

“Don’t Look Down”: Alpha-Band Activity Reveals Selection Prior to Suppression of to-be-Ignored Locations

by

Ryan Scott Williams

A thesis submitted in conformity with the requirements
for the degree of Master of Arts

Department of Psychology
University of Toronto

© Copyright by Ryan Scott Williams 2017

“Don’t Look Down”: Alpha-Band Activity Reveals Selection Prior to Suppression of to-be-Ignored Locations

Ryan Scott Williams

Bachelor of Arts

Department of Psychology
University of Toronto

2017

Abstract

To examine behavioural and electrophysiological effects associated with the intentional suppression of spatial locations, a task was employed which cued to-be-ignored locations prior to stimulus presentation. Over three experiments, participants were faster to respond to targets when such stimuli were presented alongside salient distractors at cued locations compared to uncued locations. This distractor cueing benefit, however, was time dependent as it was only observed when sufficient time was provided between cue and target displays. Possibly underlying the distractor cueing benefit, hemispheric differences in alpha-band activity gradually emerged between cue and target displays in accordance with the position of cued locations. While it was expected that electrophysiological markers associated with reactive suppression would also be influenced by distractor cueing, this was not the case; only a late stage of effortful processing was affected. Further, findings were present to suggest that both endogenous and exogenous processes contributed to the distractor cueing benefit.

Acknowledgments

I would like to thank all of my colleagues from the Cognitive Neuroscience Laboratory and the Visual Cognition Laboratory who contributed their opinions to this project through various conversations and lab meetings. I would especially like to thank Matthew Hilchey and Jason Rajsic who suggested articles of literature that were instrumental during the development of this project, as well as Sol Sun who provided plenty of feedback throughout each stage of this project. I would also like to acknowledge the contribution of Robert Newman who helped collect data for each of the experiments conducted here. Lastly, I would like to thank my advisors, Susanne Ferber and Jay Pratt, for all of their guidance over the past year.

Table of Contents

Acknowledgments.....	iii
Table of Contents.....	iv
List of Figures.....	vi
1 Introduction.....	1
1.1 Orienting Attention in Space: Endogenous versus Exogenous Spatial Attention	1
1.2 The Frontoparietal Network: Where Vision Meets Attention	3
1.3 Intentional Suppression of Task Irrelevant Information.....	5
1.4 Electrophysiological Indices of Visual Attention.....	8
1.4.1 Oscillatory Alpha-Band Activity	8
1.4.2 Lateralized Event-Related Potentials (ERPs)	10
1.5 The Present Study	11
2 Experiment 1	12
2.1 Method	12
2.1.1 Participants.....	12
2.1.2 Stimuli and Procedure.....	13
2.2 Results and Discussion	14
3 Experiment 2	16
3.1 Method	16
3.1.1 Participants.....	16
3.1.2 Stimuli and Procedure.....	16
3.2 Results and Discussion	17
4 Experiment 3	18
4.1 Method	19
4.1.1 Participants.....	19

4.1.2	Stimuli and Procedure.....	19
4.1.3	EEG Data Acquisition Processing	19
4.2	Results.....	21
4.2.1	Behavioural Results	21
4.2.2	Cue-Locked Alpha-Band Activity	21
4.2.3	Lateralized Distractor ERPs.....	25
4.3	Discussion	26
5	General Discussion.....	27
	References.....	35

List of Figures

Figure 1. Schematic of task used in Experiment 1.....	20
Figure 2. Mean reaction time for Experiment 1.....	21
Figure 3. Mean reaction time for Experiment 2.....	24
Figure 4. Time-frequency plots corresponding to the cue-target ISI in Experiment 3	29
Figure 5. Grand averaged waveforms for lateralized targets	31
Figure 6. Grand averaged waveforms for lateralized CMDs.....	32

“Don’t Look Down”: Alpha-Band Activity Reveals Selection Prior to Suppression of to-be-Ignored Locations

1 Introduction

The manner by which we identify important objects and events amidst complex visual scenes often relies on our expectations of the environment. Indeed, decades worth of research highlight the fact that visual processing is more efficient when individuals know in advance where to expect to find an imperative stimulus. Yet, little is known regarding the inverse – that is, whether one’s expectations about where not to find an imperative stimulus can reduce the number of items to be searched in the visual field, thereby increasing the efficiency with which one locates an imperative stimulus. In this thesis, behavioural and neuroscientific findings are reviewed regarding the extent to which foreknowledge of upcoming events can be utilized to enhance or suppress the deployment of visual attention to spatial locations and objects. Novel evidence is then presented with respect to the temporal dynamics of preparatory suppression mechanisms, and the outcome of such preparation on the various stages of visual processing when salient, distracting stimuli are present.

1.1 Orienting Attention in Space: Endogenous versus Exogenous Spatial Attention

Understanding the role that attentional processes play in guiding our everyday sensory experiences has been a central goal of psychological science throughout its history. Among the earliest contributors to this topic, William James (1892) proposed that the manner by which we come to attend to objects in the environment occurs both voluntarily and involuntarily. To some extent, this classification of attentional processes by James remains prominent to this day, broadly mapping onto a widely held distinction between endogenous and exogenous modes of attention. In the case of the endogenous mode, attentional processes are prioritized for a given object at the volition of the agent in accordance with his or her goals or motivations. The exogenous attentional mode, on the other hand, is more reflexive or automatic, and is largely determined by the salience of an object’s physical properties in its surrounding context.

Within the visual-spatial domain, formal investigations into the interaction of sensory inputs with endogenous and exogenous modes of attention commonly employ variants of a spatial cueing paradigm developed by Posner and colleagues (1978, 1980). In its basic form, this task requires participants to fixate centrally, and make one of two responses depending on whether a visual stimulus is presented to the left or right of fixation. In cases where endogenous attention is of interest, the target is preceded by one of two central cues: a directional arrow, or a neutral, non-directional symbol. Critically, central arrow cues predict the location of the upcoming target with high probability (e.g., 80%), which allows participants to form expectations regarding the target's location and endogenously orient attention towards the expected location. In contrast, when the exogenous mode of attention is of interest, peripheral rather than central cues precede target presentation – for example, an abrupt change in luminance may occur to the left or right of fixation (Posner & Cohen, 1984). Such peripheral cues are non-predictive of the target's location, and therefore cannot be used strategically. Attentional orienting towards the peripheral stimulus then is attributed to exogenous factors, rather than the participant's expectations.

Using the spatial cueing task described above, effects of endogenous and exogenous attentional orienting on visual processing are inferred through cost-benefit analyses of behavioural performance, depending on whether targets are presented to cued locations (i.e., validly cued targets) or uncued locations (i.e., invalidly cued targets). Under endogenous cueing conditions, target responses benefit from valid cues relative to neutral cues, but are hindered by invalid cues (Posner, 1980; Posner & Ogden, 1978). Behavioural effects produced by exogenous cueing conditions, on the other hand, greatly depend on the interstimulus interval (ISI) between cue and target stimuli. For short ISIs, a validity effect is observed, with faster reaction times (RT) for validly cued targets than for invalidly cued targets (Berger, 1999; Collie, Maruff, Yucel, Danckert, & Currie, 2000; Posner, & Cohen, 1984). At longer ISIs, however, this effect reverses and responses are consistently faster for invalidly cued targets than for validly cued targets – a phenomenon referred to as inhibition of return (IOR; Posner, & Cohen, 1984; Bennett, & Pratt, 2001; Collie et al., 2000).

The pattern of results associated with the various spatial cueing conditions suggests that visual processing is enhanced for objects and events at spatial locations to which attention is oriented, though, at the expense of efficient visual processing elsewhere. How attention comes to be oriented towards a particular location dictates the duration of the enhancement, with sustained

effects following endogenous orienting, but only transient benefits when oriented exogenously. It is important to acknowledge, though, that endogenous and exogenous modes of attentional orienting do not necessarily occur in isolation of one another. Central arrow cues, for example, continue to produce validity effects in spatial cueing tasks even when such arrows are non-predictive of the target's location, suggesting that effects of exogenous attentional orienting may be present under endogenous cueing conditions (Hommel, Pratt, Colzato, & Godijn, 2001; Ristic & Kingstone, 2006; Tipples, 2002). Conversely, while illuminant peripheral cues exogenously capture attention while one anticipates the abrupt onset of a target; such cues are less likely to do so if one is anticipating a target defined by its colour (Folk, Remington, & Johnston, 1992). Exogenous orienting, then, may not occur entirely outside of one's control. In light of these findings, it is best to think of endogenous and exogenous attentional processes as jointly contributing to one's moment-to-moment engagement with locations and objects in the visual environment to varying degrees.

The remainder of this thesis will largely focus on conditions in which the endogenous mode of attentional orienting is thought to be prominently involved – that is, conditions in which attentional processes are voluntarily deployed and under the control of the agent. Still, it is worth highlighting that works employing exogenous peripheral cueing demonstrate that attentional orienting produces both facilitative and inhibitory effects on the processing of visual inputs. To date, however, the vast majority of studies concerned with endogenous attentional orienting have considered only the extent to which visual inputs can be intentionally prioritized, while a comprehensive understanding of the extent to which inhibitory processes can be intentionally engaged is currently lacking.

1.2 The Frontoparietal Network: Where Vision Meets Attention

Behavioural tasks that are used to study interactions of vision and attention commonly involve the recognition of a change in the environment, the localization of a target stimulus, and/or a discrimination judgment regarding a target's features or orientation. Such processes largely rely on one's awareness of the visual field's sensorial content, which arises in large part from information communicated by neurons along the ventral visual stream. Along this pathway, individual neurons are tuned to respond to specific features or patterns that fall within the cell's receptive field, with the size of receptive fields and the complexity of tuned features increasing

posteriorly to anteriorly (Goodale & Milner, 1992; Hubel & Wiesel, 1959). As such, it follows that if attentional processes alter the efficiency of visual processing, then attention-based alterations should be evidenced by the activity of the ventral visual stream.

The manner by which attentional processes are thought to influence the ventral visual stream is described by the biased competition model (Desimone, 1998; Desimone, & Duncan, 1995). Central to this model is the claim that all inputs across the visual field compete for neural representation. Since not all stimuli are likely to be relevant to one's goals, "attentional templates" are endogenously maintained to bias visual processing of relevant spatial locations, features (such as colour or form), or object classes. This is achieved by anticipatorily increasing the baseline activity of neurons in the visual cortex tuned to the attentional template (e.g., Luck et al., 1997), and, to a greater extent, by suppressing the activity of neurons that code features outside of the attentional template, but whose receptive field receives input relevant to the attentional template (e.g., Moran & Desimone, 1985). In other words, endogenous attentional mechanisms work to enhance the neural signal of imperative stimuli in the visual cortex, as well as suppress the signals of distracting stimuli, particularly when such stimuli are in direct competition with imperative stimuli.

With respect to the neural source of these competitive biases, a wealth of evidence has amassed converging on a network of frontoparietal structures that are heavily involved in endogenous spatial orienting (e.g. Coull & Nobre, 1998; Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Fan, McCandliss, Fossella, Flombaum, & Posner, 2005; Hopfinger, Buonocore, & Mangun, 2000; Szczepanski, Pinsk, Douglas, Kastner, & Saalman, 2013). Among parietal structures, activation of both the intraparietal sulcus (IPS) and superior parietal lobule (SPL) are consistently implicated in the shifting and maintenance of attention. Despite the close proximity of the IPS to the SPL, the two structures serve distinct functions; the IPS is associated with the internal maintenance of attentional priority maps that correspond to one's attentional set, while the SPL is activated when attention needs to be shifted from one location or object to another (Bisley & Goldberg, 2003; Kelley, Serences, Giesbrecht, & Yantis, 2007; Molenberghs, Mesulam, Peeters, & Vandenberghe, 2007). More anteriorly, the frontal eye field (FEF) also shows consistent activation during endogenous spatial orienting. In addition to its involvement in the execution of saccadic eye movements (e.g., Everling & Munoz, 2000; Robinson & Fuchs, 1969), this region is linked to the maintenance of spatial information in working memory

(Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998). Interestingly, these frontoparietal structures that support endogenous spatial orienting, are also active during the anticipation of feature-based information (e.g., Egner et al., 2008; Giesbrecht, Woldorff, Song, & Mangun, 2003; Liu, Hospadaruk, Zhu, & Gardner, 2011).

In addition to the dorsal frontoparietal structures described thus far, a popular account of visual attention also distinguishes a right-lateralized ventral frontoparietal network (Corbetta & Shulman, 2002, 2008). This model attributes a “reorienting” function to the ventral frontoparietal network wherein attention is rapidly shifted towards behaviourally relevant stimuli in the environment not anticipated by the dorsal network. Activation of the temporoparietal junction (TPJ) is thought to be principally involved in the reorienting response (e.g. Chang et al., 2013; Corbetta et al., 2000). As Corbetta and Shulman (2002, 2008) describe, though, the ventral frontoparietal network is susceptible to distracting items in the visual field that possess target features. In such cases, the authors argue that termination of the reorienting response is carried out by dorsal frontoparietal structures.

1.3 Intentional Suppression of Task Irrelevant Information

As the previous section highlights, knowledge of spatial and featural information relevant to imperative visual stimuli can be endogenously prioritized to guide efficient visual processing. One of the primary modes by which such benefits are achieved is through the suppression of task irrelevant inputs that compete with imperative stimuli. With this being the case, one may wonder whether knowledge of distracting stimuli can similarly be used to voluntarily suppress visual signals in advance of presentation. Beginning in the last decade, a line of research has emerged concerned with this very question.

One of the first demonstrations to show anticipatory suppression of task irrelevant visual inputs was provided by Awh, Matskura, and Serences (2003). Participants in this study were cued to probable locations of briefly presented numerical digits that were relevant to an arithmetic task. Additionally, the experimenters manipulated participants’ expectations as to whether the digits would be presented alone, or within cluttered displays of distracting letters. This study revealed a benefit of distractor expectancy for cluttered displays when validly cued to the correct locations, but no effect of distractor expectancy when digits were presented alone. This was taken as

evidence that distractor expectancy selectively enhanced the suppression of task irrelevant stimuli without producing an overall attentional benefit in response to task demands, since performance was equivalent in the absence of distractors. A follow-up study employing functional magnetic resonance imaging (fMRI) later revealed greater activation in regions of the occipital cortex that retinotopically mapped to cued versus uncued locations during the cue-target interval, with this difference being greater when distractors were expected (Serences, Yantis, Culberson, & Awh, 2004). As in the study by Awh et al. (2003), no benefit of distractor expectancy was observed when digits were presented alone. It was thus suggested that the neural effect of distractor expectancy at cued locations reflected a preparatory increase in inhibitory activity surrounding the cued locations.

It has since been shown that anticipatory suppression of upcoming distractors is not only associated with functional activation of the occipital cortex, but also with those same frontoparietal structures that are involved in the maintenance of attentional templates. Ruff and Driver (2006), for example, found greater bilateral activation of the SPL and a frontal region near the FEF when a distracting item was expected to appear opposite the location of a cued target compared to when no such distractor was anticipated. Sylvester, Jack, Corbetta, and Shulman (2008) also observed an anticipatory increase of FEF activity when a distracting item was expected opposite to a cued target, though, only when difficult target discriminations were required.

Provided the described findings, as well as additional behavioural evidence (e.g., Leber, Gwinn, Hong, & O'Toole, 2016; Van der Stigchel & Theeuwes, 2006), it does seem to be the case that foreknowledge of to-be-ignored items can be used to anticipatorily reduce their competitive influence on imperative stimuli, at least when the information provided is spatial in nature. However, a drawback of such studies is that the location of target stimuli is always known, or can be predicted with high probability. As such, from these studies alone it is difficult to discern whether attentional templates can be used to selectively suppress the expected location of a distracting item in the absence of a spatial template for the target item. Take, for instance, the work by Serences et al. (2004); the authors attributed increased occipital activation to the suppression of the area surrounding expected target locations, yet, this implies that knowledge of target locations was still necessary.

Examinations of the attentional processes associated with to-be-ignored locations (or at least unlikely target locations) under conditions less confounded by target expectancies have been conducted, though, with mixed results. Tsal and Makovski (2006), for example, consistently presented distractors to a common location during a flanker task. While participants had knowledge of the distractors' locations, they nonetheless seemed to devote attentional resources towards these locations – an effect they referred to as the “attentional white bear.” This was demonstrated using an intervening temporal order judgment task, in which, among two simultaneously presented stimuli, participants were more likely to report an earlier onset for stimuli at the expected distractor location. This finding that was later replicated by Lahav, Makovski, and Tsal (2012). More recently, Jollie, Ivanoff, Webb, and Jamieson (2016) also found evidence in favour of the attentional white bear effect. Positions corresponding to the hours on an analogue clock face were cued as unlikely locations for target stimuli using numerical digits. Still, participants were faster when responding to targets presented to these cued locations compared to targets appearing at other locations. This was even the case when cued locations were associated with “no-go” targets, which should have encouraged inhibition for the cued locations.

In contrast to those studies that reported an attentional white bear effect, there are others that provide evidence in support of a benefit for cueing to-be-suppressed locations. Notably, Munneke, Van der Stigchel, & Theeuwes (2008) used central arrow cues to identify where among four possible locations a distracting stimulus resembling the target would appear (if present at the time of target display) with 100% validity. When the distracting stimulus was present, participants were faster to respond to the target if the distractor was cued in advance compared to if no information about the distractor's location was provided.

Using similar methods, Chao (2010) also found a response benefit when distractors were validly cued, compared to when they were not. Chao (2010) also conducted a number of follow-up experiments that expanded on the conditions that promote or impede active suppression of to-be-ignored locations. Among the more noteworthy findings, it was demonstrated that presenting target stimuli to the cued locations for a portion of trials (i.e., 20%) abolished the effect. This may account for the attentional white bear effect observed by Jollie et al (2016), and to some extent Lahav et al. (2012) and Tsal and Makovski (2006). Additionally, Chao (2010) found evidence to suggest that intentional suppression may be time-dependent. Specifically, the

distractor cueing benefit was observed when the cue-target ISI was long (i.e., 2120 ms), but not when it was short (i.e., 507 ms). This effect, however, was contingent on blocks employing the long ISI preceding blocks employing the short ISI, as no cueing benefit was observed when the order was reversed – perhaps reflecting a loss of motivation following ineffective attempts to inhibit the distractor. Elsewhere, Moher and Egeth (2012) also report evidence for a time-dependent suppression response, with a detrimental effect of spatially cued distractors at short ISIs (i.e., 100 ms), and a benefit at longer ISIs (i.e., 800 and 1500 ms). This study, however, cued the location of distractors by presenting squares matching the colour of the distracting item in the periphery. As such, an exogenous cueing effect may have resulted in an IOR response, rather than intentional suppression. Evidently, more work is needed to clarify whether intentional suppression of to-be-ignored locations is temporally dependent when endogenously cued.

1.4 Electrophysiological Indices of Visual Attention

Under certain conditions, target-based judgments are benefited by foreknowledge of to-be-ignored locations even when target locations are not known in advance, as the previous section outlines. However, at present, very little is established regarding the neural mechanisms that support this benefit. The use of electroencephalography (EEG) may be particularly useful in this regard given its ability to track underlying neural activity with excellent temporal resolution. In this section, EEG markers associated with various attentional processes are discussed with particular focus on those markers most relevant to intentional suppression.

1.4.1 Oscillatory Alpha-Band Activity

Neural oscillations in the alpha-band frequency range (~8–12 Hz) have long been associated with attention. This connection primarily arose from findings consistently demonstrating decreased activity in this frequency range over posterior regions both in anticipation of, and in response to the presentation of task relevant stimuli (e.g., Klimesch, Pfurtscheller, & Schimke, 1992; Lansing, Schwartz, & Lindsley, 1959; Pfurtscheller & Aranibar, 1977). Rather than simply reflecting arousal-based processes, though, it is believed that neural activity in the alpha-band also reflects the spatial distribution of attention. This is in large part due to the work of Worden, Foxe, Wang, and Simpson (2000) who examined the topography of alpha-band activity during the cue-target ISI of a spatial cueing task.

In this study, Worden et al. (2000) instructed participants to indicate the orientation of a stimulus when it appeared at a centrally-cued peripheral location, but to ignore it when it appeared opposite to the cued location. Over the cue-target interval, alpha-band activity measured at parieto-occipital electrodes was found to be greater in the hemisphere contralateral to the to-be-ignored location than in the ipsilateral hemisphere. This effect emerged about 400 ms after the onset of the cue, and steadily increased thereafter until the onset of the stimulus. Further, the topographic distribution of the preparatory alpha-band response retinotopically mapped whether the to-be-ignored location was in the upper or lower portion of the visual field. These findings by Worden et al. (2000) have since been corroborated by a number of researchers employing similar cueing methods (e.g., Gould, Rushworth, & Nobre, 2011; Rihs, Michel, & Thut, 2007; Thut, Nietzel, Brandt, & Pascual-Leone, 2006).

Interestingly, anticipatory alterations of posterior alpha-band activity may be mediated by the dorsal frontoparietal network. Evidence in favour of this possibility was provided by Capotosto, Babiloni, Romani, and Corbetta (2009), who combined EEG with repetitive transcranial magnetic stimulation (rTMS) – a non-invasive technique capable of temporarily disrupting the activity of neurons in a given region – during a typical endogenous spatial cueing task. Behaviourally, applying rTMS to the FEF and IPS at the time of cue presentation impaired accuracy and the time needed to make target discriminations, relative to a control condition, and when rTMS was applied to a ventral prefrontal area. Further, for both the control and ventral prefrontal rTMS conditions, alpha-band activity at parieto-occipital sites decreased to a greater extent in the hemisphere contralateral to the cued location. However, no such lateralization effects were observed following the cue under conditions of FEF or IPS stimulation.

In line with the findings described above, Foxe and Snyder (2011) have proposed an account that attributes an active suppression role to neural activity in the alpha-band. This account argues that such oscillatory activity gates visual processing by altering the cortical excitability of visual areas. As such, greater alpha-band activity is thought to reflect reduced sensitivity to visual inputs, with regional differences being particularly pronounced when distracting stimuli are expected at unattended locations. This being the case, one can argue that if active suppression underlies the behavioural benefit associated with cueing to-be-ignored locations, then this effect should be accompanied by topographic differences in parieto-occipital alpha-band activity.

1.4.2 Lateralized Event-Related Potentials (ERPs)

In addition to the oscillatory changes observed while one prepares to locate (or ignore) an upcoming stimulus, event-related potentials (ERPs) have been identified that are thought to index the selection of task-relevant objects and suppression of distracting objects following the presentation of visual search arrays. The most well-studied ERP component in this regard is the N2-posterior-contralateral (N2pc). The N2pc is marked by a negative voltage difference between electrodes contralateral to an attended stimulus versus ipsilateral electrodes over parieto-occipital areas, typically occurring between 180–300 ms after stimulus onset (Luck & Hillyard, 1994). As such, the N2pc allows for inferences regarding the spatial deployment of attentional processes (e.g., Eimer, 1996; Hickey, Di Lollo, & McDonald, 2009; Hickey, McDonald, & Theeuwes, 2006). Multiple neural sources are thought to contribute to the N2pc including early top-down influences from the FEF and dorsal regions of the parietal cortex, as well as subsequent activation in anterior portions of the ventral visual stream (Cohen, Heitz, Schall, & Woodman, 2009; Hopf et al., 2000). For the current purpose, the N2pc can be used to observe the efficiency of target selection when distracting stimuli are anticipatorily suppressed compared to when they are not. Conversely, the N2pc can also be used to index the extent to which distracting stimuli capture attention (Eimer & Grubert, 2014; Hickey et al., 2006; Kiss, Jolicœur, Dell'Acqua, & Eimer, 2008a).

A second ERP component of interest is the distractor positivity (P_D). Similar to the N2pc, this component is measured by comparing the voltage difference of parieto-occipital electrodes from opposite hemispheres. Unlike the N2pc, though, the P_D is exclusively considered in relation to the position of a distracting stimulus, and observed as a larger positive difference for contralateral sites relative to ipsilateral sites (Hickey et al., 2009). The presence of target stimuli is controlled for during such measurements by placing target stimuli along the vertical meridian to avoid influencing one hemisphere more than the other. The P_D is typically observed in the same time range as the N2pc, and is thought to reflect a neural mechanism that works to prevent exogenous shifts of attention towards salient, distracting stimuli (Gaspar, Christie, Prime, Jolicœur, & McDonald, 2016; Hickey et al., 2009; Jannati, Gaspar, & McDonald, 2013). However, in some cases, distracting stimuli first generate an N2pc, which is then followed by the P_D , possibly reflecting attentional suppression following attentional capture (e.g., Hilimire,

Mounts, Parks, & Corballis, 2011; Kiss, Grubert, Petersen, & Eimer, 2012). Given that the P_D reflects a reactive mechanism to suppress salient, but irrelevant stimuli, it can be anticipated that preparatory suppression of to-be-ignored locations should produce enhanced P_D amplitudes in response to distracting stimuli presented to these locations.

1.5 The Present Study

Only one experiment to date has examined electrophysiological responses under conditions in which a distracting stimulus is cued without providing spatial information about target stimuli (i.e., Noonan et al., 2016). Interestingly, this study failed to demonstrate hemispheric differences in alpha-band activity related to the anticipatory suppression of cued locations. However, it should be noted that the conclusions that can be drawn from this study are somewhat limited by methodological considerations. For example, stimuli in this experiment were presented to quadrants of a two-by-two grid. As such, hemispheric differences in alpha-band activity may not have emerged because target and distracting stimuli sometimes appeared in the same hemifield. Related to this point, this experiment did not permit isolated observations of ERP components generated by distracting stimuli since target stimuli were always present in either the same or opposite hemifield of the distractor. It thus remains unclear how an ERP component, such as the P_D , is affected by foreknowledge of to-be-ignored locations. Lastly, the task used by Noonan et al. (2016) produced a distractor cueing benefit only when the location of the distracting stimulus was held constant across a given block. It is debatable then whether preparatory suppression was actually engaged in this task or if the benefit was an unintentional consequence of the distractor's repeating position – similar to what is observed in the case of negative priming (e.g., Frings & Wühr, 2007). Thus, there is still much to be learned regarding the mechanisms that support the distractor cueing benefit.

The primary aim of the present study was to examine the electrophysiological correlates of the distractor cueing benefit under conditions better suited to isolate the anticipatory and reactive processing of cued locations. In contrast to Noonan et al. (2016), I predicted that cueing lateral locations would produce gradual hemispheric differences in posterior alpha-band activity, reflecting active endogenous suppression. Further, I hypothesized that the perceptual outcome of such activity would be manifest in at least two ways. First, I predicted that the distractor cueing benefit would be absent immediately following the presentation of the cue (presumably when

hemispheric differences in alpha-band activity are minimal), but emerge over time in accordance with topographic changes in alpha-band activity. Second, I predicted that lateralized ERP components associated with the initial selection and suppression of items in the visual field (i.e. N2pc and P_D) would vary according to whether distracting stimuli were cued or uncued. These hypotheses were tested over the course of three experiments. As will be discussed, both a behavioural distractor cueing benefit and hemispheric differences in alpha-band activity exhibited time-dependent responses, in line with my hypotheses. However, early lateralized ERPs were unaffected by whether distracting stimuli appeared at cued or uncued locations. Instead, the amplitude of a late ERP component associated with attentional effort was affected by the presence of cued versus uncued distractors, contrary to what I predicted.

2 Experiment 1

The purpose of Experiment 1 was to replicate previous findings demonstrating a benefit of trial-by-trial cueing on to-be-ignored locations. To do so, I employed a task similar to that used by Munneke et al. (2008), which involved centrally cueing one location of a visual search array where a target stimulus would not appear, providing sufficient time between the cue and target displays. I hypothesized that if participants could successfully suppress the cued locations, then salient distracting stimuli presented to these locations would have less of an interfering effect on task performance than distracting stimuli presented to uncued locations.

2.1 Method

2.1.1 Participants

Participants consisted of University of Toronto undergraduates who participated for course credit, and individuals recruited from the University of Toronto community via advertisements and online postings who received monetary compensation. In total, 22 participants completed the experiment. One participant was excluded without observation for failing to follow task instructions. Additionally, two more participants were removed from analyses who did not meet our performance criteria, as described below. The final sample consisted of 19 individuals between the ages of 18 and 28 years ($M = 21.3$ years, $SD = 2.4$; 4 male, 15 female). Written

informed consent was obtained from all participants. All experimental procedures were approved by the University of Toronto Ethics Review Committee.

2.1.2 Stimuli and Procedure

The experimental task was carried out on a Dell computer operating Windows 7. Stimuli were presented to an 18-inch ViewSonic PF790 CRT monitor with a screen resolution of 1280 x 1024 pixels, and 60 Hz refresh rate. Each participant was seated with his or her head rested in a chinrest mounted 60 cm from the computer monitor. All stimuli were displayed against a black background.

As is illustrated in Figure 1, every trial began with a fixation display consisting of a small central dot ($.09^\circ$ radius), along with outlines of 4 outer circles ($.68^\circ$ radius), and 4 inner circles ($.19^\circ$ radius). The outer circles served as placeholders for target locations, and were positioned $\pm 3.5^\circ$ from central fixation (centre-to-centre) along the horizontal and vertical meridian, respectively. The inner circles were arranged in the same manner as the outer circles ($.32^\circ$ from central fixation, centre-to-centre) and served as symbolic representations of the target locations. All stimuli at fixation were presented in grey (RGB: 128, 128, 128), and remained onscreen for the duration of the trial. Following the fixation display, one of the inner circles would fill-in, cueing one location where the target would not appear (i.e., a to-be-ignored location). Participants were explicitly told that the target would never appear at the cued location (i.e., the cue was 100% valid). The presentation of the target display relative to the cue was separated by a 1400 ms ISI though the cue remained onscreen for the duration of the target display.

Target displays consisted of four items – one target item, and three non-target items – presented to the centre of each of the placeholders. The letter “T” was used as the target stimulus (width: $.55^\circ$, height: $.55^\circ$, thickness: $.12^\circ$), and the letter “I” for non-target stimuli, with these items sharing the same visual dimensions as the target. Participants were instructed to report the orientation of the target (“upright” or “inverted”) by making two-handed “d” and “j” keypresses. Target and non-targets items were presented in four colours: red (RGB: 255, 0, 0), green (RGB: 0, 255, 0), blue (RGB: 0, 0, 255), and yellow (RGB: 255, 255, 0). For each experimental block, the target was defined by a specific colour. The order in which the four colours defined the target was randomized across participants. Target-distractor competition was manipulated via a colour-matching distractor (CMD), in which one of the non-target items possessed the target’s colour.

Three conditions involving the CMD were intermixed within each block; (a) an Absent condition in which none of the non-target items shared the target's colour, (b) a Cued condition in which the CMD was presented to the to-be-ignored location, and (c) an Uncued condition in which the CMD appeared at a possible target location. Non-target items never shared the same colour in a given target display. Each trial ended when a response was recorded, or a response limit of 2000 ms was reached. Participants were instructed to maintain central fixation throughout each trial. The task was comprised of 8 blocks, with each consisting of 54 trials (432 trials total). Prior to beginning the task, participants were given one practice block equal in length to an experimental block.

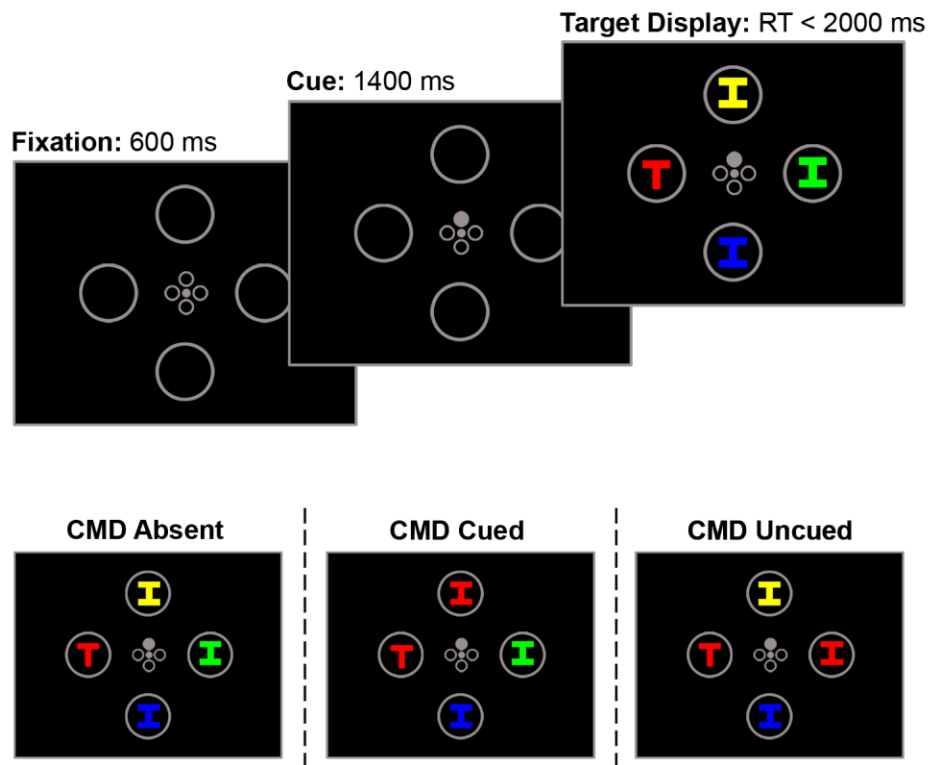


Figure 1. Schematic of task used in Experiment 1. Shown is an example of a single trial in which the target is defined as a red “T” (top panel), as well as the possible CMD configurations at the time of target display (bottom panel).

2.2 Results and Discussion

RT for correct responses were submitted to a one-way analysis of variance (ANOVA) performed on the within-subject factor of CMD (Absent, Cued, Uncued). Trials in which RT exceeded the condition mean by 2.5 SD were excluded from analyses, as were trials with RT below 200 ms.

Further, participants were excluded from analyses altogether in cases where overall task RT or error rates were outside of 2 SD from the group mean. Errors and missed responses accounted for only a small portion of trials (5.1 %) and were not influenced by experimental condition ($p = .871$) Significant effects were followed-up with two-tailed t-tests.

The main effect of CMD condition was significant [$F(2,36), p < .001, \eta p^2 = .70$]. As graphically depicted in Figure 2, follow-up comparisons revealed that responses were faster in the Absent condition compared to both the Cued [$t(18) = 6.39, p < .001, d = 1.47$], and Uncued condition [$t(18) = 7.40, p < .001, d = 1.70$]. Critically, when CMDs were present, RT was shorter when these items appeared at to-be-ignored locations compared to uncued locations [$t(18) = 2.80, p = .012, d = 0.64$]. The results from this experiment suggest that the inclusion of a CMD was successful in creating target-distractor competition, as performance in the task was markedly enhanced when such distractors were absent, regardless of whether the location of the CMD was cued in advance or not. More importantly, and in line with Munneke et al. (2008) and Chao (2010), these results suggest that prior knowledge of to-be-ignored locations can be used to suppress attention to these locations under the right conditions.

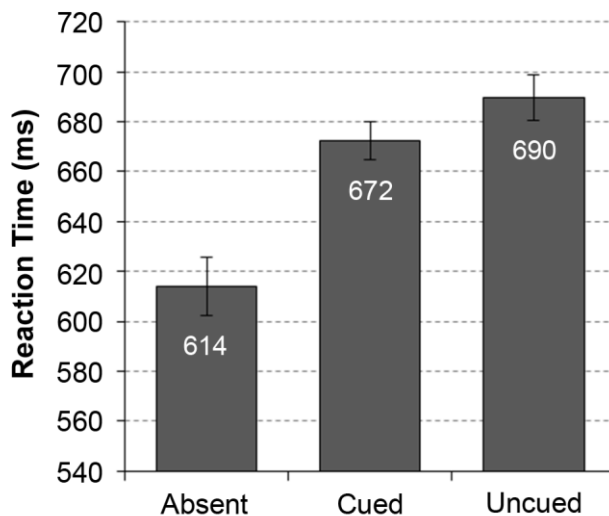


Figure 2. Mean reaction time for Experiment 1. Each column corresponds to a CMD condition. Error bars represent 95% confidence intervals corrected for within-subject designs (Loftus & Masson, 1994).

3 Experiment 2

The results from Experiment 1 demonstrated that the influence of distracting stimuli is reduced when presented to to-be-ignored locations. It is unclear, however, when this cueing benefit emerges. As described previously, Moher and Egeth (2012) report an interfering effect of cueing distractors at short ISIs, but a benefit at longer ISIs. This pattern may have been due to the exogenous nature of the cues used, though. Chao (2010) did find an effect of time on intentional suppression using endogenous cues, but only when a block employing long cue-target ISIs preceded a short ISI block. Experiment 2 was therefore aimed at further clarifying the time course of the distractor cueing benefit using informative central cues. I hypothesized that that one's ability to ignore cued locations would take time. As such, I predicted that the distractor cueing benefit would be absent for the shortest ISI, but become increasingly more pronounced as the ISI increased.

3.1 Method

3.1.1 Participants

Thirty-two participants completed the experiment. Five participants were excluded without observation for failing to follow task instructions (e.g., closing eyes during the task, not maintaining central fixation). Additionally, two participants respectively exhibited RT and accuracy more than 2 SD below the group mean and were subsequently excluded from analyses. The final sample therefore consisted of 25 participants between the ages of 18 and 25 years ($M = 20.3$ years, $SD = 1.3$; 7 male, 18 female).

3.1.2 Stimuli and Procedure

Experiment 2 was identical to Experiment 1 with one notable exception. Unlike Experiment 1, which employed a single cue-target ISI of 1400 ms, three cue-target ISIs were used in Experiment 2 (350, 700, and 1050 ms) in order to track the effect of cueing to-be-ignored locations at various time intervals. The ISIs were intermixed within blocks, and equally distributed across the three CMD conditions. Each experimental block consisted of 81 trials (648 total trials).

3.2 Results and Discussion

Trials were excluded from analyses following the same procedures as Experiment 1. A 3 [CMD (Absent, Cued, Uncued)] x 3 [ISI (350, 700, 1050 ms)] repeated measures ANOVA was carried out on RT for correct responses. As was the case in Experiment 1, errors and missed responses were low (5.0 %), and did not vary according to any experimental manipulation (p 's $\geq .222$).

Meant RT for each CMD condition crossed with the three ISIs are presented in Figure 3. Main effects of CMD [$F(2,48)$, $p < .001$, $\eta_p^2 = .78$] and ISI [$F(2,48)$, $p < .001$, $\eta_p^2 = .26$] were observed. With respect to the former, RT was shorter in the Absent condition relative to the Cued [$t(24) = 9.38$, $p < .001$, $d = 1.9$] and Uncued conditions [$t(24) = 10.23$, $p < .001$, $d = 2.0$], but equivalent for Cued and Uncued conditions [$t(24) = 1.12$, $p = .274$, $d = 0.22$]. The main effect of ISI was attributable to longer RT for the 350 ms ISI compared to the 700 ms ISI [$t(24) = 4.00$, $p < .001$, $d = 0.80$] and 1050 ms ISI [$t(24) = 2.93$, $p = .007$, $d = 0.59$]. The difference in RT for 700 ms and 1050 ms ISIs was not significant [$t(24) = .30$, $p = .766$, $d = 0.06$]. While the main effects of CMD and ISI were significant, the two effects did not interact [$F(4,96)$, $p = .077$, $\eta_p^2 = .08$]. However, because the effect of the cue on target-distractor competition was of primary interest here, a separate ANOVA was conducted that did not include the Absent CMD condition. In doing so, an interaction of CMD x ISI [$F(2, 48) = 3.43$, $p = .041$, $\eta_p^2 = .13$] was observed. For the 350 ms ISI, Cued and Uncued conditions did not significantly differ [$t(24) = 1.27$, $p = .217$, $d = 0.25$]. This was also the case for the 700 ms ISI [$t(24) = 1.05$, $p = .304$, $d = 0.21$]. For the 1050 ms ISI, though, a significant difference was present with shorter RT for the Cued than Uncued condition [$t(24) = 2.29$, $p = .031$, $d = 0.46$].

Lastly, a linear mixed effects analysis was performed to explore whether there was a linear relationship between the cue-target ISI and RT difference between Cued and Uncued CMD conditions. Using the lme4 package in R (Bates, Maechler, Bolker, & Walker, 2015), a model was created that included random effects of inter-subject variance, as well as variance in slope for the effect of ISI across participants (treating ISI as a continuous variable). The factor ISI was then entered into model as a fixed effect, which significantly improved explained variance [$\chi^2(1) = 6.23$, $p = .013$], with an observed change of 9.14 ms ($SE = 3.5$) in the RT difference between Cued and Uncued conditions with each addition of 350 ms to the cue-target ISI.

The results from this experiment provide additional support to suggest that the distractor cueing benefit is time dependent. At short ISIs, cueing a to-be-ignored location was not beneficial for the suppression of salient distractors. In fact, a numerical (but not statistically significant) disadvantage was observed at the shortest ISI (i.e., 350 ms), much like that reported by Moher and Egeth (2012). As the cue-target duration was increased, though, cueing to-be-ignored locations became increasingly beneficial, as evidenced by the linear trend of ISI on the RT difference, and significant cueing benefit for the 1050 ms ISI when Cued and Uncued conditions were directly compared.

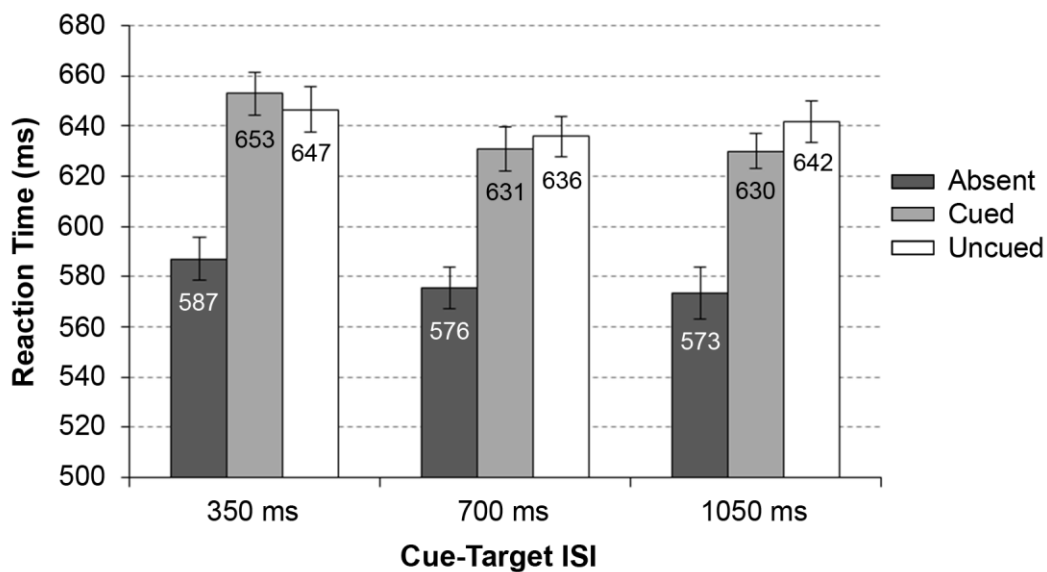


Figure 3. Mean reaction time for Experiment 2. Graph depicts each CMD condition separated by the various cue-target ISIs. Error bars represent 95% confidence intervals corrected for within-subject designs (Loftus & Masson, 1994).

4 Experiment 3

Experiments 1 and 2 demonstrated that the current task design is suitable to generate a behavioural distractor cueing benefit in that the presentation of salient distractors at to-be-ignored locations reduced their impact on behavioural performance (at least at long cue-target ISIs). As such, I used this task design to examine the electrophysiological processes underling preparatory suppression of to-be-ignored locations for Experiment 3 of my thesis. Posterior alpha-band activity was the primary marker of interest given its hypothesized role in the active suppression of visual signals (Foxe, & Snyder, 2011). Further, in addition to measuring behavioural performance in the task, lateralized ERPs were assessed to infer how attentional

selection and suppression mechanisms were modulated by the CMD conditions at the time of target presentation. I hypothesized that hemispheric differences in alpha-band activity would increase over the course of the cue-target ISI, with greater activity in the hemisphere contralateral to the to-be-ignored location, similar to that found by Worden et al. (2000).

4.1 Method

4.1.1 Participants

Twenty participants completed the experiment. One participant failed to maintain fixation during the experiment, as indicated by an excessive number of horizontal electroocular (EOG) artifacts, and was subsequently removed from all analyses. Further, one participant's mean RT exceeded the group mean by more than 2 SD, while another participant's accuracy was more than 2 SD below the group mean. As such, both participants were excluded from analyses. The final sample consisted of 17 participants between the ages of 18 and 24 years ($M = 21.1$ years, $SD = 1.9$; 4 male, 13 female; 15 right-handed).

4.1.2 Stimuli and Procedure

Stimuli were presented to a 24-inch BenQ XL2430T LCD monitor with a screen resolution of 1920 x 1080 pixels, and 60 Hz refresh rate. All stimuli were adjusted to match the visual dimensions of those used in Experiments 1 and 2 at a viewing distance of 60 cm. The task itself was modified in two ways relative to the first two experiments. First, the Absent CMD condition was removed in order to exclusively examine the effects of the cue on target-distractor competition. Second, an inter-trial interval of 1000 ms was introduced. During this time, the central fixation turned white, and participants were permitted to blink freely. As was the case in Experiment 1, a single cue-target ISI of 1400 ms was used for the experimental task. The task consisted of 8 experimental blocks of 72 trials (576 total trials) in addition to one practice block of 72 trials. All experimental procedures were otherwise identical to those used in Experiments 1 and 2.

4.1.3 EEG Data Acquisition Processing

The EEG was continuously sampled at 2048 Hz from AG-AgCl electrodes positioned at 64 standard sites using an ActiveTwo system (BioSemi; Amsterdam, Netherlands). Vertical EOG and horizontal EOG were recorded from two electrodes infraorbital to the left and right eye

paired respectively with FP1 and FP2, and two electrodes placed lateral to the external canthi of the left and right eyes. Two additional electrodes were positioned at the left and right mastoids.

Offline processing and analyses were performed using a combination of EEGLAB (Delorme & Makeig, 2004), ERPLAB (Lopez-Calderon & Luck, 2014), and Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen, 2011). EEG recordings were referenced to the average of the left and right mastoids, downsampled to 512 Hz, and bandpass filtered between .1 – 30 Hz (24 db/octave Butterworth filter). Trials excluded from behavioural analyses (i.e., errors, misses, and exceptionally slow/fast responses) were removed, as were trials in which eye movements exceeding 30 μ V were detected in the horizontal EOG between the time of fixation and 500 ms post target-onset. Participants were excluded from all analyses if horizontal eye movements were present for 50 or more trials. This was the case for one participant, as noted previously.

Time-frequency analysis was performed over the cue-target ISI. To do so, 3s-epochs locked to the cue were generated (-1000 ms cue onset to 500 ms post target onset). Eye blinks occurring within these epochs were corrected using independent component analysis (ICA) unless the eye blink occurred within \pm 100 ms of cue onset, in which case the epoch was rejected. Epochs containing extreme values (\pm 100 μ V) were also excluded, as were epochs containing artifacts detected during visual inspection. Exceptionally noisy channels were corrected using spherical interpolation. Time-frequency decomposition was then performed separately for epochs locked to left and right cues using a Hanning taper window of 500 ms, which moved in steps of 50 ms from -600 ms pre-cue to 200 ms post-target onset at 2 Hz intervals from 4 to 20 Hz. Baseline correction was performed by subtracting mean power over the fixation period (-600 to 0 ms) from each time point. Prior to baseline correction, two participants exhibited exceptionally high alpha-band power values (i.e., > 2 SD from the group mean). These participants were not included in the time-frequency analysis. Following baseline correction, time-frequency power spectrums for left and right cues were averaged to create contralateral and ipsilateral power spectrums at electrode pairs PO3/4, PO7/8, and O1/2 according to the cued location. Grand average contralateral and ipsilateral power spectrums over lateral posterior regions were then computed by averaging power spectrums for the three electrode pairs. Lastly, differences in power between contralateral and ipsilateral hemispheres were computed by subtracting the grand averaged ipsilateral power spectrum from the grand averaged contralateral power spectrum for

each participant. The resultant time-frequency power spectrums are depicted as spectrograms in Figure 4.A.

ERPs were analyzed relative to the target display. In order to examine lateralized effects of target and distractor processing, only trials in which the target appeared along the horizontal meridian with the CMD along the vertical meridian, and vice versa, were analyzed. Epochs were baseline corrected to the 100 ms period prior to the onset of the target display and extended 500 ms post target onset. Epochs were rejected following the same procedure as that used for the cue-locked epochs. ERP waveforms were averaged across trials according to whether the item of interest (i.e., target or CMD) appeared in the left or right hemifield. Using these averaged waveforms, contralateral and ipsilateral waveforms were created according to the position of the target/CMD. Difference waves were then produced by subtracting ipsilateral waveforms from contralateral waveforms. All ERP analyses were performed on the PO7/8 electrode pair.

4.2 Results

4.2.1 Behavioural Results

Mean RT for correct responses in Cued and Uncued CMD conditions were compared using a two-tailed, paired-samples t-test. This contrast revealed a significant difference [$t(16) = 3.57, p = .003, d = 0.87$], with RT being greater in the Uncued ($M = 625$ ms, $SD = 95.8$) relative to the Cued CMD condition ($M = 614$ ms, $SD = 96.8$), replicating the finding from Experiment 1. Once again, errors and misses accounted for only a small proportion of trials (5.2%), and did not vary by experimental condition [$t(16) = 1.73, p = .103, d = 0.419$].

4.2.2 Cue-Locked Alpha-Band Activity

Time-frequency analyses were limited to hemispheric differences in oscillatory alpha-band activity (8 – 12 Hz) over lateral posterior electrodes (Figure 4.B.). In order to compare changes in alpha-band activity to the observed behavioural findings from Experiments 1 and 2, the cue-target interval was divided into four time bins of 350 ms corresponding to the ISIs used previously. A 2 [Hemisphere (Contralateral, Ipsilateral)] x 4 [Time Bin (0–350 ms, 350–700 ms, 700–1050 ms, 1050–1400 ms)] repeated measures ANOVA was then performed to compare hemispheric differences in alpha-band activity over each bin. Despite finding no main effect of Hemisphere [$F(1,14) = .02, p = .902, \eta_p^2 < .01$], or Time Bin [$F(1,14) = .53, p = .663, \eta_p^2 = .04$],

there was a significant interaction of Hemisphere x Time Bin [$F(3,42) = 6.42, p = .001, \eta_p^2 = .31$]. At the first time bin, alpha-band power was greater over the hemisphere ipsilateral to the cued location than the contralateral hemisphere [$t(14) = 2.8, p = .014, d = .73$]. Hemispheric differences were not present for the second [$t(14) = 1.08, p = .298, d = .28$], nor at the third time bin [$t(14) = 1.39, p = .185, d = .36$]. At the fourth time bin, there was a trend towards greater alpha-band power for the contralateral hemisphere relative to the ipsilateral hemisphere [$t(14) = 1.9, p = .080, d = .49$].

Additionally, a linear mixed effects analysis similar to that employed in Experiment 2 was performed. This was done to examine whether hemispheric differences in alpha-band power followed a linear trend across the various time bins. A model was created that included random effects of inter-subject variance, and variance in slope for the effect of Time Bin across participants. The factor of Time Bin was then added to the model as a fixed effect, which significantly improved explained variance [$\chi^2(1) = 7.45, p = .006$]. An average power increase of $.42 \mu V^2$ ($SE = .14$) was observed for the contralateral minus ipsilateral hemispheric difference from one bin to the next.

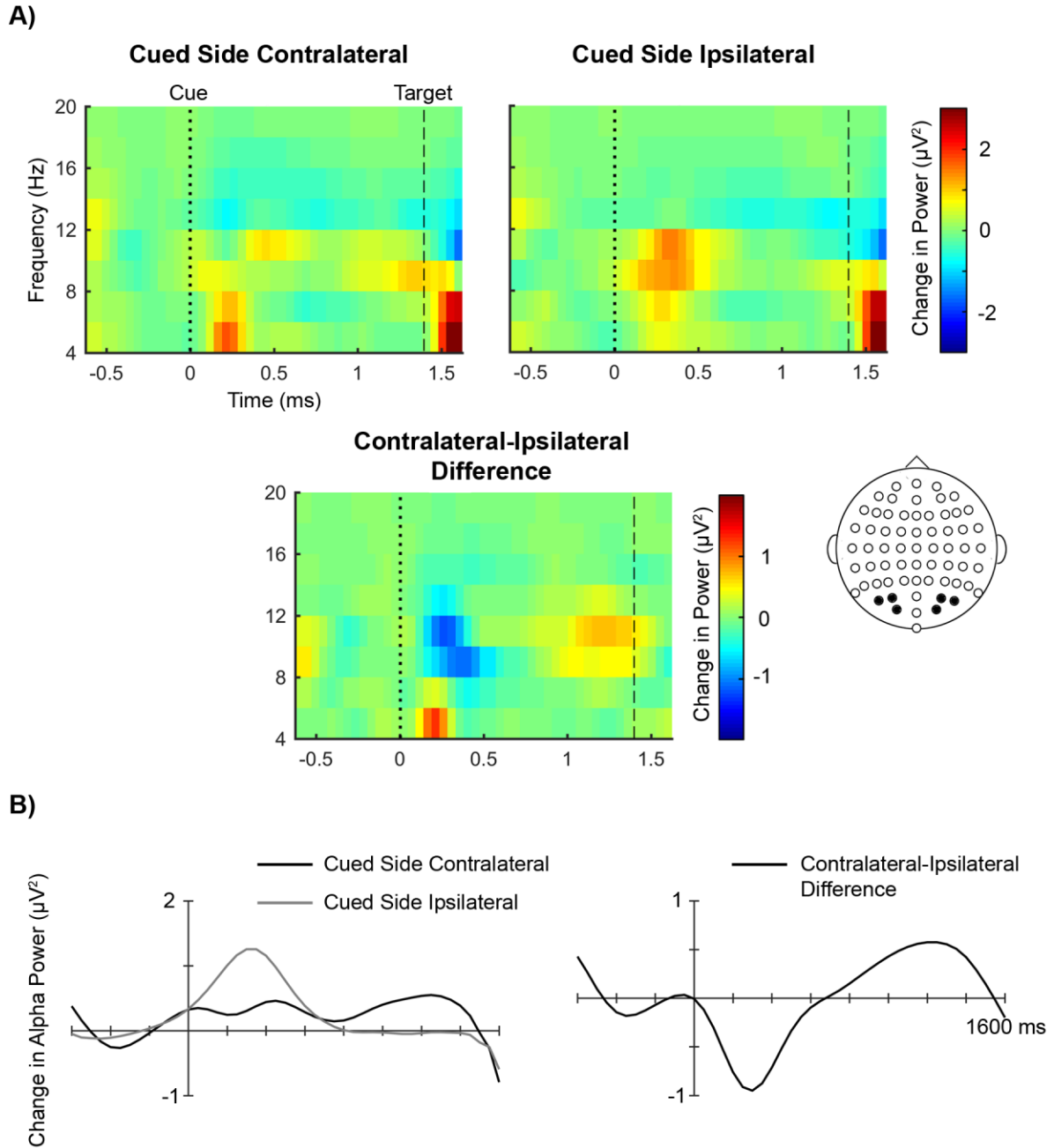


Figure 4. Time-frequency plots corresponding to the cue-target ISI in Experiment 3. Shown are (A) grand averaged spectrograms baseline corrected to the fixation period for hemispheres contralateral and ipsilateral to the side of the cued location at lateral posterior electrodes, as well as the difference between the two, and (B) line plots of the observed power values averaged over the alpha-band frequency range (8–12 Hz) for contralateral and ipsilateral hemispheres (left) and the contralateral-ipsilateral difference (right).

4.2.2.1 Lateralized Target ERPs

Inspection of the contralateral-ipsilateral difference waves for lateralized target stimuli (see Figure 5) revealed the traditional contralateral target negativity in the N2pc time range. The amplitude of this component over a 220–280 ms post-stimulus time window was entered into a 2 [Hemisphere (Contralateral, Ipsilateral)] x 2 [CMD(Cued, Uncued)] repeated measures ANOVA. A main effect of Hemisphere was found [$F(1,16) = 32.80, p < .001, \eta_p^2 = .67$], confirming that the negative difference between hemispheres was significant. The main effect of CMD, however, was not significant [$F(1,16) = .286, p = .600, \eta_p^2 = .02$], which was also the case for the interaction of Hemisphere x CMD [$F(1,16) = 1.16, p = .298, \eta_p^2 = .07$], indicating that the target N2pc was equivalent in both the CMD cued and Uncued conditions

In addition to the N2pc, a late sustained negativity was also observed in the lateralized target contralateral-ipsilateral waveform, though only in the CMD Uncued condition. This component, which emerged approximately 350 ms after stimulus onset and persisted to the end of the 500 ms epoch, was in same time range as a sustained posterior contralateral negativity (SPCN; Jolicœur, Sessa, Dell'Acqua, & Robitaille, 2006) observed elsewhere during visual search and working memory tasks (e.g., Hilimire et al., 2011; Kiss, Van Velzen, & Eimer, 2008b). The amplitude of this component was analyzed over a 350–500 ms post stimulus time window in the same manner as the target N2pc. While neither the effect of Hemisphere [$F(1,16) = 1.30, p = .272, \eta_p^2 = .08$], nor the effect of CMD was significant [$F(1,16) = 1.24, p = .282, \eta_p^2 = .07$], there was an interaction of Hemisphere x CMD [$F(1,16) = 8.93, p = .009, \eta_p^2 = .36$]. The contralateral-ipsilateral difference over the target SPCN time window was significant in the CMD Uncued condition [$t(16) = 2.43, p = .027, d = .59$], but not in the CMD cued condition [$t(16) = .41, p = .685, d = .10$].

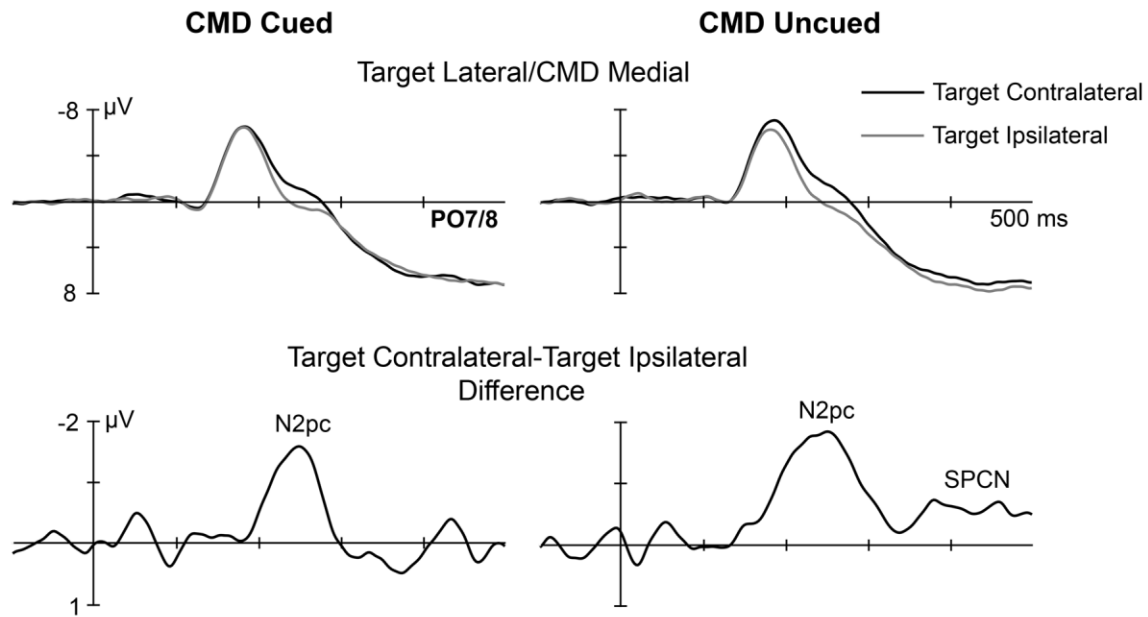


Figure 5. Grand averaged waveforms for lateralized targets. Contralateral and ipsilateral waveforms are depicted (top) as are contralateral-ipsilateral difference waves (bottom) for Cued (left) and Uncued (right) CMD conditions.

4.2.3 Lateralized Distractor ERPs

Contralateral-ipsilateral difference waveforms (see Figure 6) for lateralized distractors in both the Cued and Uncued CMD conditions exhibited a negative deflection in the typical N2pc time range, immediately followed by a positive deflection, considered here to be a late P_D component. The amplitudes of these components were separately analyzed using 2 [Hemisphere (Contralateral, Ipsilateral)] x 2 [CMD(Cued, Uncued)] repeated measures ANOVAs. As was the case for the target N2pc, the amplitude of the distractor N2pc was measured from 220–280 ms post stimulus onset, while the P_D amplitude was measured from 280–340 ms.

For the distractor N2pc, there was a main effect of Hemisphere [$F(1,16) = 11.28, p = .004, \eta_p^2 = .41$], but not CMD [$F(1,16) = .20, p = .661, \eta_p^2 = .01$]. More importantly, there was no interaction of Hemisphere with CMD [$F(1,16) = .45, p = .513, \eta_p^2 = .03$], suggesting that the distractor N2pc was equivalent for both cued and uncued CMDs. A similar pattern of results was found for the P_D , with a main effect of Hemisphere [$F(1,16) = 8.16, p = .011, \eta_p^2 = .34$], but no effect of CMD [$F(1,16) = .04, p = .843, \eta_p^2 < .01$], or interaction of Hemisphere x CMD [$F(1,16) = .06, p = .813, \eta_p^2 < .01$].

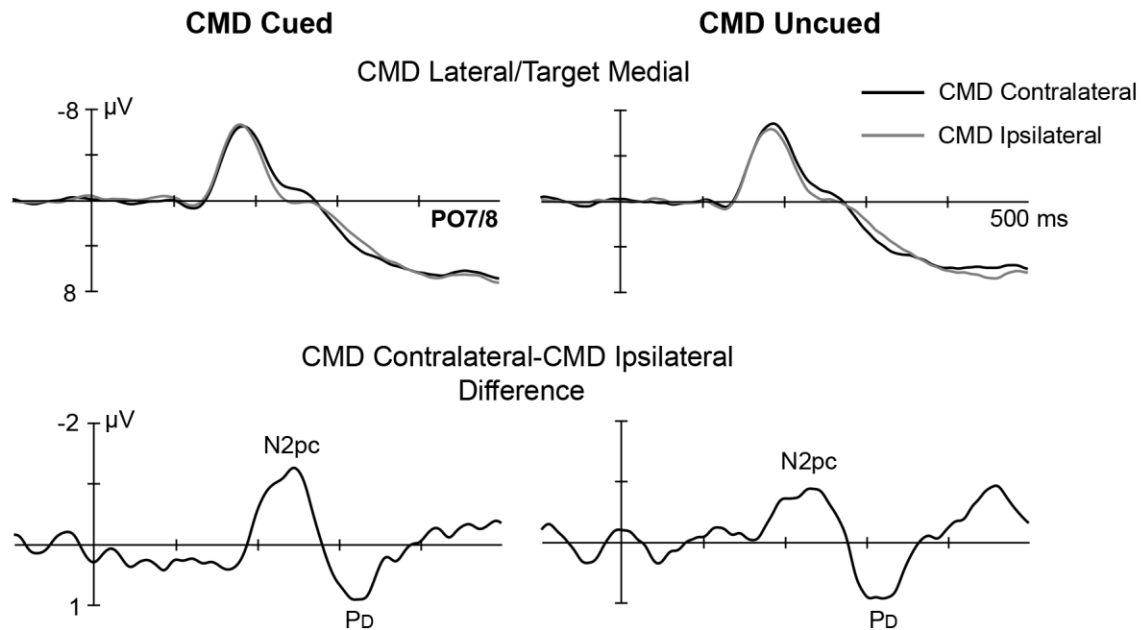


Figure 6. Grand averaged waveforms for lateralized CMDs. Contralateral and ipsilateral waveforms are depicted (top) as well as contralateral-ipsilateral difference waves (bottom) for Cued (left) and Uncued (right) CMD conditions.

4.3 Discussion

In Experiment 3, RTs benefited when salient distractors appeared at to-be-ignored locations, replicating the findings from Experiments 1 and 2. More critically, the observed electrophysiological activity illuminates the processes that underlie this benefit. Specifically, I hypothesized that hemispheric differences in alpha-band activity would be present during the cue-target ISI, with increasingly greater alpha-band activity in the contralateral hemisphere relative to the ipsilateral hemisphere. This did seem to be the case as evidenced by a linear trend of the contralateral-ipsilateral power difference over the four time bins of interest. However, somewhat unexpectedly, a significant contralateral-ipsilateral alpha-band power difference was evident over the first time bin, with greater activity in the contralateral hemisphere. If hemispheric differences in alpha-band activity are taken to reflect the spatial distribution of attentional processes, then the observed pattern suggests that participants first attended the cued location prior to active suppression. Curiously, at the time of the target display, N2pc and PD components were equivalent for Cued and Uncued CMD conditions. Instead, a late SPCN for target stimuli was the only ERP component that varied according to CMD condition. The functional significance of these results is discussed further in the following section.

5 General Discussion

Over the course of three experiments, participants performed a task in which to-be-ignored locations were centrally cued prior to the presentation of target displays. While targets never appeared at cued locations, distracting items resembling target stimuli sometimes did, which made it beneficial for participants to try to ignore these locations. Despite having no advance knowledge of the target's location, participants were able to use the cues to their advantage. In each experiment, participants were faster to locate and identify the orientation of the target when the CMD appeared at a to-be-ignored location compared to when it appeared at a possible target location. This advantage, however, was contingent on the length of time between the presentation of the cue and target display, as no benefit was observed when shorter ISIs were employed. Possibly underlying this finding, Experiment 3 demonstrated a time-dependent response involving lateralized alpha-band activity over parieto-occipital sites following the onset of the cue. However, in spite of both the behavioural benefit and preparatory alpha-band response, presenting the CMD to cued locations had no influence on the amplitude of ERPs commonly associated with attentional selection and suppression. Instead, such effects were restricted to a late sustained negativity present only for target stimuli.

The current set of experiments adds to an emerging line of research concerned with understanding whether spatial information can be used to endogenously diminish the competitive influence of distracting items in the visual field without biasing attentional processes towards target locations. Behavioural studies in this area to date have been mixed. On the one hand, some researchers have reported an attentional white bear effect, in which prior knowledge of an unlikely target location or a distracting item's location paradoxically enhances attentional priority for such locations (e.g., Jollie et al., 2016; Lahav et al., 2012; Tsal & Makovski, 2006), while on the other hand, some have found that cueing the location of a distracting item reduces its interfering influence (e.g., Munneke et al., 2008; Chao, 2010). The behavioural observations found here are in line with those of the latter. This was expected, as the methods employed were intentionally chosen to resemble those used by Munneke et al. (2008) in order to examine physiological responses under cueing conditions known to facilitate performance. Nonetheless, the current results help to resolve existing discrepancies. In particular, it has previously been argued that the behavioural benefit of cueing a distractor's location depends on imperative

stimuli never appearing at these locations (Chao, 2010). The current findings support this position as the cueing benefit was observed using a cue that was entirely valid. I assume that the observed cueing effect would have been greatly diminished, if not altogether eradicated, had this not been the case.

In addition to replicating the distractor cueing benefit, I provide further insight into the temporal nature of this effect. Previously, only one study had manipulated the ISI between cue and target stimuli when centrally cueing the locations of distractors. In particular, Chao (2010) administered two experimental blocks to participants; each associated with either a short or long ISI. When presented first, the researcher found a benefit of cueing the location of the distractor in the long ISI block, but not the short ISI block. Curiously, when the order of the blocks was reversed, cueing the location of the distractor had no effect on performance, regardless of ISI length. In the present study, the effect of time was more apparent. Using multiple ISIs intermixed across blocks in Experiment 2, the distractor cueing benefit was shown to gradually emerge over the period following the cue, and not significantly facilitate performance until sometime between 700–1050 ms. In fact, for the shortest ISI (i.e., 350 ms) performance was numerically worse when CMDs were cued compared to when they were uncued, raising the possibility that participants may have initially attended to the cued location. Interestingly, this resembles findings by Moher and Egeth (2012) who used valid peripheral cues to identify the locations of to-be-ignored items. Performance in this task was hindered when a short cue-target ISI was used, but facilitated when longer ISIs were used. Given the similarity between the results of Experiment 2 and those found by Moher and Egeth (2012), it seems as though both central and peripheral cues, when valid, are acted on in much the same manner when such cues identify locations that one is to ignore.

Overall, the behavioural findings confirm that, under the right conditions, spatially cueing to-be-ignored locations can successfully reduce the impact of distracting stimuli presented to these locations. The question, then, is how this distractor cueing benefit arises. Given the overwhelming amount of support to suggest that the prioritization of visual inputs is governed by a dorsal network of frontoparietal structures (e.g., Bisley & Goldberg, 2003; Coull & Nobre, 1998; Corbetta et al., 2000; Fan et al., 2005; Hopfinger et al., 2000; Kelley et al., 2007; Lauritzen et al., 2009; Molenberghs et al., 2007; Szczepanski et al., 2013), one can reason that top-down

signals from this network should be principally involved if active suppression is the mechanism by which the benefit comes to be.

In order to test the active suppression account, I assessed posterior alpha-band activity during the cue-target ISI in Experiment 3. I considered this to be an ideal marker of endogenous suppression as it is both influenced by the activation of frontoparietal structures (Capotosto et al., 2009) and is thought to alter the responsiveness of neurons to visual stimulation – with greater alpha-band activity reflecting decreased cortical excitability (Foxe & Snyder, 2011). As such, I predicted that hemispheric differences in this measure would increase over the course of the cue-target ISI, reflecting the time-based nature of the distractor cueing benefit. In line with my prediction, the contralateral-ipsilateral difference in posterior alpha-band activity exhibited a pattern resembling the behavioural pattern observed in Experiment 2. Specifically, the contralateral-ipsilateral power difference was negative (compared to baseline) over the first time bin, but then became increasingly more positive across each measured bin. This finding suggests that the uncued side of space was more greatly suppressed initially, but this effect reversed over time, with greater suppression of the cued side with the passage of time. It is important to acknowledge, though, that in the period immediately preceding target presentation the hemispheric difference trended towards, but did not actually reach significance.

The observed pattern of alpha-band activity, while suggestive of active suppression, also suggests that IOR may have contributed to the distractor cueing benefit. Again, this phenomenon reflects an initial enhancement in one's ability to detect and/or act on stimuli present at a location to which one is exogenously oriented towards, followed by a hindrance thereafter (Posner & Cohen, 1984). While the central cues used in the present study validly indicated where the target would not appear, they nonetheless seemed to orient attention towards the cued location. This was most strongly evidenced by the negative contralateral-ipsilateral power difference in the alpha-band over the first 350 ms of the cue-target ISI. Not only does this suggest that participants attended to the cued locations, but that they did so reflexively since hemispheric differences do not emerge until about 400 ms after the presentation of cue stimuli when attention is endogenously oriented (e.g., Worden et al., 2000). Further supporting this view is the interfering effect of cued CMDs following a 350 ms ISI that was exhibited in Experiment 2, which may have been significant had a shorter ISI been used. At the moment, then, it cannot be concluded

that the observed distractor cueing benefit is entirely voluntary, but instead may reflect both endogenous and exogenous attentional processes.

Nonetheless, the cue based modulation of alpha-band activity observed in the present study is in stark contrast to Noonan et al. (2016) who found cueing distractor locations to have no effect on the oscillatory activity of this frequency range. Perhaps this disparity is best accounted for by differences in experimental design. As previously mentioned, the layout of the target display used by Noonan et al. (2016) allowed for targets to appear in the same hemifield as the cued distractor. In this case, simple comparisons of contralateral and ipsilateral hemispheres may not have been entirely appropriate as it would not have been beneficial for participants to ignore the entire side of space corresponding to the cued location. Further, Noonan et al. (2016) consistently presented distractors to the same location in a given block. It is thus unclear whether their distractor cueing benefit was actually a cue-based response, or a byproduct of the distractor's repeated location.

Beyond observing oscillatory changes during the preparatory period in the present study, I also examined lateralized ERPs at the time of target presentation. I predicted that N2pc and P_D components would reflect differences in the efficiency of target processing, depending on whether CMDs were presented to cued or uncued locations since these components are strongly linked to early attentional processes involved in the selection of task relevant items and suppression of salient to-be-ignored items in the visual field, respectively (Eimer, 1996; Gaspar et al., 2016; Hickey et al., 2009; Hickey et al., 2006; Jannati et al., 2013; Luck & Hillyard, 1994). This, however, was not the case. Lateral targets elicited the typical N2pc response, but the amplitude of this component was equivalent in Cued and Uncued CMD conditions, suggesting that the initial deployment of attentional resources towards the target did not differ between conditions. Still, more striking was the similarity in lateral ERP components for cued and uncued CMDs, given that cued CMDs should have been the benefactors of active suppression. As with lateral target stimuli, CMDs generated the N2pc component, with the amplitude being the same in Cued and Uncued CMD conditions. While this confirms the capturing effect of the CMD evidenced in Experiments 1 and 2, the lack of a difference indicates that attentional selection of the distracting item was unaffected by one's spatial knowledge. Immediately following the distractor N2pc, a late P_D was observed, however, this component too did not differ between Cued and Uncued CMD conditions. If the late P_D is taken to reflect top-down suppression

following spurious attentional capture, then the equivalent response for cued and uncued CMDs implies that prior spatial information did not influence the reactive suppression of such stimuli.

I contend that the findings regarding N2pc and P_D ERP components reflect the nature of the stimuli used in the study in combination with the reorienting function of the ventral frontoparietal network. Specifically, I created target-distractor competition by matching target and distractor stimuli on a critical feature (i.e., colour). This was done purposely to ensure that any preparatory bias against distracting stimuli would be spatially based. If instead, for example, targets were defined by a unique colour, then participants might have maintained an attentional set to enhance visual signals corresponding to that colour, while suppressing visual signals corresponding to other colours (Giesbrecht et al., 2003; Liu et al., 2011). In which case, distractor suppression effects would be at least partially attributable to a bias in favour of target stimuli. Still, I presume that participants in the current study did maintain the colour of the target as part of the attentional set. Importantly, attentional sets defined by colour produce global attentional biases, which increase attention for all items matching the maintained colour regardless of whether such items appear in one's attended region of space or not (Andersen, Fuchs, & Müller, 2011). With this being the case, the ventral frontoparietal network, which works to reorient attentional processing towards task-relevant items (Corbetta & Shulman, 2002, 2008), may have been sensitive to CMDs independent of location, disrupting the dorsal spatial control signal. The N2pc then, which corresponds to activation of the ventral visual stream (Hopf et al., 2000), and has been shown elsewhere to be sensitive to distractors encompassing target features (i.e., Eimer & Grubert, 2014), may have represented a priority response to all task-relevant features in the visual display. If this is the case, then the late P_D observed for CMDs may have represented a terminating response from the dorsal network that worked to regain control by suppressing or disengaging from the salient, distracting stimuli.

Despite finding no influence of cueing to-be-ignored locations on these early ERP components commonly associated with the initial enhancement or suppression of visual signals, a later component did exhibit signs of modulation contingent on the CMD being cued or uncued. Specifically, the SPCN was generated by target stimuli contained in displays with an uncued CMD, but was notably absent when the CMD was present at a cued location. While the functional role of this component is not entirely established as of yet, its amplitude does appear to be sensitive to attentional and working memory demands; for example, this component is

greater when discrimination judgments are required compared to simple localization judgments (e.g., Mazza, Turatto, Umiltà, & Eimer, 2007), and when multiple items/attributes need to be assessed or remembered (e.g., Jolicœur, Brisson, & Robitaille, 2008; Maheux, & Jolicœur, 2017). In this context, it appears as though cueing distractors acted on a late stage of effortful processing. I argue that the presence of the target SPCN in the Uncued CMD condition, but not the Cued condition suggests fewer attentional resources were required in the latter condition. Although contradictory to the P_D findings, this could be due to a reduction in perceptual conflict stemming from greater suppression of cued CMDs than uncued CMDs. This is consistent with Bacigalupo and Luck (2015) who recently found the amplitude of the SPCN to scale with the physical distance between target and flanking stimuli, such that the amplitude of this component was maximal when flanking and target stimuli were close to one another (i.e., when perceptual conflict was greatest), but increasingly reduced as targets and distractors became more distant. Of course, further replication of the present finding is required before this account can be wholly accepted since the observed findings were not anticipated.

I acknowledge that the current study is not without limitations. Of note, the cue that was used to indicate to-be-ignored locations might not have been optimal for the study of endogenous attentional processes. As mentioned previously, centrally presented cues associated with direction exogenously orient attention, even when such cues are uninformative (e.g., Hommel et al., 2001; Ristic & Kingstone, 2006; Tipples, 2002). In the present study, it is possible that cue stimuli were processed in relation to central fixation, which may have prompted automatic shifts of attention towards cued locations in response to cue onset. If this was the case, then IOR effects may be attributable to the physical properties of the cue. The current study was further limited in that there was no neutral cueing condition (i.e., a condition in which participants had no advance knowledge of to-be-ignored locations). This raises the possibility that the observed distractor cueing benefit resulted not from greater suppression of cued locations, but instead from an enhancement of attention at uncued locations, resulting in greater interference from CMDs presented to these locations. While this is a valid concern, I argue that any attentional enhancement that occurred at uncued locations was minimal, since such resources would have needed to be distributed over multiple locations.

Despite the described limitations, the current study nonetheless provides valuable information regarding the use of spatial information to anticipatorily suppress cued locations without having

prior access to target locations. Still, questions remain that will need to be addressed by future studies. For example, work will need to be done to separate endogenous contributions to the distractor cueing benefit from exogenous contributions. This might be achieved using the same methods employed in the present study, replacing the central cue with a salient peripheral stimulus that participants are to ignore. If both the behavioural pattern and electrophysiological activity produced under such conditions mirrors that observed in the current study, then this would undoubtedly challenge an endogenous suppression account of the distractor cueing benefit as it would suggest that the effect occurs outside of one's intentions. Alternatively, numerical cues that do not inherently imply direction, such as those used by Jollie et al. (2016), could be employed. In this case, I would not expect reflexive shifts of attention towards the cued location, making it less likely that a distractor cueing benefit could be attributed to an exogenous effect.

In addition to isolating endogenous and exogenous influences on the distractor cueing benefit, it is also important to examine the electrophysiological response to target displays under conditions that minimize the potential for a ventral reorienting response. Again, ERP components associated with attentional selection and suppression elicited by CMDs did not differ between Cued and Uncued conditions. While this is counter to the argument that distractor cueing influences the efficiency of visual processing, it is possible that the similarity between targets and CMDs may have produced activation in the ventral frontoparietal network, temporarily disrupting spatial signals maintained by the dorsal frontoparietal network, as suggested above. To avoid this, one could use physically salient distractors distinct from target stimuli, but again this risks the possibility of participants biasing target features rather than suppressing distractor locations. One could also reduce the stimulus presentation time of target displays, which would increase the demand to suppress distracting stimuli. In the past, this has been demonstrated as an effective way to eliminate the distractor N2pc in favour of the P_D (Kiss et al., 2008a).

Overall, the findings that I present here work to extend understanding of the behavioural and electrophysiological phenomena associated with cueing to-be-ignored locations in the absence of a guiding spatial template for target stimuli. It is demonstrated cueing to-be-ignored locations with 100% validity works to reduce the influence of distracting stimuli at these locations. This effect takes time, though, as no distractor cueing benefit is observed when the time between cues and target displays is brief. Topographic changes in posterior alpha-band activity appear to underlie this time-based effect, as hemispheric differences increase over time when cued to

lateral locations. While it is tempting to claim that these effects are reflective of intentional suppression processes, this cannot be concluded at present. This is due to the possibility that exogenous rather than endogenous attentional mechanisms produce the benefit, as well as the finding that early ERP components for target displays do not differ for Cued and Uncued CMD conditions. Regardless, these findings have important implications for the interpretability of previous works of a similar nature, and offer numerous avenues for future studies to pursue.

References

- Andersen, S. K., Fuchs, S., & Müller, M. M. (2011). Effects of feature-selective and spatial attention at different stages of visual processing. *Journal of Cognitive Neuroscience*, 23, 238-246.
- Awh, E., Matsukura, M., & Serences, J. T. (2003). Top-down control over biased competition during covert spatial orienting. *Journal of Experimental Psychology: Human Perception and Performance*, 29, 52-63.
- Bacigalupo, F., & Luck, S. J. (2015). The allocation of attention and working memory in visual crowding. *Journal of Cognitive Neuroscience*, 27, 1180-1193.
- Bates, D., Maechler, M., Bolker, B., Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1-48.
- Bennett, P. J., & Pratt, J. (2001). The spatial distribution of inhibition of return. *Psychological Science*, 12, 76-80.
- Berger, A. (1999). Peripheral non-informative cues do induce early facilitation of target detection. *European Journal of Cognitive Psychology*, 11, 119-137.
- Bisley, J. W., & Goldberg, M. E. (2003). Neuronal activity in the lateral intraparietal area and spatial attention. *Science*, 299, 81-86.
- Capotosto, P., Babiloni, C., Romani, G. L., & Corbetta, M. (2009). Frontoparietal cortex controls spatial attention through modulation of anticipatory alpha rhythms. *Journal of Neuroscience*, 29, 5863-5872.
- Chao, H. F. (2010). Top-down attentional control for distractor locations: the benefit of precuing distractor locations on target localization and discrimination. *Journal of Experimental Psychology: Human Perception and Performance*, 36, 303-316.
- Cohen, J. Y., Heitz, R. P., Schall, J. D., & Woodman, G. F. (2009). On the origin of event-related potentials indexing covert attentional selection during visual search. *Journal of Neurophysiology*, 102, 2375-2386.

- Collie, A., Maruff, P., Yucel, M., Danckert, J., & Currie, J. (2000). Spatiotemporal distribution of facilitation and inhibition of return arising from the reflexive orienting of covert attention. *Journal of Experimental Psychology: Human Perception and Performance*, 26, 1733-1745.
- Coull, J. T., & Nobre, A. C. (1998). Where and when to pay attention: the neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. *Journal of Neuroscience*, 18, 7426-7435.
- Chang, C. F., Hsu, T. Y., Tseng, P., Liang, W. K., Tzeng, O. J., Hung, D. L., & Juan, C. H. (2013). Right temporoparietal junction and attentional reorienting. *Human Brain Mapping*, 34, 869-877.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews. Neuroscience*, 3, 201-215.
- Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: from environment to theory of mind. *Neuron*, 58, 306-324.
- Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neuroscience*, 3, 292-297.
- Courtney, S. M., Petit, L., Maisog, J. M., Ungerleider, L. G., & Haxby, J. V. (1998). An area specialized for spatial working memory in human frontal cortex. *Science*, 279, 1347-1351.
- Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134, 9-21.
- Desimone, R. (1998). Visual attention mediated by biased competition in extrastriate visual cortex. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 353, 1245-1255.

- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193-222.
- Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology*, 99, 225-234.
- Eimer, M., & Grubert, A. (2014). The gradual emergence of spatially selective target processing in visual search: From feature-specific to object-based attentional control. *Journal of Experimental Psychology: Human Perception and Performance*, 40, 1819.
- Egner, T., Monti, J. M., Trittschuh, E. H., Wieneke, C. A., Hirsch, J., & Mesulam, M. M. (2008). Neural integration of top-down spatial and feature-based information in visual search. *Journal of Neuroscience*, 28, 6141-6151.
- Everling, S., & Munoz, D. P. (2000). Neuronal correlates for preparatory set associated with pro-saccades and anti-saccades in the primate frontal eye field. *Journal of Neuroscience*, 20, 387-400.
- Fan, J., McCandliss, B. D., Fossella, J., Flombaum, J. I., & Posner, M. I. (2005). The activation of attentional networks. *Neuroimage*, 26, 471-479.
- Folk, C. L., Remington, R. W., & Johnston, J. C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 1030-1044.
- Foxe, J. J., & Snyder, A. C. (2011). The role of alpha-band brain oscillations as a sensory suppression mechanism during selective attention. *Frontiers in Psychology*, 2, 1-13.
- Frings, C., & Wühr, P. (2007). On distractor-repetition benefits in the negative-priming paradigm. *Visual Cognition*, 15, 166-178.
- Gaspar, J. M., Christie, G. J., Prime, D. J., Jolicœur, P., & McDonald, J. J. (2016). Inability to suppress salient distractors predicts low visual working memory capacity. *Proceedings of the National Academy of Sciences*, 113, 3693-3698.

- Giesbrecht, B., Woldorff, M. G., Song, A. W., & Mangun, G. R. (2003). Neural mechanisms of top-down control during spatial and feature attention. *Neuroimage*, *19*, 496-512.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*, 20-25.
- Gould, I. C., Rushworth, M. F., & Nobre, A. C. (2011). Indexing the graded allocation of visuospatial attention using anticipatory alpha oscillations. *Journal of Neurophysiology*, *105*, 1318-1326.
- Hickey, C., Di Lollo, V., & McDonald, J. J. (2009). Electrophysiological indices of target and distractor processing in visual search. *Journal of Cognitive Neuroscience*, *21*, 760-775.
- Hickey, C., McDonald, J. J., & Theeuwes, J. (2006). Electrophysiological evidence of the capture of visual attention. *Journal of Cognitive Neuroscience*, *18*, 604-613.
- Hilimire, M. R., Mounts, J. R., Parks, N. A., & Corballis, P. M. (2011). Dynamics of target and distractor processing in visual search: Evidence from event-related brain potentials. *Neuroscience Letters*, *495*, 196-200.
- Hommel, B., Pratt, J., Colzato, L., & Godijn, R. (2001). Symbolic control of visual attention. *Psychological Science*, *12*, 360-365.
- Hopf, J. M., Luck, S. J., Girelli, M., Hagner, T., Mangun, G. R., Scheich, H., & Heinze, H. J. (2000). Neural sources of focused attention in visual search. *Cerebral Cortex*, *10*, 1233-1241.
- Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience*, *3*, 284-291.
- Hubel, D. H., & Wiesel, T. N. (1959). Receptive fields of single neurones in the cat's striate cortex. *The Journal of Physiology*, *148*, 574-591.
- James, W. (1892). *Psychology: The briefer course*. New York: Holt.

- Jannati, A., Gaspar, J. M., & McDonald, J. J. (2013). Tracking target and distractor processing in fixed-feature visual search: evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance*, 39, 1713-1730.
- Jolicœur, P., Brisson, B., & Robitaille, N. (2008). Dissociation of the N2pc and sustained posterior contralateral negativity in a choice response task. *Brain research*, 1215, 160-172.
- Jolicœur, P., Sessa, P., Dell'Acqua, R., & Robitaille, N. (2006). On the control of visual spatial attention: Evidence from human electrophysiology. *Psychological Research*, 70, 414-424.
- Jollie, A., Ivanoff, J., Webb, N. E., & Jamieson, A. S. (2016). Expect the unexpected: a paradoxical effect of cue validity on the orienting of attention. *Attention, Perception, & Psychophysics*, 78, 2124-2134.
- Kelley, T. A., Serences, J. T., Giesbrecht, B., & Yantis, S. (2007). Cortical mechanisms for shifting and holding visuospatial attention. *Cerebral Cortex*, 18, 114-125.
- Kiss, M., Grubert, A., Petersen, A., & Eimer, M. (2012). Attentional capture by salient distractors during visual search is determined by temporal task demands. *Journal of Cognitive Neuroscience*, 24, 749-759.
- Kiss, M., Jolicœur, P., Dell'Acqua, R., & Eimer, M. (2008a). Attentional capture by visual singletons is mediated by top-down task set: New evidence from the N2pc component. *Psychophysiology*, 45, 1013-1024.
- Kiss, M., Van Velzen, J., & Eimer, M. (2008b). The N2pc component and its links to attention shifts and spatially selective visual processing. *Psychophysiology*, 45, 240-249.
- Klimesch, W., Pfurtscheller, G., & Schimke, H. (1992). Pre-and post-stimulus processes in category judgement tasks as measured by event-related desynchronization (ERD). *Journal of Psychophysiology*, 6, 186-203.

- Lahav, A., Makovski, T., & Tsal, Y. (2012). White bear everywhere: Exploring the boundaries of the attentional white bear phenomenon. *Attention, Perception, & Psychophysics*, 74, 661-673.
- Lansing, R. W., Schwartz, E., & Lindsley, D. B. (1959). Reaction time and EEG activation under alerted and nonalerted conditions. *Journal of Experimental Psychology*, 58, 1-7.
- Leber, A. B., Gwinn, R. E., Hong, Y., & O'Toole, R. J. (2016). Implicitly learned suppression of irrelevant spatial locations. *Psychonomic Bulletin & Review*, 23, 1873-1881.
- Liu, T., Hospadaruk, L., Zhu, D. C., & Gardner, J. L. (2011). Feature-specific attentional priority signals in human cortex. *Journal of Neuroscience*, 31, 4484-4495.
- Loftus, G. R., & Masson, M. E. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review*, 1, 476-490.
- Lopez-Calderon, J., & Luck, S. J. (2014). ERPLAB: An open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience*, 8, 213.
- Luck, S. J., & Hillyard, S. A. (1994). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology*, 31, 291-308.
- Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology*, 77, 24-42.
- Maheux, M., & Jolicœur, P. (2017). Differential engagement of attention and visual working memory in the representation and evaluation of the number of relevant targets and their spatial relations: Evidence from the N2pc and SPCN. *Biological Psychology*, 125, 28-35.
- Mazza, V., Turatto, M., Umiltà, C., & Eimer, M. (2007). Attentional selection and identification of visual objects are reflected by distinct electrophysiological responses. *Experimental Brain Research*, 181, 531-536.

- Moher, J., & Egeth, H. E. (2012). The ignoring paradox: Cueing distractor features leads first to selection, then to inhibition of to-be-ignored items. *Attention, Perception, & Psychophysics*, 74(8), 1590-1605.
- Molenberghs, P., Mesulam, M. M., Peeters, R., & Vandenberghe, R. R. (2007). Remapping attentional priorities: differential contribution of superior parietal lobule and intraparietal sulcus. *Cerebral Cortex*, 17, 2703-2712.
- Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Frontiers in Cognitive Neuroscience*, 229, 342-345.
- Munneke, J., Van der Stigchel, S., & Theeuwes, J. (2008). Cueing the location of a distractor: An inhibitory mechanism of spatial attention? *Acta Psychologica*, 129, 101-107.
- Noonan, M. P., Adamian, N., Pike, A., Printzlau, F., Crittenden, B. M., & Stokes, M. G. (2016). Distinct mechanisms for distractor suppression and target facilitation. *Journal of Neuroscience*, 36, 1797-1807.
- Oostenveld, R., Fries, P., Maris, E., Schoffelen, JM (2011) FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. *Computational Intelligence and Neuroscience*, 2011, Article ID 156869.
- Pfurtscheller, G., & Aranibar, A. (1977). Event-related cortical desynchronization detected by power measurements of scalp EEG. *Electroencephalography and Clinical Neurophysiology*, 42, 817-826.
- Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, 32, 3-25.
- Posner, M. I., & Cohen, Y. (1984). Components of visual orienting. *Attention and Performance X: Control of Language Processes*, 32, 531-556.
- Posner, M. I., Nissen, M. J., & Ogden, W. C. (1978). Attended and unattended processing modes: The role of set for spatial location. In H. L. Pick, & E. Saltzman (Eds.), *Modes of perceiving and processing information* (pp. 137-157). Hillsdale, NJ: Lawrence Erlbaum Associates.

- Rihs, T. A., Michel, C. M., & Thut, G. (2007). Mechanisms of selective inhibition in visual spatial attention are indexed by α -band EEG synchronization. *European Journal of Neuroscience*, 25, 603-610.
- Ristic, J., & Kingstone, A. (2006). Attention to arrows: Pointing to a new direction. *The Quarterly Journal of Experimental Psychology*, 59, 1921-1930.
- Robinson, D. A., & Fuchs, A. F. (1969). Eye movements evoked by stimulation of frontal eye fields. *Journal of Neurophysiology*, 638-648.
- Ruff, C. C., & Driver, J. (2006). Attentional preparation for a lateralized visual distractor: Behavioral and fMRI evidence. *Journal of Cognitive Neuroscience*, 18, 522-538.
- Serences, J. T., Yantis, S., Culbertson, A., & Awh, E. (2004). Preparatory activity in visual cortex indexes distractor suppression during covert spatial orienting. *Journal of Neurophysiology*, 92, 3538-3545.
- Sylvester, C. M., Jack, A. I., Corbetta, M., & Shulman, G. L. (2008). Anticipatory suppression of nonattended locations in visual cortex marks target location and predicts perception. *Journal of Neuroscience*, 28, 6549-6556.
- Szczepanski, S. M., Pinsk, M. A., Douglas, M. M., Kastner, S., & Saalmann, Y. B. (2013). Functional and structural architecture of the human dorsal frontoparietal attention network. *Proceedings of the National Academy of Sciences*, 110, 15806-15811.
- Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). α -Band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *Journal of Neuroscience*, 26, 9494-9502.
- Tipples, J. (2002). Eye gaze is not unique: Automatic orienting in response to uninformative arrows. *Psychonomic Bulletin & Review*, 9, 314-318.
- Tsal, Y., & Makovski, T. (2006). The attentional white bear phenomenon: the mandatory allocation of attention to expected distractor locations. *Journal of Experimental Psychology: Human Perception and Performance*, 32, 351-363.

Van der Stigchel, S., & Theeuwes, J. (2006). Our eyes deviate away from a location where a distractor is expected to appear. *Experimental Brain Research*, 169, 338-349.

Worden, M. S., Foxe, J. J., Wang, N., & Simpson, G. V. (2000). Anticipatory biasing of visuospatial attention indexed by retinotopically specific-band electroencephalography increases over occipital cortex. *Journal of Neuroscience*, 20, 1-6.