulus or was a mismatch. In the above example, the orientation task would be a mismatch trial as the orientation of the test stimuli did not match the orientation of the sample stimulus. (B). Population-tuning curves for V4 neurons during a match-to-sample (attended) task (black squares) and during the color (unattended) task (white circles). The x-axis represents grating orientation relative to the preferred orientation of the neuron (0 degrees = preferred orientation). The y-axis represents the normalized response from recorded neurons. The dashed lines represent the average neural activity during fixation. Figure from McAdams and Maunsell (1999).

When an animal performs an orientation discrimination task, neurons that represent goal-relevant orientations increase their firing rate (response gain), while the firing rate of neurons that represent orthogonal orientations is decreased (Desimone & Duncan, 1995; Maunsell, 2015; Reynolds & Heeger, 2009; Verhoef & Maunsell, 2017). This attentional modulation manifests as an increase in the height of the tuning function. For example, McAdams and Maunsell (1999; see

Figure 1.8A) recorded from orientation-selective neurons in cortical area V4 of rhesus monkeys while the animals performed a delayed match-to-sample task that required attending to oriented gratings or a color task that required the animals to ignore the gratings. During the match-to-sample task, the monkeys were shown a sample grating. After a short delay, a second (test) grating was presented that either matched the orientation of the sample grating or was a different orientation. The gratings were presented in the recorded neuron's receptive field or were presented in a different location. When gratings were attended and presented in the neuron's receptive field the height of the tuning function was increased relative to when the grating was in an unattended location (see Figure 1.8B). This finding suggests that the firing rate of the same population of neurons is dependent on the task at hand.

It is important to note that the biasing of sensory neurons that afford enhancement and suppression of a given stimulus, location or feature does not necessarily evoke perceptual awareness of that stimulus, location or feature. Indeed, much evidence suggests that attention works to modulate the processing of sensory input without yielding perceptual awareness. I discuss this evidence in more detail below.

1.4 What is Perceptual Awareness?

I began this chapter by describing the subjective sense of experiencing the external world. Commonly, this subjective sense is what is meant by "conscious" experience. But consciousness is used to describe many different phenomena. It can refer to the *contents of consciousness* (as in experiences upon waking), and to the *state of consciousness* (e.g., sleep versus wakefulness; Posner, 2012). Here I am interested in the former and thus, throughout the thesis, I will use the more specific term *perceptual awareness* to refer to the contents of consciousness.

1.5 Evidence in support of the three views on how attention and awareness relate

As stated above, views on how attention and perceptual awareness relate are diverse but can be loosely categorized into three main views: The no dissociation view, the single dissociation view, and the double dissociation view. Proponents of the no dissociation view argue that attention and perceptual awareness are the same processes (Chun & Wolfe, 2000; De Brigard & Prinz, 2010; Mole, 2008; O'Regan & Noe, 2001; Posner, 1994; Prinz, 2011; 2012; Wolfe, 1999). Proponents of the single dissociation view argue that while attention and perceptual awareness occur together, they can nevertheless be dissociated such that attention is the critical antecedent of perceptual awareness (Cohen, Cavanagh, Chun & Nakayama, 2012; Pitts, Lutsyshyna, & Hillyard, 2018). In short, attention can occur without perceptual awareness, but perceptual awareness cannot occur without attention. Proponents of the double dissociation view agree that attention and awareness often go together, and that attention can occur without perceptual awareness but, controversially,

they also argue that perceptual awareness can occur without attention, such that awareness is rich in content and does not require attention (Block, 2006; 2011; Koch & Tsuchiya, 2007; Tsuchiya & Koch, 2016).

1.5.1 The no dissociation view

Evidence for the no dissociation view has come principally from studies of inattentional blindness, change blindness, and how perceived contrast is modulated by attention, as described in detail below.

Inattentional Blindness

Possibly the strongest evidence in support for the no dissociation view comes from work on inattentional blindness (Devue, Laloyaux, Feyers, Theeuwes & Bredart 2009; Mack & Rock, 1998; Most, 2010; Pitts, Martinez, & Hillyard, 2012; Schelonka, Graulty, Canseco-Gonzalez, & Pitts, 2017; Shafto & Pitts, 2015; Wood & Simons, 2017; Wood, 2019). In their experiments, Mack and Rock (1998) had observers monitor a centrally located cross and asked observers to identify which arm of the cross (vertical or horizontal) was longer (see Figure 1.9A). After several trials, an additional unexpected stimulus was presented near fixation (see Figure 1.9B). Immediately following this, the experiment was interrupted, and participants were asked whether they had noticed an additional stimulus on the immediately preceding trial. Over many experiments, Mack and Rock (1998; see also Moray, 1959; Neisser, 1979; Neisser & Becklen, 1975;) found that, on average, 60-80% of participants failed to see the additional, unexpected stimulus. Critically, in subsequent trials, when participants were asked explicitly to monitor for any additional stimulus, they had no problem seeing and identifying it. Some have argued that evidence from these classic inattentional blindness studies suggest that attention and awareness are identical (De Brigard & Prinz, 2010). But Mack and Rock (1998) found that some stimulus types, such as faces and one's name, were less prone to inattentional blindness than other types of stimuli, suggesting that some stimuli may require limited, or no, attentional resources for perceptual awareness (but see below for a critical review of this interpretation).

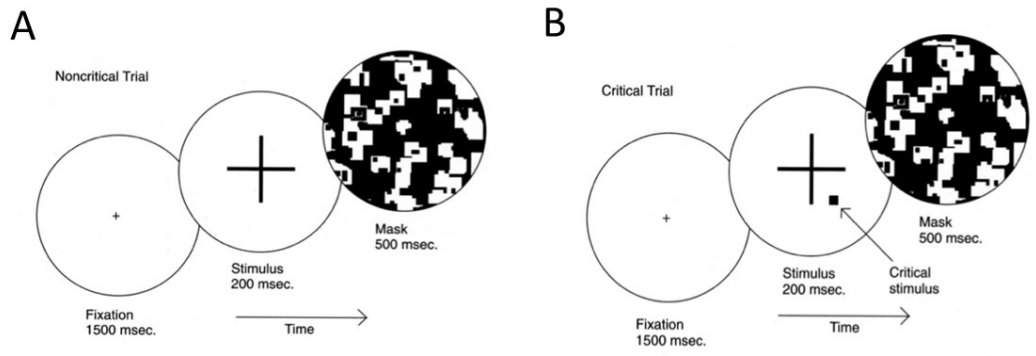

Figure 1.9. Schematic of a typical inattentional blindness task. (A) An example of a non-critical trial, in which participants are asked to indicate which arm of the cross (vertical or horizontal) is longer, and the critical stimulus is not presented. (B) An example of a critical trial, in which participants performed the cross task, and a critical (unexpected) stimulus was presented. Task diagram from Mack and Rock (1998), with permission (License number: 4730391186908).

Change Blindness

Studies of inattentional blindness have shown that a small object near fixation can go unnoticed without attention. A similar phenomenon — *change blindness* — demonstrates that observers can fail to notice large changes in a visual scene when attention is not directed to the location of the change. In the original version of the paradigm (Rensink, O'Regan & Clark, 1997; Rensink, 2000), two images of a scene are presented sequentially with a blank screen presented between the two images, or a high-contrast local mask – referred to as a 'mud-splash' – is presented simultaneously with one of the images (O'Regan, Rensink, & Clark, 1999). The two images are identical except for one (sometimes large) difference (see Figure 1.10; Rensink, 2007). The blank screen, or mud-splash, acts as a masking stimulus. If the blank screen is removed, or no mud-splashes are presented, observers are significantly more likely to detect the change (Simons, 2000). The presentation of the images repeats until the observer reports the change. Despite the change being a large object in the scene, observers often take several seconds before reporting the change. It is not until observers attend to the location of the change that they become aware of it, suggesting that attending to the change brings it into awareness. In this context it is worth noting that stimuli which are assumed to be processed holistically, such as faces, are less susceptible to change blindness than other stimuli (Wilford & Wells, 2010). In addition, changes located toward the center of the display are noticed faster than changes in the periphery (Rensink, O'Regan, & Clark, 1997), probably because attention is initially focused in this region.

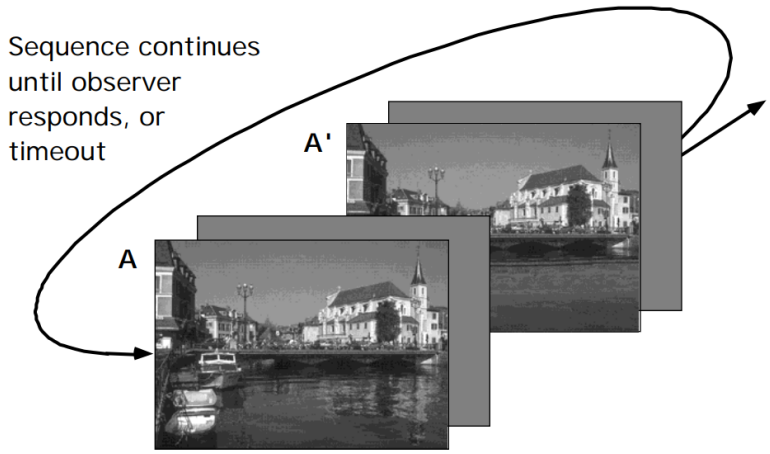

Figure 1.10. Example display used to demonstrate change blindness. An original image and a modified image alternate with a blank image presented between each scene presentation. The alternating images continue until the observer reports seeing the change, which can take several seconds. In this example the castle reflection is missing from the second image. Figure taken from Rensink (2007).

Modulation of perceived contrast by attention

Other evidence in support of the no dissociation view includes tasks that involve working memory, detecting and discriminating unexpected or unfamiliar stimuli, and verbal reportability (Koch & Tsuchiya, 2007); under these conditions, attended stimuli invariably become the content of perceptual awareness. A less obvious observation is that attention can increase contrast gain (Cameron et al., 2002; Carrasco, Penpeci-Talgar & Eckstein, 2000; Ling & Carrasco, 2006; Martinez-Trujillo & Treue, 2002; Reynolds et al., 2000). That is, attention can increase the perceived contrast of a stimulus and, consequently, has a direct influence on perceptual awareness. For example, Carrasco, Ling, & Read (2004; see Figure 1.11) presented participants with two oriented gratings (one to the left and one to the right of fixation) and had participants identify the grating that appeared higher in contrast and report its orientation (left or right). Before the gratings were presented, however, a cue was presented to the left or right of fixation. The researchers found that gratings of the same contrast value were perceived as having higher contrast when they were presented in the same location as the cue compared with when they were presented in the opposite location. These results suggest that attention was "captured" to the location of the cue and altered the appearance of the gratings by boosting their apparent contrast.

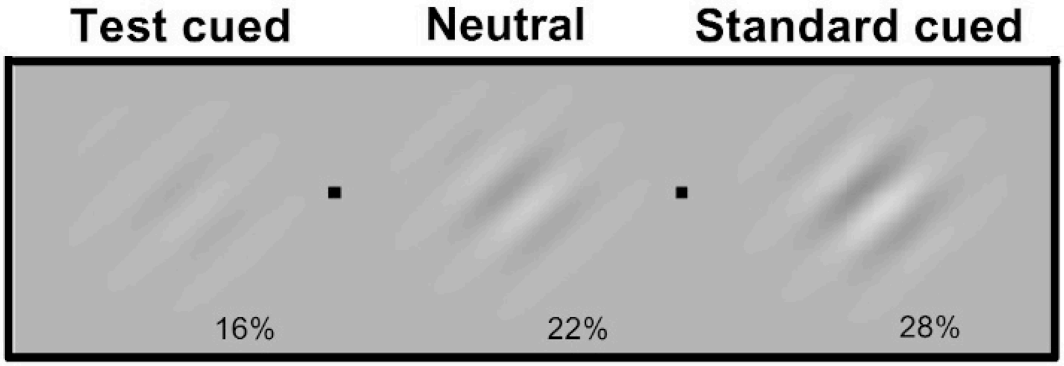

Figure 1.11. Example of the effect of attention on perceived contrast. While fixating the black fixation dot between the 16% and 22% contrast gratings and covertly attending to the 16% stimulus, the contrast of the 16% stimulus appears equivalent to that of the 22% stimulus. Similarly, while fixating the black fixation dot between the 22% and 28% contrast grating and covertly attending to the 22% stimulus, the contrast of the 22% stimulus appears equivalent to that of the 28% stimulus. Figure reproduced from Carrasco, Ling & Read (2004), with permission (License number: 4727450410297).

Summary of the no dissociation view

There have been a number of proponents of the view that attention and perceptual awareness are inextricably linked, if not identical (Chun & Wolfe, 2000; De Brigard & Prinz, 2010; Mole, 2008; O'Regan & Noe, 2001; Posner, 1994; Prinz, 2011, 2012; Wolfe, 1999). The findings outlined above in support of this view are not necessarily in opposition to the single dissociation and double dissociation views. Both the single- and the double dissociation views acknowledge that under most circumstances, attention and awareness appear to be intimately connected. The single- and double dissociation views, however, claim that under certain circumstances, attention and perceptual awareness can be dissociated at least to some degree, as outlined below.

1.5.2 The single dissociation view

Proponents of the single dissociation view argue that attended stimuli can fail to reach awareness even with goal-directed attention (Cohen, Cavanagh, Chun & Nakayama, 2012; Pitts, Lutsyshyna, & Hillyard, 2018). As well as evidence from visual search tasks, experimental evidence in support of the single dissociation view has come principally from adaptation and masked priming studies.

Adaptation

Adaptation to a visual stimulus can produce an *afterimage* – a percept that is complementary to the adapting stimulus and persists after the original adapting stimulus is removed. For example, adaptation to an oriented grating causes a subsequently presented grating to appear tilted away from the orientation of the adaptor (*the tilt aftereffect*; Gibson & Radner, 1937). Across many studies, attention has been shown to modulate the magnitude of the tilt aftereffect or the duration of a *negative afterimage* (Alais & Blake, 1999; Brascamp, van Boxtel, Knapen, & Blake, 2010a; Chaudhuri, 1990; Kanai, Tsuchiya, & Verstraten, 2006; Lak, 2008; Liu, Larsson, & Carrasco, 2007; Lou, 2001; Melcher, 2009; Montaser-Kouhsari & Rajimhehr, 2005; Mukai & Watanabe, 2001; Rees, Frith, & Lavie, 1997; Rezec, Krekelberg, & Dobkins, 2004; Shulman, 1992; Spivey & Spirn, 2000; Suzuki, 2001; Suzuki & Grabowecky, 2003; van Boxtel et al., 2010a; von Grunau, Bertone, & Pakneshan, 1998; Wede & Francis, 2007; Yeh, Chen, De Valois, & De Valois, 1996; for a review see Alais, 2005). For example, Suzuki and Grabowecky (2003) presented two overlapping inducer triangles, one upright and one slightly tilted (Figure 1.12). During adaptation, participants were asked to fixate centrally and attend to one triangle while ignoring the other. After adaptation, participants were asked to describe their afterimage experience. When the inducer triangles were presented in the same color (e.g., both blue), attention did not modulate the afterimage. When the inducer triangles were presented in different colors (e.g., one blue and one green), however, participants described the afterimage of the attended triangle as weaker than the afterimage of the ignored triangle, suggesting that focused attention somehow decreases afterimage strength.

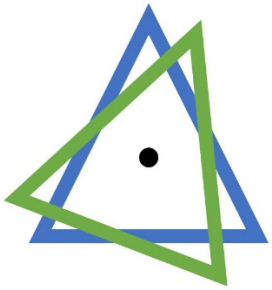

Figure 1.12. Example of an afterimage inducer stimulus. Participants fixated the central dot and attended to the upright (blue) or tilted (green) triangle during the adaptation phase. After adaptation, participants verbally described their afterimage. Figure adapted from Suzuki and Grabowecky (2003).

Recent evidence has challenged the idea that attention decreases afterimage duration, suggesting instead that the effect of attention on aftereffects depends on the type of attention deployed during a task (Baijal & Srinivasan, 2009; Kanai, Tsuchiya, & Verstraten, 2006). For

example, Kanai, Tsuchiya, and Verstraten (2006) used the tilt aftereffect (Gibson & Radner, 1937; Morant & Harris, 1965; Muir & Over, 1970) to investigate the effects of spatial and feature-based attention on afterimages. They had participants adapt to a grating and either attend to the location of the adapting stimulus (spatial attention manipulation) or attend to the specific orientation of the adapting stimulus (feature-based attention manipulation). After adaptation, participants were shown a test stimulus of varying orientations and asked whether it was tilted to the left or right. They found that both spatial and feature-based attention *increased* the magnitude of the tilt aftereffect. The authors used a masking technique called *continuous flash suppression* (CFS; Gilroy & Blake, 2005; Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006), in which awareness of the adapting stimulus was manipulated by presenting the gratings to one eye, and on unaware trials presenting a dynamic mask to the other eye (Figure 1.13). Under these conditions, an observer is more likely to consciously perceive the highly salient dynamic mask than the static grating. In Kanai, Tsuchiya, and Verstraten (2006), when the adapting stimulus was rendered invisible through CFS, the researchers found that spatial attention no longer modulated the magnitude of the afterimage. Interestingly, feature-based attention continued to modulate the magnitude of the afterimage despite participants being unaware of the adapting stimulus. These results suggest that the effects of attention might depend both on awareness of the adapting stimulus and the type of attention deployed during the task. Thus, the relationship between attention and awareness is likely more nuanced than originally supposed.

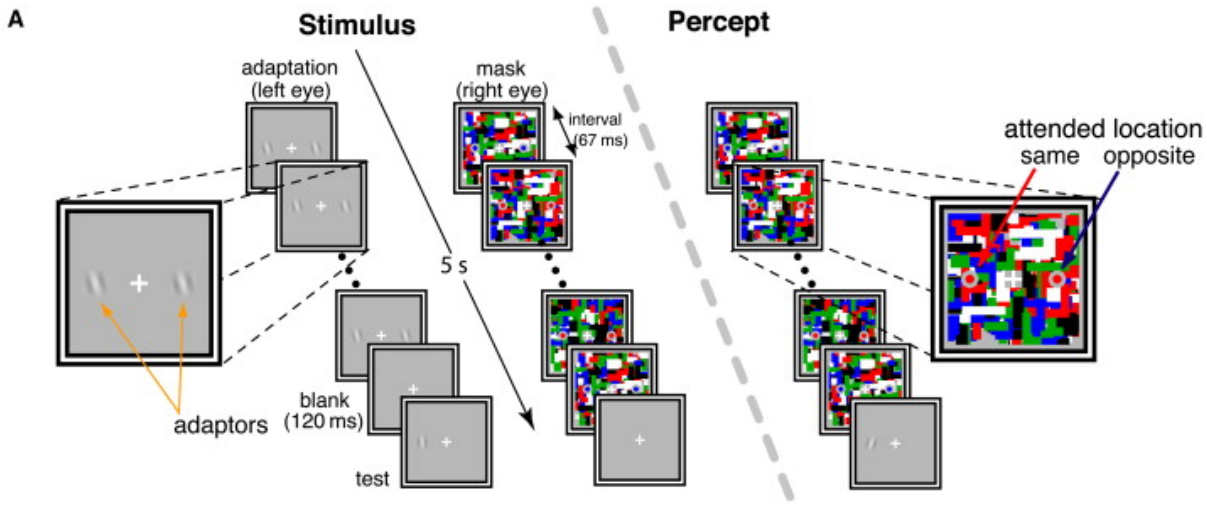

Figure 1.13. Schematic of the spatial attention task from the study by Kanai, Tsuchiya, and Verstraten (2006). The left side of the figure shows the stimulus. During adaptation, two adaptor gratings were presented to the left eye, and a high-contrast dynamic Mondrian mask was presented to the right eye. Two fixation circles were presented on top of the Mondrian masks and participants were instructed to attend to one of the circles. After adaptation, a test stimulus was presented in the attended location (attended) or in the opposite location (unattended). Participants reported whether the

test stimulus was oriented to the left or right. The right side of the figure shows participants' percept during the task. Figure reproduced from Kanai, Tsuchiya, and Verstraten (2006), with permission (License number: 4727450703367).

Masked Priming

Masked priming studies are commonly used to investigate the role of unconscious stimuli on behavior and neural responses (Forster, Mohan & Hector, 2003; Forster & Davis, 1984). Priming is a technique in which a stimulus (the prime) is presented that influences an observer's response to a subsequent stimulus. Masked priming is simply the technique of using a masking procedure to reduce the visibility of the prime. For example, Palmer and Mattler (2013) presented a central cue that indicated whether an observer should report a subsequent left- or right-sided target (see Figure 1.14). Unbeknownst to the observer, the cue was preceded by a prime that was either congruent with the cue (e.g., both were square, or both were diamond-shaped) or was incongruent with the cue (e.g., one was a square and the other a diamond). Observers were faster when the prime and cue were congruent than when they were incongruent, suggesting that the prime influenced the shifting of attention in the absence of awareness of the prime.

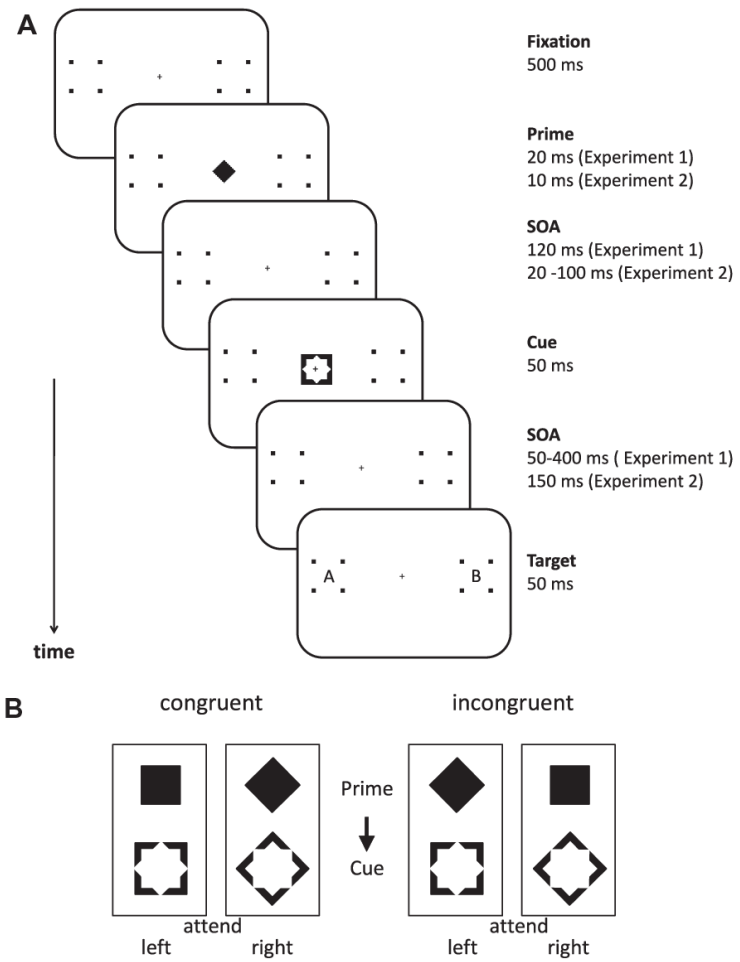

Figure 1.14. Schematic of trial sequence and stimuli from the masked priming study of Palmer and Mattler (2013). (A) Example of a trial sequence. After fixation, a brief prime was presented, followed by a cue that instructed participants to report the upcoming right or left target. In the example, square cues indicted that the left target was to be reported, whereas diamond cues indicated that the right target was to be reported. (B) The prime was either congruent with the cue (e.g., the prime was square-shaped and the cue was square-shaped) or was incongruent with the cue (e.g., the prime was diamond-shaped and the cue was square-shaped). Participants were instructed to make their response as quickly and as accurately as possible. Figure reproduced from Palmer and Mattler (2013), with permission (License number: 4727450917923).

1.5.3 The double dissociation view

Proponents of the double dissociation view argue that attention can act on sensory inputs without perceptual awareness, but they also make the more provocative claim that an observer can be perceptually aware of a stimulus without attention (Koch & Tsuchiya, 2007; Tsuchiya & Koch, 2016). As proponents of the single dissociation view and the double dissociation view agree about the first claim, much of the evidence presented in support of a double dissociation relates to the second claim that observers can be aware of a stimulus without attending to it. In this section, I

review the evidence presented in support of a double dissociation, and then present recent findings that counter that evidence.

Gist

Evidence commonly given in support of a double dissociation is that observers can readily glean the *gist* (or the meaning) of a scene that is flashed briefly (Koch & Tsuchiya, 2007; Lamme, 2004; Tononi & Koch, 2008). Even when performing a demanding attentional task, observers are able to extract the gist of a scene with similar accuracy as conditions in which no additional task is performed, suggesting that gist information does not require attention (Biederman, 1972; Li, VanRullen, Koch, & Perona, 2002; Mack & Rock, 1998; Potter, 1975; Rensink et al., 1997; Rousselet, Fabre-Thorpe & Torpe, 2002; Simons & Levin, 1997; Thorpe, Fize, & Marlot, 1996). Other work, however, has suggested that the attention tasks employed in studies of gist perception have not been particularly taxing and thus might not represent a strong test of the gist hypothesis (Cohen, Alvarez, & Nakayama, 2011; Evans & Treisman, 2005; Mack & Clarke, 2012; Marois, Yi & Chun, 2004; Rousselet, Thorpe, & Fabre-Thorpe, 2004; Slagter, Johnstone, Beets & Davidson, 2010). For example, Cohen, Alvarez, & Nakayama (2011) had observers perform a relatively difficult attentional task, in which they were required to track multiple moving objects, while checkerboard images changed in the background (Figure 1.15). On the final, critical, trial the second-to-last background checkerboard was replaced, briefly, with an image of a natural scene. Most observers (64%) were unable to identify the scene, suggesting that when an attention task is sufficiently demanding, awareness of the gist of the scene is indeed impaired. Thus, extracting the gist of a briefly presented scene seems to rely at least to some extent on the availability of attentional resources.

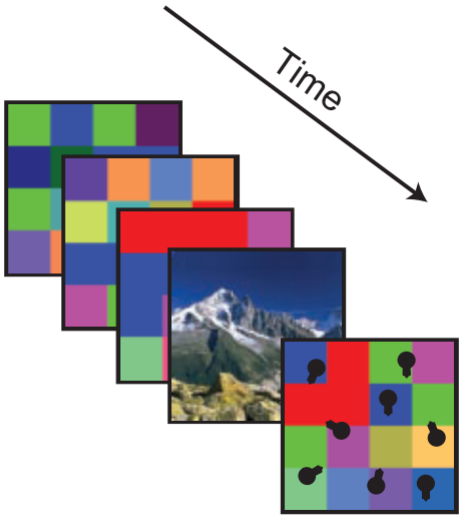

Figure 1.15. Schematic of trial sequence from a gist perception study. Eight moving dots were presented on top of rapidly changing colored checkerboards (every 67 ms). Participants were required to track the location of fours of the moving dots. On the critical trial, a checkerboard image was replaced by an image of a natural scene. After the critical trial, participants were asked questions about their subjective experience of the unexpected scene. Figure reproduced from Cohen, Alvarez, & Nakayama (2011), with permission (License number not required).

Observers' ability to rapidly extract the gist of a scene is thought to occur through ensemble encoding. Ensemble encoding is the ability to extract summary statistical information from stimuli or to process statistical regularities in visual information, such as average motion direction, speed, orientation, size, position, density, or facial expression (Whitney, Haberman, & Sweeny, 2014). Some have argued that ensemble encoding can occur without attention (Bronfman, Brezis, Jacobson & Usher, 2014; Block, 2014). As suggested above, people are efficient in extracting such information from natural scenes, but evidence suggests that observers are also able to accurately perceive the average direction of motion, average size, average orientation, the density of objects from multiple moving stimuli, or color diversity from a display of multiple colors (Chong & Treisman, 2003; Dakin & Watt, 1997; Bauer, 2009; Watamaniuk & Duchon, 1992). Claims have been made that ensemble encoding does not require attention (e.g., Bronfman, Brezis, Jacobson, & Usher, 2014), but there is evidence to contradict this view. For example, Jackson-Nielsen, Cohen & Pitts (2017) had participants perform a working memory task in which a matrix of various colored letters (4 x 6) were presented. One row in the matrix was cued and participants were required to remember and then report as many letters in the cued row as they could (single task) or report as many letters and their colors as they could (dual-task). On the critical trial, instead of reporting the cued row, participants were presented with three-letter matrices and asked to report which matrix was most like the matrix that was just presented. One matrix contained letters that were similar in

color to the just-presented matrix, while the other two matrices contained letters that were colored differently to the just-presented matrix. The authors found that participants were much less accurate at identifying the just-presented matrix under dual-task conditions relative to single-task conditions. The authors reasoned that as participants were cued to attend to just one row and the critical trial was presented unpredictably, participants had no reason to attend to the entire matrix. Thus, participants were not sensitive to the statistical regularities in the displays, suggesting that they were inattentionally blind to the ensembles.

Iconic memory

Sperling's classic iconic memory test (Sperling, 1960) is often presented in support of a double dissociation between attention and perceptual awareness. In one variant of his classic experiment, a matrix of letters is briefly presented (50ms; see Figure 1.16). If asked to report all letters in the display, observers can usually report approximately 4-6 letters. If one of the rows of the matrix is cued after the matrix disappears, the observer can typically report all letters in that row. Given that observers do not know in advance which row will be cued, Sperling argued that, for a limited amount of time, observers must have access to all the information in the matrix. Block (2005) has argued that because the matrix display is presented very briefly, there is not sufficient time for attention to exert an effect and, thus, iconic memory of the matrix does not require attention (Block, 2005; see Lamme (2003) for a similar argument). However, several studies have shown that when combined with a sufficiently taxing attentional task, iconic memory does in fact draw on attentional resources (Mack, Erol, & Clarke, 2015; Mack, Erol, Clark, & Bert, 2016; Mack, Erol & Clark, 2017).

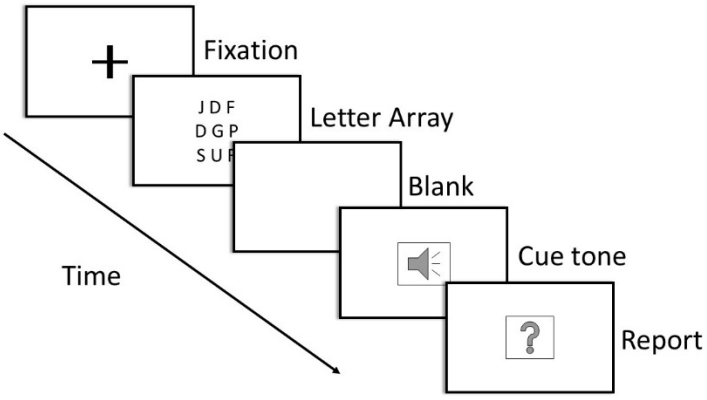

Figure 1.16. Schematic of task sequence from Sperling (1960). Observers were shown a matrix of letters and symbols followed by a blank delay of variable length. Then, in the "partial report" condition, an auditory cue was presented, with the pitch indicating which row of the matrix the observers were required to report. Figure adapted from Sperling (1960).

Familiarity

The evidence reviewed thus far suggests that the gist of a scene, ensemble encoding, and iconic memory require attention, but it might be asked whether some stimuli are so familiar that they do not require attention for awareness. The cocktail party effect provides an apt example. When in a crowded room, partygoers can focus on one conversation without being distracted by neighboring conversations. However, the mention of one's name in a neighboring conversation will immediately result in awareness of the utterance (Moray, 1959). Some have argued that highly familiar stimuli, such as one's name, do not require attention for awareness (Li, VanRullen, Koch, & Perona, 2002; Mack & Rock, 1998; Triesman & Gelade, 1980). Others, however, have shown that when engaged in a sufficiently demanding attention task, even highly familiar stimuli can go undetected (e.g., Cohen, Cavanagh, Chun, & Nakayama, 2012; Devue, Laloyaux, Feyers, Theeuwes, & Brédart, 2009). For example, using an inattentional blindness paradigm, Devue et al. (2009) presented images of the participant's own face, a friend's face, or a stranger's face, as the unexpected stimulus. Under these conditions, the researchers found no difference in inattentional blindness rates between own and other faces, suggesting that awareness of familiar faces requires attention.

Opposing effects of attention and awareness

One highly cited paper has provided seemingly strong evidence in support of the double dissociation view of attention and awareness (van Boxtel, Tsuchiya, & Koch, 2010a). In this study, the authors employed a 2 (attention vs. no attention) x 2 (aware vs. unaware) design to simultaneously investigate the effects of attention and awareness on afterimage duration. In this work, van Boxtel et al. (2010a) had observers report the duration of an afterimage, which was induced by an adapting stimulus that was either visible or rendered invisible using CFS (Figure 1.17). During adaptation, observers performed a high- or a low-load secondary task at fixation. As described earlier in this chapter, attentional load was manipulated by presenting a stream of upright and inverted crosses in various colors (see Figure 1.5). In the low-load condition, participants were asked to count the number of upright and inverted red crosses (1, 2, 3, or 4). In the more difficult high-load condition, participants were asked to count the number of upright green and inverted yellow crosses. Consistent with load theory (Lavie, 1995; 2000; 2001), the authors reasoned that under low-load, residual perceptual resources would be available to process the adaptor, whereas under high-load little or no perceptual resources would be available for processing the adapting stimulus. They found that attention and awareness had opposing effects on afterimage duration. Specifically, while awareness of the adapting stimulus increased afterimage duration, attention to

the adapting stimulus reduced afterimage duration, suggesting that attention and awareness can have opposing effects on afterimage duration and are, thus, independent processes.

1.6 Overview of this thesis

1.6.1 Re-examining the opposing effects of attention and awareness

In **Chapter 2,** I describe two experiments in which I set out to replicate the key experiments of van Boxtel et al. (2010a) to investigate whether attention and awareness do indeed have opposing effects. In doing so, I also address several weaknesses of the van Boxtel et al. study. First, the original experiments were statistically underpowered. The sampling distribution for a low-powered study is typically wider than the sampling distribution for a high-powered study (Button et al., 2013). Thus, if the null hypothesis is rejected with a low-powered study, the sample mean tends to be larger than when the null hypothesis is rejected in a high-powered study (Button et al., 2013). Therefore, a statistically significant finding from a low-powered study is less likely to reflect the true effect and more likely to overestimate the effect size when compared with a statistically significant finding from a high-powered study (Button et al., 2013). There were very low participant and trial numbers used in most of the experiments reported in van Boxtel et al. (2010a). For example, in their Experiment 3, nine participants performed just eight trials in each condition, which would be expected to yield a rather poor estimate of true afterimage duration. Moreover, after removing incorrect trials, data from approximately six trials per participant per condition were included in the final analysis. A further issue concerns the inclusion criteria adopted in van Boxtel et al. (2010a). Here, the authors relaxed their inclusion threshold such that responses equal to the correct number of targets ±1 were included in the analysis. Consequently, on one- and four-target trials, two different responses were classified as 'correct,' so that chance performance was equal to 50%. On two- and three-target trials three of the four possible responses were considered correct, so that chance performance was now equal to 75%. Despite the lenient threshold, ~30% of trials were removed from the analysis.

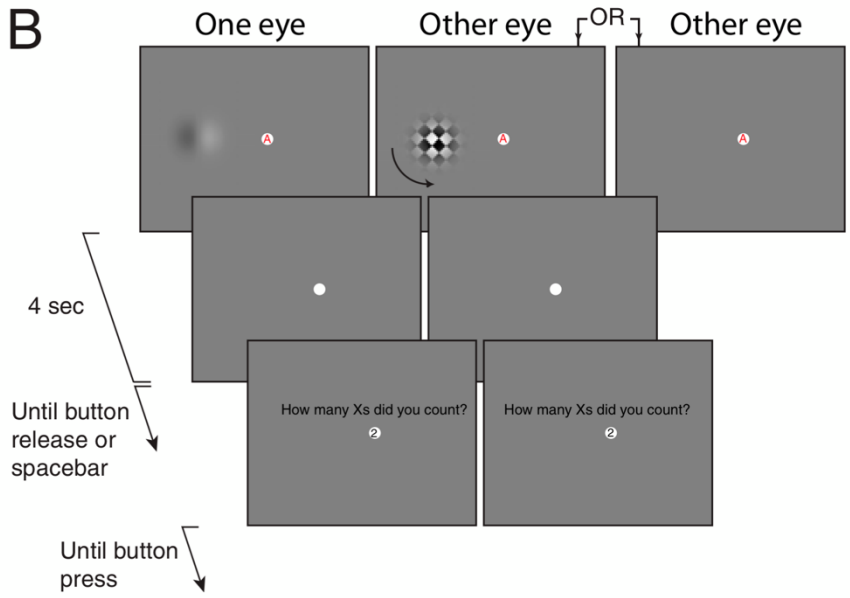

Figure 1.17. Schematic of displays used in van Boxtel et al. (2010a). Each trial began with a 4-second adaptation phase. The adaptation stimulus was a peripheral Gabor patch. Attention was manipulated by a central *rapid serial visual presentation* (RSVP) task that required relatively low attentional load (their so-called 'high attention' condition) or high attentional load (their 'low attention' condition). Visibility of the adaptor was manipulated by presenting a dynamic checkerboard mask to the eye contralateral to the adapting stimulus (unaware condition), or no mask was presented (aware condition). After the adaptation phase, observers indicated afterimage duration by pressing and releasing a mouse button. After recording the afterimage duration, observers responded to the attention task. Figure reproduced from van Boxtel, Tsuchiya, Koch, (2010a), with permission (License number not required).

1.6.2 How enhancement and suppression relate to awareness

Earlier in this chapter, I reviewed evidence suggesting that attention may involve independent processes of enhancement and suppression, and suggested that such evidence could have implications for understanding the relationship between attention and perceptual awareness. Recent work by Lamy, Alon, Carmel, & Shalev (2015) provided an interesting answer to this question. Lamy et al. (2015) combined a variant of the contingent capture paradigm with CFS masking (Figure 1.18). They presented a dynamic mask to one eye; in the same eye and in front of the dynamic mask, they displayed four white T-shaped target placeholders and a central fixation cross. In the other eye, four white cue placeholders were presented such that they were in the same retinal locations as the T-shaped target placeholders in the other eye. Toward the end of the trial, each T-shaped placeholder changed color, such that the four T-shapes were red, blue, green, and yellow. Participants searched for a target of a specific color (e.g., red) and were asked to report the orientation of the target (rotated 90° to the left or 90° to the right) as quickly as possible. Immediately before the T-shapes changed color, one of the cue-placeholders changed color to either

the target color (target-colored cue) or a different color (distractor-colored cue). After making their response to the target, participants reported their awareness of the cue on a four-point scale (0 = not visible at all; 3 = clearly visible).

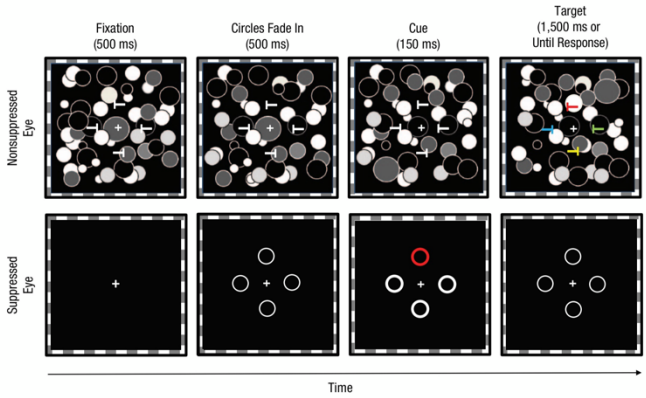

Figure 1.18. Schematic of the trial structure in the study of Lamy et al. (2015). A dynamic mask and four white T-shapes were presented to one eye throughout the experiment. After fixation, the cue-placeholders gradually increased in luminance in the suppressed eye. A colored cue was then presented to the suppressed eye. The cue either matched the target color (target-colored cue) or was a distractor color (distractor-colored cue). In the immediately following target display, each of the four T-shapes took on a unique color (red, blue, green, or yellow). Participants first indicated the orientation of the target T-shape as quickly and as accurately as possible, and then reported their awareness of the cue on a scale from 0 (not visible) to 3 (clearly visible). Figure reproduced from Lamy, Alon, Carmel, & Shalev (2015), with permission (License number not required).

In line with classic contingent capture findings (Folk et al.,1992), participants were faster at responding to the target when a target-colored cue was presented in the same location as the target relative to when a target-colored cue was presented in a different location. Interestingly, this effect occurred even when participants reported being unaware of the cue due to the CFS mask, supporting the conclusion of Kanai et al. (2006) that feature-based attention can occur independently of awareness. In contrast, when a distractor-colored cue was presented in the same location as the target, participants were slower to respond to the target than when a distractor-colored cue was presented in a different location. Surprisingly, this effect only occurred when participants were aware of the cue. There was no difference in response times between the same location and the different location distractor-colored cues when participants were not aware of these cues. These results have important implications for understanding the relationship between attention and awareness. The independence of feature-based attention from awareness depends on the stimulus feature. While the feature-based attentional enhancement of goal-relevant features can occur independently of awareness, the suppression of goal-irrelevant features depends on awareness.

In **Chapter 3** of this thesis, I extend the pioneering work of Lamy et al. (2015) by combining behavioral measures (accuracy and reaction times) with scalp-recorded EEG to investigate whether the behavioral and neural signatures of feature-based cueing effects are similar for aware and unaware cues. Considering the results of Lamy et al. (2015), I predicted that feature-based enhancement should interact with awareness differently from feature-based suppression.

1.6.3 Awareness and decision-making

When an observer reports that he or she is aware of a stimulus, there are several processing stages that contribute to the final decision: sensory evidence accumulation, decision formation, motor preparation, and response execution (Sternberg, 1969). Understanding the neuroscience of decision-making provides insight into how the brain deliberates and ultimately makes a choice. The aim of the work presented in **Chapter 4** was to understand when awareness emerges during decision-making, and how awareness interacts with the decision-making process. In this work, I employed EEG to measure brain responses to gratings that progressively increased in contrast using a *continuous flash suppression* paradigm combined with *frequency tagging* of the critical stimuli (Müller et al., 1998; Müller & Hillyard, 2000). The goal of this study was to examine the emergence of feature-specific information in neural encoding of a masked stimulus during perceptual decision making. Specifically, the stimulus consisted of a flickering grating presented to one eye that ramped up in contrast over a five-second trial while a high contrast counter-phasing rotating mask was presented to the other eye. The participant's task was to monitor the display and, when aware of the grating, report whether its orientation was rotated relative to a central cue. The frequency tagging method takes advantage of the finding that stimuli that flicker (or oscillate) at a specific frequency induce a *steady-state visual evoked potential* (SSVEP) at the same frequency (and their harmonics; Regan, 1966; Vialatte et al., 2010; Norcia et al., 2015). When multiple images are presented at different frequencies, each image can be "tagged" by its specific frequency. Thus, each stimulus can be independently tracked during task performance. In **Chapter 4** I used time-frequency analyses to quantify neural responses specific to the flickering grating. I also employed forward encoding modeling (e.g. Garcia, Srinivasan, & Serences, 2013) of the time-frequency data to generate tuning functions for orientation information across the entire trial, and analyzed the centroparietal-positivity (CPP), an ERP component thought to track evidence accumulation for determining a subsequent action independently of motor preparation signals (Kelly & O'Connell, 2013; Loughnane, et al., 2016; O'Connell, Dockree, & Kelly, 2012).

1.7 Summary of aims

The overarching aim of this thesis is to contribute to the long-standing debate as to how attention and perceptual awareness interact. The thesis is divided into three empirical chapters. In **Chapter 2**, I endeavored to replicate the key experiments reported by van Boxtel et al. (2010a), the results of which led the authors to conclude that there is a double dissociation between attention and awareness. In **Chapter 3**, I combined behavioral testing and EEG to investigate whether the effects of two aspects of attention – enhancement of goal-relevant stimuli and suppression of goal-irrelevant stimuli – depend on awareness. In **Chapter 4,** I investigated the processing stages involved in perceptual decision-making, from stimulus onset, through unaware processing stages, stimulus awareness and response. In **Chapter 5**, I provide a summary of the empirical chapters and argue that the findings align most closely with the single dissociation view, in which attention is the critical antecedent to awareness.

Chapter 2 : Re-examining the influence of attention and consciousness on visual afterimage duration

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Travis, S.L., Dux, P.E., & Mattingley, J.B. (2017). Re-examining the influence of attention and consciousness on visual afterimage duration. *Journal of Experimental Psychology: Human Perception and Performance, 43 (12)*,1944- 1949.

2.1 Abstract

The relationship between visual attention and conscious perception has been the subject of debate across a number of fields, including philosophy, psychology and neuroscience. While some researchers view attention and awareness as inextricably linked, others propose that the two are supported by distinct neural mechanisms that can be fully dissociated. In a pioneering study, van Boxtel, Tsuchiya, and Koch (2010a) reported evidence for a dissociation between attention and conscious perception using a perceptual adaptation task in which participants' perceptual awareness and visual attention were manipulated independently. They found that participants' awareness of an adapting stimulus increased afterimage duration, whereas attending to the adaptor decreased it. Given the important theoretical implications of these findings, we endeavored to replicate them using an identical paradigm, while dealing with some potential shortcomings of the original study by adding more trials and a larger participant sample. Consistent with van Boxtel et al. we found that afterimage duration was reliably increased when participants were aware of the adapting stimulus. In contrast to the original findings, however, attention to the adaptor also increased afterimage duration, suggesting that attention and awareness had the same – rather than opposing – effects on afterimage duration. We discuss possible reasons for this discrepancy.

2.2 Significance Statement

Considerable research has been devoted to understanding the nature of conscious visual experience and the processes that regulate it. Traditionally, mechanisms of attention have been assumed to play a critical role in determining whether a sensory event is experienced consciously. Specifically, it is assumed that stimuli that are attended enter awareness, whereas those that are ignored do not. More recently, however, it has been suggested that focused attention is not required for conscious perception. Here, we attempted to replicate an influential study which demonstrated that attention to, and awareness of, a visual adapting stimulus had opposing effects on the duration of the induced afterimage. Using the identical stimuli and experimental set-up, but with enhanced statistical power, we failed to replicate the attention effect, and showed instead that attention and awareness have the same effect on perception.

2.3 Introduction

There has been considerable debate in the literature on visual perception as to the relationship between attention and consciousness. Here we define *attention* as those processes that prioritize some sensory inputs over others, and *consciousness* as the reportable contents of a perceptual experience. While the terms *consciousness* and *awareness* are often used interchangeably, here we use the more specific term *perceptual awareness*[1] (or just *awareness*; Cohen, Cavanagh, Chun, & Nakayama, 2012; Kim & Blake, 2005, van Boxtel, Tsuchiya, & Koch, 2010a). While some argue that attention is necessary for awareness (e.g. Carrasco, Ling, & Read, 2004; Reynolds & Desimone, 2003; Treue, 2003), others propose that these processes are supported by distinct neural mechanisms that can be fully dissociated (e.g. Koch & Tsuchiya, 2007; van Boxtel, Tsuchiya, & Koch, 2010a, 2010b; Wyart & Tallon-Baudry, 2008).

Several previous studies have found that attending to a visual adapting stimulus reduces the duration of its afterimage (Brascamp et al., 2010; Suzuki & Grabowecki, 2003; van Boxtel et al., 2010a; Wede & Francis, 2007). For example, in one prominent and widely cited study, van Boxtel et al. (2010a) had observers report the duration of an afterimage after they had been exposed to a peripheral Gabor (the adaptor) that was either visible, or was rendered invisible using continuous flash suppression (CFS; Gilroy & Blake, 2005; Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006). During adaptation, observers also undertook a central visual attention task that was either easy (low-load), allowing limited perceptual resources to spill over to the adaptor, or difficult (high-load), leaving little or no capacity for processing of the adaptor (Bahrami, Carmel, Walsh, Rees, & Lavie, 2008; Lavie, 1995; Lavie, Hirst, de Fockert, & Viding, 2004, Macdonald & Lavie, 2008). The authors found that their observers' afterimages lasted longer when the adaptor was visible than when it was invisible. By contrast, afterimage duration was reduced under low- versus high-central load, implying that any residual attentional resources available for processing the adapting stimulus actually *reduced* the influence of the adapting stimulus on afterimage duration. In a further experiment, the authors varied the visibility of the adapting Gabor by manipulating the contrast of the CFS mask, and again found that afterimage duration increased with awareness of the adaptor, but was reduced under low attentional load. van Boxtel et al. concluded that attention and awareness are independent processes, based on the opposing effects they exert on afterimage duration, consistent with conclusions from previous

[1]We follow Kanwisher (2001) in defining perceptual awareness as the extraction of perceptual information from a stimulus that is experienced consciously.

investigations (Bachmann & Murd, 2010; Brascamp et al., 2010; Lou, 2001; Suzuki & Grabowecki, 2003; Wede & Francis, 2007; Wyart & Tallon-Baudry, 2009).

Given the influential contribution of the van Boxtel et al. (2010a) findings to the attention versus awareness debate, we aimed to replicate their key results. In Experiment 1 we set out to replicate Experiment 2a from their paper. The authors kindly sent us their experimental code so we could reproduce their stimuli with high fidelity. Trial number and sample size were small in van Boxtel et al., an issue we return to in the Discussion, so we increased these. Critically, we also included an awareness test to verify the effectiveness of the masking stimulus, a manipulation check not included in the original study. No changes were made to the critical experimental conditions or event timing. In Experiment 2, we sought to replicate Experiment 3 from van Boxtel et al. (2010a), again adhering strictly to their original protocol.

2.4 Experiment 1

2.4.1 Methods

2.4.1.1 Participants

Twenty individuals (11 Female; mean age = 23.61 years, SD = 4.63) participated. All reported normal or corrected-to-normal vision, were naïve to the experimental hypotheses, and provided informed written consent. The University of Queensland Human Research Ethics Committee approved the studies.

2.4.1.2 Stimuli and apparatus

Stimuli were presented on a 24-inch LCD monitor (refresh rate 60 Hz, mean background luminance 51 cd/m^2, without gamma correction). Stimulus delivery and response recording were controlled using a Dell PC running Cogent software (Cogent 2000 toolbox: Functional Imaging Laboratory, Institute of Cognitive Neuroscience, and Wellcome Department of Imaging Neuroscience) in Matlab under Windows XP. Participants viewed dichoptic displays through a mirror stereoscope, at a viewing distance of ~57 cm.

Stimuli, which were identical to those used in Experiment 2a of van Boxtel et al. (2010a; Figure 2.1), were displayed against a uniform gray background (Figure 2.1). During the entire presentation, a white fixation dot was presented to both eyes. Each trial began with a 4-second adaptation phase. The adaptor was a greyscale 34% Michelson-contrast Gabor (carrier spatial frequency = 0.23 cycles per degree). The full width at 1/2 height of the Gaussian envelope was 1.43°. Gabor orientation was randomly assigned on each trial. During adaptation the Gabor was presented to one eye (counterbalanced) 4.9° from the central fixation dot in one of eight cardinal or inter-cardinal directions. To minimize carry-over adaptation from previous trials, the location of the Gabor shifted counter-clockwise by 45° between trials. On half of the trials, the CFS mask was

presented to the other eye. The mask was a black (1.4 cd/m^2) and white (214 cd/m^2) Gaussian-windowed (σ = 1.43°) checkerboard (0.78 cycles per degree) that counterphased (every 67 ms) and continuously rotated (150 degrees per second).

Fifteen colored crosses [red (CIE .607, .365, 42.9 cd/m2), green (CIE .294, .651, 158 cd/m^2), blue (CIE .144, .083, 16.7 cd/m^2), yellow (CIE .396, .561, 198 cd/m^2), cyan (CIE .226, .395, 173 cd/m^2), magenta (CIE .314, .184, 57.2 cd/m^2)] measuring 1.9° in height and 1.4° in width were presented at 3.76 Hz binocularly at fixation.

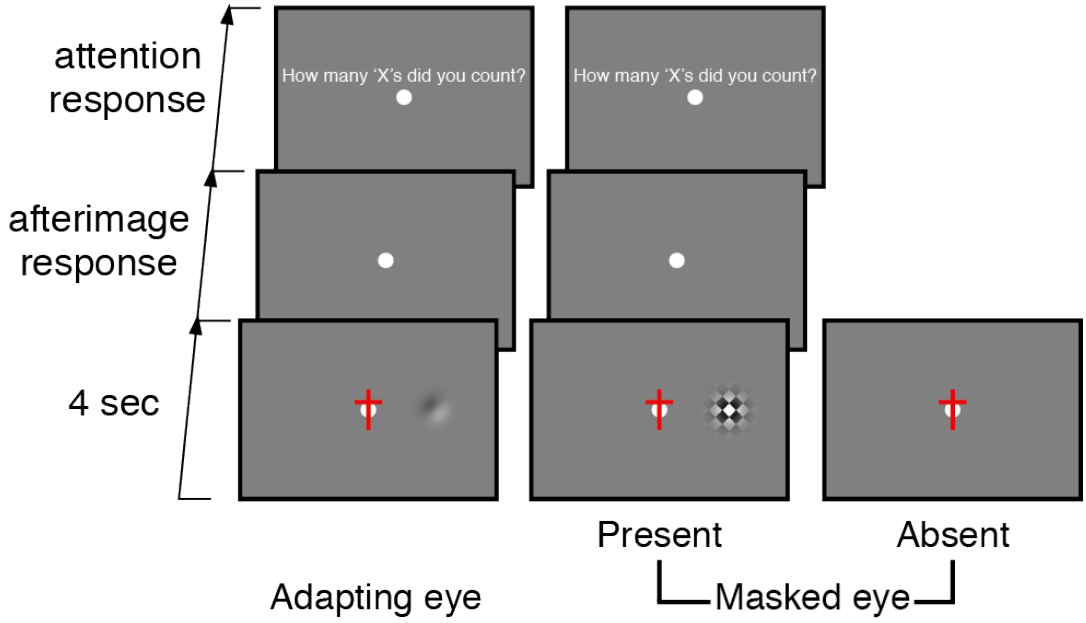

Figure 2.1. Schematic of displays used in Experiment 1. Each trial began with a 4-second adaptation phase. The adaptation stimulus was a peripheral Gabor patch. Attention was manipulated by a central rapid serial visual presentation (RSVP) task, in which observers were required to count the number of upright and inverted red crosses (low-load) or upright yellow and inverted green crosses (high-load). Visibility of the adaptor was manipulated by presenting a rotating and counter-phasing checkerboard mask to the eye contralateral to the adapting stimulus (unaware condition), or no mask was presented (aware condition). After the adaptation phase, observers indicated afterimage duration by pressing and releasing a mouse button. After recording afterimage duration, observers reported the number of targets presented out of a possible four targets.

2.4.1.3 Procedure

Participants performed 16 practice trials, followed by 8 blocks of 16 experimental trials. During adaptation, attention was manipulated by a rapid serial visual presentation (RSVP) task in which participants counted the number of upright and inverted red crosses (low-load), or upright yellow and inverted green crosses (high-load; see Schwartz et al., 2004). Target numbers on each trial could be 1, 2, 3, or 4 and were separated by at least one non-target. After adaptation, participants indicated the duration of their afterimage using a mouse held in the right hand. They

then used their left hand to indicate on a keyboard the number of targets. Accuracy feedback was provided during practice, but not during the experiment.

2.4.1.4 Awareness test

Following the experiment, participants performed 4 blocks of 16 awareness test trials. Here, stimuli were identical to those in the experimental trials, except that there was no RVSP stream, and a counter-phasing mask was presented for 100 ms after the Gabor to reduce any afterimage at that location. A second Gabor was then presented at fixation in a random orientation. On half the trials the initial Gabor was masked using CFS, and on the other half of trials there was no CFS mask. Participants used a mouse to rotate the second Gabor to match the orientation of the first Gabor.

2.4.2 Results

Two participants were excluded from the analysis because their accuracy in the attention task was not significantly above chance (25%). Overall RSVP accuracy was well above chance (25%) for both the low-load (77.17%), $t(17)=533.99$, $p<.001$, and high-load (59.03%) tasks, $t(17)=730.07$, $p<.001$. Accuracy was also significantly higher in the low- than in the high-load task, $t(17)=6.17$, $p<.001$, 95% confidence interval (CI)=[11.94,24.34], confirming the effectiveness of the load manipulation.

Afterimages persisted for longer when participants were aware of the adapting Gabor (no CFS) than when they were unaware of it (CFS; Figure 2.2). Likewise, afterimages lasted longer in the low-load than in the high-load condition. This difference in afterimage duration with attention is in the opposite direction to that reported by van Boxtel et al. (2010a).

Mean afterimage durations were calculated for each participant in each condition, excluding incorrect responses. Responses greater than 3 standard deviations above the participant's mean for each condition were removed (~68% of all trials were included). Mean afterimage durations were then subjected to a repeated-measures analysis of variance (ANOVA) with the factors of adaptor condition (aware, unaware) and attentional load (low-load, high-load). There was a significant main effect of adaptor condition, $F(1,17)=12.10$, $p=.003$, $\eta^2_p=.416$, 95% CI=[229.33,936.14]. Mean afterimage duration was 582 ms longer for aware trials (M=2262 ms, SD=977) than for unaware trials (M=1680 ms, SD=876).

There was also a significant main effect of attentional load, $F(1,17)=5.47$, $p=.032$, $\eta^2_p=.243$, 95% CI=[13.01,252.43]. Mean afterimage duration was shorter for high-load (M=1905 ms, SD=968) than for low-load trials (M=2037 ms, SD=930). This effect was opposite to that reported by van Boxtel et al. (2010a). Adaptor condition and attentional load did not interact, $F(1,17)=.63$, $p=.438$, $\eta^2_p=.036$.

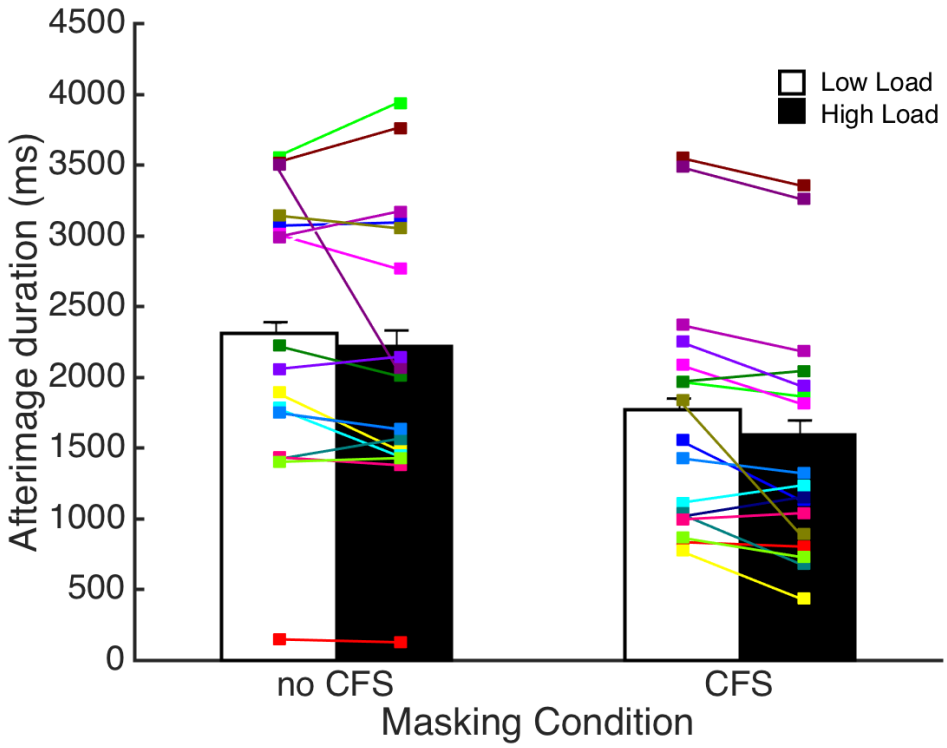

Figure 2.2. Mean afterimage duration in Experiment 1. Aware (no CFS) trials produced longer afterimage durations than unaware (CFS) trials. Afterimage duration was reduced under high-attentional load relative to low-attentional load conditions. Colored squares indicate mean responses for individual participants. Error bars represent within-subjects standard errors of the means (Masson and Loftus, 2003).

2.4.2.1 Awareness test

Orientation judgments in the awareness test – normalized to the orientation of the first Gabor – were randomly distributed for the condition in which the CFS mask was present (Figure 2.3A), and aligned close to zero degrees (perfect performance) on trials in which no mask was presented (Figure 2.3B). We calculated the difference in orientation between the first and the second Gabors, and then tested these distributions for uniformity. A V-test for non-uniformity, with a mean direction of 0 radians, showed that the population of responses was uniformly distributed around the circle for CFS trials ($v = 19.907$, $p = .120$), but was not distributed uniformly for non-CFS trials ($v = 483.228$, $p < .0001$). The mean resultant vector for non-CFS trials was .90 (median = .40)

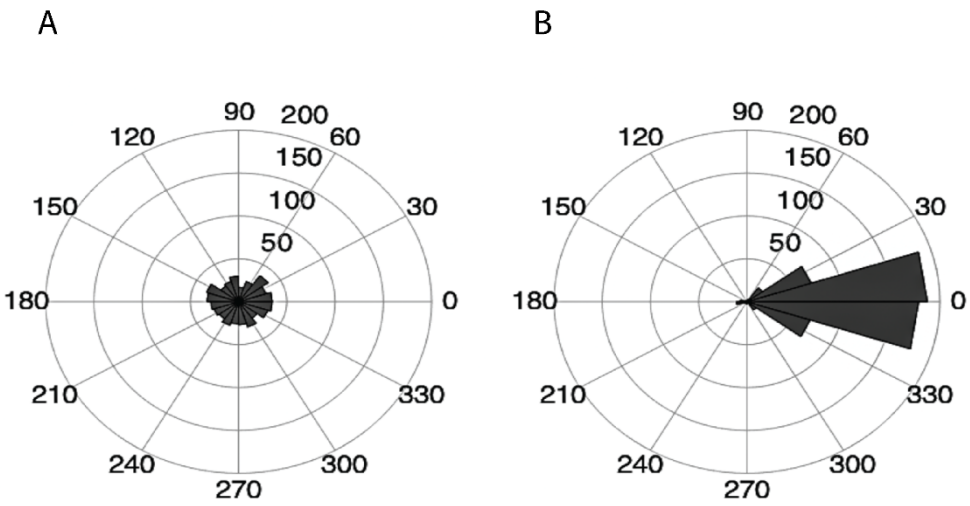

Figure 2.3. Polar plot showing the distribution of normalized directional orientation judgments in the awareness test. Values are grouped in 20 bins according to their angular range in polar coordinates. The angle of each bin represents the difference in degree between the orientation of the first Gabor and participants' orientation choice. The extent of each bin represents the number of trials that fall within each bin. Participant orientation responses were random with respect to the alignment of the initial Gabor on trials in which the CFS mask was present (**A**), but were well aligned on trials in which the CFS mask was absent (**B**).

2.5 Experiment 2

Experiment 2 was an exact replication of Experiment 3 from van Boxtel et al. (2010a), in which the contrast of the CFS mask – and thus the visibility of the adapting Gabor – was varied across trials.

2.5.1 Methods

2.5.1.1 Participants

Twenty new individuals (16 Female; mean age = 23.44 years, SD = 5.40) participated.

2.5.1.2 Stimuli, apparatus, and procedure

The methods were the same as those of Experiment 1, except that the CFS mask was presented at eight different contrast levels (0, 1.6, 3.1, 6.3, 12.5, 25, 50, and 100%), and after the practice participants completed two sessions, each of which consisted of 8 blocks of 32 trials.

2.5.2 Results

Attention and awareness again had similar effects on afterimage duration, as in Experiment 1, but contrary to the findings of van Boxtel et al. (2010a). As shown in Figure 2.4, afterimage duration decreased with increases in mask contrast, and afterimage duration was longer under low attentional load than under high load.

Overall RSVP accuracy, pooled across the different contrast levels, was above chance for both the low- (87%), $t(19)=857.96$, $p<.001$, 95% CI=[81.18,92.96], and high-load (69%), $t(19)=562.22$, $p<.001$, 95% CI=[60.46,78.56] conditions. Accuracy was also significantly higher in the low- than in the high-load task, $t(19)=4.25$, $p<.001$, 95% CI=[8.91,26.21] (paired samples *t*-test).

After removing incorrect trials and outliers (~22% of trials removed; see Experiment 1 for procedure), mean afterimage duration was subjected to a repeated-measures ANOVA with the factors of adaptor condition (eight contrast levels) and attentional load (low-load, high-load). There was a significant main effect of adaptor condition, $F(7,133)=10.61$, $p<.001$, $\eta^2_p=.358$, $BF_{10}=1.718e+10$. Null-hypothesis testing revealed no statistical difference in afterimage duration for the low- (M=2026 ms, SD=883) versus high- load (M=1971, SD=908) conditions, $F(1,19)=3.17$, $p=.091$, $\eta^2_p=.143$, 95% CI=[-9.68,119.85]. We also performed a Bayes factor analysis using JASP (Version 0.8.0.0, https://jasp-stats.org/) to quantify the strength of evidence for the null hypothesis. The Bayes factor for the main effect of attentional load was $BF_{10}=4.133$. Thus, while the inferential analysis suggested no effect of attentional load, the Bayes factor analysis revealed that attention did moderately increase afterimage duration. Critically, however, there was no evidence that attention *decreases* afterimage duration. There was also no interaction between adaptor condition and attentional load, $F(7,133)=.56$, $p=.787$, $\eta^2_p=.029$. An ANOVA on Bayes factors revealed that the main effects model was preferred to the interaction model by a factor of 51.22.

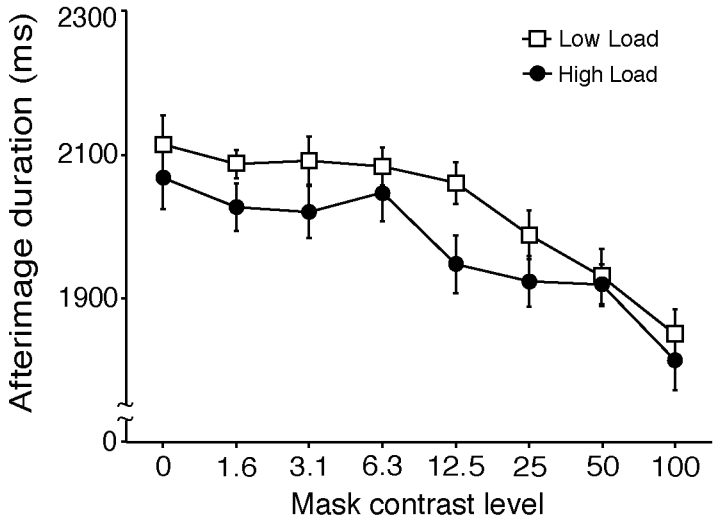

Figure 2.4. Mean afterimage duration in Experiment 2. Afterimage duration varied as a function of awareness, such that low rates of awareness (i.e., higher contrast CFS masks) produced shorter afterimages than high rates of awareness. The CFS mask was presented at eight different contrast levels (0, 1.6, 3.1, 6.3, 12.5, 25, 50, and 100%). Afterimage duration was shorter under high-central load compared with low-central load conditions. Error bars represent within-subjects standard errors of the means (Masson and Loftus, 2003).

2.6 Discussion

Here we sought to replicate an influential and widely cited study by van Boxtel et al. (2010a), in which the authors found that visual attention and awareness have opposing effects on perceived afterimage duration. Specifically, van Boxtel et al. found that afterimage duration increased when observers were aware (versus unaware) of the adapting stimulus, but *decreased* when residual attention was available for processing the adaptor, compared with a condition in which attention was fully expended on a central visual task. We replicated two of the key experiments from the original study, and found instead that attention and awareness both increased afterimage duration.

Our finding that attention increased afterimage duration is in contrast with the findings of van Boxtel et al. (2010a), as well as other studies that used different stimuli and experimental protocols (e.g. Brascamp et al., 2010; Suzuki & Grabowecki, 2003; Wede & Francis, 2007) and found that attention decreased afterimage duration. In this context, we note the work of Baijal and Srinivasan (2009), which suggests that perceived afterimage duration is sensitive to the particular type of attention directed toward the inducing stimulus. In light of this previous research, we would conclude that while the present results suggest that attention does not decrease afterimage duration, we acknowledge that afterimage durations are evidently decreased in other experimental contexts.

Further work will be required to determine what kinds of stimuli, tasks and attention manipulations are required to yield such reliable reductions.

Given the theoretical importance of the van Boxtel et al. (2010a) study, and our failure to replicate the opposing effect of attention and awareness they observed, it is important we consider some of the factors that might have led to the discrepant findings. One explanation comes from work by Brascamp et al. (2010), who suggested that the enhanced adaptation that accompanies attention to a stimulus can simultaneously facilitate the formation of an afterimage, thereby increasing afterimage duration, and augment the elevation of the observer's detection threshold, thereby decreasing (perceived) afterimage duration. It is possible that the balance between these two putative effects was different for our study and that of van Boxtel et al., which might in turn have caused the differential effects of attention on afterimage duration. Given that we used the same stimuli and the same experimental procedures as van Boxtel et al., however, this seems somewhat unlikely.

Another possibility is that the experiments in van Boxtel et al. were statistically underpowered, both in terms of the number of participants tested and the number of trials included in the critical conditions (see Table 1). An a priori power analysis performed with G*Power, for the main effect of attention on afterimage duration (f = .30, and α-error equal to .05, and a power of .80) calls for a sample size of 24 participants. The sample size used in van Boxtel et al. was 8 in Experiment 2a and 9 in Experiment 3. As the sampling distribution for a low-powered study is typically wider than the sampling distribution for a high-powered study, the sample mean needs to be larger in a low-powered study to reject the null hypothesis. Thus, a statistically significant finding from a low-powered study is more likely to overestimate the effect size when compared with a statistically significant finding from a high-powered study (Button et al., 2013). It should be noted in this context that our own study was also somewhat underpowered – we included data from 18 and 20 participants in Experiment 1 and 2, respectively – though considerably less so than in the original investigation.

Table 2.1 – Number of participants and trials in van Boxtel et al. (2010a)

	N	Trials per cell	Mean trials per cell in analysis
Experiment 2a	8	16	~13.6
Experiment 3	9	8	~5.6

A second possible reason for the discrepant findings concerns the relatively low trial numbers used in the van Boxtel et al. study (see Table 1). In their Experiment 3, for example,

participants performed only 8 trials in each condition, which would likely have yielded a somewhat imprecise estimate of the true afterimage duration. Moreover, after removing incorrect trials, data from only around 6 trials per condition were included in the final analysis. In the current study, after removing incorrect trials and outliers, data from ~22 trials (Experiment 1) and ~25 trials (Experiment 2) per condition were included in the final analysis, potentially improving estimates of observers' true performance in each condition.

In summary, our findings suggest attention and awareness have similar – rather than opposing – effects on afterimage duration, at least within the context of the specific paradigm introduced by van Boxtel and colleagues. While our failure to replicate suggests caution in using this specific approach to support the argument that attention and awareness are dissociable processes, there is nevertheless a diverse literature in support of this general conclusion (for reviews see Koch & Tsuchiya, 2007; Tallon-Baudry, 2012). Future work should be directed toward understanding the specific conditions under which attention and awareness operate together or in opposition. Such investigations will provide important insights into the relationship between attention and awareness in human vision.

Chapter 3 : Neural correlates of goal-directed enhancement and suppression of visual stimuli in the absence of conscious perception

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3.1 Abstract

An observer's current goals can influence the processing of visual stimuli. Such influences can work to enhance goal-relevant stimuli and suppress goal-irrelevant stimuli. Here we combined behavioral testing and electroencephalography (EEG) to examine whether such enhancement and suppression effects arise even when the stimuli are masked from awareness. We used a feature-based spatial cueing paradigm, in which participants searched four-item arrays for a target in a specific color. Immediately before the target array, a non-predictive cue display was presented in which a cue matched or mismatched the searched-for target color, and appeared either at the target location (spatially valid) or another location (spatially invalid). Cue displays were masked using continuous flash suppression. The EEG data revealed that target-colored cues produced robust N2pc and N_T responses – both signatures of spatial orienting – and distractor-colored cues produced a robust P_D – a signature of suppression. Critically, the cueing effects occurred for both conscious and unconscious cues. The N2pc and N_T were larger in the aware versus unaware cue condition, but the P_D was roughly equivalent in magnitude across the two conditions. Our findings suggest that top-down control settings for task-relevant features elicit selective enhancement and suppression even in the absence of conscious perception. We conclude that conscious perception modulates selective enhancement of visual features, but suppression of those features is largely independent of awareness.

3.2 Introduction

The relationship between attention and perceptual awareness has been the subject of a lengthy and intense debate (Chica & Bartolomeo, 2012; Chun & Wolfe, 2000; Cohen et al., 2012; De Brigard & Prinz, 2010; Dehaene et al., 2006; Iwasaki, 1993; Koch & Tsuchiya, 2007, 2012; Lamme, 2003, 2006; Mole, 2008; Posner, 1994; Prinz, 2011; Tallon-Baudry, Campana, Park, Babo-Rebelo, 2018; van Boxtel, 2017; van Boxtel et al., 2010b; Wyart & Tallon-Baudry, 2008). Many theorists have suggested that the two processes are inseparable, if not identical (Cohen et al., 2012; Chun & Wolfe, 2000; De Brigard & Prinz, 2010; Mack & Rock, 1998; Merikle & Joordens, 1997; Mole, 2008; O'Regan & Noe, 2001; Posner, 1994; Prinz, 2011; Velmans, 1996), whereas others have argued that attention and awareness are supported by distinct neural processes, and are readily dissociated from one another (Baars, 1997 & 2005; Bachmann, 2006; Block, 2005; Dehaene et al., 2006; Iwasaki, 1993; Kentridge et al., 1999a; Kentridge et al., 2004; Koch, 2004; Lamme, 2003; Maier et al., 2008; Naccache et al., 2002; Koch & Tsuchiya, 2007; van Boxtel et al., 2010b; Watanabe et al., 2011; Woodman & Luck, 2003a).

A central dilemma in the debate is that under normal circumstances, attended stimuli tend to be consciously perceived; likewise, salient stimuli that occupy conscious perception frequently become the focus of attention. Koch and Tsuchiya (2007) have proposed that the optimal approach for investigating associations and dissociations between attention and awareness is to use a two-by-two crossed experimental design. Under this framework, participants are instructed either to attend to or ignore sensory stimuli, and these events are presented so that they are either consciously perceived or manipulated (via masking, etc.) so that they cannot be consciously reported. Here we addressed the question of the relationship between spatial attention and perceptual awareness using a recently developed feature-based cueing paradigm (Lamy, Alon, Carmel & Shalev, 2015) in which cue events were masked so that they were not available for conscious report on roughly half the trials. We combined reaction time (RT) measures of performance with electroencephalography (EEG) to examine the independent effects of attention and awareness on feature-based cueing effects (e.g., Folk & Remington, 1999; Folk, Remington & Johnston, 1992; Folk, Remington, & Wright, 1994; Gibson & Amelio, 2000; Gibson & Kelsey, 1998; Yantis & Egeth, 1999).

As is typical in feature-based cueing experiments (e.g., Folk & Remington, 1999; Folk, Remington & Johnston, 1992; Folk, Remington, & Wright, 1994; Gibson & Amelio, 2000; Gibson & Kelsey, 1998; Yantis & Egeth, 1999), targets presented at the same location as a target-colored cue (valid trials) produce faster RTs than targets presented at a different location (invalid trials). Interestingly, this feature-based cueing effect seems to occur even when cues are not consciously perceived due to masking (e.g., Ansorge & Neumann, 2005; Hsieh, Colas, & Kanwisher, 2011; Ivanoff & Klein, 2003; Lamy, Alon, Carmel & Shalev, 2015). In most previous studies, the feature-

based cueing effect has been quantified by comparing differences in reaction times (RTs) between valid and invalid cue conditions (e.g., Folk & Remington, 1999; Folk, Remington & Johnston, 1992; Folk, Remington, & Wright, 1994; Gibson & Amelio, 2000; Gibson & Kelsey, 1998; Yantis & Egeth, 1999). However, RT measures index the end result of an accumulated sequence of processing stages between stimulus onset and motor response (Sternberg, 1969). It is thus desirable to incorporate a more continuous measure of attentional allocation to examine the time-course of feature-based cueing effects in such experiments. To this end, several investigators have employed event-related potentials (ERPs), such as the N2 posterior contralateral (N2pc) component, to measure the neural dynamics of feature-based spatial cueing effects (Eimer, 1996; Eimer & Kiss, 2008; Heinze, Luck, Mangun & Hillyard, 1990; Kiss, van Velzen & Eimer, 2008; Luck, 2005; Luck & Hillyard, 1994; Woodman & Luck, 1999, 2003b).

Several feature-based cueing studies have found evidence for an N2pc response to target-relevant cues that were masked from awareness (e.g., Ansorge, Horstmann, & Worschech, 2010; Ansorge, Kiss, & Eimer, 2009; Woodman & Luck, 2003a). There are, however, some important limitations with the designs used in these studies that limit the extent to which clear conclusions can be drawn regarding the relationship between spatial attention and perceptual awareness. Ansorge, Horstmann, and Worschech (2010) and Ansorge, Kiss, and Eimer (2009) found that masked cues captured attention when they were task-relevant, but not when they were task-irrelevant, suggesting that feature-based cueing effects can be elicited even when cues are not consciously perceived. In these studies, however, spatial orienting was not measured under both aware and unaware conditions, so the independent effects of selective attention and awareness could not be assessed.

Woodman and Luck (2003a) presented search displays that contained targets and distractors that were masked using object substitution masking (OSM). They measured N2pc responses to the targets and distractors under delayed offset and co-termination masking conditions. Interestingly, the authors found an N2pc response for both delayed offset and co-termination trials, and this response did not differ in magnitude between the masking conditions, suggesting that feature-based cueing effects might be independent of awareness. Critically, however, their participants' performance on the search task was significantly above chance even in the critical delayed-mask offset condition, suggesting that their participants might have been aware of the target and distractor stimuli in the "unaware" condition (see Crouzet et al. (2017) for evidence in support of this view).

Lamy, Alon, Carmel & Shalev (2015) addressed some of the issues with these previous studies by using continuous flash suppression (CFS; Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006) to mask brief visual cues presented to one eye in a feature-based cueing task. In their task, a cue display containing a single colored stimulus, which either matched the target color or was a distractor color, was presented to one eye. This cue display was masked by

presenting a high-contrast flickering stimulus in the other eye. Importantly, stimulus parameters were held constant for every trial throughout the experiment and participants were asked to report their awareness of the cue on each trial. After the cue display, targets appeared at valid or invalid locations. Participants searched for a color-defined target and reported its orientation, before indicating their awareness of the preceding cue. Valid target-colored cues produced faster RTs to targets than invalid target-colored cues, as expected. Critically, however, Lamy et al. (2015) found that the validity effect was similar in magnitude for consciously perceived and unperceived cues, suggesting that the feature-based cueing effect arises even in the absence of conscious perception of the triggering cues. The authors also found that spatially valid distractor-colored cues increased RTs to the target compared with invalid distractor-colored cues, resulting in a same location cost (see also Anderson & Folk, 2012; Belopolsky, Schreij, & Theeuwes, 2010; Carmel & Lamy, 2014; Lamy, et al., 2015; Eimer, Kiss, Press, & Sauter, 2009; Folk & Remington, 2008; Lamy & Egeth, 2003; Lamy, Leber, & Egeth, 2004; Schoeberl, Ditye & Ansorge, 2018; Schönhammer & Kerzel, 2013). Interestingly, the same location cost was found for aware trials but not for unaware trials, suggesting that the same-location cost depends on awareness of relevant cue stimuli.

Here we sought to replicate and extend the pioneering work of Lamy et al. (2015) using a feature-based cueing task combined with CFS to manipulate participants' awareness of visual cues. We combined behavioral testing and electroencephalography (EEG) to ask whether goal-relevant stimuli in a feature-based spatial attention task produce cueing effects even when the "cueing" events are not consciously perceived. In Experiment 1 we ran a direct replication of the behavioral task developed by Lamy et al. (2015), as described in detail above, but using a larger sample of participants and more experimental trials per condition. In Experiment 2 we recorded EEG while participants performed the same behavioral task as in Experiment 1, with the aim of investigating whether the neural signatures of feature-based cueing effects are similar for aware and unaware cues. Finally, in Experiment 3 we modified the spatial cueing task to determine whether the observed effects of aware and unaware cues on RTs and ERPs reflected selective enhancement of task-relevant features and/or active suppression of task-irrelevant features.

3.3 Experiment 1

Experiment 1 was a direct replication of Experiment 1 from Lamy et al. (2015). Cues could appear at the same location as the target or at a different location, and they either matched the target color or were a different color. Cues were masked using CFS, such that participants were only aware of the cues on approximately half of the trials. Participants were asked to identify the target's orientation as quickly as possible and, following this, report their awareness of the cue. In line with the findings of Lamy et al. (2015), we predicted that valid target-colored cues would elicit faster

responses to targets than invalid target-colored cues, and the magnitude of this same location benefit would not differ between aware and unaware trials. We also hypothesized that valid distractor-colored cues would elicit slower responses to targets than invalid distractor-colored cues, but only when the cues were consciously perceived, in line with the findings of Lamy et al. (2015).

3.3.1 Methods

3.3.1.1 Participants

Twenty-seven individuals participated in Experiment 1 (16 females, mean age = 22.74 years, SD= 3.50). To increase statistical power and, therefore, the probability of finding potentially small effects, we increased sample size considerably compared to the original study by Lamy et al. (2015; 14 participants). All participants reported normal or corrected-to-normal vision and all were naïve to the experimental hypotheses. Each provided informed written consent. The University of Queensland Human Research Ethics Committee approved the studies.

3.3.1.2 Apparatus, stimuli, and procedure

Participants were tested in a dimly illuminated room. Stimuli were presented on a 24-inch LCD monitor with a resolution of 1920 x 1200 and a refresh rate of 60 Hz. Stimulus delivery and response recording were controlled using a Dell PC running Cogent software (Cogent 2000 toolbox: Functional Imaging Laboratory, Institute of Cognitive Neuroscience, and Wellcome Department of Imaging Neuroscience) using Matlab operating under Windows XP. Participants viewed a dichoptic display through a mirror stereoscope, at a viewing distance of approximately 57 cm. To promote stable binocular fusion, the mirrors were adjusted for each individual observer at the beginning of the experimental session.

Participants performed a spatial cueing task, in which they were asked to identify the orientation of a target-colored T shape (rotated counterclockwise (“left”) or clockwise (“right”) by 90°; see Figure 3.1). Before the target display, a cue display was presented but masked using continuous flash suppression (CFS), such that participants were aware of the cue on approximately half of the trials only (as found by Lamy et al., 2015, and confirmed in the current study following pilot testing). Cues did not predict the target location, and either matched the target color or appeared in a distractor color instead. The observers’ task was to identify the orientation of the target-colored T shape (left or right) and indicate their response via a keypress. Following this response, observers provided a subjective report of their perception of the cue, using a scale from 0 (not aware) to 3 (clearly visible). Observers were informed that on some trials no cue would be presented.

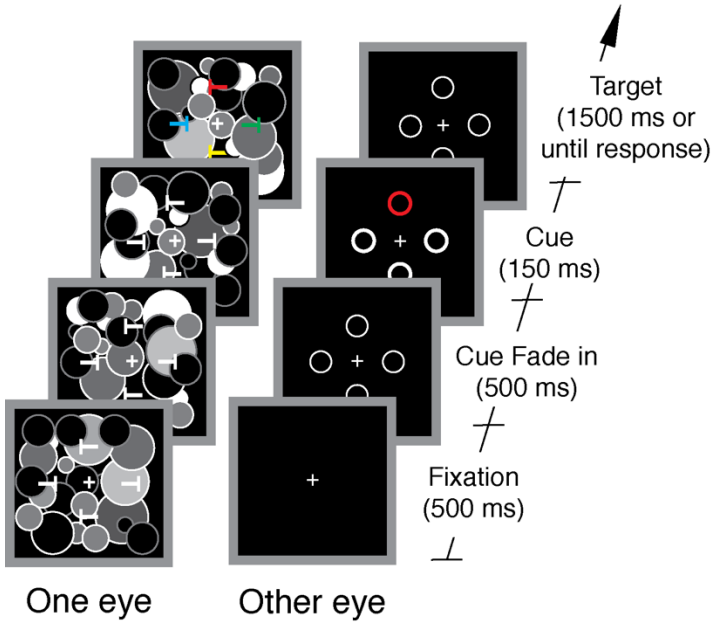

Figure 3.1. Schematic of individual trial events in Experiment 1. The participants' task was to report the orientation of the target T-shape and then to indicate whether they were aware of a colored cue stimulus. A flickering mask display (20 or 22 Hz) and four white T-shapes (two rotated 90 degrees clockwise and two rotated 90 degrees counter-clockwise) were presented to one eye throughout the experiment. Each trial began with a 500 ms fixation cross, followed by a 500 ms period in which the cue-placeholders faded in to the suppressed eye. Colored cues were then presented to the suppressed eye for 150 ms. All placeholders thickened, and on cue-present trials one of the four placeholders changed color so that it either matched the target color (target-colored cue) or was a distractor color (distractor-colored cue). In the immediately following target display, each of the four T-shapes took on a unique color (red, blue, green, or yellow) for 1500 ms or until response. Participants first indicated the orientation of the target T-shape as quickly and as accurately as possible, and then reported, without time pressure, their perception of the cue on a scale from 0 (not aware of the cue) to 3 (clearly aware of the cue).

Stimuli were displayed against a black background (CIE: .304, .259, 1.4 cd/m^2). During the entire presentation, two white (CIE: .305, .389, 214 cd/m^2) fixation crosses and two grey (CIE: .305, .389, 59 cd/m^2) and white (CIE: .305, .389, 214 cd/m^2) striped squares (7.3º x 7.3 º x .2 º of visual angle) were presented on each side of the screen, such that one fixation dot and one square was visible to each eye. The task consisted of a fixation display, a cue display, and a target display.

The fixation display (500 ms) was presented to one eye (pseudo-randomly to the left or right eye on each trial) and consisted of a central fixation cross (CIE: .305, .389, 214 cd/m^2; 0.5 º x 0.5 º) surrounded by four peripheral circles (CIE: .305, .389, 214 cd/m^2; 1 pixel thick; 1 º radius and 2.5 º from fixation). These circles were placed at the top, bottom, left and right of the fixation cross. The peripheral circles appeared gradually from 0% contrast to 100% contrast over the 500 ms fixation display. The mask was presented to the other eye at 20 Hz. Each masking display was made of circles of various sizes (.5 º to 1.5 º radius) and shades of grey (light grey CIE: .299, .399,

107cd/m^2; dark grey CIE: .276, .342, .2 cd/m^2; mid-dark grey CIE: .254, .479, 6.0 cd/m^2; mid-grey CIE: .277, .446, 48.3 cd/m^2). Four T shapes (CIE: .305, .389, 214 cd/m^2; 0.5º x 0.5º), two oriented 90° to the left and two 90° to the right, were superimposed on the masks.

In the cue display (150 ms) the peripheral circles thickened (2 pixels thick). On cue-present trials, one circle changed color (red: CIE: .607, .365, 43 cd/m^2, green: CIE: .294, .651,158 cd/m^2, blue: CIE: .144, .083, 17 cd/m^2 or yellow: CIE: .396, .561,198 cd/m^2). The target color was consistent throughout the experiment. For observers searching for a red or green target, cues were either red (40% of trials), green (40% of trials), or no cue was presented (20% of trials). For observers searching for blue or yellow targets, cues were either blue (40% of trials), yellow (40% of trials), or no cue was presented (20% of trials). During the target display, T shapes changed color, such that each T was rendered in a different color (red: CIE: 607, .365, 43 cd/m^2, green: CIE: .294, .651,158 cd/m^2, blue: CIE: .144, .083, 17 cd/m^2 or yellow: CIE: .396, .561,198 cd/m^2).

On 25% of cue trials the target-colored cue was presented in the same location as the target (valid trials), and on 75% of trials, the target-colored cue was presented in a different location (invalid trials). Thus, the cue display did not predict the location of the target. Participants performed a practice block of 32 trials. During the practice block, performance was monitored to ensure participants understood the task. If required, feedback was provided verbally. Following the practice block, participants performed 10 blocks of 64 trials (for a total of 640 experimental trials; 240 more experimental trials than in Lamy et al., 2015)

3.3.2 Results

Five participants were excluded from the analysis because they reported that they were consciously aware of the cue on fewer than 10% of trials. Data from the remaining 22 participants were included in the final analyses. Awareness ratings are presented in Table 1. In line with Lamy et al. (2015), we grouped cue-present trials rated 1, 2, and 3 together to form the aware trials and those rated 0 as the unaware trials. Thus, participants were aware of the cue on approximately half of cue-present trials.

Table 3.1. Awareness ratings for cue absent and cue present trials in Experiments 1 - 3

	Experiment 1		Experiment 2		Experiment 3	
	Cue Absent	Cue Present	Cue Absent	Cue Present	Cue Absent	Cue Present
0	69%	49%	83%	41%	67%	44%
Unaware	**69%**	**49%**	**83%**	**41%**	**67%**	**44%**
1	14%	13%	9%	13%	15%	15%
2	9%	14%	4%	11%	6%	8%
3	9%	25%	5%	34%	13%	33%
Aware	**32%**	**52%**	**18%**	**58%**	**33%**	**56%**

Figure 3.2 shows mean correct RTs as a function of awareness (aware or unaware), cue type (target-colored cue or distractor-colored cue), and cue validity (valid or invalid). We conducted a 2 (awareness) x 2 (cue type) x 2 (cue validity) ANOVA on mean correct RTs. Results revealed a significant main effect of awareness, $F(1,21) = 26.294$, $p = .\ 0.00004$, $\eta^2_p = .556$, $BF_{10} = 1.637e+10$ (Bayesian analysis performed with JASP: Version 0.8.0.0, https://jasp-stats.org/). Mean correct RTs were faster when participants were unaware of the cue (M = 732 ms, SD = 67 ms) than when they were aware of the cue (M = 793 ms, SD = 82 ms). We ran an additional analysis that included all four awareness levels and found that RTs increased as cue awareness increased, $F(3,54) = 16.73$, $p < .00001$.

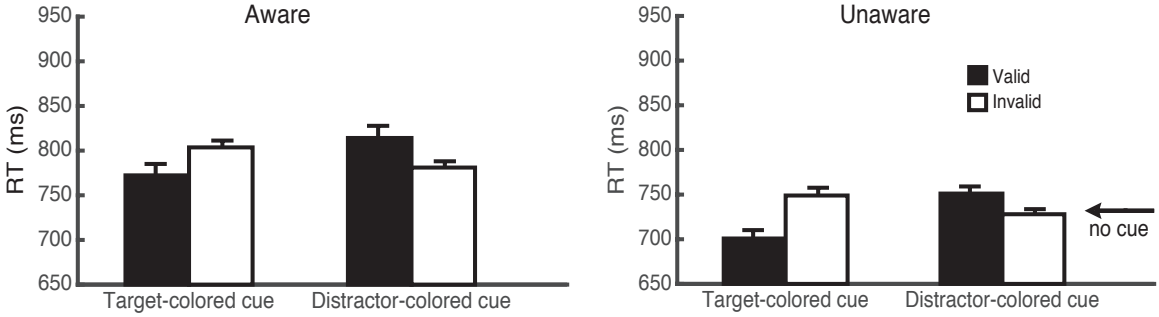

Figure 3.2. Mean correct RTs to targets in Experiment 1, shown as a function of cue color, cue condition, and cue awareness. Cue color either matched the target color (target-colored cue) or was a distractor color (distractor-colored cue). Cue location either matched the target location (valid) or was different to the target location (invalid). The aware condition included trials in which participants reported having some awareness of the cue (i.e., awareness ratings of 1, 2 or 3). The unaware condition included only those trials in which participants indicated they were not aware of the cue (i.e., an awareness rating of 0). The small arrow on the right indicates the mean reaction time for the no-cue condition (M = 736 ms, SE = 14.28). Error bars represent within-subjects standard errors of the mean.

The main effects of cue type ($F(1,21) = 3.591$, $p = .072$, $\eta^2_p = .146$, $BF_{10} = .371$) and cue validity ($F(1,21) = .725$, $p = .404$, $\eta^2_p = .033$, $BF_{10} = .191$) did not reach significance. Importantly, however, there was a significant two-way interaction between cue type and cue validity, $F(1,21) = 30.619$, $p = .00002$, $\eta^2_p = .593$, $BF_{inclusion} = 772.99$). In line with previous work on feature-based cueing effects (e.g., Folk & Remington, 1999; Folk, Remington & Johnston, 1992; Folk, Remington, & Wright, 1994; Gibson & Amelio, 2000; Gibson & Kelsey, 1998; Yantis & Egeth, 1999), there was a same-location benefit for target-colored cues, such that RTs were faster when target-colored cues were presented in the same location as targets (M = 737 ms, SD = 70 ms) than when they were presented in a different location (M = 776 ms, SD= 77 ms), $t(21) = -3.671$, $p = .001$, d = -.783, $BF_{10} = 24.779$. Results also revealed a same-location cost for distractor-colored cues. RTs were slower when cues were presented in the same location as the target (M = 783 ms,

SD = 83 ms) than when they were presented in a different location (M = 755 ms, SD = 75 ms), $t(21) = 3.933$, $p = .0008$, d = .839, $BF_{10} = 43.694$.

The other two-way interactions did not reach significance (awareness and cue validity, $F(1,21) = 1.251$, $p = .276$, $\eta^2_p = .056$, $BF_{inclusion} = .498$; awareness and cue type, $F(1,21) = .169$, $p = .685$, $\eta^2_p = .008$, $BF_{inclusion} = .756$). Finally, the three-way interaction between awareness, cue type, and cue validity did not reach significance ($F(1,21) = .171$, $p = .683$, $\eta^2_p = .008$, $BF_{inclusion} = .244$), suggesting that the same-location benefit for target-colored cues and the same-location cost for distractor-colored cues were not differentially affected by awareness.

An analogous ANOVA on error rates (see Table 2) revealed a significant main effect of awareness, $F(1,21) = 5.758$, $p = .026$, $\eta^2_p = .215$, $BF_{10} = 2441.679$. Mean error rates were higher when participants were aware of the cue (M = 16.31%, SD = 16.72) than when they were unaware of the cue (M = 10.21%, SD = 9.57). None of the other main effects or interactions reached significance, suggesting there was no speed-accuracy trade off. (Main effect of cue type, $F(1,21) = .905$, $p = .352$, $\eta^2_p = .041$, $BF_{10} = .213$; main effect of cue validity, $F(1,21) = 2.879$, $p = .105$, $\eta^2_p = .121$, $BF_{10} = .231$; awareness x cue type, $F(1,21) = .208$, $p = .653$, $\eta^2_p = .010$, $BF_{inclusion} = .103$; awareness x cue validity, $F(1,21) = .558$, $p = .463$, $\eta^2_p = .026$, $BF_{inclusion} = .108$; cue type x cue validity, $F(1,21) = 2.228$, $p = .150$, $\eta^2_p = .096$, $BF_{inclusion} = .032$; awareness x cue type x cue validity, $F(1,21) = .031$, $p = .862$, $\eta^2_p = .001$, $BF_{inclusion} = .004$).

Table 3.2. Mean reaction times and error rates for the different cue color and awareness conditions of Experiment 1

	Target-colored cue				Distractor-colored cue			
	Unaware		Aware		Unaware		Aware	
Cue validity	RT (ms)	Error rate (%)	RT (ms)	Error rate (%)	RT (ms)	Error rate (%)	RT (ms)	Error rate (%)
Valid	701 (16)	9.0 (2.6)	772 (19)	16.4 (4.0)	751 (15)	12.0 (2.6)	814 (24)	18.0 (4.2)
Invalid	749 (17)	9.8 (2.1)	804 (18)	15.7 (3.6)	728 (15)	10.1 (2.5)	781 (19)	15.2 (3.5)

Note: Standard errors are given in parentheses.

3.3.3 Discussion

The results from Experiment 1 demonstrate that attention can be oriented to task-relevant cues even when those cues are not consciously perceived, and that the magnitude of this orienting effect is largely independent of cue awareness. Task-irrelevant cues caused a same-location cost. Interestingly, the magnitude of the cost was also independent of cue awareness, a finding that is not consistent with Lamy et al. (2015), who found a same-location cost for aware cues, but not for unaware cues (see, however, Schoeberl et al., 2018). Given that we used the same methodological design as Lamy et al., this finding is surprising. Having said this, the same location cost for unaware cues is a small effect. Thus, as we used a larger sample and had observers perform more trials than

Lamy et al., our results likely reflect that we simply had more statistical power to uncover this small effect.

In Experiment 1, feature-based cueing effects were operationalized in terms of RT differences between valid and invalid cues. Response times, however, represent the final outcome of several information-processing stages, from initial encoding and selection of sensory inputs to response execution (Schmidt, 1988). It is possible that some of these processes are modulated by cue awareness, while others remain largely independent of it. We investigated this possibility in Experiment 2 by comparing neural activity associated with consciously perceived versus unperceived cues.

3.4 Experiment 2

In Experiment 2 we employed EEG to examine the timing and magnitude of cue-related evoked responses in an analogous feature-based cueing paradigm to that employed in Experiment 1. We focused our analyses on the N2pc component, consistent with previous investigations of spatial orienting (Eimer, 1996; Kiss, van Velzen & Eimer, 2008; Luck & Hillyard, 1994; Woodman & Luck, 1999, 2003b).

3.4.1 Methods

3.4.1.1 Participants

Twenty new individuals participated in Experiment 2 (17 females, mean age = 21.00 years, SD = 1.00).

3.4.1.2 Apparatus, stimuli, and procedure

The stimuli and procedure were similar to those of Experiment 1, except for the following changes. Our aim in Experiment 2 was to measure an N2pc to the cue displays. Thus, to accommodate the measurement of N2pc responses, all cue and target stimuli (.05º x .05º) were lateralized so that they appeared at the top left, bottom left, top right and bottom right corners (2.5º distant from fixation; Figure 3.3) of the display. Cue-present trials consisted of a target-colored cue, a distractor-colored cue, and two neutral cues. As in Experiment 1, target and distractor colors were consistent throughout the experiment. For observers searching for red or green targets, cues were red or green. For observers searching for blue or yellow targets, cues were blue or yellow. To ensure any cue-related N2pc response was driven by top-down attentional biasing and not by stimulus differences, target-colored cues and distractor-colored cues were always presented in opposite hemifields (left/right). Target displays consisted of one target-colored T, one distractor-colored T, and two white Ts. As with the cue display, each hemifield contained one colored T-shape (target or distractor). The CFS mask was presented at 20 or 22 Hz (10 participants each).

Participants completed 12 blocks of 64 trials (for a total of 768 experimental trials; 368 more than in Lamy et al., 2015).

For observers searching for red or green targets, one cue was red and one cue was green (640 trials; 83%), or no cue was presented (128 trials; 17%). For observers searching for blue or yellow targets, one cue was blue and one cue was yellow (640 trials; 83%), or no cue was presented (128 trials; 17%). During the target display, two T shapes changed color. For participants searching for red or green, one T shape was red (red: CIE: 607, .365, 43 cd/m^2) and one was green (CIE: .294, .651,158 cd/m^2). For participants searching for blue or yellow, one T shape was blue (CIE: .144, .083, 17 cd/m^2) and one was yellow (CIE: .396, .561,198 cd/m^2). The other two T shapes remained white.

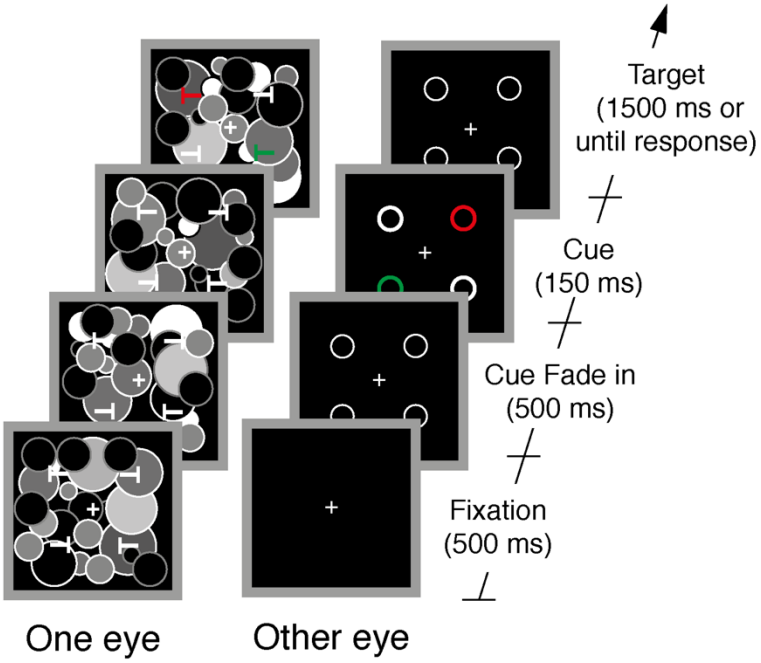

Figure 3.3. Schematic of individual trial events in Experiment 2. The participants' task was to report the orientation of the target T-shape and to indicate whether they were aware of a colored cue. A flickering mask display (20 or 22 Hz) and four white T-shapes (two rotated 90 degrees clockwise and two rotated 90 degrees counter-clockwise) were presented to one eye throughout the experiment. Each trial began with a 500 ms fixation cross, followed by a 500 ms period in which the cue-placeholders faded in to the suppressed eye. Colored cues were then presented to the suppressed eye for 150 ms. All placeholders thickened, and on cue-present trials, two of the four placeholders changed color so that one matched the target color (target-colored cue) and another matched the distractor color (distractor-colored cue). Neutral cues remained white. These colored circles were always presented in different hemifields. In the immediately following target display, two of the four T-shapes changed color such that one matched the target color (target) and another was the distractor target (distractor). The target display was presented for 1500 ms or until response. Participants first indicated the orientation of the target T-shape as quickly and as accurately as possible, and then reported, without time pressure, their perception of the cue on a scale from 0 (not aware of the cue) to 3 (clearly aware of the cue).

Electroencephalography. EEG data were recorded continuously from 64 active Ag/AgCl scalp electrodes. The electrodes were arranged according to the international standard 10-10 system for electrode placement (Oostenveld & Praamstra, 2001) using a nylon cap. Eye movements were monitored using bipolar horizontal and vertical electrooculography (EOG). EEG and EOG signals were amplified by Biosemi Active Two amplifiers and sampled at 1024 Hz with 24-bit A/D conversion. Standard reference and ground electrodes were used during recording.

Offline preprocessing of the EEG data was performed using Brain Electrical Source Acquisition (BESA 5.3; MEGIS Software GmbH, Gräfelfing, Germany). Noisy channels were identified via visual inspection and replaced by interpolation of the voltages recorded at all other scalp electrodes. A maximum of four electrodes were interpolated for each participant. Data were then subjected to a 0.1 Hz high-pass filter and a 100 Hz low-pass filter. The data were re-referenced to the average of all 64 scalp electrodes and segmented into 1 s epochs spanning 200 ms before cue onset to 800 ms after cue onset. The average voltage in the 200 ms precue interval was used as a baseline for each epoch. Epochs with excessive noise from eye blinks or other muscle activity were identified by visual inspection and rejected from further analysis. An average of 18% of epochs were rejected using this criterion, with no more than 25% rejected for any individual participant. Incorrect trials were also excluded from the analysis. The remaining epochs were averaged for each participant separately for each condition.

The N2pc response to the cue was quantified within the time period of 200-300 ms after cue onset. This time window was chosen to match that of Lien, Ruthruff, Goodin, & Remington (2008), who conducted a similar experiment (but without the awareness manipulation), and is also consistent with those adopted in previous research on the N2pc (e.g., Eimer, 1996; Hopf, Luck, Boelmans, Schoenfeld, Boehler, Rieger, & Heinze, 2006; Luck & Hillyard, 1994; Wascher & Wauschkuhn, 1996; Wauschkuhn, Verleger , Wascher , Klostermann, Burk, Heide, & Kömpf, 1998). The N2pc was calculated as the mean amplitude from electrodes contralateral to the target-colored cue minus the mean amplitude for the homologous electrodes ipsilateral to the target-colored cue. To determine electrode sites for analysis, we calculated the average response for each electrode site during the cue-related time window, separately for trials in which the target-colored cue was presented in the right visual hemifield and trials in which the target-colored cue was presented in the left visual hemifield. We then collapsed across hemispheres such that responses contralateral to the target-colored cue were represented in the right hemisphere and responses ipsilateral to the target-colored cue were represented in the left. We chose the three electrode sites with the highest responses in the right hemisphere (P8, P10, and PO8) and the homologous electrode sites in the left hemisphere (P7, P9, PO7) for analysis.

3.4.2 Results

3.4.2.1 Behavioral analysis

The behavioral results from Experiment 2 replicated those of Experiment 1. Awareness ratings can be seen in Table 1. We found faster RTs to targets that were validly cued by target-colored cues than neural cues. This pattern of results was found for both aware and unaware target-colored cues. We also found slower RTs to targets that were validly cued by distractor-colored cues than by neutral cues. This pattern of results was found for both aware and unaware distractor-colored cues. Again, we grouped cue-present trials rated 1, 2, and 3 to form the aware trials, and those rated 0 as the unaware trials.

Figure 3.4 shows mean correct RTs as a function of awareness (aware or unaware) and cue condition (target-colored cue in target location, distractor-colored cue in target location, or neutral cue in target location). To analyze these patterns statistically, we conducted a 2 (awareness) x 3 (cue condition) repeated-measures ANOVA on mean correct RTs (see Table 2). Results revealed a significant main effect of awareness, $F(1,19) = 26.444$, $p = .00006$, $\eta^2_p = .582$, $BF_{10} = 9.274e+6$. Mean correct RTs were faster for unaware trials (M = 778 ms, SD = 115) than aware trials (M = 847 ms, SD = 111). There was also a significant main effect of cue condition, $F(2,38) = 27.429$, $p = .00000004$, $\eta^2_p = .591$, $BF_{10} = 4419.50$. Follow-up tests using Bonferroni correction revealed that RTs were faster when targets were presented in the same location as the target-colored cue (M = 773 ms, SD = 104) than when they were presented in a neutral cue location (M = 823 ms, SD = 118, $t(19) = -4.743$, $p = .0001$, d = -1.060, $BF_{10} = 204.13$). Furthermore, RTs were slower when distractor colored cues were presented in the same location as the target (M = 842 ms, SD = 122) than when they were presented in the location of a neutral colored cue ($t(19) = 3.811$, $p = .001$, d = .852, $BF_{10} = 31.69$). The interaction between awareness and cue condition was not significant, $F(2, 38) = .496$, $p = .530$ (Greenhouse-Geisser corrected), $\eta^2_p = .025$, $BF_{inclusion} = .615$, suggesting that the effect of cue condition did not depend on awareness. Thus, top-down attentional settings were involved in feature-based cueing even when cues were not consciously perceived.

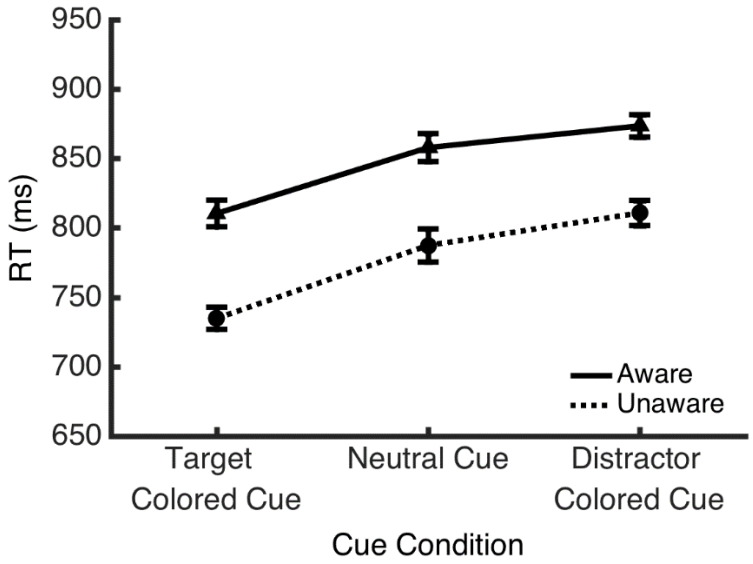

Figure 3.4. Mean correct RTs to targets in Experiment 2, shown as a function of cue condition and cue awareness. Target location either matched the target-colored cue location (target-colored cue), the distractor-colored cue location (distractor-colored cue), or a neutral cue location (neutral cue). The aware condition included trials in which participants reported having some awareness of the cue. By contrast, the unaware condition included only those trials in which participants indicated they were not aware of the cue. Error bars represent within-subjects standard errors of the means

A further ANOVA on error rates (see Table 3) revealed no significant main effect of awareness ($F(1,19) = .182$, $p = .675$, $\eta^2_p = .009$, $BF_{10} = .270$), but a significant main effect of cue condition, $F(2,38) = 5.823$, $p = .006$, $\eta^2_p = .235$, $BF_{10} = .670$. Follow-up tests using Bonferroni correction revealed that the main effect of cue condition was driven by a significantly higher mean error rate for trials in which the target was located in the distractor-colored cue location (M = 9.40%, SD = 6.21) than for trials in which the target was located in the target-colored cue location (M = 7.21%, SD = 6.38, $t(19) = -3.462$, $p = .003$, d = -.774, $BF_{10} = 15.948$). The interaction between awareness and cue condition was also significant, $F(2,38) = 5.328$, $p = .009$, $\eta^2_p = .219$, $BF_{inclusion} = .180$. This significant interaction was followed up by evaluating the simple main effects of cue condition separately for aware and unaware trials. Mean error rates did not differ between cue conditions for aware trials, $F(2,38) = 1.172$, $p = .321$, $\eta^2_p = .058$, but they did differ significantly between cue condition for unaware trials, $F(2,38) = 11.71$, $p = .0001$, $\eta^2_p = .381$. We performed follow-up *t*-tests with Bonferroni correction, to assess these differences. For unaware cues, error rates were significantly lower when targets were located in the same location as target-colored cues (M = 5.85%, SD = 4.39) than when targets were located in the same location as distractor-colored cues (M = 9.52%, SD = 5.36), $t(19) = -4.144$, $p = .0006$, d = .927, $BF_{10} = 61.551$), or when targets were located in the same location as neutral cues (M = 8.55%, SD = 5.47), $t(19) = -3.203$, $p = .005$,

d = -.716, BF_{10} =.9.694). Thus, the interaction between awareness and cue condition appears to be driven by fewer errors in the unaware target-colored cue condition. Overall these results suggest there was no speed accuracy trade off in Experiment 2.

Table 3.3. Mean reaction times and error rates for the different cue and awareness conditions of Experiment 2

	Unaware		Aware	
Cue condition	RT (ms)	Error rate (%)	RT (ms)	Error rate (%)
Target-colored cue	735 (24)	5.8 (1.0)	810 (24)	8.6 (2.2)
Distractor-colored cue	811 (30)	9.5 (1.2)	874 (28)	9.3 (1.9)
Neutral	787 (27)	8.5 (1.2)	858 (27)	7.9 (1.6)

Note: Standard errors are given in parentheses.

3.4.2.2 ERP analysis

As we were interested in the effect of awareness on the neural signatures of attentional orienting, we focused our ERP analyses on cue-related responses. The ERP data were analyzed as a function of cue awareness (aware or unaware) and electrode laterality (contralateral or ipsilateral to the target-colored cue location). An N2pc component was evident for both aware and unaware trials, but with a slightly larger negative amplitude for the aware trials (Figure 3.5). ERP data for the cue-related response were submitted to a 2 (awareness) x 2 (electrode laterality) repeated measures ANOVA on the mean response during the cue-related N2pc time window.

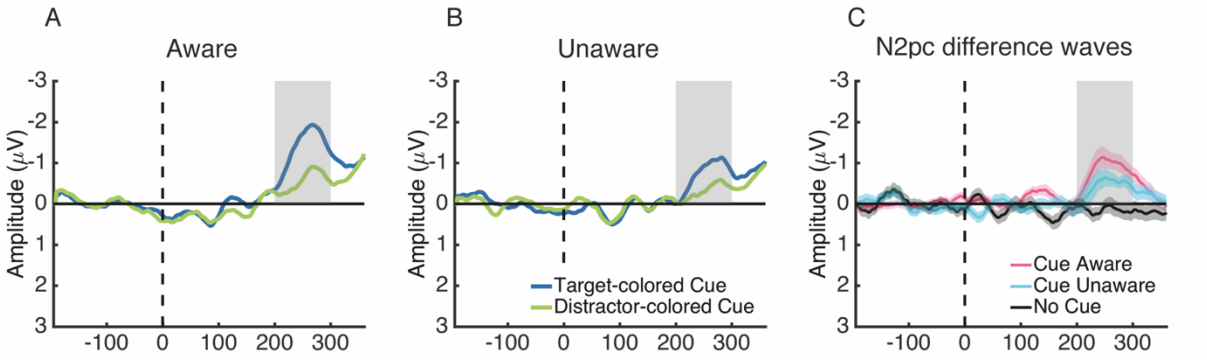

Figure 3.5. Grand average event-related potentials (ERPs) and difference waves for target-colored cues. (**A** & **B**) ERPs averaged across posterior electrode sites (P7/P8, P9/P10, PO7/PO8) contralateral to the target-colored cue location (blue) and distractor colored cue location (green), as a function of awareness (aware vs unaware). **(A)** Average ERPs when participants were aware of the cue. **(B)** Average ERPs when participants were unaware of the cue. **(C)** Difference waves calculated by subtracting ipsilateral from contralateral ERPs for the aware (magenta), unaware (cyan), and no-cue trials (black), showing the cue-induced N2pc. Cue onset is at time zero. Shaded areas represent analyzed time window for the cue-related response (200-300 ms after cue onset). Data have been smoothed using a sliding Boxcar for display only. All analyses were performed on the unsmoothed data. Note that here the label *Target-colored cue* represents responses that were contralateral to the target-colored cue, but also ipsilateral to the distractor-colored cue; likewise, the label *Distractor-colored cue* represents responses that were contralateral to the distractor-colored cue, but also ipsilateral to the target-colored cue.

There was a significant main effect of awareness on cue-evoked ERP magnitude, $F(1,19) = 10.14$, $p = .005$, $\eta^2_p = .348$, $BF_{10} = 11.330$. Responses were more negative for aware trials (M = -.968, SD = 1.109) than for unaware trials (M = -.520, SD =1.384). There was also a significant main effect of electrode laterality, $F(1,19) = 20.65$, $p = .0002$, $\eta^2_p = .521$, $BF_{10} = 1293.948$. Responses at electrode sites contralateral to the target-colored cue (ipsilateral to distractor-colored cue) were more negative (M = -1.062, SD = 1.325) than responses at electrode sites ipsilateral to the target-colored cue (contralateral to distractor-colored cue; M = -.426, SD = 1.178), indicating a significant N2pc response. Critically, there was also a significant interaction between awareness and electrode laterality, $F(1,19) = 13.66$, $p = .002$, $\eta^2_p = .418$, $BF_{inclusion} = 3.310$. To investigate whether there was an N2pc to both aware and unaware trials, we followed up this interaction with pairwise t-tests. When participants were aware of the cue, mean ERPs were significantly more negative at electrode sites contralateral to the target-colored cue location (M = -1.384, SD = 1.204) than at electrode sites ipsilateral to the target-colored cue location (M = -.553, SD = 1.181), $t(19) = -5.206$, $p = .00005$, d = -1.164, $BF_{10} = 514.330$. Critically, this pattern was also found for unaware trials. When participants were unaware of the cue, mean ERPs were significantly more negative at electrode sites contralateral to the target-colored cue location (M = -.740, SD = 1.580) than responses at electrode

sites ipsilateral to the target-colored cue location (M = -.300, SD = 1.315), $t(19) = -3.172$, $p = .005$, d = -.709, $BF_{10} = 9.136$. Thus, there was a significant N2pc to target-colored cues both when participants were aware of the cue, and also when the cue was not consciously perceived; however, the magnitude of the N2pc was greater for aware cues (mean difference = -.805, SD = .598) than for unaware cues (mean difference = -.428, SD = .514; see Figure 3.5C).

The difference in N2pc magnitude between aware and unaware cues was driven by a larger negative response at electrode sites contralateral to aware target-colored cues than those contralateral to unaware target-colored cues, $t(19) = -4.082$, $p = .0006$, d = -.913, $BF_{10} = 514.330$. Responses at electrode sites contralateral to the distractor-colored cue (ipsilateral to the target colored cue) did not differ between aware and unaware conditions, $t(19) = -1.771$, $p = .093$, d = -.396, $BF_{10} = 9.136$. Thus, the difference in N2pc magnitude between aware and unaware cues was likely driven by differences between processing aware and unaware target-colored cues, but not between aware and unaware distractor-colored cues.

3.4.3 Discussion

In Experiment 2 we recorded EEG while participants performed a behavioral task with stimuli and design similar to that used in Experiment 1. We found an RT benefit for valid versus invalid target-colored cues, with no difference in the magnitude of this feature-based cueing effect for cue-aware and cue-unaware trials. These findings are consistent with our Experiment 1 findings and those of Lamy et al. (2015). We also found an RT cost for valid versus invalid distractor-colored cues. We found no difference in the magnitude of this same location cost for cue-aware and cue-unaware trials. Our finding that the same location cost does not depend on awareness aligns with recent research by Schoeberl, Ditye, & Ansorge (2018), in which the authors found that valid cues that mismatched the observers' goals produced a same location cost for unaware cues.

The ERP data revealed an N2pc response to both aware and unaware cues. The N2pc is thought to reflect target enhancement (Eimer, 1996; Shedden & Nordgaard, 2001). Thus, the results from Experiment 2 suggest that attention was allocated to the location of items that share features with observers' task-goals even in the absence of awareness[2]. Interestingly, the magnitude of the

[2] There was no N2pc in no-cue trials ($p > .05$). Thus, there was a neural difference between unaware cue-present trials and unaware no-cue trials. It might be argued that participants' actual level of awareness, as indexed by subjective ratings, differed between unaware cue present and unaware cue absent trials. In interpreting the awareness ratings, however, we followed the reasoning of Lamy et al. (2015) and took the participants' subjective awareness ratings in the cue-present trials at face value – that is, when participants gave a zero rating, we defined their experience as *unaware of the cue.*

N2pc response in Experiment 2 was larger for cue-aware trials than for cue-unaware trials. This magnitude difference was driven by a larger negative response at electrode sites contralateral to aware target-colored cues than those contralateral to unaware target-colored cues. Responses at electrode sites contralateral to the distractor-colored cue did not differ between aware and unaware cues. Thus, our findings suggest that neural measures of target processing are modulated by awareness, but those associated with distractor suppression are not — a finding that is reversed in relation to the behavioral results reported in Lamy et al. (2015).

In Experiment 2, each trial involved the presentation of a target-colored cue in one hemifield and a distractor-colored cue in the opposite hemifield. We reasoned that by using these balanced displays any lateralized effects would be attributable to influences from participants' current task set as opposed to stimulus-driven effects. There was, however, a downside to using such a balanced-display design. As the N2pc is by definition a difference between contralateral and ipsilateral responses, the balanced displays used in Experiment 2 may have yielded N2pc waveforms that reflected a combination of responses elicited by the target-colored cue and the simultaneously presented distractor-colored cue. Consistent with this, Hickey, Di Lollo and McDonald (2009) have suggested that the N2pc is a combination of two ERP components: the N_T, a negative ERP component associated with target enhancement, and the P_D, a positive ERP component associated with distractor suppression (e.g. Cosman, Lowe, Woodman, & Schall, 2018; Gaspelin & Luck, 2018b). Although in Experiment 2 we were able to measure neural responses separately for contralateral and ipsilateral electrode sites, we were not able to determine whether these responses reflected processing of the target-colored cue, the distractor-colored cue, or a combination of both. We sought to address this issue in Experiment 3.

3.5 Experiment 3

While much of the literature on feature-based cueing has focused on attentional allocation in terms of the selective enhancement of task-relevant information (e.g., Wolfe, 1994), suppression of task-irrelevant information is also a key component of selective processes (Braithwaite & Humphreys, 2003; Lleras, Kawahara, Wan, & Ariga, 2008). Indeed, a large volume of research supports the idea that selective attention both modulates activity in sensory processing areas by enhancing relevant features (Bisley & Goldberg, 2010; Corbetta et al., 1990; Corbetta & Shulman, 2002; Desimone & Duncan, 1995; Fries et al., 2001; Gruber et al.,1999; Hillyard & Anllo-Vento, 1998; Kastner et al., 1998; Kastner & Ungerleider, 2000; Luck et al., 2000; Raz & Buhle, 2006; Reynolds & Chelazzi, 2004; Siegel et al., 2008; Tallon-Baudry et al., 2005; Treue, 2003) and suppressing irrelevant features (Andersen & Muller, 2010; Chelazzi et al., 1993; Hopf et al., 2006; Luck et al., 1997; Moran & Desimone, 1985; Reynolds et al.,1999; Thut et al., 2006; Vanduffel et

al., 2000; Worden et al., 2000). This idea that selection involves both enhancement and suppression is central to prominent theories of attention, such as the biased competition model (Desimone & Duncan, 1995) and the notion of priority maps (Itti & Koch, 2001).

In Experiment 3, we tested whether the N2pc response reported in Experiment 2 is the result of an N_T to the target-colored cue, a P_D to the distractor-colored cue, or a combination of both components. The design was similar to that employed in Experiment 2, except that only one cue was presented on each cue-present trial (either a target-colored or a distractor-colored cue). This design allowed us to investigate lateralized neural responses separately for target-colored and distractor-colored cues under aware and unaware conditions. In line with our findings from Experiments 1 and 2, we expected to observe an RT benefit for valid target-colored cues and an RT cost for valid distractor-colored cues, for both aware and unaware trials. For the ERPs, we expected to observe an N_T to target-colored cues, which would be larger in magnitude for aware trials than for unaware trials. We also predicted a P_D in response to distractor-colored cues, but not target-colored cues.

3.5.1 Methods

3.5.1.1 Participants

Twenty-four new individuals participated in Experiment 3 (12 males, mean age = 21.37 years, SD = 1.53).

3.5.1.2 Apparatus, stimuli, and procedure

The stimuli and procedure were the same as those of Experiment 2, with the following exceptions. To accommodate the measurement of the N_T and P_D components, cue-present trials consisted of a single target-colored cue in one of the four locations, with three neutral cues in the remaining locations (320 trials; 41.67%), or a single distractor-colored cue in one location with three neutral cues (320 trials; 41.67%). In an additional 128 trials (16.67%), no cue was presented. The CFS mask was presented at 20 Hz for each participant.

Electroencephalography

Offline preprocessing of the EEG data was performed using EEGlab (Delorme & Makeig, 2004). Muscle, eye movement and blink artifacts were identified and removed using independent component analysis. Incorrect trials were also excluded from the analysis. An average of 18% of epochs were rejected using this criterion, with no more than 25% rejected for any individual participant. The remaining epochs were averaged for each participant separately for each condition.

The N_T responses to the target-colored cue and the P_D responses to the distractor colored cue were quantified within the time period of 200-300 ms after cue onset. The N_T was calculated as the mean amplitude from electrodes contralateral to the target-colored cue minus the mean amplitude for the homologous three electrodes ipsilateral to the target-colored cue. The P_D was calculated as

the mean amplitude from electrodes contralateral to the distractor-colored cue minus the mean amplitude for the homologous three electrodes ipsilateral to the distractor-colored cue. To determine electrode sites for analysis, we calculated the average response for each electrode site during the cue-related time window, separately for trials in which the cue was presented in the right visual hemifield and trials in which the cue was presented in the left visual hemifield. We then collapsed across hemispheres such that responses contralateral to the cue were represented in the right hemisphere and responses ipsilateral to the cue were represented in the left. We chose the three electrode sites with the highest responses in the right hemisphere (P8, P10, and PO8) and the homologous electrode sites in the left hemisphere (P7, P9, PO7) for analysis.

3.5.2 Results

Data from five participants were excluded from the analysis because these individuals reported being aware of the cue on more than 50% of no-cue trials. Data from the remaining 19 participants were included in the following analyses.

3.5.2.1 Behavioral analysis

Awareness ratings are presented in Table 1. As in Experiments 1 and 2 we grouped cue-present trials rated 1, 2, and 3 together to form the aware trials, and those rated 0 as the unaware trials.

Figure 3.6 shows mean correct RTs as a function of awareness (aware or unaware), cue type (target-colored cue or distractor-colored cue), and cue validity (valid or invalid). We conducted a 2 (awareness) x 2 (cue type) x 2 (cue validity) ANOVA on mean correct RTs (see Table 4). There was a significant main effect of awareness, $F(1,18) = 28.473$, $p = .000045$ $\eta^2_p = .613$, $BF_{10} = 2.464e+7$), with mean correct RTs faster when participants were unaware of the cue (M = 796 ms, SD = 117 ms) than when they were aware of the cue (M = 855 ms, SD = 109 ms).

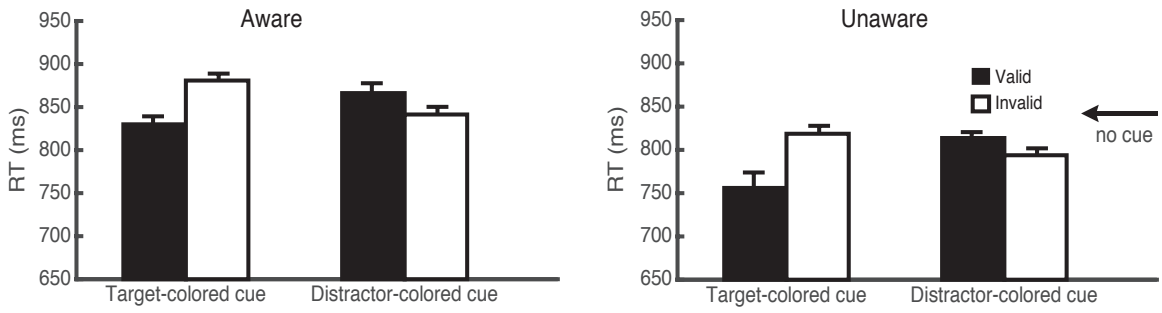

Figure 3.6. Mean correct RTs to targets in Experiment 3, shown as a function of cue color, cue condition, and cue awareness. Cue color either matched the target color (target-colored cue) or was a distractor color (distractor-colored cue). Cue location either matched the target location (valid) or was different to the target location (invalid). The aware condition included trials in which participants reported having some awareness of the cue. By contrast, the unaware condition included only those trials in which participants indicated they were not aware of the cue. The arrow on the right indicates the mean reaction time for the no-cue condition (M = 842 ms, SE = 26.83). Error bars represent within-subjects standard errors of the means.

The main effects of cue type ($F(1,18) = .569$, $p = .460$, $\eta^2_p = .031$, $BF_{10} = .221$) and cue validity ($F(1,18) = 4.113$, $p = .058$, $\eta^2_p = .186$, $BF_{10} = .660$) did not reach significance. Again, however, there was a significant two-way interaction between cue type and cue validity, $F(1,18) = 26.414$, $p = .000069$, $\eta^2_p = .595$, $BF_{inclusion} = 3048.43$). Specifically, there was a same-location benefit for target-colored cues, such that RTs were faster when target-colored cues were presented in the same location as targets (M = 793 ms, SD = 126 ms) compared to when they were presented in a different location (M = 850 ms, SD= 124 ms), $t(18) = -4.192$, $p = .000548$, d = -.962, $BF_{10} = 62.505$. Results also revealed a same-location cost for distractor-colored cues. RTs were slower when cues were presented in the same location as the target (M = 840 ms, SD = 107 ms) than when they were presented in a different location (M = 818 ms, SD = 117 ms), $t(18) = 2.518$, $p = .021$, d = .578, $BF_{10} = 2.775$.

The other two-way interactions did not reach significance (awareness and cue type, $F(1,18) = 3.591$, $p = .074$, $\eta^2_p = .166$, $BF_{inclusion} = .600$; awareness and cue validity, $F(1,18) = .412$, $p = .529$, $\eta^2_p = .022$, $BF_{inclusion} = .974$). Finally, the three-way interaction between awareness, cue type, and cue validity did not reach significance ($F(1,18) = .127$, $p = .726$, $\eta^2_p = .007$, $BF_{inclusion} = .334$), suggesting that the same-location benefit for target-colored cues and the same-location cost for distractor-colored cues were not differentially affected by awareness. Thus, as in the previous two experiments, we found behavioral evidence for feature-based cueing effects and distractor costs even when the evoking events were not consciously perceived.

We ran an analogous ANOVA on error rates (see Table 4). There were no significant main effects of awareness, $F(1,18) = .134$, $p = .719$, $\eta^2_p = .007$, $BF_{10} = .194$, cue type, $F(1,18) = 1.426$, $p = .248$, $\eta^2_p = ..073$, $BF_{10} = .321$; or cue validity, $F(1,18) = .279$, $p = .604$, $\eta^2_p = .015$, $BF_{10} = .209$). There was, however, a significant interaction between cue type and cue validity, $F(1,18) = 8.042$, $p = .011$, $\eta^2_p = .309$, $BF_{inclusion} = .300$). Follow up pairwise t-tests revealed that this two-way interaction was due to the fact that there were more errors when invalid cues were target-colored (M = .104, SD = .099) than when they were distractor-colored (M = .080, SD = .070), but this difference did not survive Bonferroni correction with an alpha level of .0125, $t(18) = -2.322$, $p = .032$, d = -.533, $BF_{10} = 2.006$). None of the other interactions were significant (awareness x cue type, $F(1,18) = .148$, $p = .705$, $\eta^2_p = .008$, $BF_{inclusion} = .028$; awareness x cue validity, $F(1,18) = .912$, $p = ..352$, $\eta^2_p = .048$, $BF_{inclusion} = .026$; awareness x cue type x cue validity, $F(1,18) = 2.229$, $p = .153$, $\eta^2_p = .110$, $BF_{inclusion} = .008$).

Table 3.4. Mean reaction times and error rates for the different cue color and awareness conditions of Experiment 3

	Target-colored cue				Distractor-colored cue			
	Unaware		Aware		Unaware		Aware	
Cue validity	RT (ms)	Error rate (%)	RT (ms)	Error rate (%)	RT (ms)	Error rate (%)	RT (ms)	Error rate (%)
Valid	756 (34)	7.3 (7)	830 (26)	9.4 (8.2)	814 (26)	9.2 (6.7)	867 (25)	8.9 (9.1)
Invalid	819 (29)	10.8 (11.5)	881 (29)	9.9 (8.5)	794 (28)	7.8 (6.2)	841 (27)	8.2 (8.3)

Note: Standard errors are given in parentheses.

3.5.2.2 ERP analysis

The ERP data were analyzed as a function of cue awareness (aware or unaware), electrode laterality (contralateral or ipsilateral to the cue location), and cue condition (target-colored cue or distractor-colored cue). As seen in Figure 3.7, starting approximately 200 ms after cue onset a negative component (N_T) was evident for all conditions, but with a slightly larger negative amplitude for the target-colored cue trials than the distractor-colored cue trials. Interestingly, starting approximately 350 ms after cue onset a positive component (P_D) was also evident for distractor-colored cue trials, but not for target-colored cue trials. To capture the sequence of these laterality effects we analyzed mean ERP amplitudes during two time windows: an earlier time window focused on the N_T component (200 to 300 ms after cue onset, to match the cue-related time window analyzed in Experiment 2), and a later time window focused on the P_D component (350 to 500 ms after cue onset). Past research has shown that the P_D component can vary over a broad time range that depends on the evoking stimulus and experimental task (e.g., Burra & Kerzel, 2014; Cosman, Lowe, Woodman, & Schall, 2018; Gaspelin & Luck, 2018a; Gaspar & McDonald, 2014; Hickey, Di Lollo, & McDonald, 2009; Hilimire, Mounts, Parks, & Corballis, 2012; Sawaki, Geng,

& Luck, 2012; Sawaki & Luck, 2010). To be sure any P_D effect was not canceled out by the opposite-polarity of the N_T component, we chose a time window that was outside the N_T time window. Note also that the cue-related ERP responses were always collapsed across valid and invalid trials (with respect to subsequent target location), so any evoked activity arising from the subsequent onset of target events was effectively canceled out.

ERP data for the N_T and P_D responses were submitted to separate 2 (awareness) x 2 (electrode laterality) x 2 (cue condition) repeated measures ANOVAs on the mean amplitude for each participant during each time window.

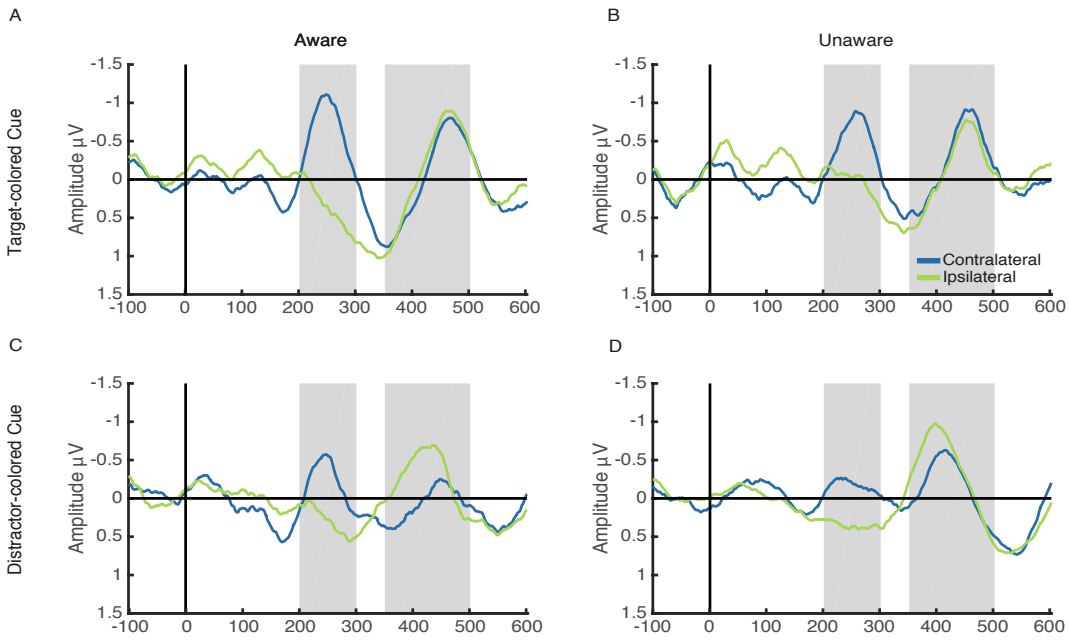

Figure 3.7. Grand average event-related potentials (ERPs) in response to cue events, averaged across posterior electrode sites (P7/P8, P9/P10, PO7/PO8) contralateral to the cue location (blue) and ipsilateral to the cue location (green). The ERPs are shown as a function of awareness (aware vs unaware) and cue condition (target-colored cue vs distractor-colored cue). (A) Average ERPs when a target-colored cue was presented and participants were aware of the cue. (B) Average ERPs when a target-colored cue was presented and participants were unaware of the cue. (C) Average ERPs when a distractor-colored cue was presented and participants were aware of the cue. (D) Average ERPs when a distractor-colored cue was presented and participants were unaware of the cue. Cue onset is at time zero. Shaded areas represent analyzed time windows for the cue-related response (200-300 ms after cue onset and 350-500 ms). Data have been smoothed using a sliding Boxcar for display only. All analyses were performed on the unsmoothed data.

N_T component. There was no significant main effect of awareness on cue-evoked ERPs during the earlier time window, $F(1,18) = .011$, $p = .918$, $\eta^2_p = .001$, $BF_{10} = .175$. Responses did not differ between aware trials (M = -.090, SD = .931) and unaware trials (M = -.104, SD = .664). There was a significant main effect of electrode laterality, $F(1,18) = 18.402$, $p = .000441$, $\eta^2_p = .506$, $BF_{10} = 1.254e+6$. Responses at electrode sites contralateral to the cue were more negative (M

= -.439, SD = .942) than responses at electrode sites ipsilateral to the cue (M = .246, SD = .703). There was also a significant effect of cue condition, $F(1,18) = 5.096$, $p = .037$, $\eta^2_p = .221$, $BF_{10} = 1.762$. Overall responses for target-colored cue trials were more negative (M = -.236, SD = .854) than those for distractor colored-cue trials (M = .043, SD = .745). There was no significant interaction between cue condition and electrode laterality, $F(1,18) = 2.739$, $p = .115$, $\eta^2_p = .132$, $BF_{inclusion} = .861$, between cue condition and awareness, $F(1,18) = 1.247$, $p = .279$, $\eta^2_p = .065$, $BF_{inclusion} = .112$, or between awareness and cue laterality, $F(1,18) = 1.420$, $p = .249$, $\eta^2_p = .073$, $BF_{inclusion} = .146$. There was, however, a significant three-way interaction between cue condition, awareness, and electrode laterality, $F(1,18) = 9.639$, $p = .006$, $\eta^2_p = .349$, $BF_{inclusion} = .050$. To investigate this three-way interaction, we analyzed the interaction between cue condition and cue laterality at each awareness level.

For aware trials, there was no significant effect of cue condition, $F(1,18) = 1.854$, $p = .190$, $\eta^2_p = .093$, $BF_{10} = .359$. There was, however, a significant effect of cue laterality, $F(1,18) = 13.943$, $p = .002$, $\eta^2_p = .436$, $BF_{10} = 2443.150$, as well as a significant interaction between cue condition and cue laterality, $F(1,18) = 9.643$, $p = .006$, $\eta^2_p = .349$, $BF_{inclusion} = 1.231$. To investigate whether there was an N_T to both target-colored and distractor-colored cues for aware trials, we followed up this interaction with pairwise t-tests. On target-colored cue trials, mean ERPs were significantly more negative at electrode sites contralateral to the cue location (M = -.720, SD = 1.445) than at electrode sites ipsilateral to the cue location (M = .349, SD = .962), $t(18) = -3.950$, $p = .000939$, d = -.906, $BF_{10} = 39.032$. This pattern was also found for distractor-colored cue trials, such that ERPs were significantly more negative at electrode sites contralateral to the cue location (M = -.255, SD = 1.054) than at electrode sites ipsilateral to the cue location (M = .267, SD = .850), $t(18) = -2.872$, $p = .010$, d = -.659, $BF_{10} = 5.145$. We performed permutation tests, which verified these results (see supplemental material).

To determine whether the magnitude of the N_T response differed between target- and distractor-colored cues for aware trials, we computed a difference score by subtracting responses at ipsilateral electrode sites from responses at contralateral sites, separately for target- and distractor-colored cue trials. The magnitude of this difference (i.e., the size of the N_T) was greater for target-colored cues (mean difference = -1.069, SD = 1.180) than for distractor-colored cues (mean difference = -.522, SD = .792), $t(19) = -3.105$, $p = .006$, d = -.712, $BF_{10} = 7.859$. Thus, there was a significant N_T to both target- and distractor-colored cues in aware trials, but the magnitude of the response was larger for target-colored cues. There was no evidence of a P_D component during this earlier time window.

For the unaware trials, there was a significant effect of cue condition, $F(1,18) = 5.775$, $p = .027$, $\eta^2_p = .243$, $BF_{10} = 2.386$. There was also a significant effect of cue laterality, $F(1,18) = 14.493$,

p = .001, η^2_p =.446, BF_{10} = 118.123, but there was no significant interaction between cue condition and cue laterality, $F(1,18)$ = .062, p = .807, η^2_p =..003, $BF_{inclusion}$ =1.030. Pairwise t-tests showed that on target-colored cue trials, mean ERPs were significantly more negative at electrode sites contralateral to the cue location (M = -.588, SD = 1.086) than at electrodes ipsilateral to the cue location (M = .014, SD = .712), $t(18)$ = -2.597, p = .018, d = -.596, BF_{10} = 3.171. This pattern was also found for distractor-colored cues in unaware trials, such that mean ERPs were significantly more negative at electrode sites contralateral to the cue location (M = -.194, SD =.709) than at electrodes ipsilateral to the cue location (M = .354, SD =.822), $t(18)$ = -4.379, p = .000362, d = -1.005, BF_{10} = 89.846. Thus, there was a significant N_T to both target- and distractor-colored cues, but this did not differ between the two cue conditions. Once again there was no evidence of a P_D component during this time earlier window.

P_D Component. There was no significant effect of awareness on cue-evoked ERPs during the later time window (350 to 500 ms after cue onset), $F(1,18)$ = .763, p = .394, η^2_p = .041, BF_{10} = .298. Responses did not differ between aware trials (M = -.114, SD = .821) and unaware trials (M = -.232, SD = .902). In addition, there was no significant main effect of electrode laterality, $F(1,18)$ =3.653, p = .072, η^2_p = .169, BF_{10} = .396. Responses did not differ between electrode sites contralateral to the cue (M = -.099, SD = .817) and those at electrodes ipsilateral to the cue (M = .246, SD = .838). Finally, there was no significant effect of cue condition, $F(1,18)$ = .057, p = .815, η^2_p = .003, BF_{10} = .186. Overall responses for target-colored cue trials (M = -.150, SD = -.682) did not differ from those for distractor colored-cue trials (M = -.196, SD = 1.091). There was, however, a significant interaction between cue condition and electrode laterality, $F(1,18)$ = 6.002, p = .025, η^2_p =.250, $BF_{inclusion}$ = .562. To investigate whether there was a P_D to both target- and distractor-colored cues, we followed up this interaction with pairwise t-tests (collapsed across the awareness condition). In target-colored cue trials, mean ERPs did not differ between electrode sites contralateral to the cue location (M = -.151, SD = .720) and electrode sites ipsilateral to the cue location (M = -.150, SD =.730), $t(19)$ = -.013, p = .990, d = -.003, BF_{10} = .238. In contrast, in distracter-colored cue trials, ERPs were significantly more positive at electrode sites contralateral to the cue location (M = -.048, SD = 1.133) than at electrode sites ipsilateral to the cue location (M = -.343, SD = 1.077), $t(19)$ = 3.693, p = .002, d = .847, BF_{10} = 23.795. Thus, there was a significant P_D for distractor-colored cues, but not for target-colored cues. None of the other interaction terms approached significance (cue condition x awareness, $F(1,18)$ = .288, p = .598, η^2_p = .016, $BF_{inclusion}$ = .026; awareness x electrode laterality, $F(1,18)$ = 2.204, p = .155, η^2_p = .109, $BF_{inclusion}$ = .049; cue condition x awareness x electrode laterality, $F(1,18)$ = .149, p = .704, η^2_p = .008, $BF_{inclusion}$ = .003). We performed permutation tests, which verified these results (see supplemental material).

3.5.3 Discussion

In line with the findings of Experiments 1 and 2, we found an RT benefit for valid versus invalid target-colored cues, with no difference in magnitude between cue-aware and cue-unaware trials. Target-colored cues and distractor-colored cues elicited an N_T response for both cue-aware and cue-unaware trials. In line with our findings from Experiment 2, the magnitude of the N_T response to target-colored cues was reliably larger for cue-aware trials than for cue-unaware trials. We also found that distractor-colored cues elicited an equivalent P_D response for both cue-aware and cue-unaware trials, whereas target-colored cues did not elicit a reliable P_D. Thus, at the neural level, target processing is modulated by awareness, but distractor processing is not. Taken together, the results of Experiment 3 suggest that top-down task goals can elicit selective enhancement of task-relevant features (as measured by the N_T) and active suppression of task-irrelevant features (as measured by the P_D), even in the absence of cue awareness. Interestingly, enhancement occurred earlier (200-300 ms after cue onset) than suppression of task-relevant features (350-500 ms after cue onset), suggesting that the N2pc results reported in Experiment 2 are not likely to reflect a combined N_T and P_D response.

3.6 General Discussion

A key debate in the visual attention literature concerns how attention and perceptual awareness are related. Some researchers propose that attention and consciousness are intimately linked (Chun & Wolfe, 2000; Cohen et al., 2012; De Brigard & Prinz, 2010; Mack & Rock, 1998; Merikle & Joordens, 1997; Mole, 2008; O'Regan & Noe, 2001; Posner, 1994; Prinz, 2011; Velmans, 1996), whereas others suggest that the two processes can act independently (Baars, 1997 & 2005; Bachmann, 2006; Block, 2005; Dehaene et al., 2006; Iwasaki, 1993; Kentridge et al., 1999b; Kentridge, Heywood, & Weiskrantz, 2004; Koch, 2004; Koch & Tsuchiya, 2007; Lamme, 2003; Maier et al., 2008; Naccache et al., 2002; van Boxtel et al., 2010b; Watanabe et al., 2011; Woodman & Luck, 2003a). Here we investigated the independent effects of spatial attention and perceptual awareness on feature-based cueing effects. Specifically, we were interested in whether the relationship between attention and perceptual awareness was consistent across behavioral and neural signatures of feature-based cueing effects. Previous research has shown that behavioral measures of feature-based cueing effects are independent of perceptual awareness (e.g., Ansorge & Neumann, 2005; Hsieh, Colas, & Kanwisher. 2011; Ivanoff & Klein, 2003; Lamy, Alon, Carmel & Shalev, 2015), but there has been little work on the effects of attention and perceptual awareness on neural measures of feature-based cueing effects.

In Experiment 1 we ran a direct replication of Lamy et al. (2015, Exp. 1), in which participants searched for a color-defined target that was preceded by a cue that was masked via

CFS. Like Lamy et al. (2015), we found an RT benefit for valid target-colored cues, the magnitude of which did not differ between aware and unaware cues. We also found an RT cost for distractor-colored cues, which did not differ with cue awareness. This latter finding is in contrast to that of Lamy et al. (2015), who found an RT cost for distractor-colored cues on aware trials but not on unaware trials. Our findings suggest that when measured behaviorally, attentional mechanisms of selective enhancement and active suppression appear to act independently from perceptual awareness. Importantly, we replicated these behavioral results across all three experiments.

In Experiment 2, we presented a pair of colored cues, one in each visual hemifield, and found that target-colored cues evoked an N2pc response for both consciously perceived and unperceived cues. The magnitude of this N2pc response was larger for aware cues than for unaware ones. The N2pc is widely assumed to index attentional orienting to a specific location in space (Heinze, Luck, Mangun, & Hillyard, 1990; Luck, 2005; Luck & Hillyard, 1994; but other processes have also been implicated; see Naughtin, Mattingley & Dux, 2017). Since both aware and unaware cues in our study produced a significant N2pc response, it seems reasonable to conclude that selective attention is required to resolve competition between goal-relevant and distractor stimuli even when those stimuli are not consciously perceived.

In Experiment 3, we presented just one cue (either target-colored or distractor-colored) within each cue display, and measured N_T and P_D responses to the cue stimuli. We found an N_T to target- and distractor-colored cues when observers were both aware and unaware of those cues. In line with predictions, the magnitude of the N_T response was larger for aware target-colored cues than unaware target-colored cues. Interestingly, we also found an N_T to distractor-colored cues, the magnitude of which did not differ between aware and unaware trials. Previous research has found that the N2pc/N_T response is evoked when stimuli are goal-relevant, but not when stimuli are task-irrelevant (Eimer & Kiss, 2008; Eimer, Kiss, Press, & Sauter, 2009; Kiss et al., 2008; Lien et al., 2008). Thus, our finding of an N_T response to distractor-colored cues might seem unexpected. However, one important component of our design is that we asked participants to report their awareness of the cue on every trial. Thus, all cues, both target- and distractor-colored, were relevant to the awareness task in our experiments. Previous research has shown that cues that have some task-relevant features produce an N2pc response, even when those cues do not share all task-relevant features (Kiss, Grubert, & Eimer, 2013). Given that an N_T is typically not found for distractor-colored cues in feature-based cueing studies, our finding of an N_T response to distractor-colored cues highlights how different this version of the paradigm is from the original paradigm introduced by Folk, Remington & Johnston, (1992). The presence of the N_T response to distractor-colored cues suggests that attention was directed to the location of the distractor-colored cue. This finding might seem contradictory to our observation of a same-location RT cost for distractor-

colored cues. We suspect that the N_T response reflects an early stage of processing, whereas the RT measure captures a later stage in the stimulus-response chain (as we discuss in detail below).

In Experiment 3, we also observed a P_D response to distractor-colored cues that occurred later in time than the N_T response. The magnitude of the P_D response did not differ between aware and unaware cues. Importantly, we found no evidence of a P_D response to target-colored cues. The timing of the P_D in our study was somewhat later than has been observed previously (Burra & Kerzel, 2014; Gaspelin & Luck, 2018a; Gaspar & McDonald, 2014; Hickey, Di Lollo, & McDonald, 2009; Hilimire, Mounts, Parks, & Corballis, 2012; Sawaki, Geng, & Luck, 2012; Sawaki & Luck, 2010). According to the signal suppression hypothesis (Sawaki & Luck, 2010), top-down suppression is typically initiated even before a stimulus is presented. Thus, once participants are informed of their task goal (e.g., "find the red T-shape and ignore the green T-shape"), top-down signals act to enhance firing rates of neurons involved in processing goal-relevant features (e.g., red), and to attenuate the firing of neurons involved in processing goal-irrelevant features (e.g., green; e.g., Maunsell & Cook, 2002). When a target-colored cue is then presented, neurons involved in processing critical stimulus features are more likely to fire and neurons involved in processing goal-irrelevant stimuli are less likely to fire (Hamker, 2005; Treue & Martínez-Trujilllo, 1999). As all cues were relevant to the awareness task in our experiments, however, active suppression was not required until after cue onset. Thus, it is possible that cues were initially enhanced in order to perform the cue awareness task, but then were quickly suppressed for target processing and rapid response.

3.6.1 The relationship between attention and perceptual awareness

Lamy et al. (2015) found an RT benefit for target-colored cues that was independent of perceptual awareness, and an RT cost for distractor-colored cues that depended on perceptual awareness. Across the three experiments presented here, we failed to replicate the independent effects of perceptual awareness on RT costs. Given that we used the same methodological design as Lamy et al., this finding is surprising. We note that the RT cost for unaware cues is quite small in numerical terms (mean cost of 23 ms across the three experiments). As we used a larger sample and had observers perform more trials than Lamy et al. (2015), we may have simply had more statistical power to find this small effect. Interestingly, a recent paper by Schoeberl, Ditye, & Ansorge (2018) also found that the same location cost was independent of cue awareness. Thus, converging evidence suggests that, when measured behaviorally, the attentional mechanisms of selective enhancement and active suppression both appear to be independent of awareness.

Interestingly, our neural data provide a different story as to the relationship between attention and perceptual awareness. We found that the neural responses associated with enhancement (the N2pc/N_T; Hickey, Di Lollo, & McDonald, 2009) were dependent on awareness,

whereas the neural response associated with suppression (the P_D; Hickey, Di Lollo, & McDonald, 2009) was independent of awareness. Thus, our findings suggest that while the neural signatures of top-down enhancement of sensory processes are modulated by awareness, the neural signatures of top-down suppression are not.

Overall our findings have two important implications for understanding the relationship between attention and perceptual awareness. The first is that conclusions about the manner in which attention and awareness relate are likely contingent on how any effects on behavior and brain activity are measured. The variance in neural responses and the variance in RT measures might be assumed to arise from a common source. Thus, it might be expected that the pattern of ERP responses would match those of the behavioral responses (i.e., RTs). The N2pc/N_T component, however, represents an early stage in the stimulus-response chain, whereas RTs represent the final outcome of that chain (or conceivably one of many consequences of stimulus processing). It is possible, therefore, that N2pc/N_T amplitude is determined by one stage of processing, whereas the RT effect is determined by later processing stages involved in decision making, response selection and/or execution. Our findings suggest that these later stimulus-processing stages are largely independent of the magnitude of responses during the early processing of visual features.

The second implication of our work is that the mechanisms of selective attention are likely the combination of (at least) two processes — selective enhancement and active suppression — and these processes seem to relate in different ways to perceptual awareness. While the neural measures of selective enhancement appear to depend on awareness, the neural measures of active suppression do not.

To claim that perceptual awareness is entirely independent of attention, it must be shown that all forms of attentional bias involved in all stages of processing are independent of whether a stimulus will be consciously perceived. Our findings suggest that the relationship between attention and perceptual awareness is a complex one that depends on the type of processing involved in any given task. Future research on the relationship between attention and perceptual awareness should focus on how these different mechanisms interact at different stages of the information processing hierarchy.

3.7 Supplemental material

We ran a permutation test on the EEG results from Experiment 3 to estimate the distribution of values that would be expected under the null hypothesis (as in Gaspelin & Luck, 2018; Sawaki, Geng, & Luck, 2012). The results of this analysis are shown below. Figure S1 is from the analysis of the negative waveform (N_T). Here, the area under the negative waveform was measured over a broad window (200 to 600 ms after cue onset) and compared with the distribution of the area that would be expected by chance. Figure S2 shows the results from the same test applied to the positive waveform (P_D). The results of these tests support the findings of our original analysis.

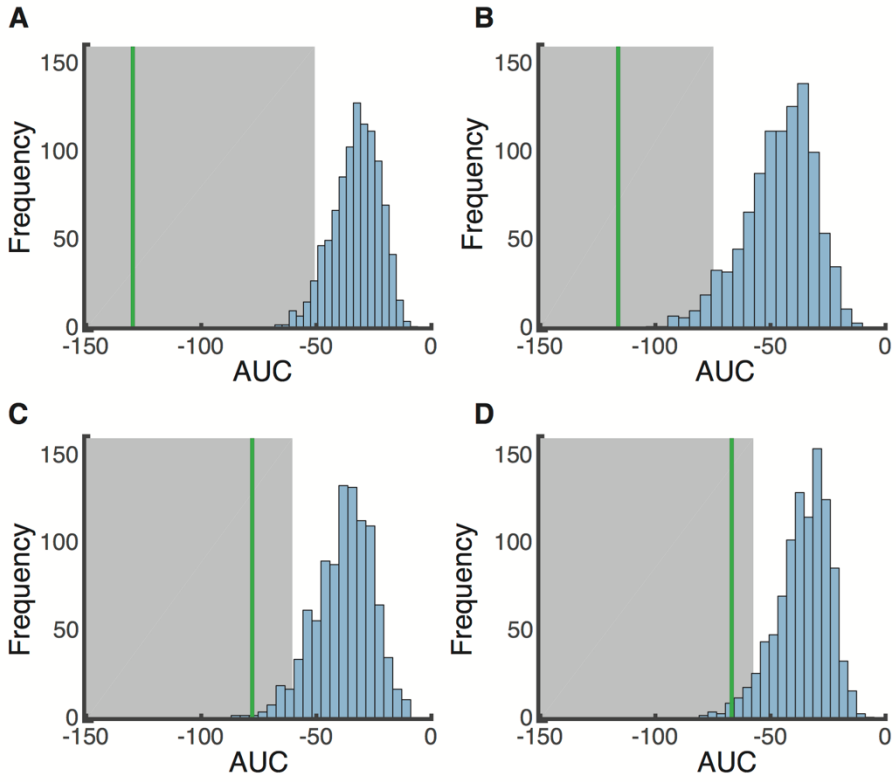

Figure 3.8 Permutation tests of the negative area (N_T) under the difference wave from 200 to 600 ms postcue onset in the four key conditions of Experiment 3. **A** Aware target-colored cue. **B** Unaware target-colored cue. **C** Aware distractor-colored cue. **D** Unaware distractor-colored cue. The blue histograms represent the estimated null distribution from 1,000 permutations. The green lines mark the observed values from the grand average waveforms. The gray areas mark the extreme 5% of the permutation distribution. The green lines fall within the gray area, suggesting that the observed values are significantly different from chance, confirming the outcomes of the original analyses

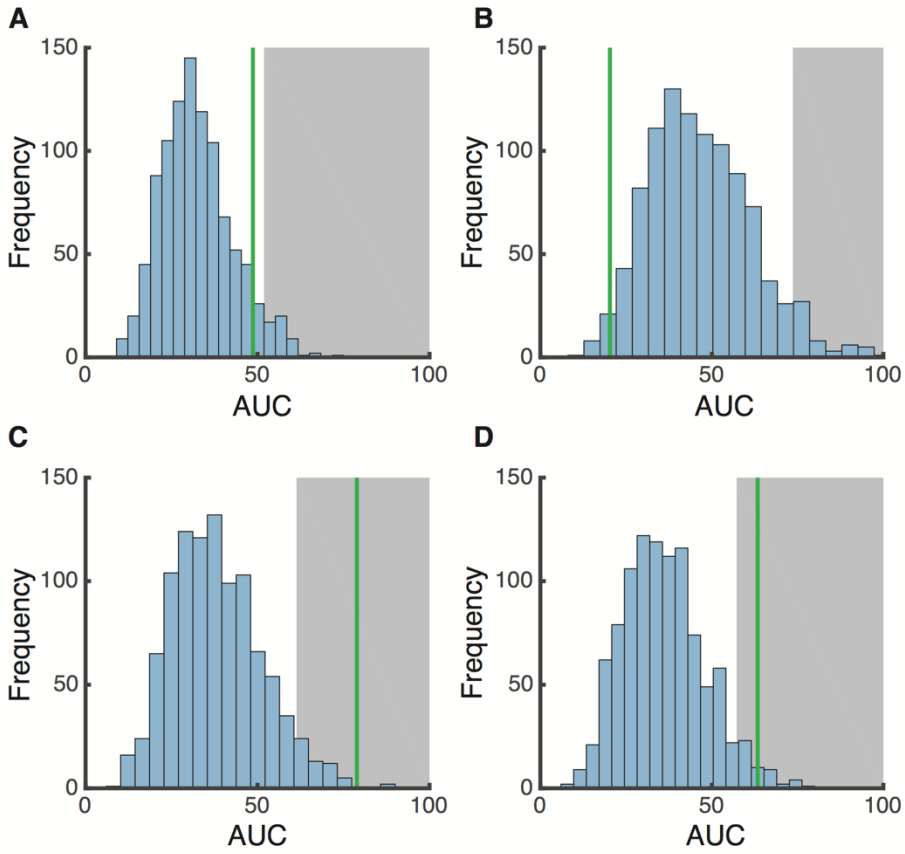

Figure 3.9. Permutation tests of the positive area (P_D) under the difference wave from 200 to 600 ms postcue onset in the four key conditions of Experiment 3. **A** Aware target-colored cue. **B** Unaware target-colored cue. **C** Aware distractor-colored cue. **D** Unaware distractor-colored cue. The blue histograms represent the estimated null distribution from 1,000 permutations. The green lines mark the observed values from the grand average waveforms. The gray areas mark the extreme 5% of the permutation distribution. The green lines fall within the gray area in the distractor-colored cue conditions (**C** & **D**), but not in the target-colored cue conditions (**A** & **B**), confirming the outcomes of the original analysis.

Chapter 4 : Forward encoding of neural activity reveals feature-selective orientation responses under continuous flash suppression

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Travis, S. L., Dux, P. E., & Mattingley, J. B. (submitted). Forward encoding of neural activity reveals feature-selective orientation responses under continuous flash suppression.

4.1 Abstract

To what extent do visual stimuli that are not consciously perceived affect perceptual decisions? There is a rich history of psychophysical and neurophysiological research on the mechanisms by which visual information is accumulated in simple decision-making tasks. This work has focused almost exclusively on decisions made under conditions where the stimuli to be judged are clearly visible to the observer, as exemplified by the widely studied random-dot motion discrimination task. Here we asked how featural information is represented in a decision-making task in which the stimuli to be judged were masked from awareness via continuous flash suppression (CFS). Participants made forced-choice judgments on the orientation of gratings whose contrast was gradually increased so that they eventually broke CFS and emerged into awareness. We recorded brain activity concurrently using electroencephalography (EEG), and flickered the grating and mask stimuli at different frequencies so that we could track their associated neural signals over time. Using forward encoding modeling, we characterized feature-selective neural activity to the gratings prior to, during and after observers made their explicit orientation judgments. Robust orientation-selective responses emerged well before observers' explicit perceptual reports, and this selection was associated with differences in a neural index of evidence accumulation as well as the speed of perceptual judgments. Overall our findings suggest that elementary featural information is extracted from unconscious stimuli, and that this information influences the efficiency of simple perceptual decisions.

4.2 Significance Statement

It is widely recognized that unconscious processing plays an important role in human decision-making. While much research has investigated unconscious perception and evidence accumulation processes, little work has examined how elementary features of stimulus inputs accumulate from unaware to aware states during the decision-making process. Forward encoding models provide a way to investigate this gap by generating feature-specific responses from patterns of brain activity recorded using electroencephalography (EEG). Here we show that orientation-specific responses to visual gratings that are masked via continuous flash suppression are evident in ongoing brain activity well before observers are aware of the orientation information. These results suggest that unconscious processing of elementary perceptual information plays an important role in decision-making.

4.3 Introduction

Much research has been directed toward understanding the human brain's capacity to process sensory information unconsciously (for reviews see Ansorge, Kunde, & Kiefer, 2014; Overgaard, 2017; Sterzer, et al., 2014). Traditionally, cognitive neuroscience has studied unconscious processing by contrasting brain responses evoked under aware and unaware conditions (Overgaard, 2017). While this approach has been important in yielding understanding of information processing under each awareness state, it is inherently limited in its ability to assess how evidence accumulates during unaware states to reach awareness. Although there has been much research on evidence accumulation during perceptual decision making (for reviews see Gold & Shadlen, 2007; Hanks & Summerfield, 2017), much of this work has used visible stimuli to show that perceptual decisions involve optimizing noisy signals until a response threshold is reached. Research investigating how input signal-optimization develops through unaware states is limited and, thus, not well understood.

A popular technique for assessing stimulus processing during unaware states is known as *continuous flash suppression* (CFS; Gilroy & Blake, 2005; Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006), in which a dynamic mask is presented to one eye while a low-contrast target stimulus is slowly ramped in contrast to the other eye (Jiang et al., 2007). The time it takes for the target to be consciously perceived (known as *breaking CFS*) is used as a proxy for awareness (although there is ongoing debate as to the source of the difference in break times, see Stein et al., 2011; Gayet et al., 2014). While neuroimaging studies have shown breaking the suppression is preceded by a specific neural marker (del Rio et al., 2018), whether responses prior to breaking of CFS reflect functionally relevant unconscious processing is currently debated (Stein et al., 2011; Stein & Sterzer, 2014). What is lacking, therefore, is research that investigates whether neural responses measured under suppression are task-relevant, mediate access to awareness, and facilitate perceptual decision-making (Sterzer, et al., 2014).

Previous work has used electroencephalography (EEG) to track decision-related neural activity in response to visual stimuli (O'Connell et al., 2012). This work has identified a centro-parietal positivity (CPP), which averages activity across stimulus features to provide important task-general correlates of evidence accumulation (O'Connell et al., 2012; Pisauro et al, 2017). The CPP component peaks at response time and increases at a rate that depends on task difficulty (O'Connell et al., 2012; Pisauro et al, 2017). Combining this general correlate of evidence accumulation with a measure that reveals the subtle differences in neural activity patterns associated with encoding specific target features can provide important insights into how the brain encodes specific target features during the decision-making process.

To measure how target features are encoded during decision-making, Ho et al. (2012) used fMRI to measure neural activity while participants performed a simple orientation discrimination task on unmasked high-contrast gratings. A forward encoding model was used to quantify orientation-selective processing, which predicted performance accuracy and the rate of sensory evidence accumulation. While this research provides evidence that stimulus-specific encoding can be tracked for clearly visible stimuli, it remains unknown whether stimulus-feature encoding can be tracked prior to awareness in a decision-making context.

Here we used EEG to track orientation-selective neural responses to visual targets presented under CFS. Participants were presented with a flickering target grating to one eye, which progressively ramped up in contrast until it broke the suppressive effect of a dynamic mask presented to the other eye. We analyzed CPP responses to the flickering target to assess evidence accumulation. We also used forward encoding modeling to generate feature-specific functions from brain response patterns across the entire trial. Single-cell recordings in cats and monkeys have revealed that neural responses increase with increased contrast (Albrecht & Hamilton, 1982; Dean, 1981; Sclar & Freeman, 1982). We therefore expected that orientation selectivity would increase gradually as the grating increased in contrast, and that earlier onset of orientation-specific functions would be associated with faster reaction times. We also predicted that orientation-specific responses would be evident for the suppressed target prior to perceptual awareness. Our approach provides a sensitive and continuous readout of feature-specific information that can be used to track unconscious information processing in a variety of contexts.

4.4 Materials and Methods

4.4.1 Participants

Data were collected from twenty-four individuals (18 females, mean age = 22.42 years, SD = 2.59). All participants reported normal or corrected-to-normal vision and all were naïve to the experimental hypotheses. Each provided informed written consent. The experimental protocol was approved by The University of Queensland Human Research Ethics Committee.

4.4.2 Apparatus, stimuli, and procedure

Participants were tested in a dimly illuminated room. Stimuli were presented on a 24-inch LCD monitor with a resolution of 1920 x 1080 and a refresh rate of 100 Hz. Stimulus delivery and response recording were controlled using a Dell PC running Cogent software (Cogent 2000 toolbox: Functional Imaging Laboratory, Institute of Cognitive Neuroscience, and Wellcome Department of Imaging Neuroscience) in Matlab under Windows XP.

After providing informed consent, participants viewed a dichoptic display through a mirror stereoscope, at a viewing distance of approximately 57 cm (see Figure 4.1). A pair of white,

horizontally aligned circular frames (10° diameter) was presented on the monitor. To promote stable binocular fusion, the mirrors were adjusted for each observer at the beginning of the experimental session, such that when viewed through the mirror stereoscope the two circular frames appeared as one single frame.

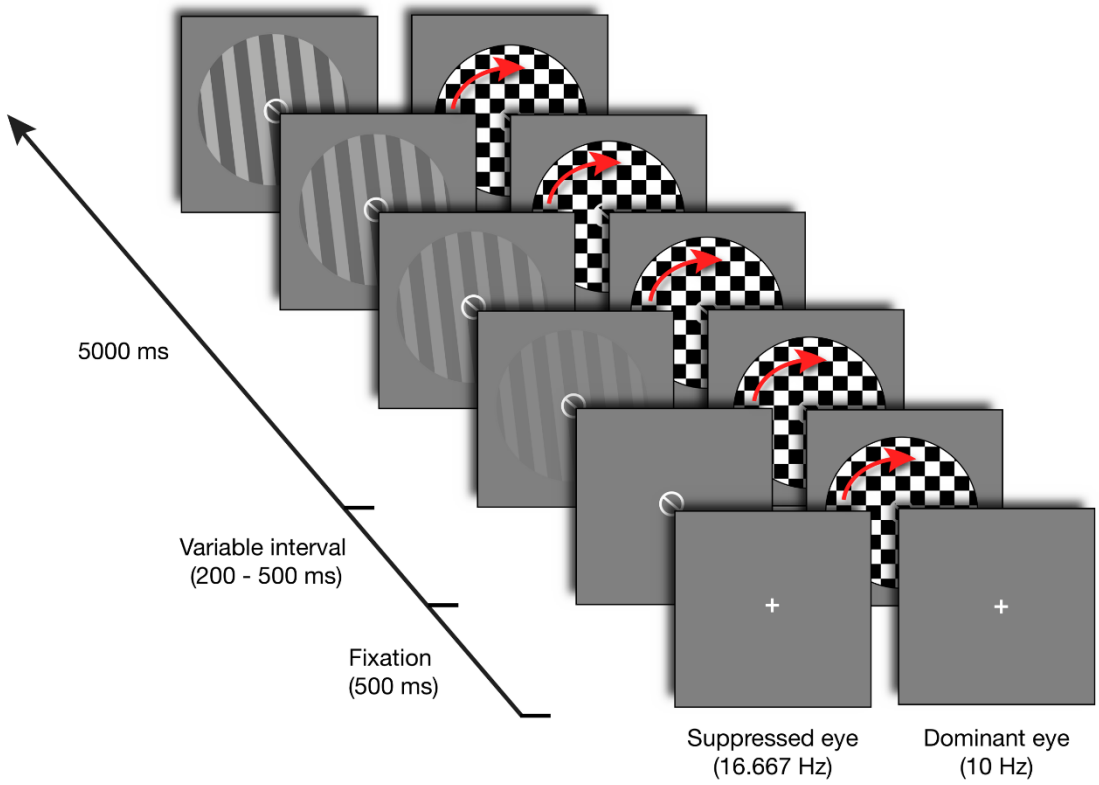

Figure 4.1. Schematic of the trial sequence. Trials began with a 500 ms fixation period followed by a variable interval of 200-500 ms, during which a high contrast rotating checkerboard flickering at 10 Hz was presented to the participant's dominant eye, while a central orientation cue was presented to both eyes. A flickering grating (16.667 Hz) which gradually increased in contrast was then introduced to the suppressed eye over 5,000 ms. Participants were asked to indicate whether the grating was rotated clockwise ("right") or counterclockwise ("left") with respect to the orientation cue. Red arrows are for illustrative purposes only, and indicate the direction of motion of the rotating mask.

The CFS mask was a counter-phasing flickering (10 Hz) black (CIE: .304, .259, 1.4 cd/m^2) and white (CIE: .305, .389, 214 cd/m^2) circular checkerboard (10° diameter) that rotated at 250° per second. The target was a counter-phasing flickering (16.667 Hz) black and white grating (10° diameter). The orientation cue consisted of a white (CIE: .305, .389, 214 cd/m^2) circle (1°) with a white (CIE: .305, .389, 214 cd/m^2) diameter line which served as the orientation cue.

Each trial began with a 500 ms fixation cross, followed by a variable interval of 200-500 ms, during which the CFS mask was presented to one eye and an orientation cue was presented centrally to both eyes. Following this interval, the grating was presented to the other eye and ramped linearly

from 0% contrast to 50% contrast over 5,000 ms. Grating orientation was pseudo-randomly selected from one of 9 orientations (0-160° in 20° increments) and was presented either 20° clockwise or 20° counter-clockwise relative to the orientation cue (counter-balanced across grating orientations). Participants performed an orientation discrimination task in which they were asked to identify as quickly and as accurately as possible whether the orientation of the grating was counterclockwise ("left") or clockwise ("right") relative to the orientation cue.

Prior to the main experiment participants performed a practice block of 36 trials. During the practice block, performance was monitored to ensure participants understood the task and that the grating broke suppression at some point during the trial. If required, participants performed a second practice block until performance was above 80% correct. During practice, feedback was provided on accuracy for each trial. Following the practice block, participants performed 10 blocks of 36 trials (for a total of 360 experimental trials). During the experimental trials, feedback on accuracy was provided at the end of each block.

Electroencephalography. EEG data were continuously recorded from 64 active Ag/AgCl scalp electrodes, arranged according to the international standard 10-10 system for electrode placement (Oostenveld & Praamstra, 2001) using a nylon cap. Eye movements were monitored using bipolar horizontal and vertical electrooculography (EOG). EEG and EOG signals were amplified by Biosemi Active Two amplifiers and sampled at 1024 Hz with 24-bit A/D conversion. Standard reference and ground electrodes were used during recording.

Offline pre-processing of the EEG data was performed using EEGlab (Delorme & Makeig, 2004). A high pass 0.1 Hz filter was applied, and data were re-referenced to the average of all common electrodes. Then, 7,000 ms epochs were extracted beginning 1,000 ms before grating onset to 1,000 ms after grating offset, separately for each of the nine grating orientations. Muscle, eye-movement and blink artifacts were identified and removed using independent component analysis with the Amsterdam Decoding and Modeling (ADAM) toolbox (The toolbox can be downloaded from https://github.com/fahrenfort/ADAM). Incorrect trials were excluded from the analysis.

4.4.3 *CPP Analysis*

To measure decision-related neural activity, we analyzed the CPP component by averaging the extracted epochs from electrode site CPz and baseline-correcting to the 200 ms interval before target onset. A notch filter was applied to the ERPs to remove the 10 Hz mask frequency, the 16.667 Hz grating frequency, and the 50 Hz line noise (and their harmonics up to 100 Hz; note that a notch filter was not applied to the data for the SSVEP analysis below). We used a jackknife procedure (Miller, Patterson, & Ulrich, 1998) to examine whether the onset and accumulation rate of the CPP differed between fast- and slow-RT trials (as described in detail below). As suggested by Miller, Patterson, & Ulrich (1998), the onset latency of the CPP was defined as the latency to reach

50% of the waveform's peak amplitude, and the accumulation rate was calculated by taking the latency of the CPP $\pm$ 500 ms as coordinates (x_0, y_0) and (x_1, y_1) and calculating the linear interpolant between these points (Equation 1):

$$b = \frac{y_1 - y_0}{x_1 - x_0} \quad (1)$$

4.4.4 *SSVEP Analysis*

We analyzed SSVEP responses to the flickering gratings as a measure of stimulus-specific evidence accumulation. We performed a wavelet analysis on the unfiltered ERP data, to assess the SSVEP response across time. As in the CPP analysis, we sorted the data into fast- and slow-RT trials relative to each participant's median RT, in order to assess whether SSVEP responses were correlated with response times. We used a complex Morlet wavelet with a length of 10 cycles to estimate the power of the SSVEP response averaged over eight occipital electrodes (Oz, POz, PO3, O1, PO4, O2, PO7, PO8), for the 16.667 Hz (grating) and 10 Hz (mask) frequencies (z-scored with respect to 200 ms pre-stimulus baseline), separately for fast- and slow-RT trials. We used a similar jackknife procedure as described above to examine whether the onset and accumulation rate of the wavelets differed between fast- and slow-RT trials. As suggested by Miller, Patterson, & Ulrich (1998), we defined the onset of the increase in SSVEP power as the latency at which the power reached 50% of the minimum to maximum power, beginning 500 ms after stimulus onset.

4.4.5 Forward Encoding Analyses

We used a forward encoding model based on the 16.667 Hz wavelet results to estimate the dynamic feature-selective response function of the grating response. We used a similar procedure to that described in Brouwer and Heeger (2009), in which a 10-fold cross-validation was performed. A training set of EEG data was used to model the response in each of 9 hypothetical orientation channels (corresponding to the 9 presented grating orientations), composed of half-rectified sinusoids raised to the 5th power.

During training, the following general linear model was used (Equation 2):

$$\boldsymbol{B_1 = WC_1} \quad (2)$$

Where B_1 is the matrix (electrodes x time x trials) containing the power values for each electrode at each time point in each trial of the training set, C_1 (channels x time x trials) is the matrix of predicted responses for each channel at each time point on each trial, and W (electrodes x channels x time) is the matrix of weights resulting from the least-squares regression as follows (Equation 3):

$$\boldsymbol{W = B_1 C_1^T (C_2 C_1^T)^{-1}} \tag{3}$$

The observed test data (B_2; electrodes x time x trials) were then transformed by the inverse of the model to estimate the channel responses (C_2; channels x time x trials) using the weights from the training set (W). C_2 was calculated using Equation 4:

$$\boldsymbol{C_2 = (W^T W)^{-1} W^T B_2} \tag{4}$$

This procedure was repeated until all data had been used as the testing set. Estimated responses in C_2 were then shifted to align to 0° and averaged across trials to yield the estimated channel responses over time.

We conducted circular statistical analysis to assess the estimated orientation-specific response functions using CircStat: A Matlab Toolbox for Circular Statistics (Berens, 2009). We z-transformed the data and, since the data were axial, we multiplied each orientation by two before calculating the mean angular direction and the mean resultant vector across the 5-second trial. We converted the data from degrees to radians and took the cosine of the mean angular direction as the measure of angular direction. Thus, angular direction values close to +1 represent mean resultant vectors that point toward the presented orientation, and values close to -1 represent vectors that point 180 degrees from the presented orientation.

The length of the mean resultant vector was calculated as a measure of circular spread. Values close to 1 represent data that are concentrated around the angular mean, and those close to 0 represent a uniform distribution. As the estimated angular mean direction is biased when using binned data, we applied Equation 5 to correct for this bias:

$$\boldsymbol{c = \frac{d}{2\sin\left(\frac{d}{2}\right)}} \tag{5}$$

where d is the spacing between orientations.

To obtain a single measure of orientation-specific response across the 5-second trial we weighted the mean resultant vector length by the cosine of the mean angular direction. Thus, the adjusted mean resultant vector length could vary between -1 and +1, where positive values represent orientation-specific responses toward the presented orientation (0°), negative values represent orientation-specific responses toward the opposite direction (180°), and a value of 0

represents a uniform distribution. (Note that a value of 0 could also be due to orientation-specific responses that are orthogonal to the presented orientation, i.e. 90°).

4.5 Results

Data from two participants were excluded from the analysis. One participant's performance on the task was not significantly above chance, and another participant chose not to complete the experimental session. Data from the remaining 22 participants were included in the final analyses.

4.5.1 Behavioral Results

Participants registered a response (grating clockwise vs. counterclockwise relative to the cue) on 92% of trials. For these trials, mean accuracy was 96.45% (chance = 50%; SD = 3.38%), indicating that participants were able to accurately discriminate the orientation of the target grating before the end of the trial. As expected, response latencies were variable (M = 3091 ms; SD = 687 ms; see Figure 4.2A).

4.5.2 ERP Results

To quantify the accumulation of neural evidence associated perceptual decisions, we measured the onset latency and slope of the CPP component. To assess whether the timing and slope of the CPP component predicted response times, we sorted the data into fast- and slow-RT trials relative to each participant's median RT. We then averaged waveforms from the CPz electrode, separately for fast- and slow-RT trials (baseline corrected to a 200 ms interval before target onset).

The ERP analysis revealed a robust CPP component for both fast- and slow-RT trials time-locked to grating onset (Figure 4.2B) and to response (Figure 4.2C). The mean time of onset of the CPP – determined at 50% of the waveform's peak amplitude – occurred significantly earlier for fast RT trials (M = 947 ms, SD = 40 ms) than for slow-RT trials (M = 1124 ms, SD = 78 ms), (M_{diff} 177 ms, SD = 58 ms, $t(21) = 3.027$, $p = .0064$. To investigate whether response times were predicted by the rate of neural evidence accumulation, we quantified the slope of the CPP separately for fast- and slow-RT trials. This analysis revealed that the slope of the CPP (calculated as the linear interpolant between $\pm$ 500 ms of its onset latency) was significantly steeper for fast-RT trials than for slow-RT trials, $t(21) = 7.461$, $p < .0001$), suggesting that the CPP grew at a faster rate on trials in which participants were quicker to judge the orientation of the grating stimulus. Importantly, this difference in onset latency and slope between fast- and slow-RTs occurred despite identical sensory input on all trials.

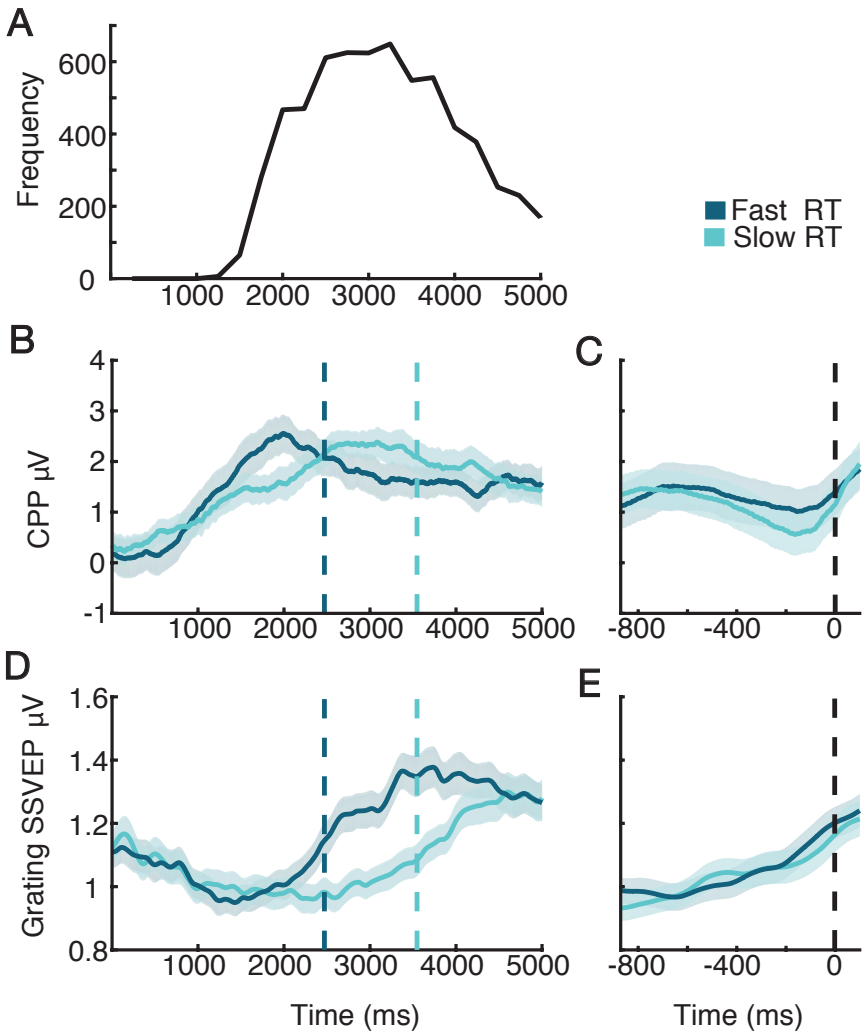

Figure 4.2. Reaction times and neural signatures of evidence accumulation (CPP) and sensory processing (SSVEPs) relative to the onset of the target grating. (A) Reaction time distribution for all participants (N = 22). For subsequent analyses, trials were sorted into fast- and slow-RT trials relative to each participant's median RT. (B) CPP component of the EEG, aligned to grating onset. (C) CPP component of the EEG, aligned to participants' responses. (D) SSVEP responses to the target grating (16.667 Hz), aligned to grating onset. (E) SSVEP responses to the target grating, aligned to response. Vertical dashed lines represent mean reaction times for the fast-RT trials (M = 2563 ms, SD = 453 ms; dark blue) and slow-RT trials (M = 3685 ms, SD = 495 ms; light blue). Black vertical lines indicate the time of response (C, E).

4.5.3 SSVEP Results

To assess sensory processing of the target, we measured the onset latency and slope of the SSVEP response at the flicker frequency of the grating stimulus. As with the CPP component we sorted trials into fast- and slow-RT trials relative to each participant's median RT, to assess whether the timing and slope of the SSVEP predicted response times. SSVEP responses were time-locked both to the grating onset (Figures 4.2D), and to participant's responses (Figure 4.2E).

As seen in Figure 4.2D, the onset of the SSVEP for the target grating (16.667 Hz) was earlier for fast-RT trials (M = 2502 ms, SD = 33 ms) than for slow-RT trials (M = 3677 ms, SD = 38 ms). Using a jackknife procedure, we found that the mean onset difference was significant, (M_{diff} 1176 ms, SD_{diff} = 31 ms, $t(21) = 38.518$, $p < .00001$. The slope of SSVEP power was also significantly steeper for fast-RT trials than for slow-RT trials ($t(21) = 2.376$, $p = .027$), again indicating that the increase in SSVEP power occurred earlier and at a faster rate when participants responded earlier in the trial. The onset of the mean SSVEP response (M = 2990 ms, SD = 137 ms) occurred significantly later than the onset of the mean CPP component (M = 1046 ms, SD = 45 ms, $t(21) = 13.881$, $p < .00001$).

4.5.4 Encoding Results

Having established that SSVEP power covaried with response time, we investigated whether SSVEP power could be used to construct a population orientation-specific function. We used a similar procedure to that described in Brouwer and Heeger (2009), in which the magnitude of the response at each electrode is estimated as a weighted sum of a hypothetical orientation-specific response function. We used these weights to estimate the SSVEP response for each presented orientation, as described in detail in the Methods. We expected that responses would initially be unable to discriminate between orientations, but as the contrast of the grating increased, orientation-specific responses would progressively emerge across the trial. Figure 4.3A shows the modeled orientation-selective response function for all trials, time-locked to grating onset, and Figure 4.3B shows the same results time-locked to the participants' responses.

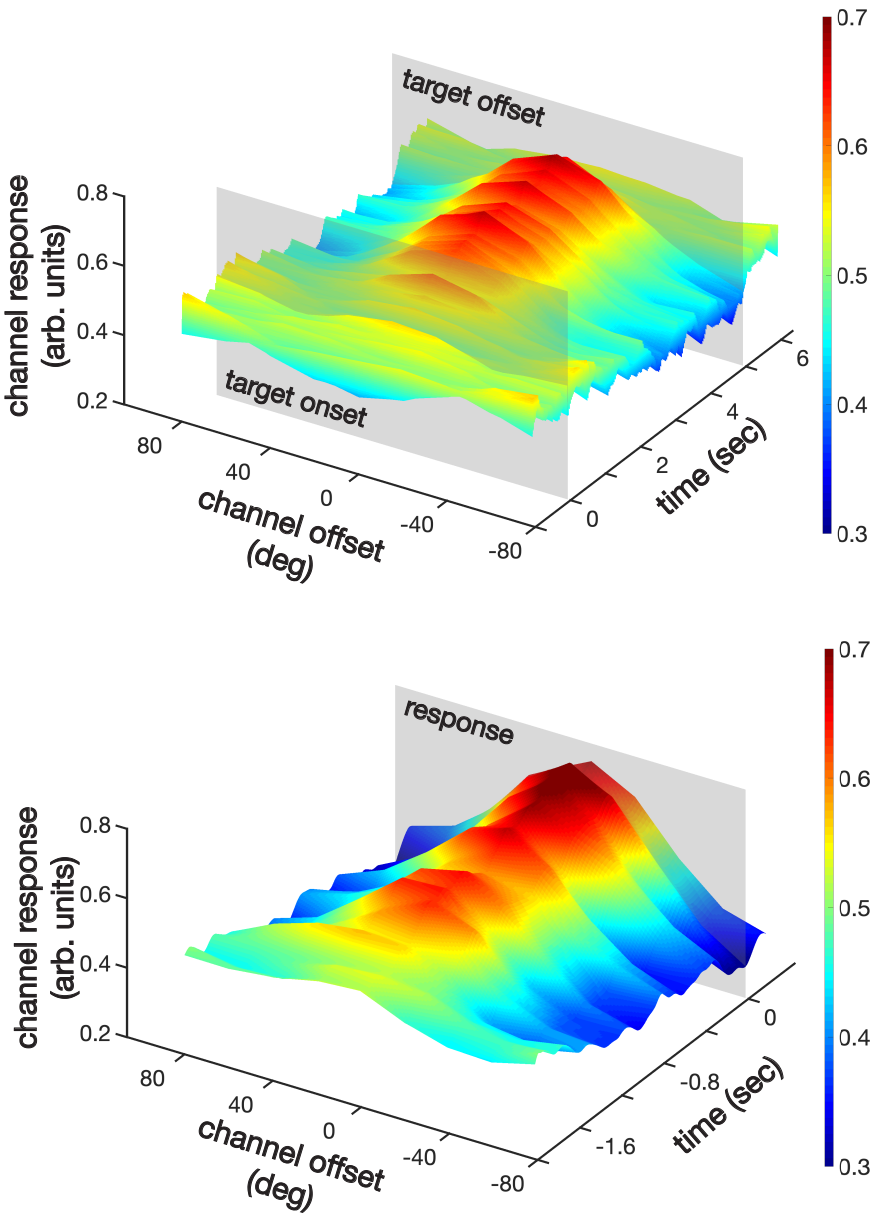

Figure 4.3. Normalized forward encoding modeling results from wavelet decomposition of the SSVEP response. Channel response functions for each presented orientation were shifted so that they were centered on over a common point (i.e. 0 degrees on the channel offset axis). (A) All trials time-locked to grating onset. Grey planes mark grating onset and grating offset. (B) All trials time-locked to response (-2000 ms to 200 ms). Grey plane marks response. See section 4.4.5 for more information on the forward encoding analyses. Note: As the channel weighted matrix computes the linear transform of observations into the hypothetical space of the basis function (C_1 in Equation 2), the parameters of the idealized tuning curve are determined from the basis set. Consequently, the unit of measurement for the channel response (C_2 in Equation 2) is expressed in arbitrary units.

To assess the estimated orientation-specific response function, we calculated the cosine of the mean angular direction, the length of the mean resultant vector, and the adjusted vector length across the 5-second trial. The cosine of the mean angular direction is a measure of precision; values

close to +1 represent orientation-selection towards the presented orientation and values close to -1 represent orientation-selection at 180˚ from the presented orientation. As can be seen in Figure 4.4A, the cosine of the mean angular direction of the orientation-specific response function increased significantly, indicating a gradual increase in orientation selectivity over the duration of the trial. The length of the mean resultant vector is a measure of circular spread. Values close to 1 represent data that are concentrated around the angular mean, and a value of 0 represents a uniform distribution. The mean resultant vector length (Figure 4.4B) also increased across the 5-second trial, indicating that the variance in circular spread decreased over the trial. To obtain a weighted measure of the orientation-specific response function we calculated an adjusted mean resultant vector by multiplying the mean resultant vector length by the cosine of the mean angular direction. The adjusted mean resultant vector increased positively across the 5-second trial and was significantly different from zero beginning at 813 ms (Figure 4.4C; FDR corrected). To summarize, the results of the forward encoding analyses suggest that while orientation-specific responses were not evident at the onset of the masked target grating, orientation selectivity increased gradually across the trial. The modeled orientation-specific response function was undetectable early in the trial, but orientation-specific responses gradually emerged as the contrast of the grating increased.

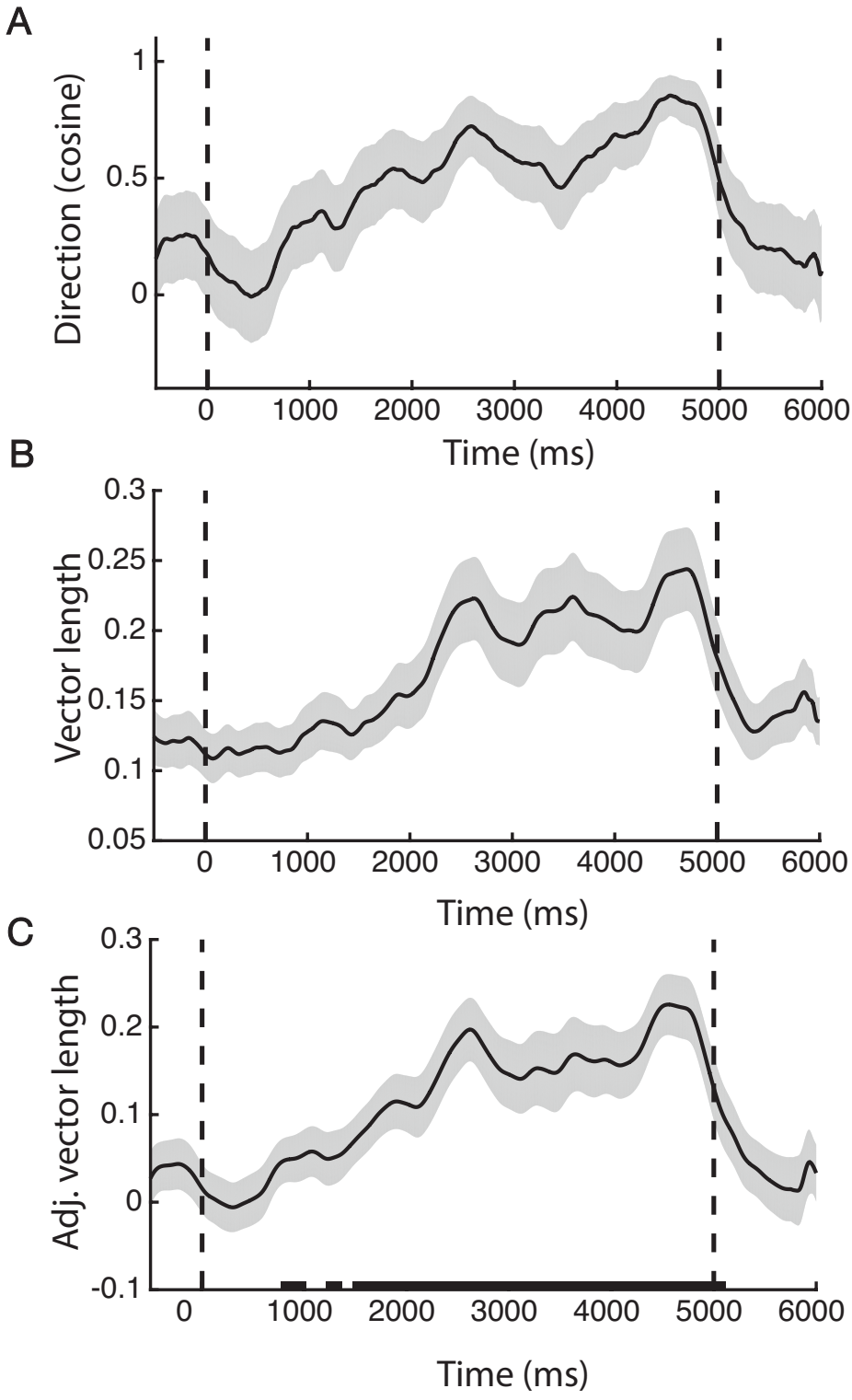

Figure 4.4. Vector parameters during the 5,000 ms trial. (A) Cosine of the mean angular direction. (B) Mean resultant vector length. (C) Adjusted mean resultant vector length, calculated by multiplying the mean resultant vector by the cosine of the mean angular direction. Black markers on the x-axis in panel C indicate time points at which the adjusted vector length was significantly different from zero ($p < .05$, FDR corrected). Data have been smoothed for the figure, but all analyses were performed on unsmoothed data.

4.5.5 Encoding for Fast and Slow RT trials

As with the CPP component and the SSVEP response, we sorted trials into fast- and slow-RT trials relative to each participant's median RT to assess whether the orientation-specific response functions covaried with response times. As shown in Figure 4.5, there were clear orientation-specific responses for both fast- (Figure 4.5A) and slow-RT trials (Figure 4.5B). Responses were aligned to the presented grating orientation, and the amplitude of these responses increased earlier and reached a larger magnitude for fast-RT trials than slow-RT trials.

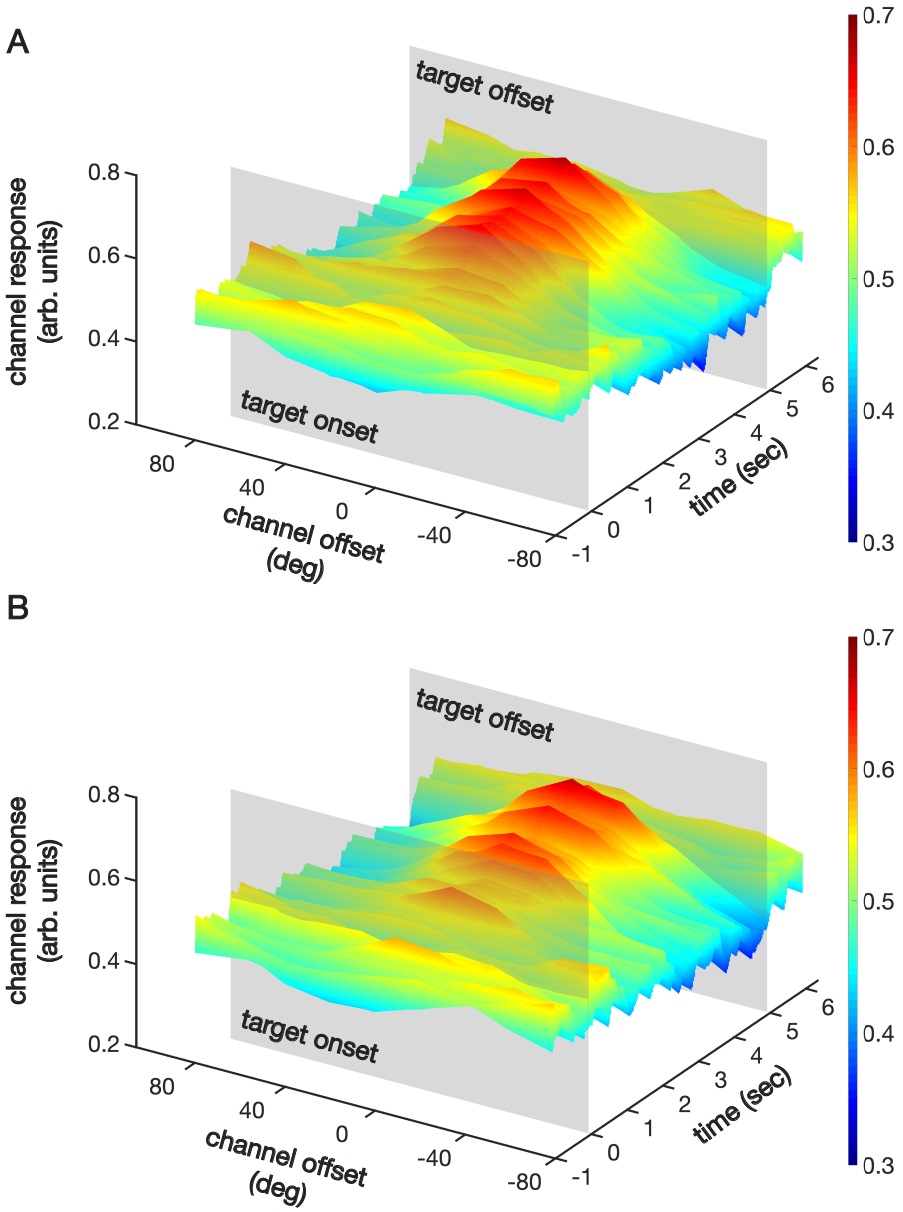

Figure 4.5. Normalized forward encoding modeling results from the wavelet decomposition of the SSVEP response. (A) Fast-RT trials time-locked to grating onset. (B) Slow-RT trials time-locked to grating onset. Grey planes mark grating onset and grating offset.

4.5.6 Comparison of neural activity during aware vs unaware trial intervals

In a final set of analyses, we asked whether the dynamics of orientation-specific responses to the target grating varied between intervals in which participants were consciously aware of the target and intervals in which the target was suppressed due to the CFS mask. In the current task we did not ask participants to make explicit awareness judgments, so instead we operationalized awareness by dividing trials based upon the time of participants' responses to the target grating. Our rationale was to bin trial epochs over which the contrast of the grating was within a fixed range (e.g., 20-25%), thus allowing us to remove any effects related to physical properties of the target. We then compared orientation-specific responses for epochs over which participants had responded to the target, which we took as a reasonable proxy for awareness, and epochs over which no response had yet been registered (as a proxy for unawareness).

To do this we chose a narrow time-window close to each participant's median RT (see Figure 4.6A). Since motor execution typically occurs within around 200 ms for such simple responses (e.g. Welford, 1980), we offset the time-window by a buffer of 200 ms to allow for any non-visual contributions to response times (e.g., motor execution time). Thus, for example, if a participant's median RT was 2.7 s, by definition on half of all trials a response was made between target onset and 2.7 s (hereafter "fast-RT" trials), and on the other half of trials a response was made between 2.7 s and the end of the trial (5 s; "slow-RT" trials). Taking a 500 ms time window from 2 secs to 2.5 secs (with a 200 ms buffer from the median RT), by definition participants had already registered their response to the target on fast-RT trials, but over the same interval (and thus over the same contrast range) they had yet to register their response on slow-RT trials. In this manner, we separated the orientation-specific response functions over a fixed contrast range for each individual based upon their own median RT, and compared the functions for epochs over which they were aware of the target (having already responded to its presence) or were still unaware of the target (because they were yet to respond). While this approach might have allowed some epochs in which the participant was in fact aware of the target to contribute to the "unaware" category due to especially cautious or otherwise slow responding, it is important to note that this would have the effect of *reducing* the likelihood of any difference in response functions between aware and unaware trials.

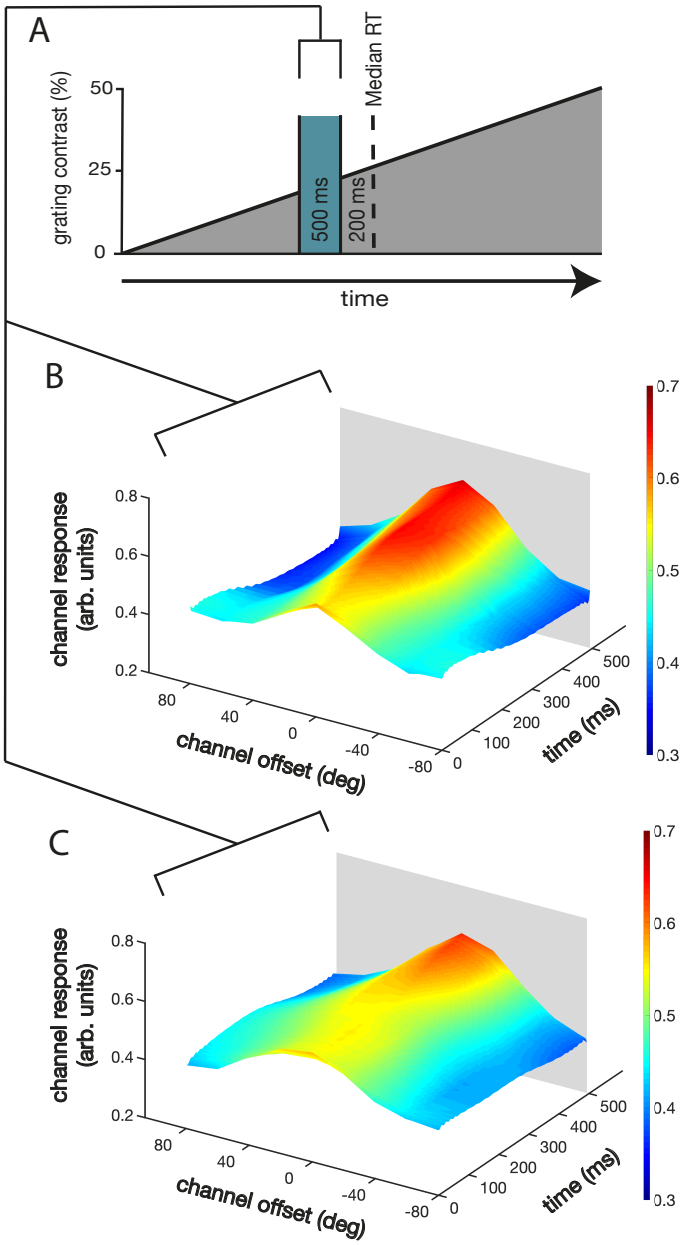

Figure 4.6. Normalized forward encoding modeling results from the wavelet decomposition of the SSVEP response. (A) Schematic showing 500 ms window for comparison of orientation-specific responses in "aware" (fast-RT) and "unaware" (slow-RT) trials based upon each participant's median RT. (B) Orientation-specific responses for aware trials during the 500 ms epoch of interest. (C) Orientation-specific responses for unaware trials during the 500 ms epoch of interest. Grey planes mark the end of the 500 ms time window (which was always 200 ms before each participant's median RT).

As seen in Figures 4.6B and 4.6C, there were clear orientation-specific responses for both aware and unaware trials. Responses were selective for the presented grating orientation and increased gradually over time, although this increase occurred earlier and was larger for aware trials than unaware trials.

To determine whether orientation-specific response functions were different for aware and unaware trials, we measured the mean angular direction and the mean resultant vector length across the selected 500 ms epoch, separately for aware and unaware trials. The cosine of the mean angular direction is plotted in Figure 4.7A and the mean resultant vector length is plotted in Figure 4.7B. To obtain a weighted measure of the orientation-specific response function for aware and unaware trials we multiplied the mean resultant vector by the cosine of the mean angular direction (Figure 4.7C). The weighted mean resultant vector for aware and unaware trials diverged such that the adjusted length was greater for aware trials than unaware trials from 207 to 500 ms (2-tailed t-test, black x-axis lines represent significant differences, FDR corrected).

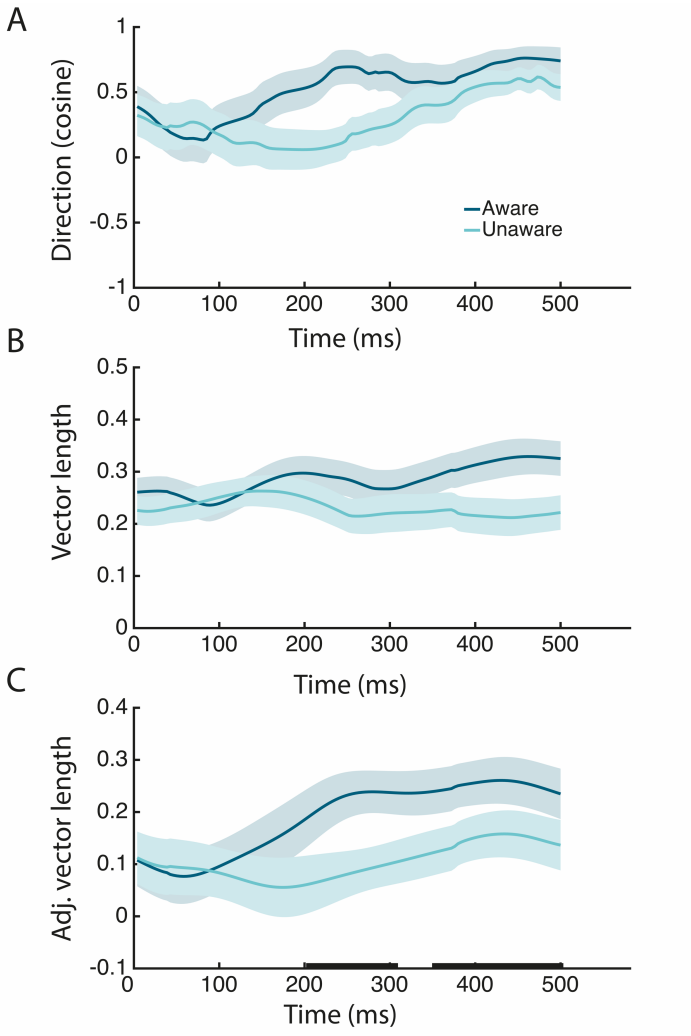

Figure 4.7. Vector parameters during the 500 ms time window of interest for aware and unaware trials. (A) Cosine of the mean angular direction. (B) Mean resultant vector length. (C) Adjusted mean resultant vector length, calculated by multiplying the mean resultant vector by the cosine of the mean angular direction. Black markers on the x-axis in panel C indicate time points over which orientation-specific response was significantly different between aware and unaware trials ($p < .05$, FDR corrected). Data have been smoothed for the figure, but all analyses were performed on unsmoothed data.

4.6 Discussion

Here we investigated how feature-selective visual information processing develops and is optimized through the decision-making process from unaware states through to aware states. To do this we used EEG to track brain activity to target gratings that were masked using CFS. We measured the CPP, an ERP component that is thought to track evidence accumulation during decision formation (O'Connell et al., 2012; Pisauro et al, 2017; Tagliabue, et al., 2019), and employed forward encoding modeling to track orientation-selective neural activity (e.g. Garcia et al., 2013).

As expected, we found that the CPP component onset earlier and grew at a faster rate in fast-RT relative to slow-RT trials. These findings are consistent with past research in humans which found that the CPP component reflects a domain-general measure, independent of stimulus features, and tracks evidence accumulation in terms of observers' subjective experience as opposed to the physical intensity of the stimulus (O'Connell et al., 2012; Tagliabue, Veniero, Benwell, Cecere, Savazzi & Thut, 2019).

These results are also consistent with evidence from single-cell recordings from non-human primate studies (e.g. Roitman & Shadlen, 2002; see also Mazurek, Roitman, Ditterich & Shadlen, 2003; Gold & Shadlen, 2007). For example, Roitman & Shadlen (2002) found that activity in area LIP tracks the decision process leading to choice initiation. In their study, rhesus monkeys performed a motion-discrimination task in which they reported the direction of motion of a random dot kinematogram by making a saccadic eye movement to one of two targets that was either in the response field of the recorded neuron or in a different location. Neural modulation prior to the saccadic eye movement predicted the monkey's choice. Interestingly, the slope of the increase in spike rate varied for trials in which the same motion coherence level was presented. Similar to the current findings, when the monkeys' responses were aligned to target onset the response slope was steeper for fast RT trials than slow RT trials. When responses were aligned to saccade initiation, the level of activity aligned ~70 ms prior to response initiation for all trials, within and across motion-coherence levels. This common level of activity prior to the monkeys' choice response suggests an activity threshold that is independent of stimulus strength which must be reached before a choice is executed. The findings of Roitman and Shadlen (2002) are conceptually similar to those of our study. We found that while response times varied with the rate of evidence accumulation (measured as the slope of the orientation-selection response) they were aligned to a common threshold (measured as the peak of the orientation-selection response curve, the CPP, and the SSVEP responses; see Figure 4.2).

Methodological differences between Roitman and Shadlen (2002) and the current study highlight implications and importance of our CPP findings. While Roitman and Shadlen had

monkeys perform a discrimination task on motion stimuli, our participants performed an orientation discrimination task. Thus, the similarity in findings across studies suggests that the predictability in the slope of responses and threshold is not strictly contingent on stimulus type. Furthermore, unlike Roitman and Shadlen we used displays in which the target stimuli were masked using CFS. Thus, our findings support the view that the accumulation of evidence during decision-making occurs before that information is available for conscious report (Haggard, 2008; Shadlen & Kiani, 2011; 2013). Finally, Roitman and Shadlen used LIP spike rates to predict the timing and the direction of the saccade. As the CPP component we measured reflects overall activity for all presented orientations, the CPP response can be used to predict task response times but cannot differentiate between target features.

To overcome this limitation, we presented targets in one of nine different orientations, allowing us to generate orientation-specific responses from distinct patterns in the EEG data. To do this we conducted a forward encoding analysis to predict the orientation-selective information available during the trial. The forward encoding analyses revealed that at the start of the trial, orientation-specific information could not be extracted from the EEG signal, but as the target grating increased in contrast, orientation-selective responses progressively emerged. When measured across the trial, the slope of the increase in orientation-selective responses varied with RT, suggesting that the responses measured were not merely stimulus-evoked.

The overall onset of the orientation-selective response was evident early in the decision-making process (M = 1,724 ms), more than 1.3s before participants made their orientation-discrimination response (mean RT minus the mean adjusted vector onset), suggesting that visually responsive neurons already prioritize orientation-specific information well before observers are explicitly aware of their presence. To test this possibility, we took a 500 ms time window before each observer's median RT (with a 200 ms buffer). We then split the trials into fast- and slow-RT trials. Thus, during this time window, participants would have registered their response to the target on fast-RT trials (aware trials), but over the same time window (and thus over the same contrast range) they had yet to register their response on slow-RT trials (unaware trials). Using this approach, we effectively separated trials over a fixed contrast range for each individual based on their own median RT and examined the orientation-selective functions during the time window for aware trials and unaware trials. Crucially, there was significant orientation-selectivity for both aware and unaware trials. However, this orientation selectivity (as measured by the weighted mean angular direction) emerged earlier for aware versus unaware trials, despite the fact that grating contrast was held constant across this comparison. Our findings suggest that the degree to which the system gathers data for decision-making is not entirely stimulus-driven, as the weighted angular direction measure varied as a function of response time. Furthermore, our findings suggest that a

preference for the target orientation may occur much earlier than explicit awareness of those sensory data.

Our results suggest that in humans, orientation-selective information is extracted from sensory inputs before it is available for conscious report. We can assume that perceptual awareness of the target would have occurred at some time before participants indicated their response. We included a 200 ms buffer before each participant's median RT to account for processes involved in response preparation that occur after awareness, but the exact time between perceptual awareness and response is unknown. Thus, we cannot be certain that participants were unaware of the grating targets during the entirety of the slow-RT epoch. Overly cautious or otherwise slow responding might have led to some "aware" epochs being included in the unaware condition. But this would have had the effect of *reducing* the likelihood of finding any difference between orientation-selectivity for aware and unaware trials; it would have also had the effect of *increasing* the likelihood of finding orientation-selectivity in the unaware condition. Future research may consider implementing a dual-task approach in which participants perform a detection task (i.e., report their awareness of the target without reference to its features; for example, when the participant is first aware of the presence of the target), followed by a discrimination task, in which they discriminate the target on the basis of its features (i.e., orientation; for example, was the target oriented to the right or left, relative to the orientation of the cue). Detection tasks require significantly less processing than discrimination tasks (Grill-Spector & Kanwisher, 2005; Hol & Treue, 2001). Including both measures would not only allow measurement of orientation-selectivity before detection, but would also allow quantification of orientation-selectivity during the period from detection to perceptual discrimination.

The present findings are consistent with previous work in non-human primates which has shown that neurons in early processing areas (V1 and V2) respond to orientation information independently of awareness, whereas orientation-selective cells in later-stage processing areas (e.g., V4) track changes in awareness, such that their firing rate increases when the animal is aware of the stimulus and decreases when the animal is unaware of it (Leopold & Logothetis, 1996; Logothetis & Schall, 1989). Similarly, human neural responses measured via EEG are higher when observers consciously perceive targets than when the same stimuli are not perceived (Haynes, Deichmann, & Rees, 2005; Tononi & Edelman, 1998; Zhang, Jamison, Engel, He, & He, 2011). Our findings extend this research, suggesting that unaware orientation-selective information accumulates during the decision-making process at a rate that is predictive of response times. There is reason to believe, therefore, that at least some of the mechanisms that underlie the decision-making process also play a role in unconscious processing.

Here we have provided data that has important implications for understanding how input signal optimization develops through unaware and aware states during the decision-making process. The approach used here provides a non-invasive method to measure stimulus-specific encoding of unaware stimuli in the human cortex. We show that using the forward encoding approach with EEG data provides an important tool for measuring the temporal dynamics of signal optimization during decision-making, from unaware to aware states. Applying this method to investigate whether evidence accumulation during the decision-making process differs in neurological patients who are chronically unaware of portions of their visual field, such as those with unilateral spatial neglect (Driver & Mattingley, 1998; Driver & Vuilleumier, 2001) or blindsight (Weiskrantz, 1986), could help to elucidate the underlying role of awareness during the decision-making process.

Chapter 5 : General Discussion

5.1 General Discussion

Our ability to process the vast amount of information received by the senses is an essential function that underpins what is perceived, learned, and acted on. An observer's ability to pay attention – to enhance processing of relevant information while inhibiting irrelevant information – affords a reduction in complexity and avoids information overload. Intuitively, this attention mechanism seems to determine what we see. How attention relates to our perceptual awareness, however, has been the subject of much recent debate. While the majority of the empirical evidence supports the view that attention is required for perceptual awareness (the single dissociation view; e.g., Cohen, Cavanagh, Chun & Nakayama, 2012; for a review see Pitts, Lutsyshyna, & Hillyard, 2018), some have argued that attention and perceptual awareness are one and the same process (the no dissociation view; e.g., Chun & Wolfe, 2000; De Brigard & Prinz, 2010; Mole, 2008; O'Regan & Noe, 2001; Posner, 1994; Prinz, 2011; 2012; Wolfe, 1999), or that attention and awareness are distinct processes that can occur independently (the double dissociation view; e.g., Koch & Tsuchiya, 2007; Tsuchiya & Koch, 2016). In this context, the main aim of my thesis was to resolve this long-standing debate, with an emphasis on investigating whether the relationship between attention and perceptual awareness is contingent on the task and the dependent measure employed during the experiment.

5.2 Overview of the main findings

In **Chapter 2**, I attempted to replicate a prominent study by van Boxtel et al. (2010a) which found that attention and perceptual awareness have opposing effects on afterimage duration. In this work, observers reported the duration of an afterimage, which was induced by an adapting stimulus that was either visible or rendered invisible using CFS. During adaptation, observers performed a high- or a low-load central secondary task. The results suggested that while perceptual awareness increased afterimage duration, attention decreased afterimage duration. As attention and perceptual awareness had opposing effects, the authors claimed that the two processes must be different, thus supporting the double dissociation view. Despite using the same experimental code, and increasing statistical power (more participants and more trials), in **Chapter 2** I failed to replicate the central findings of van Boxtel et al. (2010a). Instead, I found that both attention and perceptual awareness *increased* afterimage duration. Interestingly, attention increased afterimage duration even when the adapting stimulus was masked from awareness, suggesting that attention can have enhancing effects even when the adapting stimulus is masked from awareness. Thus, the findings from **Chapter 2** support the single dissociation view.

In **Chapter 3** I explored the idea that different types of attention may relate to perceptual awareness in different ways. There has been recent evidence suggesting that the relationship

between attention and perceptual awareness may depend on the type of attention employed during a task (Baijal & Srinivasan, 2009). In **Chapter 3**, I was specifically interested in whether the enhancement of task-relevant features relates to perceptual awareness in a similar way to the suppression of task-irrelevant features. To investigate this question, I replicated a prominent study by Lamy et al. (2015), which combined a variant of the contingent capture paradigm (Folk et al., 1992) with CFS masking such that participants were aware of the cues on approximately half of the trials, and unaware of them on the remaining trials. I conducted three experiments. In the first, I measured behavioral responses to the target. In the second and third experiments, I measured both behavioral responses and evoked neural activity to the cues using EEG. Behaviorally, across the three experiments, participants were faster when targets were preceded by valid target-colored cues than invalid target-colored cues. In contrast, participants were slower to respond to targets preceded by same-location versus different-location distractor-colored cues. Interestingly, the magnitude of the validity benefits and costs in behavior did not differ under aware and unaware conditions. That is, neither enhancement of goal-relevant features nor suppression of goal-irrelevant features were modulated by awareness of the cues. Interestingly, a different pattern was evident for the cue-evoked neural responses measured with EEG. While the amplitude of the enhancement response was larger under aware conditions than unaware conditions, the magnitude of the suppression response did not depend on awareness. Overall, these results suggest that enhancement and suppression arise from different underlying processes that relate to awareness in different ways, as I discuss in more detail later.

In the final empirical study of this thesis (**Chapter 4)**, I investigated how information processing develops and is optimized through unaware to aware states. I was particularly interested in whether orientation-specific visual encoding can be extracted from EEG signals associated with stimuli that elude awareness, and if so whether this information tracks the physical stimulus input or subjective experience. Previous studies have demonstrated that the firing rates of orientation-selective neurons track changes in the awareness of a stimulus (Leopold & Logothetis, 1996; Logothetis & Schall, 1989). In **Chapter 4,** I used a breaking CFS approach in which a grating was presented to one eye and ramped in contrast over a 5-second trial, and a dynamic high-contrast mask was presented to the other eye. Participants were required to make a simple discrimination judgment on the orientation of the grating. As participants did not perform a secondary task, their attention could be allocated entirely to the task-relevant display. Under these conditions, response times varied from trial to trial. Using forward encoding modeling, I measured feature-selective neural activity to the gratings before, during, and after participants made their response. Robust orientation-selective responses emerged well before participants registered their responses, and these orientation-selective responses were associated with differences in a neural index of evidence

accumulation (the centroparietal positivity) as well as the speed of perceptual judgments. Overall the findings suggest that elementary featural information is extracted from unconscious stimuli and that this information influences the efficiency of simple perceptual decisions.

5.3 Implications of Findings and Future Directions

The findings presented here contribute to our understanding of the relationship between attention and perceptual awareness. Most recent evidence supports the single dissociation view (Pitts, Lutsyshyna, & Hillyard, 2018), and some evidence suggests that the relationship depends on how attention is employed during a task (e.g., Baijal & Srinivasan, 2009; Kanai, Tsuchiya, & Verstraten, 2006). The results of the studies presented in this thesis support both of these views. By contrast, the evidence presented here casts doubt on the idea that attention and awareness can have opposing effects (**Chapter 2**). It also suggests that two different mechanisms – an enhancing and a suppressing mechanism – relate to awareness differently (**Chapter 3**), and implies that variation in stimulus-specific encoding during unaware states can predict awareness (**Chapter 4**).

5.3.1 Support for the single dissociation view

The results presented in this thesis demonstrate that attention can increase afterimage duration that is induced by an unaware adapting stimulus (**Chapter 2**), and that attention can be captured to the location of an unaware cue (**Chapter 3**). These findings provide support for the single dissociation view, and are consistent with a large body of previously published work (see Pitts, Lutsyshyna, & Hillyard, 2018, for a review). Much of the evidence for the double dissociation view has come from studies that compared performance during an attended condition and an unattended condition, and which found that awareness did not differ under the two conditions. As outlined in **Chapter 1**, much of this work has recently come under question, as new evidence suggests that awareness is affected when significant attentional demands are placed on the observer (see Pitts, Lutsyshyna, & Hillyard, 2018 for a review).

It is important to note, however, that my conclusions about the relationship between attention and awareness drawn from **Chapter 2** are based on the finding that attention increased afterimage duration. Although there is some evidence that attention can increase afterimage duration (e.g., Baijal & Srinivasan, 2009), other studies have found that attention has the effect of decreasing afterimage duration (Brascamp et al., 2010; Lou, 1999; Suzuki & Grabowechi, 2003; Wede & Francis, 2007). In many of these studies, however, the location of the adapting stimulus was relevant and, thus, likely attracted the attention of participants. For example, Suzuki and Grabowecki (2003) presented a central RSVP stream of numbers surrounded by a color-changing inducer triangle. During the attended condition, observers were required to attend to the inducer

triangle and count the number of times the triangle turned grey. During the unattended condition, observers were required to attend to the central RSVP stream and count the number of times the central number changed to "5". Independent of the main task being performed, on each trial observers were required to report the duration of the afterimage induced by the adapting triangle. Thus, even during "unattended" trials, the location of the adapting stimulus was task-relevant and, thus, may have received some attention.

Interestingly, Baijal & Srinivasan (2009) have shown that focused and distributed modes of attention have different effects on afterimage duration. In their study, participants performed a central task in which they identified small, large, local, or global letters. An adapting square surrounded the central task. The researchers found that afterimage duration was longer when participants performed the small letter task, which required highly focused attention to the central letter, relative to the global letter task (which presumably involved a broader distribution of attentional resources across the visual field). Baijal & Srinivasan (2009) concluded that focused and distributed attention produce different awareness effects on afterimage duration, and suggested that future research should consider the type of attention employed during a task.

Other recent findings suggest that increasing working memory load on one task can improve performance on a secondary task (Lin et al., 2010; Swallow & Jiang, 2010; Swallow & Jiang, 2013). For example, Swallow and Jiang (2013) presented a stream of symbols displayed overlaid on a stream of natural scenes. Participants were required to press a button when they detected a target symbol among distractor symbols. To increase perceptual load, the similarity between the target symbols and the distractor symbols was increased. Although participants' reaction times increased under the high perceptual load condition, in a subsequent probe test, their memory for the irrelevant scenes was better under conditions of high perceptual load than low perceptual load (i.e., when target symbols and distractor symbols were perceptually distinct). These observations challenge traditional findings from perceptual and cognitive load studies, in which increasing load on one task interferes with performance on a secondary task. Findings such as these, and those of Baijal and Srinivasan (2009), raise interesting questions about whether different task goals influence sensory neurons differently. Furthermore, they highlight the notion that when it comes to what we perceive, the particular type of attention recruited to perform the task matters to awareness.

While the findings presented in **Chapter 2** provide evidence against the double dissociation view, the findings presented in **Chapter 3** provide evidence in favor of the single dissociation view. Neural and behavioral responses showed that the enhancement of goal-relevant features (measured as the N2pc/NT and behaviorally as a same-location benefit for target-colored cues) and suppression of goal-irrelevant features (measured as the PD and a same-location cost for distractor-colored cues) were evident even when observers were unaware of the cues. These results suggest

that attention – both enhancing and suppressing mechanisms – modulates processing even when stimuli are not consciously perceived, supporting the single dissociation view.

It is important to note that in the experiments reported in **Chapter 3**, participants were asked to report their awareness of the cue on every trial. Thus, all cues, both target- and distractor-colored, were relevant to the awareness task. That is, for the awareness report, distractor colored cues were relevant and, thus, this task would benefit from enhancing mechanisms. In contrast, for the target task, distractor colored cues were irrelevant and, thus, would benefit from suppressive mechanisms. Consequently, distractor-colored cues may have received the modulation of both enhancement and suppression. The observation that distractor-colored cues evoked an early N_T response (response associated with target enhancement) followed by a later P_D response (response associated with distractor suppression), supports this notion. An intriguing question for future research is whether the act of reporting one's awareness of cues modulates the neural processes associated with these stimuli.

Despite the absence of an explicit attention manipulation in the study reported in **Chapter 4**, below I provide some speculations as to the role attention might have played in these experimental findings. Evidence from previous research suggests that the observed variation in responses across trials (response times and neural activity) may be due to variation in task engagement from trial to trial, as attention typically waxes and wanes while observers perform such tasks (e.g., Macdonald, Mathan, & Yeung, 2011; Monto et al., 2008; Robertson et al., 1997; Gilden, 2001; Wagenmakers et al., 2004). It is possible that the trials in which participants focused on the task at hand and attended to the grating targets were also the trials in which the CPP and orientation-selective responses emerged early in the trial. As discussed in **Chapter 1**, when monkeys are trained to attend to oriented gratings, the responses of orientation-selective cells increase (see Figure 1.8B), reflecting a biasing mechanism that enhances relevant information and suppresses irrelevant information (McAdams & Maunsell, 1999). The orientation-selective responses reported in **Chapter 4** also reflect the degree to which the system is biased toward the presented orientation. The results from **Chapter 4**, therefore, could be interpreted as reflecting the fidelity of attentional allocation throughout the trial. As noted above, in the absence of an explicit manipulation of attention this interpretation must be acknowledged as speculative. Nevertheless, if my assumptions are correct, the results from **Chapter 4** provide evidence that attention (as measured by orientation-selective responses) is necessary for awareness (as measured by response times). Indeed, the results from **Chapter 4** would suggest that a certain threshold of attention (orientation-selective responses) is required before a response is given. This interpretation would support the single dissociation view as, under this view, attention is the critical biasing mechanism necessary for awareness.

5.3.2 Enhancement and suppression are distinct mechanisms that interact with perceptual awareness in different ways

In **Chapter 1** of this thesis, I discussed James' (1890) definition of attention as "*withdrawal from some things in order to deal effectively with others*", implying that attention is a selective mechanism that enhances relevant things and suppresses irrelevant things. At a cellular level, this selection is achieved because neurons can flexibly change their firing rates in accordance with task demands (Duncan, 2001; Fedorenko et al., 2013). While mechanisms that enhance processing seem highly relevant to this neural biasing, suppressive mechanisms are ubiquitous in the brain (Markram et al., 2004), and likely play an important role in information processing (Jensen & Mazaheri, 2010). There is much research investigating how excitatory and inhibitory circuits function in the visual system (see Noonan, Crittenden, Jensen, & Stokes (2018) for a recent review). Task relevance has been shown to bias such circuits in favor of relevant features (Bundesen, 1990; Desimone & Duncan, 1995; Posner, 1980). While facilitation of neurons that represent goal-relevant features is most likely involved (Chelazzi et al., 1998), enhancement might be best understood in relation to goal-irrelevant suppression (Reynolds & Heeger, 2009).

The general mechanisms fundamental to enhancement and suppression are currently an active topic of investigation in the literature. One interesting question is whether information processing is the cause of one mechanism that simultaneously enhances relevant information and suppresses irrelevant information, or whether information processing is the cause of (at least) two distinct mechanisms. In a limited capacity system, suppression may be the inevitable consequence of the enhancing process. That is, if limited resources are directed to enhance some stimuli, other stimuli inevitably receive less processing resources, which may appear as suppression but is simply the inevitable consequence of the limited-capacity resource. According to this view, any appearance of suppression should mirror that of enhancement. On the other hand, suppression may be an active and separate mechanism that can be directly applied to specific stimuli independently of enhancement. The findings presented in **Chapter 3** support this second view. In those experiments, neural responses to goal-relevant cues did not mirror neural responses to goal-irrelevant cues, suggesting that enhancement and suppression are distinct processes that relate to awareness in different ways. Findings from recent studies support the view that attention is not a unitary function, suggesting that enhancement and suppression reflect different underlying mechanisms (e.g., Bettencorut & Somers, 2009; Couperus & Mangun, 2010; Slagter, Prinssen, Reteig, & Mazaheri, 2016). The findings support and extend previous findings by suggesting that enhancement and suppression are distinct processes that interact with awareness differently.

Recent empirical evidence has shown that when observers are aware of a stimulus, suppression can be directed to a specific spatial location (Arita, Carlisle, & Woodman, 2012; Awh, Matsukura, & Serences, 2003; Braithwaite et al., 2010; Sylvester et al., 2008;), or can act indirectly on goal-irrelevant stimuli by suppressing items that share similar irrelevant features across the visual filed (Duncan & Humphreys, 1989; Feldmann-Wustefeld, & Schubo, 2013; Nothdurft, 1992; Mazza, Turatto, & Caramazza, 2009). The results reported in **Chapter 3** extend these findings by suggesting that suppression can also operate on unaware stimuli. Whether suppression mechanisms can modulate unaware stimuli at a given spatial location and for a specific feature is an intriguing question for future research. Although the results reported in **Chapter 3** suggest that suppression mechanisms can have their effects even when stimuli are outside awareness, it is difficult to determine whether the suppression effect is due to a spatial or feature-based effect (or a combination of both). Contingent capture, like many cueing effects, is thought to be spatial in nature, even though the particular stimulus event that captures an observer's attention is contingent on the feature to which the observer is cued. Thus, contingent capture likely involves both spatial and feature-based attention (but see Theeuwes, 2013 for a critical review of this interpretation).

5.3.3 *The relationship between attention and awareness can vary depending on the measures used*

Empirical evidence reported in this thesis suggests that investigations into the relationship between attention and perceptual awareness may not always tell a consistent story. As discussed above, the results presented in **Chapter 3** imply that enhancement and suppression relate to perceptual awareness in distinct ways. It is important to note, however, that the distinct patterns of results for enhancement and suppression was only evident for evoked neural activity in response to visual cues. Specifically, the amplitude of the neural signature of enhancement was modulated by awareness, such that during aware trials, the amplitude of the N2pc/N_T response was increased compared with that observed in unaware trials. The neural signature of suppression (P_D), however, was not modulated by awareness. As discussed above, this distinction in the pattern of results suggests that enhancement and suppression are distinct processes that relate to awareness in different ways. In the same experiment, however, a distinction between the effects of enhancement and suppression was not evident in the behavioral measures (accuracy and reaction times). Any conclusions drawn from these findings would seem to support the notion that enhancement and suppression relate to awareness in similar ways and, thus, are likely the same mechanism. In sum, the findings from the studies reported in **Chapter 3** suggest that conclusions made about the way attention and perceptual awareness relate are likely dependent upon how the effects are measured.

It might be expected that the pattern of responses from neural measures and those from behavioral measures would match, as the variance in responses from each measure should arise

from a common source. The ERP components identified in the studies reported in **Chapter 3**, however, represent an early stage in the stimulus-response chain, whereas behavioral responses represent the outcome of the entire chain of processing from stimulus encoding through to response execution. It is possible, therefore, that the amplitude of the ERPs was determined by early stages of stimulus processing, whereas behavioral responses were determined by later stages in the decision-making chain.

In **Chapter 4** of this thesis, I used a breaking continuous flash suppression approach and had participants perform a simple orientation discrimination task on a grating that ramped in contrast over a five-second trial. I then used participant response times as an indication of the time at which participants became aware of the critical grating stimulus. There is much debate in the literature about how and when sensory awareness arises. Does a conscious visual experience happen all at once as a fully formed percept, or does awareness emerge more gradually? Some researchers have suggested that once an object is detected, the identity of that object is known (Grill-Spector & Kanwisher, 2005), while others have argued that detecting an object does not necessarily imply knowledge of its identity (Mack, Gauthier, Sadr, & Palmeri, 2008). As my aim was to construct orientation tuning functions from recorded EEG data, I was interested in the time at which participants were aware of the orientation of the grating. Thus, implementing a task in which participants identified the time at which they were aware of the orientation of the grating was more appropriate than a detection task in which participants may have been reporting their detection of something else (e.g., the overall grating shape or the stimulus flicker), but not necessarily their awareness of the grating's orientation. Whether the findings reported in **Chapter 4** might differ depending on whether participants are asked to detect or discriminate the critical target stimulus will be an important question for future research.

Resolving and understanding any distinction between detection and discrimination tasks has important implications for studies on perceptual awareness. Typically, experiments investigating the neural mechanisms of perceptual awareness contrast brain responses when participants are aware of a stimulus with conditions in which that stimulus is rendered invisible (see Bisenius, Trapp, Neumann, & Schroeter, 2015 for a meta-analysis and Koivisto & Revonsuo, 2010 for a review). There is an assumption underlying this approach, namely, that observers are either aware of the stimulus or they are not. But as outlined above, there is considerable debate in the literature as to whether perceptual awareness arises in an all-or-none fashion or a gradual manner. Findings presented in **Chapter 4** suggest that perceptual awareness can result from a gradual increase in neural activity, and once a threshold is reached, a response is made. Previous research supports this view, showing continuous, as opposed to abrupt, changes in neural activity as participants become aware of a stimulus (Bar et al., 2001; Moutoussis & Zeki, 2002; Overgaard et al., 2006; Sergent &

Dehaene, 2004). Despite the gradual neural responses from unaware to aware states, participants often report awareness in an all-or-none fashion even when asked to report awareness on a continuous scale (Sergent & Dehaene, 2004). Thus, whether perceptual awareness is gradual or all-or-none remains a topic of debate.

An answer to this question has important implications for our understanding of the relationship between attention and perceptual awareness. When investigating the relationship, a common methodology is to implement a 2 x 2 design in which participants are either aware or unaware of a stimulus and either attend or ignore a critical target stimulus. This approach was hailed as the gold standard in investigations into the relationship between attention and awareness by Koch and Tsuchiya (2012). They claimed that this allows for investigation of the independent contributions of attention and awareness. Indeed, this is the methodological design used in the studies reported in **Chapters 2** and **3** of this thesis. However, if neural processing underlying awareness is a gradual phenomenon, attention may interact with this process differently at different stages of the processing chain. Indeed, the results from the studies reported in **Chapter 3** suggest this may be the case, as neural measures that were taken early in the processing stream were modulated by attention, but behavioral measures presumed to be the combination of later processing stages were not modulated by attention. This explanation might account for the variation in how attention and perceptual awareness are purported to relate in the literature. While some studies define the relationship between attention and awareness by investigating a measure taken at an early processing point (e.g., Watanabe et al., 2011), other studies define the relationship by investigating measures taken later in the processing chain. If the conclusions drawn from the findings reported in **Chapter 3** are correct, attention interacts with awareness differently depending on when the measures are taken in the decision-making process.

Methodologies such as those used in **Chapter 4** in which neural responses are measured over time might provide an important tool for investigating the question of how attention relates to awareness at different stages of the decision-making process. It is important to note that participants in the experiment reported in **Chapter 4** performed the task under full attention conditions. As such, a comparison between attended and unattended conditions could not be made. Including an attentional manipulation in the design would be an important addition to any future investigation. Such research, however, will need to overcome the problem of how best to have participants ignore a stimulus while simultaneously measuring their awareness of that stimulus. Logically, if participants are asked to report their awareness of a stimulus, it stands to reason that they would allocate their attention to that stimulus, and thus it is no longer ignored. Recent research has tried to overcome this problem by employing an inattentional blindness paradigm, in which questions about a critical stimulus are asked after the final trial (e.g., Harris, Dux, & Mattingley, 2018; Pitts,

Martínez, & Hillyard, 2012; Pitts, Padwal, Fennelly, Martínez, & Hillyard, 2014). Others have used a no-report paradigm in which awareness is measured from known neural measures, or from pupil size and gaze direction, which are well-established markers of perceptual awareness (e.g., Frässle, Sommer, Jansen, Naber, & Einhäuser, 2014; Koivisto & Revonsuo, 2009; Pitts, Martínez, & Hillyard, 2012; see Tsuchiya, Wilke, Frässle, & Lamme, 2015 for a review; although see Laeng, Sirois & Gredeback (2012) for a review arguing that pupil diameter is better used as a measure of preconscious processing).

5.4 Conclusion

The central aim of the empirical work presented in this thesis was to investigate the relationship between visual attention and perceptual awareness. Overall the results revealed that attention modulates the processing of unaware stimuli, supporting the single dissociation view. The results also suggest that attentional modulation reflects the operation of (at least) two underlying mechanisms: an enhancing mechanism that is modulated by awareness, and a suppressing mechanism that modulates activity independently of awareness. These attentional mechanisms likely modulate activity differently at different stages of the decision-making process until a threshold is reached, and a response is made. Overall, the research presented here provides key insights into the complexity of the relationship between attention and perceptual awareness.

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Appendix A