DOCTOR OF PHILOSOPHY

The spatiotemporal distribution of inhibition in visual attention

Korolczuk, Inga

Award date:
2020

Awarding institution:
Bangor University

The spatiotemporal distribution of inhibition in visual attention

Inga Korolczuk

Thesis submitted to the School of Psychology, Bangor University, in partial fulfilment of the requirements for the degree of Doctor of Philosophy

Bangor, United Kingdom

January 2020

DECLARATION

Yr wyf drwy hyn yn datgan mai canlyniad fy ymchwil fy hun yw'r thesis hwn, ac eithrio lle nodir yn wahanol. Caiff ffynonellau eraill eu cydnabod gan droednodiadau yn rhoi cyfeiriadau eglur. Nid yw sylwedd y gwaith hwn wedi cael ei dderbyn o'r blaen ar gyfer unrhyw radd, ac nid yw'n cael ei gyflwyno ar yr un pryd mewn ymgeisiaeth am unrhyw radd oni bai ei fod, fel y cytunwyd gan y Brifysgol, am gymwysterau deuol cymeradwy.

I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

ACKNOWLEDGMENTS

First and foremost, I would like to thank my supervisors, Dr George Houghton and Prof. Charles Leek, for the opportunity to undertake this PhD but also for your enthusiasm throughout. You have encouraged me to think and work independently, which was a valuable experience from which I benefited both personally and scientifically.

I would like to thank Dr David Carey, my PhD committee Chair, for his support, good energy and insightful comments throughout my PhD. I am also grateful to Mark Roberts for his patience and guidance with the ERP analysis.

My appreciation goes to the wider Psychology Department for providing a collaborative, inspiring and stimulating research environment. Especially, I feel extremely happy to meet here wonderful friends who made this journey unforgettable. This work would not have been possible without your unconditional support, genuine care and brilliant sense of humour.

Last but not least, I would like to express my enormous gratitude to all people, inside and outside academia, who have inspired me to undertake this step. Your example motivates me to constantly grow both personally and professionally, and I feel exceptionally lucky to have met you in my life.

TABLE OF CONTENTS

LIST OF FIGURES AND TABLES

SUMMARY

Selective attention allows to effectively process large amounts of visual input by selecting relevant information and filtering out irrelevant one. Whereas most current models of visual attention emphasise the role of prioritisation of items that are essential for our current tasks and goals, an equally important facet of adaptive behaviour is the suppression of competing, yet irrelevant, stimuli. The goal of the following set of experiments is to better characterise the inhibitory mechanisms of selective visual attention by employing behavioural and event-related brain potentials methods. The first empirical chapter (Chapter II) presents a behavioural investigation examining how inhibition can be utilised to realign covert and overt attentional systems. The second empirical chapter (Chapter III), uses the behavioural approach to probe the sensitivity of inhibition to top-down processes such as statistical probabilities of the target location. Chapter IV, in turn, integrates behavioural and electrophysiological methods to elucidate the neural basis of modulatory effects of objects presence on the spatiotemporal distribution of inhibition. Finally, in Chapter V this approach is further used to examine the effects of the object complexity on inhibitory distribution. Overall, the findings indicate that inhibition acts to realign covert and overt attention by biasing reorienting towards the (central) fixation point and that it is relatively resistant to top-down modulations such as statistical priors of target location. Furthermore, stronger inhibitory signal to locations that are occupied by objects is implemented by a dynamic neural process encompassing perceptual and decision-related stages of target processing. However, object complexity appears not to affect inhibition. In sum, results from this thesis advocate the critical role of inhibition in visual attention and have important implications for cognitive fields, whenever selecting relevant items is required.

CHAPTER I

GENERAL INTRODUCTION

1.1. Overview

The human visual system must process vast amounts of sensory data. The attention system plays a fundamental role in the prioritisation and selective processing of this information. Selective attention critically relies on complementary mechanisms of facilitation and inhibition to regulate information processing. Facilitation may be defined as the enhancement of information processing, and inhibition as the suppression of information processing.

Electrophysiological and behavioural studies (Anton-Erxleben & Carrasco, 2013; Hopfinger, Luck, & Hillyard, 2004; Moran & Desimone, 1985; Niklaus, Nobre, & Van Ede, 2017; van Ede, Chekroud, Stokes, & Nobre, 2018) support the idea of competitive nature of perceptual systems. In this context, attention can be understood as the set of mechanism(s) that favours the most relevant targets (facilitation) and suppresses distractors (inhibition) by a gain control system. In the visual domain, these biases can be driven by spatial, object-based, feature-based and temporal attention (Chelazzi, Miller, Duncan, & Desimone, 1993; Coull & Nobre, 1998; Moran & Desimone, 1985; Posner & Cohen, 1984; Tipper, Driver, & Weaver, 1991). For instance, spatial attention can inhibit the selection of the stimulus by biasing certain populations of neurons in the receptive field corresponding to the unattended location (i.e., assigning negative weights to certain population of units).

Importantly, selection and inhibition of relevant items does not necessarily require

directing one's eyes towards it (overt attention), but instead, can happen independently of eye movements by focusing attention on the particular target (James, 1890). Such covert attention was first studied over a century ago by Herman von Helmholtz (1867) who demonstrated that attention can be voluntarily and selectively oriented toward a given location without making saccades. It is noteworthy that although covert and overt attentional systems have been studied separately, they are generally subserved by overlapping neural substrates (Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001; Corbetta et al., 1998; Nobre, Gitelman, Dias, & Mesulam, 2000; Nobre et al., 1997; Rizzolatti, Riggio, Dascola, & Umiltá, 1987).

The aim of this thesis is to elucidate the mechanisms underlying inhibitory spatial orienting. Our goal was to examine three important, and unresolved, theoretical issues: (1) the mechanisms by which covert and overt selection systems are brought into spatial alignment; (2) the extent to which the reorienting of covert shifts of attention is permeable to top-down processes; (3) whether spatial distributions of inhibition are modulated by objects in the visual field. We provide evidence of the critical role of inhibitory mechanisms in selective attention. These findings add to our understanding of covert orienting of attention but also provide the insight into more general basis of selective mechanisms by demonstrating the dual nature (excitatory/inhibitory) of cognitive functions.

The thesis is organised as follows: In the first chapter, a theoretical framework of selective attention is provided. Section 1.2.1. describes a general introduction to selective attention mechanisms, comprising history, approaches, and models of selective attention. Section 1.2.2. outlines the Theory of Visual Attention (TVA) by Desimone and Duncan (1995) which highlights the importance of facilitatory biases in enhancing neural systems in selecting the appropriate targets. Section 1.2.3. discusses the IOR effect in the context of covert attention

and Section 1.2.4. provides the evidence of separate inhibitory mechanisms of space- versus object-based attention. Section 1.2.5. outlines the alternative, but not mutually exclusive model of inhibitory mechanisms in selective attention (Houghton & Tipper, 1994) which recognises the dual nature of selection with a central mechanism of active inhibition of distractive information. Finally, Section 1.3. presents research questions of the current project and the overview of the thesis. Chapters 2-5 comprise two behavioural (Chapters 2 and 3) and two electrophysiological studies (Chapters 4 and 5) that investigate the critical role of the IOR using the adapted version of the Posner cueing paradigm (Posner, 1980). Finally, Chapter 6 provides a general discussion of the results and their possible implications.

1.2. Selective attention

1.2.1. What is visual selective attention?

We constantly receive large amounts of visual sensory input. In order to process it effectively, we filter out what is irrelevant and focus on information which is either salient or essential to our current goals or tasks. To achieve this in an enormously complex environment, we are able to selectively process information across the visual field. Selective attention can be thus understood as a set of mechanisms that allows for adaptive behaviour by prioritising and selecting relevant information and inhibiting irrelevant one.

One of the first empirical studies on selective attention were conducted by Herman von Helmholtz (1867). In his studies, Helmholtz (1967) demonstrated that object identification depends on the locus of attention which and can be directed voluntarily and selectively to a specific region in space independently of eye movements. He further argued that stimuli around fixation are not detected when attention was directed to some other location. In turn, James (1890) assumed that attention can be directed to both a peripheral stimulus as well as the current fixation point, which corresponds to the present distinction between covert and overt attentional systems, respectively (Corbetta, 1998; Smith & Schenk, 2012; Van Der Stigchel & Theeuwes, 2007). The attentional focal point has been investigated extensively since then, with the example of Titchener's work and his Law of Two levels (Titchener, 1908) which states that an observer can choose between two different attentional states according to the task at hand. If attention is focused on the particular location or object, it can be confined on some central point. In turn, if attention does not focus on a specific location, then it can spread across most of visual field.

In this context, attention can be conceptualised by a spotlight metaphor (Eriksen & Eriksen, 1974). This account assumes that information has to fall within the ray of the spotlight in order to be processed further. In the same vein, the zoom lens model further adapted this idea with the notion that we can flexibly adjust the size of the area of focus depending on the task demands. Whereas these two accounts argue for more discrete distribution of attentional resources, the concept of 'attentional field' by LaBerge and Brown (1989) proposes that attention can be described as a distribution of processing resources that changes across space and time in a more continuous manner. In the simplest case, the field gradient may be a monotonically decreasing function of distance from the current focal region. However, there are also other possibilities. For instance, the attentional field may take the form of a 'Mexican hat' distribution characterised by surrounding inhibition (Müller, Mollenhauer, Rösler, & Kleinschmidt, 2005). Alternatively, a distribution can be similar to a retinal photoreceptor density map which is spread in a log-linear fashion (Eriksen, Pan, & Botella, 1993; Harmening, Tuten, Roorda, & Sincich, 2014).

Although distinct in their specifications, these accounts share a common dimension - the kind of mechanism used in selection. They all postulate that selection is based on amplificatory top-down signals that modulate the gain of the system by facilitating the selection of targets. This notion is widely reflected in The Theory of Visual Attention (TVA). The next section will describe its assumptions in more detail.

1.2.2. The Theory of Visual Attention

In its first version, the Theory of Visual Attention (Desimone & Duncan, 1995) was a formal computational theory aimed at explaining the attentional effects in mind and behaviour. This theory is based on a principle called "biased competition". The model postulates that all possible visual categorisations, which ascribe features to objects in the visual field, compete against one another to be embedded in visual short-term memory (VSTM). However, this process is biased, as the competition may become less "fair" due to perceptual biases that may be present, and because certain objects may have a higher probability than others of being consciously perceived.

TVA holds that visual categorization comprises both recognition *and* selection of the objects that are present in the visual field. Therefore, the processes of selection and recognition, which are occurring simultaneously, can be understood of as two different facets of the same mechanism. Once completed, the categorised object is encoded into the VSTM which can store only a limited number of objects. Visual information stored in VSTM is available for other processes even when the sensory stimulation that triggered it is no longer present. That mechanism is in line with Hebb's (1949) account of short-term memory, conceptualised as a sustained activity of neural representation of the selected information. VSTM can be understood as a continuous circuit of feedback that lasts beyond the initial sensory stimuli. In our daily functioning when complex scenes are continuously present, the objects or categorisations "race" with one another continuously, with the assumption that one object can fall into more than one categorisation and therefore, boost its chances in the "race". The rate of the race is determined by three components: (1) the strength of the sensory evidence that a given object belongs to a given category, (2) a perceptual decision bias associated with this category and (3) a relative attention weight of the object. The weight is further conceptualised

as the importance of attending to a particular object that belongs to a given category (i.e., *pertinence* values). Targets can be thus tagged as to be reported or responded to, while distractors are typically defined as elements to ignore. Every target has approximately the same attention weight as any other target, just as every distractor also has the same attentional weight as any other distractor. When this is the case, the efficiency of top-down selection is defined using the ratio between the attentional weight of a distractor and a target.

Importantly, the rate and weight terms refer to two different mechanisms of selection – filtering (selection of objects) and pigeonholing (selection of categories), respectively. Filtering is represented by pertinence values and attentional weights. The weight equation asserts that if a given feature has a high pertinence, then objects possessing that feature gets high attentional weights. Processing objects with a prioritized feature is fast and therefore, objects that possess this feature are more likely to "win the race" and be coded into VSTM. While pertinence values determine which objects are selected (*filtering*), perceptual biases determine how the objects are categorised through the *pigeonholing* mechanism. In other words, the bias values of the prioritised categories are set to be high.

TVA has been further developed to enhance the original model such that it can also explain attentional selection at the neural level. The Neural Theory of Visual Attention and Short-Term Memory (NTVA) (Bundesen, Habekost, & Kyllingsbæk, 2005, 2011) provides a neural interpretation of how rate and weight can be represented at the single-cell level. NTVA proposes that the typical neuron in the visual system is "specialised" to represent a single feature. Neural filtering is assumed here to affect selection by altering the number of neurons representing a given object, whereas the mechanisms of neural pigeonholing by modulating the firing rate of feature-specific neurons. Importantly, the model predicts that an object can

gain dominance in different systems at the same time (i.e., competition between systems is integrated *and* visual processing is occurring in parallel).

To summarize, TVA emphasises that (1) brain systems are competitive in nature (i.e., a gain of representation for a particular visual object will be at the expense of other objects' representations); (2) competition is controlled by top-down (e.g., assigning higher weights to prioritised targets) and bottom-up mechanisms (e.g., principles of perceptual organization); and (3) competition is unified across systems (i.e., the gain of the given object is similar in different systems).

The Theory of Visual Attention provides a compelling model of visual processing by proposing facilitation as the main mechanism of selection and assuming that recognition and selection processes are occurring simultaneously. Notwithstanding the empirical validity of the model, it appears to neglect the inhibitory facet of the selection processes. Indeed, there is extensive evidence that activation processes are accompanied by inhibitory mechanisms (Davranche et al., 2007; Klein, Petitjean, Olivier, & Duque, 2014; Los, 2013; Quoilin & Derosiere, 2015; Tandonnet, Garry, & Summers, 2011). For example, Burle and colleagues (2004) have demonstrated that inhibition is consistently found in choice RT tasks, and selection and inhibition mechanisms are even assumed to reflect the same mechanism (Mostofsky & Simmonds, 2008). Furthermore, studies on negative priming have shown that inhibition is applied to stimuli that have previously been ignored (D'Angelo, Thomson, Tipper, & Milliken, 2016; Tipper, 1985; Tipper & Driver, 1987). In his seminal experiment, Tipper (1985) found that participants named target objects more slowly when they had previously ignored them. In his study, participants were presented with two superimposed objects (the prime display). Based on its colour, one of the objects was to be selected, whereas the other to be ignored.

After the interval, again two superimposed were presented and participants' task was to select the target based on its colour (the probe display). Importantly, the target could be the same as the distractor needed to be ignored in the prime display (ignored repetition). The results revealed that latencies in naming the object that previously had to be ignored were slower, indicating inhibitory mechanisms during the selection process. These findings have been replicated in numerous experiments with different settings (Beech, Agar, & Baylis, 1989; Fuentes & Tudela, 1992; Gernsbacher & Faust, 1991; Tipper & Driver, 1987).

1.2.3. Inhibition of return in the covert attention

In the field of selective attention, the empirical evidence for suppression is evident in the spatial cueing paradigm by the effect known as the inhibition of return (IOR). This section will describe the origins of the spatial cueing paradigm and the facilitatory and inhibitory (IOR) effects commonly found in its results.

The seminal studies on classical conditioning by Pavlov (Pavlov, 1927), raised interest in the orienting response toward a stimulus that captures attention. This reaction was called 'investigating' and referred to the body, head and/or eye movements. Since then, the term 'orienting' was used to distinguish between shifts of attention that are accompanied by body position movements and shifts of attention that occur independently of changes in the body position. Following this distinction, overt orienting includes attentional shifts occurring altogether with body movements. Covert orienting, in turn, refers to attentional shifts in the absence of body movements (Posner, 1980; Wurtz, Goldberg, & Robinson, 1982). The present investigation is concerned with the nature of distribution of the covert attention.

Covert orienting requires shifting attention to a particular location within space. One of

the first studies that incorporated both cueing to a location and attention aimed to measure the capacity of short-term visual memory (Sperling, 1960). Participants were exposed for a short time to boards containing three letter rows. After the 50 ms presentation, the letters disappeared, and a blank display appeared for a window ranging 50 ms - 100 ms. Then, participants were given an auditory cue indicating the letter row to report (a high-pitched, medium-pitched and low-pitched tone indicated, high, medium and low row, respectively). The results showed that the cue improved the number of words reported by directing attention to a particular row. These results were replicated in several experiments, including the ones from the visual domain (Averbach & Coriell, 1961).

The paradigm developed by Posner and colleagues (Posner, 1980) is one of the milestones in the studies on covert location. In their spatial cueing paradigm, participants are instructed to stay fixated on a central point throughout each trial. They make simple key responses to targets in a detection or discrimination task. Before the target, a cue appears either on the same side as a following target (e.g. cue left, target left) or on the opposite side (e.g. cue left, target right). Trials when the target appears on the same side as the preceding cue are called valid (or cued), whereas trials when the target appears on the opposite side as the preceding cue are called invalid (or uncued).

There are many variants of Posner's cueing paradigm. One distinction relates to the voluntary shifts of attention versus involuntary attention capture. By using symbolic cues (predictive/endogenous cues), which are usually centrally presented arrows, attention can be directed in a top-down manner to a specific location. These cues were assumed to initiate endogenous (voluntary/goal-driven/intrinsic) attention. In contrast, attention can be directed in a more bottom-up manner by using peripheral cues (non-predictive/exogenous cues), like

thickening of placeholders outlines or just stimuli presented abruptly in the same location as the expected target location. These cues are considered to initiate exogenous (involuntarily/ stimulus-drive/extrinsic) attention. Although this distinction has been assumed for a long time, it appears that arrows are, in fact, similar to exogenous peripheral cues (Hommel, Pratt, Colzato, & Godijn, 2001; Ristic, Kelland Friesen, & Kingstone, 2002; Tipples, 2002). More specifically they orient attention even when non-predictive. Yet, the debate on whether they evoke inhibitory processes (see below) remains open (Bayliss, Pellegrino, & Tipper, 2005). The present thesis is concerned with the exogenous attention elicited by an abrupt stimuli presentation.

The empirical data have shown that a target appearing at the same spatial location as a preceding peripheral non-predictive cue, is detected *faster* and more accurately than when a target is preceded by a cue shown at a different location (Muller & Findlay, 1988; Nakayama & Mackeben, 1989; Eimer, 2000; Martínez et al., 2001; Posner, Snyder, & Davidson, 1980; Soto & Blanco, 2004). This spatial cueing *benefit* in target detection tasks is typically found with cue-target stimulus onset asynchronies (SOAs) approximately about 100 ms (He, Humphreys, Fan, Chen, & Han, 2008; Posner, 2012; Posner & Cohen, 1984; Posner et al., 1980; Taylor, Chan, Bennett, & Pratt, 2015). It has been assumed to reflect spatial facilitation of processing a previously cued location. In contrast, at longer SOAs (> 300 ms), target detection is slower at cued than at uncued locations – an effect widely known as inhibition of return or IOR (Abrams & Dobkin, 1994; Bennett & Pratt, 2001; Posner & Cohen, 1984; Posner et al., 1980; Pratt, Spalek, & Bradshaw, 1999). This time *cost* likely reflects inhibition of processing at the cued location. In this manner, the IOR can be perceived as the mechanism of selection that enhances the efficiency of visual search by suppressing recently attended target locations.

Yet, in daily life, targets can equally frequently appear in the location in the proximity to the one we are attending to or have already attended. Consequently, a more comprehensive manner of conceptualising attention was proposed by LaBerge and Brown (1989). They described a spatiotemporal distribution of resources across the whole visual field as the "attentional field". According to this account, attention can disperse around the cued locations with the strongest effect on the previously attended locations and somewhat weaker in magnitude effects in the nearby locations (Bennett & Pratt, 2001; Pratt, Spalek, & Bradshaw, 1999; Taylor, Chan, Bennett, & Pratt, 2015; Wascher & Tipper, 2004). Nevertheless, the exact functions underlying this effect remain uncertain. Wascher and Tipper (2004) have proposed that such a pattern of results may stem either from the spatial gradient around the cued locations or two distinct inhibitory components – one operating over the cued location and the second one affecting the cued visual field. More studies are required to disentangle between these two possibilities.

1.2.4. Space- versus object-based IOR

While the vast number of studies have focused on location-based IOR (Bennett & Pratt, 2001; Collie, Maruff, Yucel, Danckert, & Currie, 2000; Lupiáñez, Milán, Tornay, Madrid, & Tudela, 1997; Jay Pratt & Fischer, 2002; Prime, Visser, & Ward, 2006; Samuel & Kat, 2003), there is a strong evidence that attention operates over object representations (Egly, Driver, & Rafal, 1994; Houghton & Tipper, 1994; Jordan & Tipper, 1998; Leek, Reppa, & Tipper, 2003; Macquistan & Macquistan, 1997; Ro & Rafal, 1999; Tipper et al., 1991; Tipper, Jordan, & Weaver, 1999; Tipper et al., 1997; Tipper, Weaver, Jerreat, & Burak, 1994). Indeed, different accounts of space- and feature-based attention claim that attention can be directed to specific

locations and/or features to enable them to be processed in more detail. However, in real-world settings, multiple objects with a variety of features are often superimposed in space, which necessitates a remarkably efficient selection. Therefore, an adaptive functioning in complex world must require a more parsimonious mechanism. One account would be that detailed object representations, which comprise subordinate dimensions such as features and location, are necessary to guide adaptive behaviour (Houghton & Tipper, 1994). Generating such object representations may not critically depend on attention, but rather be directly linked to the appropriate action by selection and suppression mechanisms (Houghton & Tipper, 1994).

Behavioural and neural evidence support the existence of object-based attention. In one of the first studies that investigated the object representations, Neisser and Becklen (1975) asked participants to focus on two superimposed videos. If they focused on one video only, unusual events happening in the other were not noticed, even though the objects in two videos had the same spatial location. These results suggested the existence of an attentional mechanism that focuses specifically on object representations. In turn, Duncan (1984), asked participants to report either one dimension of the superimposed object (e.g., colour), two dimensions of one superimposed object (e.g., colour and size), or one dimension from two separate superimposed objects (e.g., the colour of one object and the location of another one). Interestingly, participants' performance was impaired when asked to report one feature from each of two objects even though stimuli were spatially aligned. These results were further replicated using different types of stimuli (Baylis & Driver, 1993; Sohn, Papathomas, Blaser, & Vidnyánszky, 2004), and clearly suggest that spatial-based mechanisms do not comprehensively explain the findings.

In the classic study of Egly, Driver and Rafal (1994), a target located in a cued object

was detected faster and more accurately than a target located the same distance away from the cue, but in an uncued object, thereby suggesting the deployment of a dedicated, object-based system. Similarly, studies that used an adapted version this task have found object-based IOR effects for longer SOAs (Jordan & Tipper, 1998; Leek et al., 2003; Possin, Filoteo, Song, & Salmon, 2009). However, as an object can be described by its location and shape, one could argue that the target is detected based on spatially coded representations rather than the object's representation. Vecera and Farah (1994), for instance, found that the effect of "objectness" can be diminished or can even disappear when subjects are instructed to ignore objects. Based on their results, the term *grouped location* was proposed as a possible mechanism for attentional selection. It assumes that attention operates over spatial representations and more specifically, on the object's contours within a particular location. However, the task properties used in their study required primarily the localisation, rather that identification. Consequently, it might be that object-based effects can be found when identification is required, but not under different task demands (Vecera & Farah, 1994). Nevertheless, although space-based accounts offer a parsimonious explanation of mechanisms of visual selection, they cannot account for empirical findings demonstrated in object-based literature such as additive space-based and object-based effects (Jordan & Tipper, 1998; Leek et al., 2003; Possin et al., 2009; Tipper et al., 1999, 1994).

One of the most compelling pieces of evidence for object-based attention was provided in the studies of Tipper and colleagues. They used carefully designed tasks to separate an object's identity from its location (Tipper, Driver, & Weaver, 1991). For the first time, dynamic, instead of static, displays were used. In their study, three squares were presented, one located at the centre and two located peripherally, equidistantly from fixation. The peripheral squares' positions were changed such that they appeared to move in a clockwise fashion. One of the squares was cued (i.e., flickered) at the beginning of the trial. Then, attention was

reoriented to a central square. Finally, a target would appear on two-thirds of the trials after one of two equiprobable SOAs (430 ms or 695 ms). The results showed that RTs to previously cued square were slower; hence demonstrating that IOR to previously cued objects moved with the object to its new location.

Support for a separate space-based and object-based IOR comes also from neuropsychological studies on Parkinson's disease (PD) patients. It has been demonstrated that PD patients exhibit impairments in attentional inhibitory processes (Filoteo, Maddox, Ing, & Song, 2007; Marí-Beffa, Hayes, Machado, & Hindle, 2005). Possin, Filoteo, Song and Salmon (2009) examined spatial and object-based IOR effect in PD patients and a control group. They have demonstrated that although inhibition to already scanned environmental locations was impaired in PD patients confirming previous reports (Filoteo et al., 1997; Gurvich, Georgiou-Karistianis, Fitzgerald, Millist, & White, 2007), their object-based inhibition was intact. Therefore, these results provide another compelling evidence of distinct space-based and object-based inhibitory representations.

This section presented the origins of spatial cueing paradigm as well as experimental paradigms that have investigated object-based attentional mechanisms. Importantly, though, the evidence presented here clearly showed that attention appears to recruit distinct inhibitory mechanisms demonstrated as the IOR effect in both space-based and object-based attentional systems. The next section will describe the account that identifies inhibitory mechanisms as central to selective attention.

1.2.5. A model of inhibitory mechanisms in selective attention

Whereas the TVA assumes that adaptive behaviour is achieved through excitatory biases that boost the gain to prioritised targets (Desimone & Duncan, 1995), a model of inhibitory mechanisms in selective attention proposes two mechanisms of selection: amplification and inhibition. Consequently, the dual nature of attention would allow for efficient processing of the visual field by assigning high gain to targets and low gain to distractors.

While other theoretical accounts propose that attention is necessary for perceptual processes such as object categorization (Bundesen, 1990; Grill-Spector, Kourtzi, & Kanwisher, 2001; Oliver, 2017), this model offers an alternative approach. Here, attention is proposed to operate over already processed visual representations and even after the semantic analysis stage, as demonstrated convincingly by the negative priming task in which inhibition was applied also to category-related targets (Tipper, 1985). In other words, the main role of attention is inhibiting the distractors at later stages of processing rather than gating the information such that it can be further processed by higher-order systems. Selective attention may thus critically mediate the interaction between perception and action by top-down inhibitory signals in a more global manner. Indeed, this holistic approach is the key characteristic of the model of inhibitory mechanisms in selective attention (Houghton & Tipper, 1994) and implies that the central role of selection is to balance the complex environmental demands in order to guide adaptive behaviour.

Notably, the model does not predict that attention is crucially involved in perceptual processes, which are assumed to occur in parallel (Houghton & Tipper, 1994). Instead, it argues that object- or action-centred representations are facilitated by schema-based representations (Treisman, 1986) such that attention is not necessary for their perceptual analysis.

Consequently, the model assumes that visual processing must operate over object representations rather than separate features that require to be combined for each object separately. Critically, the model proposes that attention aids in selecting the appropriate response to prioritised targets by enhancing their representations and inhibiting the representations of competing objects. Operating in unison, facilitation and suppression can more efficiently modulate selection by boosting the gain difference between a target and a distractor. With the maximum and minimum range amplitudes in the processing system, disentangling two high-level (or low-level) signals would be simply impossible without suppressing (or enhancing) one of them to achieve a strong enough signal to noise ratio (Houghton & Tipper, 1994). Apart from discussed previously behavioural evidence, another account of inhibitory mechanism in selection comes from neurophysiological studies which reported suppressed response of the cell in the receptive field of ignored stimulus in relative to attended stimulus (Moran & Desimone, 1985).

Similarly to TVA, the model also has its neuropsychological interpretation. It specifically proposed that parietal and occipital cortices are involved in the coding of visual information with the inclusion of inferior temporal lobes at the highest level. The key gain-control system is suggested to be implemented within local cortex as the inherent quality of cells or, alternatively, by the cortical-thalamus pathway. Top-down signals are proposed to originate from prefrontal cortex which is consistently found to engage in goal-directed behaviour (Brass & Haggard, 2008; Duque, Labruna, Verset, Olivier, & Ivry, 2012; Kam, Solbakk, Endestad, Meling, & Knight, 2018; Kolling & O'Reilly, 2018). Binding the affordances with a particular object might, in turn, be executed in the premotor cortex and supplementary motor area.

In summary, the model of inhibitory mechanisms in selective attention accommodates empirical findings of suppressed processing such as negative priming and IOR. Whereas it builds upon the facilitatory accounts of enhanced target processing, it also emphasises the critical role of inhibitory signals which act to suppress distractors.

1.3. Thesis outline

In the current Chapter (Chapter I), I provided a summary of the theoretical and methodological framework of selective visual attention. I put an emphasis on the adaptive function of inhibitory signals in processing of the attention-guided information. The goal of the following chapters is to empirically test outstanding questions regarding the nature of inhibition of return (IOR) in covert exogenous cueing tasks using behavioural (Chapters II and III) and ERP (Chapters IV and V) methods. Finally, I will discuss the overall findings (Chapter VI).

In our ERP experiments, we complemented standard event-related potential analyses by additionally performing mass univariate analyses (Groppe, Urbach, & Kutas, 2011; Guthrie & Buchwald, 1991; Murray, Brunet, & Michel, 2008). Instead of using selected clusters of electrodes, MUA contrast two conditions using all electrodes for each time point. Therefore, by allowing to identify the time course of differences across conditions at each single electrode site, MUA provide a complementary statistical measure of event-related activity.

In the current project, we formulated and aimed to answer the following research questions:

(1) How inhibitory mechanisms are utilised to realign covert and overt attention?

(2) Can the spatiotemporal distribution of inhibitory mechanisms in covert attention be

modulated by statistical priors?

(3) What is the neural basis of the interaction between space- and object-based inhibition?

Chapter II investigates how inhibitory mechanisms are used to control covert and overt attentional systems. In three main (Experiments 1-3) and one control (Experiment 4) behavioural studies, the functional role of the location of a re-orienting event in realigning covert and overt attention is elucidated.

Chapter III presents the behavioural investigation of the mechanisms of spatiotemporal distribution of inhibition. More specifically, it tests in the context of spatial cueing paradigm, whether the statistical knowledge of possible target locations modulates the bottom-up orienting across space and time in the context of the spatial cueing paradigm.

Chapter IV provides an ERP investigation into the neural basis of the interaction between space- and object-based attentional systems using static displays. This is one of few studies employing a spatial cueing paradigm to evaluate how inhibition spreads across a visual field to affect the processing of adjacent locations. We performed a standard waveform analysis as well as mass univariate analysis to be able to confidently evaluate the time course and functional differences across spatial and object experimental manipulations.

Chapter V builds-on experimental findings from Chapter IV to further explore the electrophysiological differences across space and object inhibitory mechanisms by the means of standard waveform analysis and a mass univariate analysis. In this experiment, objects are varied as a function of their complexity to test whether the objects' shape may modulate the

strength of inhibition in a given location or object, as well as within a visual field.

The final chapter (**Chapter VI**) provides the overall discussion of the findings, presents how the current studies add to the existing knowledge, and offers possible new directions for future investigations.

CHAPTER II

Central versus peripheral reorienting cues elicit stronger IOR: evidence that both temporal and spatial factors determine the realignment of covert and overt attention in human vision

2.1. Introduction

One fundamental aspect of the human attention system is the distinction between the overt and covert visual orienting - that is, spatiotemporal shifts in the selective processing of sensory input that are either associated with or independent of, saccadic eye movements. A large body of previous research has shown that overt and covert attention can be decoupled by exogenous (i.e., peripheral) abrupt stimulus onsets (e.g., Klein, 2000; Posner & Cohen, 1984; Posner, Rafal, Choate, & Vaughan, 1985). This has been widely studied using the spatial cueing paradigm (e.g., Posner & Cohen, 1984; Posner, Snyder, & Davidson, 1980). Typically, in the standard variant of this task, a non-predictive (alerting) cue is presented at one of two peripheral locations whilst the observer maintains central fixation. The alerting cue decouples overt and covert attention. After a variable interval, a target appears either at the same (cued) or at the opposite (uncued), location as the preceding alerting cue. At relatively short cue-target intervals (e.g., < 300 ms) RTs for target onset detection are faster at cued than at uncued locations. At longer intervals, this pattern can reverse such that RTs for target onset detection are slower at cued than at uncued locations. This latter effect is often referred to as inhibition of return or

IOR (e.g., Klein, 2000; Posner & Cohen, 1984; Posner et al., 1985). These contrast effects have been widely assumed to reflect facilitatory and inhibitory mechanisms subserving visual selection (Houghton & Tipper, 1994; Klein, 2000; Lupiáñez, Milliken, Solano, Weaver, & Tipper, 2001; Posner et al., 1985; Posner et al., 1980).

Notably, faster target detection at relatively short cue-target lags is assumed to reflect the enhancement (i.e., facilitation) of sensory processing at the cued location. In contrast, slower target detection at relatively long cue-target lags reflects the suppression (i.e., inhibition) of sensory processing at the cued location – one function of which is to prevent repeated sampling of input at previously cued (and covertly attended) locations – hence, IOR (Posner & Cohen, 1984; Tipper, Weaver, Jerreat, & Burak, 1994). In this context, there is a fundamental assumption underlying accounts of IOR that, following the initial orienting cue, covert and overt attention are centrally realigned (and subsequently inhibited from returning to the initial peripheral cue location). This realignment is typically elicited experimentally, in the spatial cueing paradigm, by a central (re)orienting cue shown prior to a variable target onset (e.g., Klein, 2000; List & Robertson, 2008; Posner & Cohen, 1984; Posner et al., 1980; Pratt & Fischer, 2002; Prime, Visser, & Ward, 2006; Reppa, Schmidt, & Leek, 2012, although see Lupiáñez, 2010). This reorienting process itself is assumed to play a fundamental role in the realignment of overt and covert attention (e.g., Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001; Corbetta, 1998; Rizzolatti, Riggio, Dascola, & Umiltá, 1987; Smith & Schenk, 2012; Van Der Stigchel & Theeuwes, 2007). However, one fundamental, and unresolved, issue concerns the factors that mediate the process of spatial (attentional) realignment.

As noted above, it has been well-documented that facilitatory or inhibitory cueing effects in exogenous spatial orienting are time-dependent. It might be assumed that once overt

and covert attention are decoupled by an abrupt peripheral cue onset, they are involuntarily realigned to a centrally fixated location over time (that is, time since cue onset). This hypothesis is consistent with other data showing that the presentation of a central reorienting cue is not required for eliciting IOR (Martín-Arévalo, Kingstone, & Lupiáñez, 2013; Prime et al., 2006). But time may not be the only determining factor. We might also hypothesise that the *direction* of reorienting (i.e., typically from an initial peripheral cue location to a central fixation position) also plays an important role in this process. We know of no previous empirical studies on spatial orienting that speaks to this possibility.

We tested this hypothesis in the context of IOR across three experiments using the spatial cueing paradigm with cue-targets lags (SOA) of 150, 650 and 1,150 ms. The aim of Experiment 1 was to establish a 'baseline' measure of inhibitory cueing in the absence of a secondary reorienting cue. Based on previous reports (Martín-Arévalo et al., 2013; Prime et al., 2006), we expected to find IOR at the SOA of 650 and 1,150 ms. In Experiments 2 and 3, a peripheral or central reorienting cue was presented during the trial stimulus sequence in addition to the initial (alerting) cue while we manipulated target onset lag relative to the most recently presented cue. If the magnitude of IOR is modulated independently by the spatial location of the reorienting cue, we would expect to observe stronger inhibition (i.e., more negative cueing effects) after a central versus peripheral reorienting cue. Finally, we conducted a control study (Experiment 4) to reliably distinguish attentional effects from effects of perceptual processing. More specifically, we contrasted response times when detecting peripheral and central targets that varied in saturation levels (in steps of 20%). We assumed that any difference between central and peripheral reorienting of attention in Experiments 2 and 3 can be reliable provided that the results of Experiment 4 prove no significant differences in detection of peripheral and central targets.

2.2. Experiment 1

In Experiment 1, SOA was varied within a block of trials at three levels (150, 650 and 1,150 ms). The target could appear at the same location as the preceding alerting cue (cued trials) or at the opposite location (uncued trials). No reorienting cue between the alerting cue and the target was used.

2.2.1. Methods

2.2.1.1. Participants

Twenty (15 women, 5 men, M_{age} = 20.4 years, age range 18-28) participants were recruited from the Psychology Department at Bangor University and took part in the study for course credit. The study was conducted under the School of Psychology Ethics Protocol. All participants had normal or corrected-to-normal visual acuity. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971).

2.2.1.2. Apparatus

Data acquisition was conducted using a PC and 1024 x 768 Mitsubishi Diamond Pro 2060u (120 Hz, 40cm) monitor. A standard QWERTY PC keyboard was used for the responses. An SR 1000 eye tracker (1000 Hz) was used to monitor eye movements. The experiments were programmed in Experiment Builder (SR Research Ltd.).

2.2.1.3. Stimuli

The fixation point was a red cross (RGB: 255, 0, 0) of 13 x 13 pixels subtending 0.5 degrees of visual angle. The vertical and horizontal bars in the cross were each 2 pixels wide. The fixation cross was situated in the centre of the display. The background was grey (RGB: 127,127,127). Alerting cues comprised a white square of 13 x 13 pixels (RGB 255, 255, 255) subtending 0.5 degrees of visual angle. Alerting cues were positioned along the horizontal axis 5 degrees left or right from the central fixation. Targets comprised a 13 x 13-pixel black square (RGB: 0, 0, 0) displayed at the same locations as the first cue. Viewing distance was fixed at 57cm using a chinrest.

2.2.1.4. Design

Experiment 1 comprised two repeated measures factors: validity (cued, uncued); SOA (150 ms, 650 ms, 1150 ms). For each SOA, there were 60 cued, 60 uncued and 12 no target (10%) trials. There were 18 practice trials followed by two blocks each containing 198 trials. Trial presentation order was fully randomised within subjects.

2.2.1.5. Procedure

Participants first completed eye tracker calibration. They then completed the spatial cueing task. They were told to fixate centrally throughout each trial. Fixation was monitored on each trial with an eye-tracker. Trials were automatically terminated if the observer's fixation drifted outside of a non-visible circular region-of-interest (diameter equalled 2 degrees of visual angle) around the fixation point at any time prior to target onset. Each trial was initiated via the spacebar after which the central blue fixation cross turned red. The fixation cross remained in the centre for 1,000 ms. Next, an alerting cue was presented randomly at one of the two positions (right/left) for 50 ms. Then, after a variable period of 150, 650 or 1,150 ms

(SOA), a target appeared at one of two possible locations (right/left) until response or 1,000 ms had elapsed. There was a response deadline of 3,000 ms. Trials where the target appeared on the same side as a cue were defined as cued. Trials where a target appeared on the opposite side that the cue were defined as uncued. There was a jittered inter-trial interval between 400-1,000 ms. The task instructions were to detect the target as quickly as possible by pressing the spacebar whilst minimising errors. Participants were told to maintain central fixation, and where told that trials would be aborted if an eye movement was detection during the trial sequence.

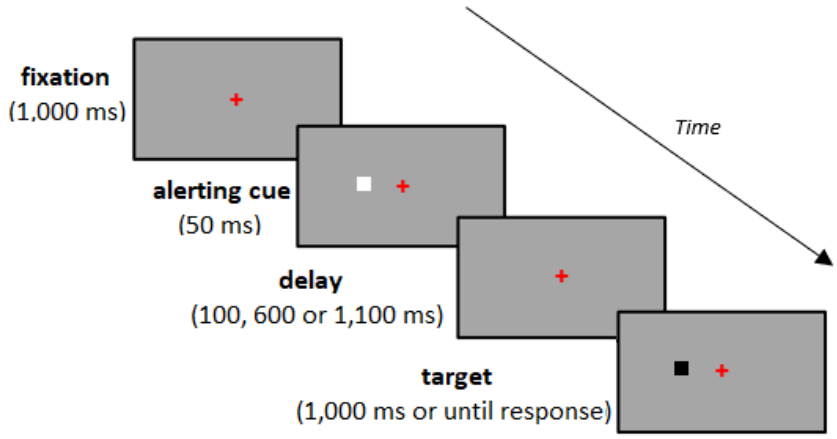


Figure 1. The trial timeline in Experiment 1. On every trial, the fixation appeared at the centre location for 1,000 ms followed by an alerting cue appearing at one of the two positions (right/left) for 50 ms, after 150, 650 or 1,150 ms after the alerting cue onset. Trials when a target appeared in the same side as a cue (i.e., right) were considered cued. Trials when a target appeared on the opposite side that a cue (i.e., cue right/target left) were considered uncued. The participants' task was to detect the target as quickly as possible while minimising errors. The illustration above is an example of the cued trial.

2.2.1.6. Data Analysis

Errors (false positives: responses to no-target trials), omissions and trials with RTs less than 100 ms and greater than 1,000 ms were excluded from the analysis. RTs were calculated separately for cued and uncued conditions for each SOA. Effects of cueing (mean uncued RT – mean cued RT), were analysed using two-way repeated measures ANOVA involving validity (cued, uncued) and SOA (150ms, 650ms and 1,150ms). Bonferroni adjustments were made for pairwise comparisons. Effect sizes were estimated using partial eta-squared (η_p^2). Significance was determined relative to an a priori alpha criterion of $p < .05$, two-tailed).

2.2.2. Results

Errors were very infrequent (0.2 %), similarly omissions (0.2 %). Trials with RTs faster than 100 ms and slower than 1,000 ms equalled to 0.4%. Table 1 shows RTs in all conditions.

Table 1

Mean RTs and cueing effects (and standard errors) in ms for two cueing conditions (cued, uncued) at each SOA (150ms, 650ms and 1,150 ms) in Experiment 1

	SOA 150	SOA 650	SOA 1,150
Cued	395 (54)	397 (50)	377 (48)
Uncued	384 (60)	364 (58)	359 (58)

There were significant main effects of validity, F (1, 19) = 27.46, $p < .001$, $\eta_p^2 = .59$, and SOA, F (2, 19) = 14.23, $p < .001$, $\eta_p^2 = .43$. Mean RTs were slower for cued versus uncued trials. Also, mean RTs were slower at SOA 150 ms ($p < .001$) and SOA 650 ms ($p = .001$) than SOA 1,150 ms. There was also a significant Validity × SOA interaction, F (2, 19) = 10.82, $p < .001$, $\eta_p^2 = .36$. In the cued condition, participants responded significantly faster to targets after 1,150 SOA than 150 ms SOA ($p = .017$) and SOA 650 ms ($p = .001$). There was no difference between SOA 150 ms and SOA 650 ms ($p = 1.00$). In the uncued condition, RTs were slower after SOA 150 ms than SOA 650 ms ($p = .001$) and SOA 1,150 ms ($p = .001$). Again, no significant difference was found between SOA 650 ms and SOA 1,150 ms ($p = .22$).

We used a t-test to compare cued and uncued trials for each of three SOAs. The IOR was found for SOA 150 ms ($p = .040$), SOA 650 ms ($p < .001$) and SOA 1,150 ms ($p < .001$). The magnitude of inhibition of return was computed by subtracting performance on uncued

from cued trials (Fig. 2). The analysis showed stronger inhibition to SOA 650 ms than to SOA 150 ms (p = .002) and to SOA 650 ms than to SOA 1,150 ms (p = .001). No difference in the IOR strength was observed between SOA 150 ms and SOA 1,150 ms (p = .174)

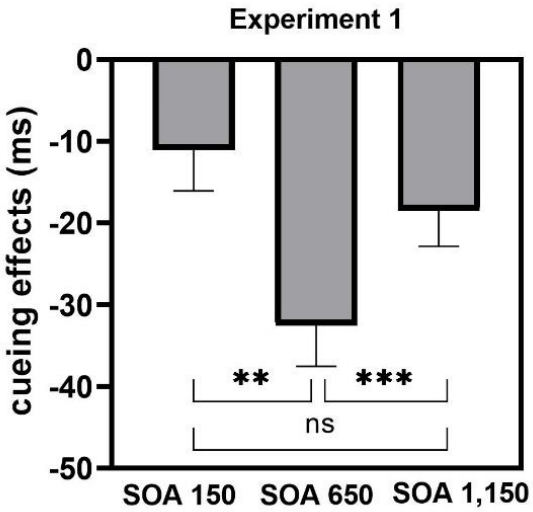


Figure 2. Mean cueing effects (uncued – cued RT) and standard error for each SOA. The more negative the value, the stronger the inhibition.

2.2.3. Discussion

The results showed inhibitory cueing effects at all three SOA. In other words, the cueing effects values were negative indicating slower RT at cued as compared to uncued locations following all three cue-target lags with the effect sizes comparable to previous reports of peripheral cueing in detection tasks (see Chica, Martín-Arévalo, Botta, & Lupiáñez, 2014, for a detailed comparison of spatial cueing experiments). Inhibition appeared to build-up incrementally with the strongest inhibitory signal at SOA of 650 ms, but no further increase at SOA of 1,150 ms. Our results Overall, the obtained robust effects of IOR without a reorienting cue further reinforce the previous hypotheses that IOR can be elicited by a mere manipulation of temporal interval between a cue and a target, suggesting that redirecting attention back to the centre is a general mechanism (see Introduction).

2.3. Experiment 2

Although the pattern of results of Experiment 1 demonstrated that IOR can be successfully measured in the paradigm that does not include the reorienting event between the alerting cue and the target, a critical point remains to what extent the reorienting cue affects the distribution of inhibition as measured in the cueing paradigm. The reorienting cue is hypothesised to direct attention away from the initial event so that the inhibition can occur at the previously attended location. However, our understanding of mechanisms underlying the modulatory effects of the reorienting cue is still incomplete. One of them is the role of the reorienting cue's location when disengaging attention from the initial place. To address this problem, the current experiment aimed to distinguish between the effects of the reorienting cue location on IOR, by presenting the reorienting cue either centrally or peripherally (while maintaining the same distance from the subsequent target).

2.4.1. Methods

The same methods were used as in the Experiment 1 unless specified otherwise.

Twenty-three (12 women, 11 men, M_{age} = 20.5 years, age range 19-29) participants took part in the study. There was a reorienting cue presented between the alerting cue and the target. The reorienting cue was a square of 13 x 13 pixels red (RGB: 255, 0, 0), positioned along the horizontal axis either at the central fixation or 10 degrees left or right from the central fixation. Only trials when a reorienting cue appeared at the centre or on the same side as a target were included in the analysis. Thus, the distance of the reorienting cue from the subsequent target was kept 5 degrees in two conditions (i.e., peripheral and central). Experiment 2 comprised three repeated measures factors: validity (cued, uncued); SOA (150, 650 or 1,150 ms) and

reorienting cue location (central, peripheral). In the central condition, for each SOA there were 30 cued, 30 uncued and 6 no target (10%) trials. In the peripheral condition (i.e., left and right locations), for each SOA there were 60 cued, 60 uncued and 12 no target (10%) trials but only half of these trials were included in the analysis (i.e., when a reorienting cue appeared on the same side as a target). There were 18 practice trials followed by two blocks each containing 297 trials.

In the experimental procedure, a reorienting cue was presented in the middle of the first (alerting) cue and target onset (SOA) which equalled 150, 650 or 1,150 ms (see Figure 3). A three-way ANOVAs involving validity (cued, uncued), SOA (150 ms, 650 ms and 1,150 ms) and reorienting cue location (central, peripheral) was conducted.

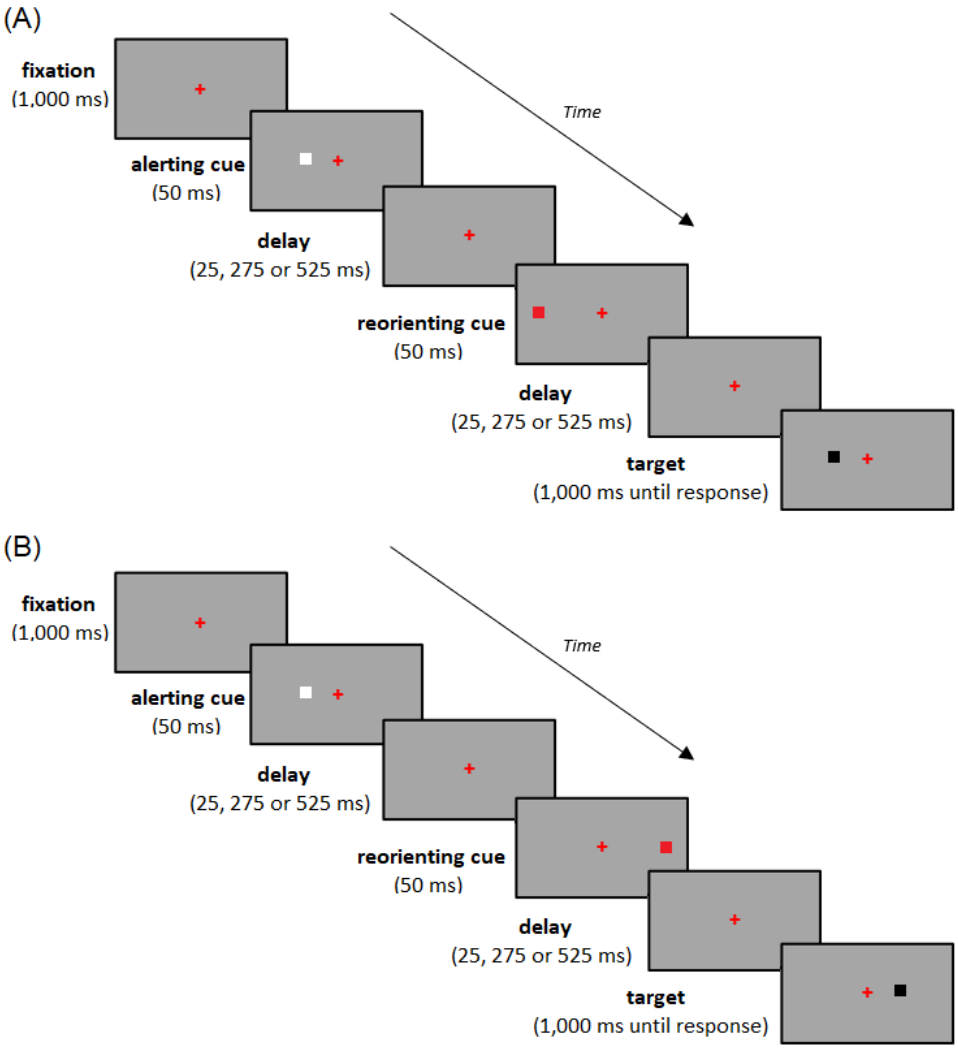


Figure 3. The trial timeline in Experiment 2 in cued (A) and uncued (B) conditions. The fixation appeared at the centre location for 1,000 ms. Next, a cue appeared randomly at one of the two positions (right/left) for 50 ms. Then, a reorienting cue appeared 75, 325 or 575 ms after the first cue onset (SOA) at one of the three positions (centre/right/left). Finally, a target appeared at one of the two positions (right/left) either 75, 325 or 575 ms after the reorienting cue onset (SOA). Only trials in which a reorienting cue appeared at the centre or on the same side as a target were included in the analysis.

2.4.2. Results

The number of errors was moderate (8.28%). Omissions were very infrequent (0.01 %). Trials with RTs faster than 100 ms and slower than 1,000 ms were 0.91 %. Table 2 shows RTs in all conditions.

Table 2

Mean RTs (ms) with standard errors as a function of condition: cued, uncued at each SOA (150, 650, 1,150) and reorienting cue position (central, peripheral)

	Reorienting cue position	SOA 150	SOA 650	SOA 1,150
Cued	Central	423 (64)	376 (53)	381 (52)
	Peripheral	417 (58)	359 (50)	383 (55)
Uncued	Central	409 (68)	355 (50)	358 (61)
	Peripheral	408 (60)	350 (51)	372 (44)

There were significant main effects of validity, $F(1, 22) = 35.25$ $p < .001$, $\eta_p^2 = .62$, and SOA, $F(2, 44) = 57.10$, $p < .001$, $\eta_p^2 = .72$. Participants were slower in the cued versus uncued conditions. They were also slower after 150 SOA than 650 SOA ($p < .001$) and 1,150 SOA ($p < .001$), as well 1,150 than 650 SOA ($p = .048$). Critically, there was a significant Validity × Reorienting Cue Position interaction, $F(1, 22) = 8.58$, $p = .008$, $\eta_p^2 = .28$. Significant IOR (slower RT to cued versus uncued targets) was found following both central ($p < .001$) and peripheral ($p = .022$) reorienting cues. However, the inhibitory cueing effects were larger for central than peripheral cues ($p = 0.008$). This finding shows that the magnitude of inhibitory cueing effects is modulated by the spatial location of a reorienting cue. There was also a SOA × Reorienting Cue Position interaction, $F(2, 44) = 4.31$, $p = .019$, $\eta_p^2 = .16$. After the peripheral

reorienting cue, RTs were longer at SOA 1,150 than SOA 650 (p = 0.007), whereas the central cue cancelled out this effect (p = 1.00). There was no main effect of location, F (1, 22) = 0.34, p = .567, η_p^2 = .02, neither a significant Validity × SOA interaction, F(2, 44) = 0.50, p = .611, η_p^2 = .02, or Validity × SOA × Reorienting Cue Position interaction, F(2, 44) = 0.42, p = .657, η_p^2 = .02.

Figure 4 shows the cueing effects for each of the experimental conditions. We used a t-test to compare cued and uncued trials across of three SOAs. In the central condition, the IOR was found for SOA 150 ms (p = .003), SOA 650 ms (p = .002) and SOA 1,150 ms (p < .001). In the peripheral condition, the IOR was also observed for SOA 150 ms (p = .037), SOA 650 ms (p = .041) but not SOA 1,150 ms (p = .079). The strength of IOR was computed by subtracting performance on uncued from cued trials. The analysis showed that at SOA 150 ms there were no differences in the magnitude of IOR between central and peripheral conditions (p = .192). Importantly, however, the IOR was stronger following central versus peripheral cue after SOA 650 ms (p = .045) and SOA 1,150 ms (p = .036).

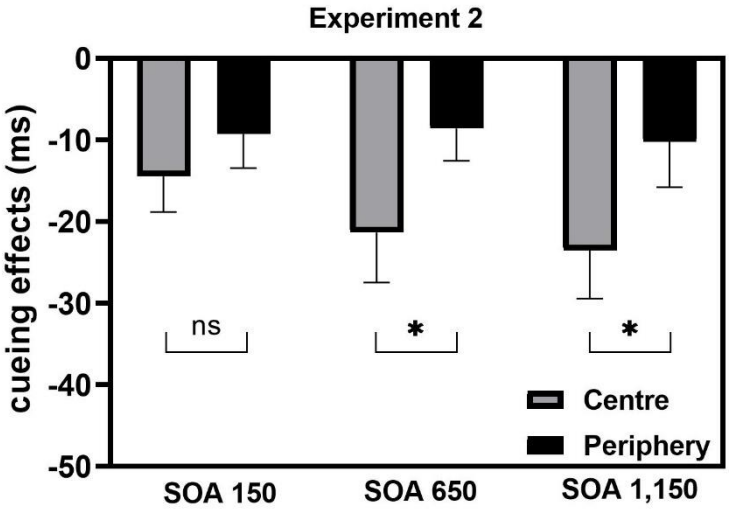


Figure 4. Mean cueing effects (uncued – cued RT) and standard error for each of reorienting cue locations (centre, periphery) and SOA (150, 650, 1,150 ms). Overall, inhibition was stronger after the central versus peripheral reorienting cue.

2.4.3. Discussion

The Experiment 2 revealed a pattern of enhanced IOR elicited by central as compared to peripheral reorienting cues. Our results present a novel empirical finding as, according to our knowledge, no previous study has investigated the influence of a reorienting cue's position on inhibitory effect. Furthermore, this modulation did not interact with SOA – which appears to suggest that it is independent of time. One may hypothesise that such a bias of attention to the central fixation may potentially stem from the existence of an operating mechanism realigning overt and covert attentional systems. Nevertheless, in order to be able to understand the novel findings in more detail, the following experiments replicating the results and examining their potential limitations would prove particularly informative.

2.4. Experiment 3

The results of Experiment 2 revealed a novel empirical finding that IOR is stronger (i.e., more negative cueing effect values) after the central versus peripheral reorienting cue. The aim of Experiment 3 was to replicate this finding, using different experimental settings to probe the robustness of observed data. More specifically, we used different SOA than in Experiment 2. Indeed, it has been highlighted that time since the most recent cue can modulate the strength of IOR (List & Robertson, 2008). In fact, whereas Experiment 2 used the same intervals as the Experiment 1, the time since the most *recent* cue (i.e., the alerting cue in Experiment 1 and the reorienting cue in Experiment 2) was different. Therefore, Experiment 3 used the same timing since the most recent cue (i.e., the reorienting cue) and a target that Experiment 1 to allow for comparisons.

2.5.1. Methods

The same methods were used as in the Experiment 1 and Experiment 2 unless specified otherwise.

Twenty participants (12 women, 8 men, M_{age} = 21, age range 19-27) took part in the study. Here, the SOA was 225, 975 or 1,725 ms such that the time since the onset of the most recent cue (reorienting cue) was 150, 650 or 1,150 ms (see Figure 5). Consequently, Experiment 3 comprised three repeated measures factors: validity (cued, uncued); SOA (225 ms, 975 ms or 1,725ms) and reorienting cue location (central, peripheral).

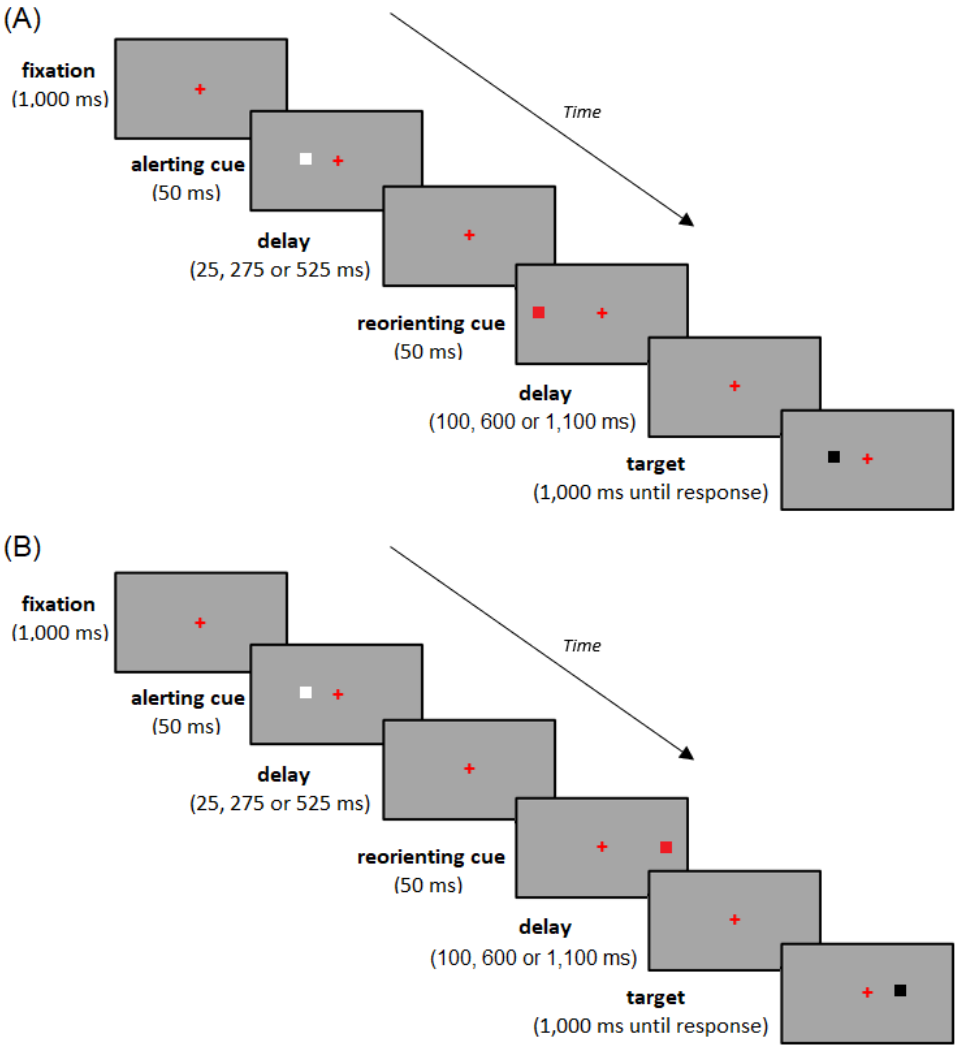


Figure 5. The trial timeline in Experiment 3 in cued (A) and uncued (B) conditions. A reorienting cue appeared 75, 325 or 575 ms after the alerting cue onset (SOA), and then, in contrast to Experiment 2, a target appeared 150, 650 or 1,150 ms after the reorienting cue onset (SOA). Therefore, the time since the most recent cue (i.e., the reorienting cue) was equal to Experiment 1.

2.5.2. Results

The number of errors was moderate (5.10%). Omissions were very infrequent (0.01 %). Trials with RTs faster than 100 ms and slower than 1,000 ms were 0.56%. Table 3 shows RTs in all conditions.

Table 3

Mean RTs (ms) with standard errors as a function of condition: cued, uncued at each SOA (225, 975, 1,725) and reorienting cue position (central, peripheral)

	Reorienting cue position	SOA 225	SOA 975	SOA 1,725
Cued	Central	400 (43)	386 (30)	379 (33)
	Peripheral	380 (47)	391 (28)	384 (34)
Uncued	Central	377 (50)	356 (31)	361 (36)
	Peripheral	379 (45)	374 (37)	369 (29)

There were significant main effects of validity, $F(1, 19) = 55.81$ $p < .001$, $\eta_p^2 = .75$. Participants were slower in the cued versus uncued conditions. Importantly, there was again a significant Validity × Reorienting Cue Position interaction, $F(1, 19) = 20.29$, $p < .001$, $\eta_p^2 = .28$. Similarly to Experiment 2, IOR was observed in both central ($p < .001$) and peripheral ($p = .003$) reorienting cue conditions, but this effect was more pronounced for central than peripheral cues ($p < .001$). Therefore, we replicated the main finding of the Experiment 2, namely that the strength of inhibitory cueing effects is modulated by the location of a reorienting cue. There was also a SOA × Reorienting Cue Position interaction, $F(2, 38) = 8.85$, $p < .001$, $\eta_p^2 = .32$. In the central reorienting cue condition, participants were slower after SOA 225 than SOA 1,725 SOA ($p = .055$), which was not the case in the peripheral cue condition

(p = 1.00). There was no main effect of a reorienting cue position, $F(1, 19) = 0.75$, p = .399, η_p^2 = .04, SOA, F (1, 19) = 1.93, p = .16, η_p^2 = .10, neither a significant Validity × SOA × Reorienting Cue Position interaction, $F(2, 38) = 1.21$, p = .310, η_p^2 = .06. Figure 6 shows the cueing effects for each of experimental conditions.

Again, the analysis of cueing effects was performed (Fig. 6). T-tests contrasting cued and uncued trials revealed the IOR for SOA 225 ms (p < .001), SOA 975 ms (p < .001) and SOA 1,725 ms (p = .011) in the central condition. In the peripheral condition, the IOR was observed for SOA 975 ms (p = .010) and SOA 1,725 ms (p < .001) but not SOA 225 ms (p = .757). The IOR magnitude was computed by subtracting performance on uncued from cued trials. The IOR was stronger after central than peripheral reorienting cue for SOA 225 ms (p < .001) and 975 ms (p = .050). No such effect was present for SOA 1,725 ms (p = .302).

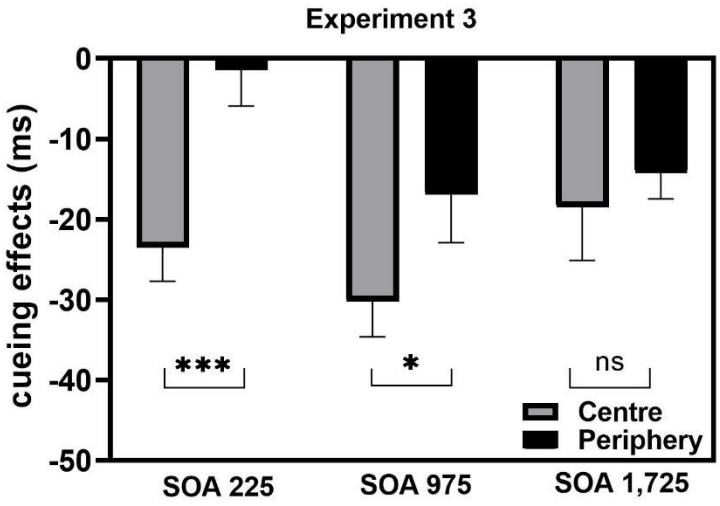


Figure 6. Mean cueing effects (uncued – cued RT) and standard error for each of reorienting cue locations (centre, periphery) and SOA (225, 975, 1,725 ms). The main findings of Experiment 2 were replicated, yielding stronger inhibition for central versus peripheral reorienting cue condition.

2.5.3. Discussion

Experiment 3 replicated the main finding of the Experiment 2, once again revealing a pattern of enhanced IOR elicited by central as compared to peripheral reorienting cues even when the intervals between an alerting cue and a target were prolonged. Similarly, the SOA did not modulate this effect, repeating our previous results and demonstrating that more robust inhibition originating from centrally located cues appears to be intact by temporal structure of the task. As previously discussed, the magnified inhibitory effects following a central reorienting of attention may potentially represent a dynamic mechanism which controls the efficacy of covert and overt attentional systems by converging their focus on central locations. Alternatively, but not mutually exclusively, this mechanism may act through covert and overt attention realignment regardless of the properties of the focal point, i.e., it is not a central location per se that triggers a stronger inhibitory signal but the current fixation point.

In the context of visual processing, an alternative account is equally plausible though. The more pronounced inhibition observed following a central than peripheral reorienting cue might derive from an increased contrast sensitivity for central versus peripheral stimuli. The question of whether the reduction in IOR associated with the peripheral cues simply reflects a reduction in its effectiveness due to lower contrast (light/dark spatial frequency) at peripheral eccentricities on the retina was tested in the following experiment.

2.5. Experiment 4

The aim of this study was to compare the contrast sensitivity for centrally and peripherally presented stimuli. This control experiment was conducted to verify whether there was any difference in cue onset sensitivity between central and peripheral reorienting cues that could potentially explain the main scientific finding of Experiments 1-3, namely that the location of the reorienting event alone can modulate the robustness of the inhibitory signal. Although replicated, such a pattern of results may stem from a more acute vision in the centre versus periphery. To exclude such a possibility, we conducted a simple detection task experiment presenting a target that varied across five levels of colour saturation in the centre versus periphery. We formulated two hypotheses. If our previous findings were due to an increased cue onset sensitivity for central versus peripheral reorienting cue, we would expect to find a significant difference in RT to peripheral versus central targets at 100% saturation level of red colour (i.e., RGB 255, 0, 0; the same as used for the reorienting cue in our experiments). On the contrary, if we failed to find such results, the observed difference in the strength of IOR can be attributable to the reorienting cue position.

2.6.1. Methods

2.5.1.1. Participants

Twenty participants were recruited from the Psychology Department at Bangor University and took part in the study for course credit. The study was conducted under School of Psychology Ethics Protocol. All participants had normal or corrected-to-normal visual

acuity. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). There were 20 subjects (13 women, 7 men, M_{age} = 20.3 years, age range 18-26).

2.5.1.2. Apparatus

Data acquisition was conducted using a PC and 1024 x 768 Mitsubishi Diamond Pro 2060u (120 Hz, 40cm) monitor. A standard QWERTY PC keyboard was used for the responses. An SR 1000 eye tracker (1,000 Hz) was used to monitor eye movements. The experiments were programmed in Experiment Builder (SR Research Ltd.).

2.5.1.3. Stimuli

The fixation point was a red cross (RGB: 255, 0, 0) of 13 x 13 pixels which equals 0.5 degrees of visual angle on a 1024 x 786 monitor (of 40 cm horizontal dimension) viewed from 57cm where the vertical and horizontal bars in the cross are each 2 pixels wide. The fixation cross was situated in the centre of the display. The background was grey (RGB: 127,127,127). A target was a square 13 x 13 pixels with RGB varied as a function of the saturation: 153, 102, 102 (20% saturation), 179, 77, 77 (40% saturation), 204, 51, 51 (60% saturation), 230, 26, 26 (80% saturation) and 255, 0, 0 (100% saturation). The higher the saturation, the more intensely red the target was on the grey background. Targets were placed on the horizontal line 10 degrees from the central fixation on the right or left side, or at the centre of the display. The viewing distance was fixed at 57 cm using a chinrest.

2.5.1.4. Design

The experiment comprised three repeated measures factors: SOA (150, 650, 1,100 ms), target location (peripheral, central) and saturation level (20%, 40%, 60%, 80%, 100%). For each SOA, there were 60 cued, 60 uncued and 12 no target (10%) trials. There were 18 practice

trials followed by two blocks each containing 198 trials. There were 20 trials per each combination of SOA, target location and saturation Level factors. The catch trials constituted 10% of all trials. There were 18 practice trials followed by four blocks of 248 trials each.

2.5.1.5. Procedure

Participants first completed eye tracker calibration. They were instructed to fixate centrally on each trial (fixation was monitored with an eye-tracker and trials were terminated if the observer's fiction fell outside of an invisible circular region-of-interest prior to target onset (with diameter of 2 degrees of visual angle around the fixation point). The trial was started by a participant by pressing the spacebar after which the blue cross turned red. The fixation point remained in the centre for 50 ms (Fig. 7). Then, after 150, 650 or 1,150 ms after the cue onset (SOA), a target appeared at one of three possible locations (right/left/centre). The trial ended with a jittered interval (400-1,000 ms). Participants' task was to detect the target as quickly as possible while minimising errors. Presentation order was randomised within subjects.

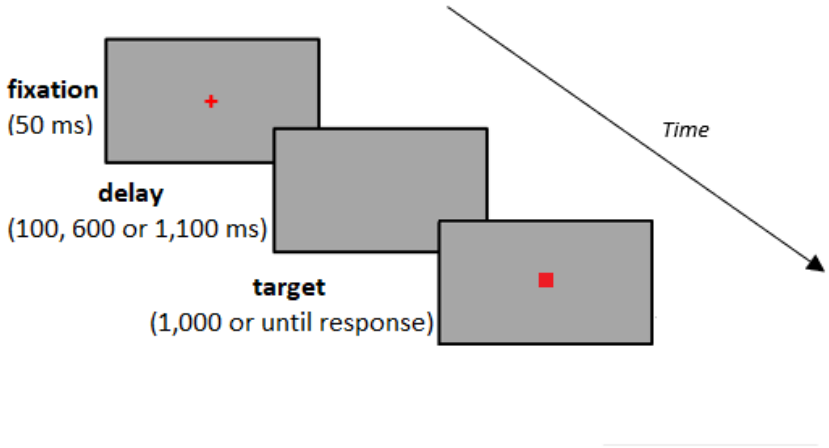


Figure 7. The trial timeline in the control Experiment 4. In the beginning of the trial, the fixation appeared at the centre location for 50 ms. After 150, 650 or 1,150 ms after the fixation onset (SOA), a target appeared randomly for 1,000 ms or until the response at one of the two positions (periphery: right/left, or centre). A target was a square 13 x 13 pixels wide and was placed on the horizontal line 10 degrees from the central fixation on the right or left side, or at the centre of the screen. The redness of the target was varied as a function of its saturation such that it gradually decreased its contrast from 100% saturation to 20% saturation (steps of 20% saturation). The participants' task was to detect the target as quickly as possible while minimising errors.

2.5.1.6. Data Analysis

Errors (false positives: responses to no-target trials), omissions and trials with RTs less than 100 ms and greater than 1,000 ms were excluded from the analysis. RTs were calculated separately for each of three SOAs, separately for central and peripheral target locations and each of five saturation levels. A three-way repeated measures ANOVA involving SOA (150,

650 and 1,150 ms), target location (central, peripheral) and saturation level (20%, 40%, 60%, 80%, 100%) was conducted. Bonferroni adjustments were made for pairwise comparisons. Effect sizes were estimated using partial eta-squared (η_p^2). Significance was determined relative to an a priori alpha criterion of $p < .05$, two-tailed).

2.6.2. Results

The number of errors was moderate (3.40%). Omissions were very infrequent (0.02 %). Trials with RTs faster than 100 ms and slower than 1,000 ms were 0.46%. Tables 4 and Figure 8 show RTs in all conditions.

Table 4

Mean RTs (ms) with standard errors as a function of condition: cued, uncued at each SOA (225, 975, 1,725) and reorienting cue position (central, peripheral).

	Saturation 20%		Saturation 40%		Saturation 60%		Saturation 80%		Saturation 100%	
SOA	Centre	Periphery	Centre	Periphery	Centre	Periphery	Centre	Periphery	Centre	Periphery
150	471 (18)	480 (18)	456 (17)	438 (16)	444 (16)	436 (17)	435 (15)	437 (17)	440 (16)	441 (17)
650	435 (16)	449 (17)	408 (11)	400 (14)	414 (14)	391 (15)	400 (13)	393 (13)	405 (14)	402 (13)
1,150	418 (13)	435 (13)	405 (10)	396 (12)	395 (12)	391 (11)	395 (14)	388 (12)	394 (13)	402 (1)

As expected, there was a significant main effect of saturation, F (4, 76) = 42.78, p < .001, η_p^2 = .70. Participants detected slower targets with the lowest saturation level (20%) when compared to targets with 40% saturation level (p < .001), 60% saturation level (p < .001), 80% saturation level (p < .001) and 100% saturation level (p < .001). There was also a main effect of SOA, F (2, 38) = 30.58, p < .001, η_p^2 = .62, with slower RT after SOA 150 than SOA 650 (p < .001) and SOA 1,150 (p < .001). There was a significant Location × Saturation interaction, F(4, 76) = 6.10, p < .001, η_p^2 = .24. Importantly, however, there was no significant difference in cue onset detection latencies between central and peripheral locations at any saturation level including 100% saturation level (p = .817). There was no main effect of target location, F (1,

19) = 0.92, p = .765, η_p^2 = .01 nor any other significant interactions. Therefore, any difference found between central and peripheral reorienting conditions in the previous experiments, could not be attributable to cue onset sensitivity.

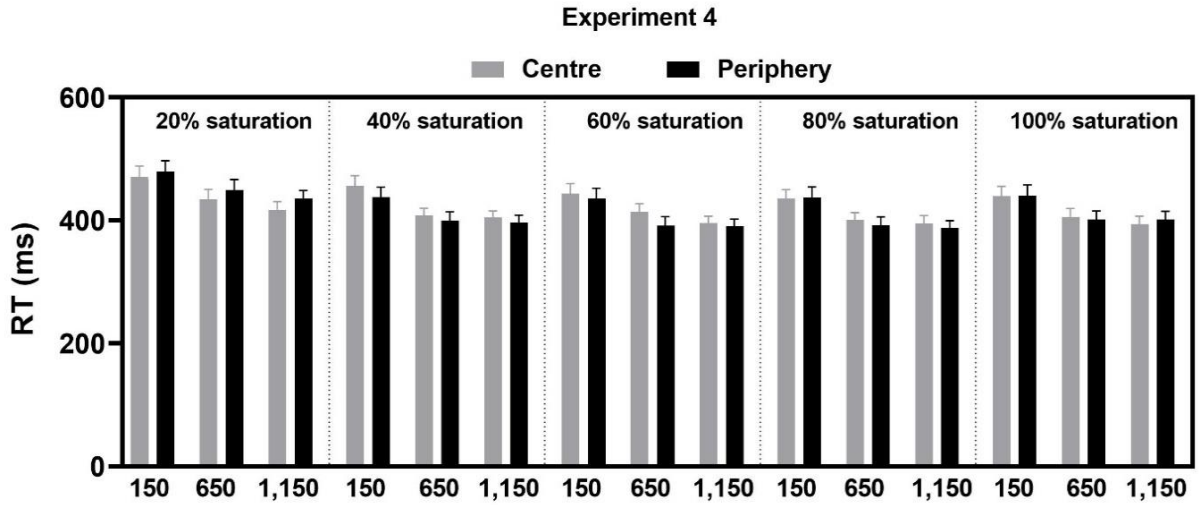


Figure 8. Mean RT in ms and standard error for each of target locations (centre, periphery), SOA (150, 650, 1,125 ms) and saturation level (20%, 40%, 60%, 80%, 100%). There was no difference in detection RT between central versus peripheral target locations for any of the saturation levels. Therefore, stronger IOR after central versus peripheral reorienting event found in Experiments 2 and 3 was not due to a reduction in its effectiveness due to lower contrast at peripheral eccentricities on the retina.

2.6.3. Discussion

Experiment 2 and Experiment 3 revealed a pattern of reduced IOR elicited by peripheral as compared to central reorienting cues. However, the obtained results could equally stem from the differences in central versus peripheral perceptual processing. The goal of the present study was to differentiate the effects of contrast sensitivity for central and peripheral stimuli by using a simple detection task. By manipulating the saturation of the red target, we were able to establish relative differences of response times when detecting central versus peripheral stimuli. Crucially, the results revealed no differences for any level of the manipulated colour saturation. Such consistent findings suggest that a stronger inhibitory signal after a central than peripheral reorienting cue does not simply result from increased contrast sensitivity for central cues on retina. Indeed, the current study provided further evidence that central reorienting of attention produces stronger inhibition of previously attended locations.

2.6. General discussion

The goal of this set of experiments was to use the effect of slower RTs to previously cued locations (i.e., IOR) in a spatial cueing paradigm to elucidate the underlying processes that mediate interaction between the overt and covert attention systems. More specifically, we hypothesised that the central redirection of attention would elicit stronger inhibition. To examine this question, we presented a reorienting cue, following an initial alerting cue, both centrally and, unlike any previous study of visual attention, peripherally. Our results showed that IOR (i.e., longer RT to cued than uncued targets) was indeed significantly stronger (i.e., more negative cueing effects) after central versus peripheral reorienting of attention. These novel findings shed a new light on factors that play a role in eliciting inhibition to previously attention locations. Whereas the time (i.e., SOA) has been well documented to contribute to this effect (Chica et al., 2014; Lupiáñez et al., 1997; Reppa et al., 2012), we demonstrated that the *spatial position* of a reorienting event also modulates the magnitude of IOR. Notably, this modulation did not interact with SOA, indicating that its mechanism is independent of time.

One could argue that the observed results may potentially stem from the contrast sensitivity difference, whereby the reduction in IOR associated with the peripheral cues could simply reflect a reduction in their effectiveness due to lower contrast (light/dark spatial frequency) at peripheral eccentricities on the retina. However, this explanation was discarded as the control study revealed no differences in detection latencies between peripherally and centrally located targets for saturation levels of the same hue as used in the experiments. Therefore, it can be concluded that stronger inhibitory signals after a central shift of attention were due to a manipulation of a reorienting cue location. Similarly, whereas previous studies revealed that the time since the most *recent* cue may play a role in the magnitude of IOR (List

& Robertson, 2008), we replicated our effects across different timings since the most recent cue.

The study also confirmed previous results that IOR can be found even in the absence of a reorienting cue (Chica et al., 2014; Martín-Arévalo et al., 2013; Prime et al., 2006), suggesting that central realignment of covert and overt attention might be involuntary in nature. However, the results suggest that this realignment can also be modulated by a subsequent peripheral cueing event. Critically, these consistent and complementary results might indicate the existence of a mechanism that acts to realign overt and covert attention by biasing attention shifts towards central fixation.

Intriguingly, no facilitation was found in cued trials at the shortest SOA (150 ms) in any of the experiments. However, it was suggested that facilitatory effects to previously cued locations are restricted to certain experimental manipulations. For example, the cue offset and target onset must overlap temporally (Chica et al., 2014), which was not the case in our experiments. In fact, the vast majority of studies on spatial cueing (Posner et al., 1980; Pratt & Fischer, 2002; Pratt, Hillis, & Gold, 2001, Eimer, 2000) consistently used placeholders in which a cue (e.g., flash of the outlines) and target were presented. In contrast, in our experiments, stimuli appeared in no spatially-constraint manner (i.e., no placeholders were used).

It may be argued that placeholders might have large effects on the distribution of attention and thus, might influence its facilitatory and inhibitory pattern. Indeed, in their recent study, Taylor, Chan, Bennett and Pratt (2015), using a spatial cueing paradigm directly compared the effects of placeholders on attentional distribution by presenting cues and targets within the placeholders or on displays in which no placeholders were present. The results

revealed that the spatial cueing benefit was found only for targets appearing within the placeholder. In turn, presenting a target on displays that did not comprise placeholders led to slower response times for cued targets even after a short time interval, suggesting that the IOR can occur even at the short SOA. Our results provide further evidence for a key role of experimental manipulation in eliciting facilitatory effects.

Finally, in the context of temporal preparation, in all our experiments, we found a typical pattern with faster response times after long versus short SOA, so-called "hazard function" (Los, Kruijne, & Meeter, 2014). Typically, in a task in which the interval between a cue and a target is varied within a block (i.e., variable foreperiod paradigm), the elapse of time itself informs participants that a target will appear soon given that it has not yet occured ("hazard function"). Therefore, the probability that a target will appear soon is increased for targets appearing after long intervals, experimentally translating into faster response times after long versus short time intervals. Importantly, temporal effects are functionally independent from space-related inhibition over time (IOR) (Gabay & Henik, 2010; Los, 2004; although see Tipper & Kingstone, 2005). These temporal preparation benefits were observed in all our experiments, highlighting yet again that salient events occur in continuous flow of time and attention should be conceptualised as dynamic changes in stimuli processing rather than the ability to select relevant events in the still environment.

To conclude, our experiments used an adapted spatial cueing task to examine whether the realignment towards a fixated (central) can be represented at the level of inhibitory attentional mechanisms. We examine this in the context of inhibition of return (IOR) - i.e., slower target detection at previously cued locations. Following a central cue (located at the position of the ocular fixation) resulted in greater IOR than when a peripheral cue was

presented. This indicates that the direction of realignment modulates inhibition of previously cued locations. We propose that stronger inhibition arising from central reorienting cues reflects a fundamental bias to realign covert and overt attention through shifts towards central fixation.

CHAPTER III

The effects of target location probability on spatiotemporal distribution of attention

3.1. Introduction

Spatial attention allows for enhanced processing of salient sensory stimuli by prioritising and selecting relevant information as well as inhibiting an irrelevant one in the service of adaptive behaviour. Although two distinct operating mechanisms of attentional orienting have been proposed, namely the endogenous (top-down) and exogenous (bottom-up) systems, the relative contribution of these representations to guided selection is still being probed. In the current study, we aimed to elucidate the effects of top-down manipulation (i.e., endogenous attention) of the target side location (left/right) probability on the spatiotemporal distribution of attention as measured by the behaviour to non-predictive targets (i.e., exogenous attention).

The Posner cueing paradigm has been successfully utilised to measure endogenous and exogenous systems by presenting central cues directing attention to a particular location in space, or when advance location is provided by the means of a stimulus presented in the in the subsequent target location, respectively (Posner et al., 1980). Importantly, even in the paradigm designed to probe the exogenous cueing effects, the endogenous processes might come into play, making it difficult to separate their overlapping effects. For instance, the paradigm's parameters such as the probability of target presence across trials affects alertness, leading to the modulation of the magnitude of inhibition.

The goal of our experiment was to investigate whether the target detection is improved when it is more likely to appear on the same display side (e.g., left) as a preceding noninformative cue. More specifically, we used an adapted Posner cueing task in which targets were presented not only at the same or opposite location as a cue but also at the upper and lower locations on both sides of the display (i.e., contralateral condition) or on the same side of the display as a preceding cue (i.e., ipsilateral condition).

Indeed, in real-life settings, targets are unevenly distributed across the visual field and this information can be utilised to guide our attention (Chun, 2000). Previous studies have reported that visual search is enhanced when the targets are more likely to appear in certain locations. This phenomenon called the "probability cueing effect", has been extensively studied in the context of visual search tasks (Druker & Anderson, 2010; Fecteau, Korjoukov, & Roelfsema, 2009; Geng & Behrmann, 2002, 2005; Hoffmann & Kunde, 1999; Kabata & Matsumoto, 2012; Maljkovic & Nakayama, 1996; Sayim, Grubert, Herzog, & Krummenacher, 2010; Shaw & Shaw, 1977). Two mechanisms have been proposed to account for these effects: learning of the statistics inherent in the task structure or alternatively but not mutually exclusively, the facilitation of target location carried over the task course. Indeed, whereas there are studies supporting the first (Druker & Anderson, 2010; Geng & Behrmann, 2002; Hoffmann & Kunde, 1999; Sayim et al., 2010) or the second account (Geng et al., 2006; Hillstrom, 2000; Maljkovic & Nakayama, 1996; Walthew & Gilchrist, 2006), there is also evidence that their joint effect underlies the probability cueing effect (Kabata & Matsumoto, 2012).

Irrespective of the rules that govern the use of the probability cueing, the study of their effects has been generally limited to visual search tasks with multiple objects on the display.

On the contrary, in the Posner cueing task, only one target is present on the screen requiring a simple detection task. Therefore, target location probability might differentially modulate visual attentional distribution. In their spatial cueing task, Tipper and Kingstone (2005) demonstrated that decreasing the probability of target presence across trials led to a diminished magnitude of IOR. Yet, they also manipulated the temporal preparation indexed by a variable foreperiod (FP) effect with faster RTs after long rather than short cue-target intervals (Niemi & Naatanen, 1981; Woodrow, 1914). As a reduced IOR was accompanied by the absence of a variable FP effect, the authors concluded that although IOR is an intrinsically reflexive phenomenon, it can be modulated by top-down processes such as temporal preparation. In turn, another study (Gabay & Henik, 2008) that varied the probability of target presence within trials, and at the same time maintained the high probability of target appearance across trials, demonstrated that the intact IOR was present even when the variable FP effect disappeared. Thus, Gabay and Henik (2008) proposed that a decrease of IOR strength observed for low target occurrence across trials by Tipper and Kingstone (2005) might have stemmed from the lower tonic alertness. To reconcile these findings, Hayward and Ristic (2013), manipulated the target occurrence probability both across and within trials in the Posner cueing paradigm. The results indicated that increasing the rate of overall target presence leads to stronger arousal (Coull, 1998; Gabay & Henik, 2008; Weinbach & Henik, 2012) and greater inhibition (Hayward & Ristic, 2013).

The goal of our experiment was to probe the effects of target location probability, relative to a preceding cue location in the spatial cueing paradigm. As in a typical exogenous spatial cueing paradigm (Posner & Cohen, 1984; Posner et al., 1980) a target could appear at the same (cuedON condition) or at the opposite location as a preceding cue (uncued condition). Importantly, in contrast to previous studies (Gabay & Henik, 2008; Hayward & Ristic, 2013;

Tipper & Kingstone, 2005), a target could also appear either at one of two other locations which were on the same side as a cue location (ipsilateral condition) or at one of four other locations, two at the same side as a preceding cue and two at the opposite side as a preceding cue (contralateral condition). Thus, in the ipsilateral condition, the probability of target occurring at the same side as a preceding cue was two times higher than in the contralateral condition. Only response times to targets appearing at the same as a cue (cuedOFF condition) were compared across contralateral and ipsilateral target presentations.

Based on previous findings, we expected to observe a modulation of cueing effects by top-down effects of target location probability. More specifically, we hypothesised that although inhibition would be present in both contralateral and ipsilateral conditions, the IOR magnitude (i.e., slower RTs to cued versus uncued trials) would be stronger for the ipsilateral condition. Put simply, in the ipsilateral condition, participants should expect a target to appear more frequently on the same side as a cue which would result in high tonic alertness (Gabay & Henik, 2008). Empirically, it would translate into more negative cueing effects (i.e., uncued – cuedON and uncued – cuedOFF response times) values in ipsilateral versus contralateral condition. Alternatively, if the probability of target location does not affect the IOR, no differences in cueing effects between contralateral and ipsilateral conditions should be observed.

3.2. Methods

3.3.1. Participants

Forty students (28 women, 12 men, M_{age} = 23.7 years, age range 18-42) from the Psychology Department at the Bangor University participated in the study for course credit, 20 participants in the contralateral condition and 20 participants in the ipsilateral condition. Participants were recruited through the SONA system in exchange for course credit. The study was conducted under School of Psychology Ethics Protocol (2015-15549). All participants had normal or corrected-to-normal visual acuity. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971).

3.3.2. Apparatus

Data acquisition was conducted using a PC and 1024 x 768 Mitsubishi Diamond Pro 2060u (120 Hz, 40 cm) monitor. A standard QWERTY PC keyboard was used for the responses. The SR 1000 eye tracker (1,000 Hz) was used to monitor central fixation. The experiments were programmed in Experiment Builder (SR Research Ltd.).

3.3.3. Stimuli

The fixation point was a red cross (RGB: 255, 0, 0) of 13 x 13 pixels subtending 0.5 degrees of visual angle. The vertical and horizontal bars in the cross were each 2 pixels wide. The fixation cross was situated in the centre of the display. The background was grey (RGB: 127,127,127). Alerting cues comprised a white square of 13 x 13 pixels (RGB 255, 255, 255) subtending 0.5 degrees of visual angle. Alerting cues were positioned along the horizontal axis 5 degrees left or right from the central fixation. Targets comprised a 13 x 13 pixel black square (RGB: 0, 0, 0) displayed at one of four locations (ipsilateral condition) or six locations (contralateral condition) on the invisible circle. Crucially, all targets were placed 5 degrees

from the central fixation (Fig. 17). In the ipsilateral condition, a target could appear at the same location as a preceding cue (cuedON), at the same side but different locations up or down relative to a preceding cue (cuedOFF) or at the opposite location as a preceding cue (uncued). In the contralateral condition, a target could additionally appear at the opposite side up and down relative to a cue position (uncuedOFF). Viewing distance was fixed at 57cm using a chinrest.

3.3.4. Design

The experiment was structured using a mixed factorial ANOVA, with group (contralateral, ipsilateral) as a between-subject factor and stimulus onset asynchrony (SOA) (150, 650 ms) and validity (cuedON/cuedOFF/uncued) as within-subject factors.

In the contralateral condition, each of the SOA (150, 650ms) and validity (cuedON, cuedOFF, uncued, uncuedOFF) configurations were presented 30 times in two blocks, resulting in 396 trials per participant (including 36 no target trials). Note, however, that in the cuedOFF condition, only targets that appeared on the same side as the cue were included in the analysis. In the ipsilateral condition, each of the SOA (150ms, 650ms) and validity (cuedON, cuedOFF, uncued) configurations were presented 30 times in two blocks, resulting in 264 trials per participant (including 24 no target trials). Therefore, in the contralateral condition, the target appeared equally on the same (50%) and opposite (50%) side as the cue. In turn, in the ipsilateral condition, it appeared on the same side as the cue in 75% of trials and on the opposite side relative to the cue in 25% of trials. Trial presentation order was fully randomised within subjects.

3.3.5. Procedure

Participants first completed eye tracker calibration. They then completed the spatial cueing task/s. For all three experiments, they were told to fixate centrally throughout each trial. Fixation was monitored on each trial with an eye-tracker. Trials were automatically terminated if the observer's fixation drifted outside of a non-visible circular region-of-interest (diameter equalled 2 degrees of visual angle) around the fixation point at any time prior to target onset. These trials were recycled at the end of the experiment. Each trial was initiated via the spacebar after which the central blue fixation cross turned red. The fixation cross remained in the centre for 1,000 ms. Next, an alerting cue was presented randomly at one of the two positions (right/left) for 50 ms. Then, after a variable period of either 150 or 650 ms since cue onset (SOA), a target appeared at one of four or six possible locations depending on the experimental condition until response or 1,000 ms had elapsed. There was a response deadline of 3,000 ms. There was a jittered inter-trial interval between 400 ms-1,000 ms. The task instructions were to detect the target as quickly as possible by pressing the spacebar whilst minimising errors. Participants were told to maintain central fixation, and where told that trials would be aborted if an eye movement was detection during the trial sequence. Figure 9 illustrates the trial sequence.

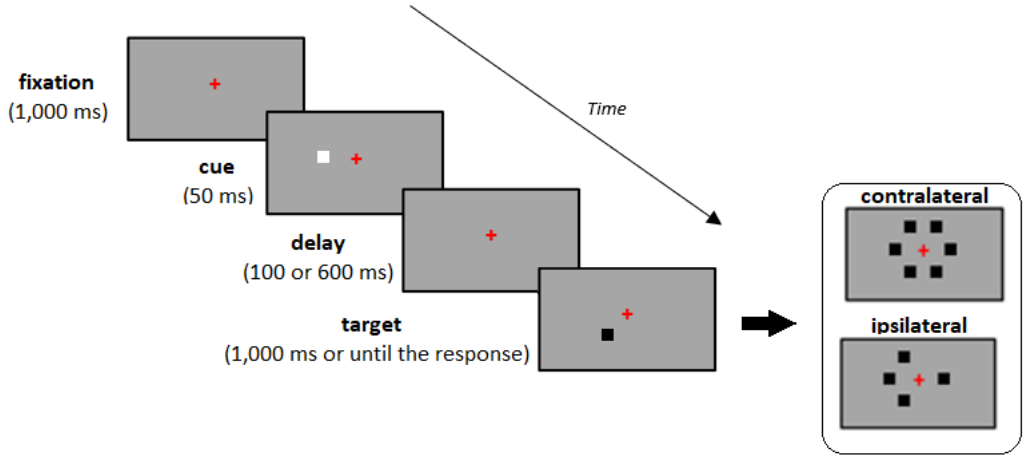


Figure 9. Illustration of trial sequence. On every trial, the fixation appeared at the centre location for 1,000 ms. Next, a cue appeared randomly at one of the two positions (right/left) for 100 ms. A target appeared randomly 150 or 650 ms after the cue onset (SOA) for 1,000ms or until the response. In the contralateral condition, a target could appear at one of two cue locations (right/left) or at one of four locations placed on the invisible circle 5 degrees from the fixation. In the ipsilateral condition, the target could appear at one of two cue locations or at one of two locations placed on the invisible circle 5 degrees from the fixation, on the same side as the proceeding cue. Trials, when a target appeared at the same location as a cue (i.e., right), were considered as cuedON. Trials when a target appeared on the opposite side that a cue (i.e., cue right/target left) were considered uncued. Finally, trials, when a target appeared at one of two remaining locations at the same side as the cue, were considered cuedOFF. In the contralateral condition, trials when targets appeared at one of two locations placed on the invisible circle were not analysed. The illustration above is an example of the trial in which a target appeared at the adjacent location to the cue (cuedOFF).

3.3.6. Data Analysis

Errors (false positives: responses to no-target trials), omissions and trials with RTs less than 100 ms and greater than 1,000 ms were excluded from the analysis. RTs were calculated separately for cuedON, cuedOFF and uncued conditions for each SOA.

Effects of cueing were analysed using three-way mixed factorial ANOVA, with group (contralateral, ipsilateral) as a between-subject factor and validity (cuedON, cuedOFF, uncued) and SOA (150, 650ms) as within-subject factors. Bonferroni adjustments were made for pairwise comparisons. Effect sizes were estimated using partial eta-squared (η_p^2). Significance was determined relative to an a priori alpha criterion of p =/< .05, two-tailed).

3.3. Results

3.4.1. Contralateral and Ipsilateral validity effects

Errors (responses to no-target trials) were very infrequent (0.28%), similarly omissions (approximately 0.003%). Trials with reaction time (RT) faster than 100 ms and slower than 1,000 ms were excluded from the analysis (0.35%).

Table 5 shows RTs in contralateral and ipsilateral conditions, respectively. A 3(validity: cuedON, cuedOFF, uncued) × 2(SOA: short, long) × 2(Group: contralateral, ipsilateral) mixed ANOVA showed a main effect of validity, $F(2, 76) = 56.56$, $p < .001$, $\eta_p^2 = .60$ and SOA, $F(1, 38) = 4.92$, $p = .033$, $\eta_p^2 = .12$. Participants were slower to cuedON than uncued targets ($p < .001$), indicating that inhibition was present across two SOAs. They were also slower to cuedOFF than uncued targets ($p = .011$). At the same time, RTs were faster in long SOA trials (i.e., the variable foreperiod effect). Also, there was a significant Validity × SOA interaction, $F(2, 76) = 9.35$, $p < .001$, $\eta_p^2 = .20$. In the uncued condition, participants responded significantly slower at SOA 150 ms than at SOA 650 ms ($p < .001$). In parallel, there was no difference in RTs to cuedOFF versus uncued targets (thus no inhibition) at SOA 150 ($p = 1.00$), whereas RTs to cuedOFF versus uncued targets were significantly slower at SOA 650 ($p < .001$). Importantly, no main effect of the group, $F(1, 38) = 1.81$, $p = .19$, $\eta_p^2 = .04$, nor any interaction with group were observed, indicating that the probability of target location did not affect attentional deployment.

Figure 10 illustrates cueing effects (uncued-cued trials). Positive values indicate facilitatory cueing effects (i.e., faster RTs to cued versus uncued trials), whereas negative values indicate IOR effects (i.e., longer RTs to cued versus uncued trials). In the contralateral condition, the classic IOR effect (cuedON versus uncued) was found for both SOA 150 ms (p

= .003) and SOA 650 ms ($p < .001$). In turn, the IOR for adjacent targets (cuedOFF versus uncued) was present for SOA 650 ms ($p = .002$) but not for SOA 150 ms ($p = .604$). In the ipsilateral condition, we observed similar results with the classic IOR effect (cuedON versus uncued) present for both SOA 150 ms ($p < .001$) and SOA 650 ms ($p < .001$). The IOR for adjacent targets (cuedOFF versus uncued) was again observed for SOA 650 ms ($p = .002$), but not for SOA 150 ms ($p = .630$). Importantly, the analysis did not show any significant differences between contralateral and ipsilateral conditions for any of the SOAs.

Table 5

Mean (and standard error) reaction times for each condition

	Contralateral		Ipsilateral	
Validity	Short SOA	Long SOA	Short SOA	Long SOA
CuedON	420 (16)	405 (15)	388 (13)	375 (12)
CuedOFF	387 (16)	384 (14)	362 (13)	369 (12)
Uncued	391 (16)	362 (12)	364 (14)	345 (13)

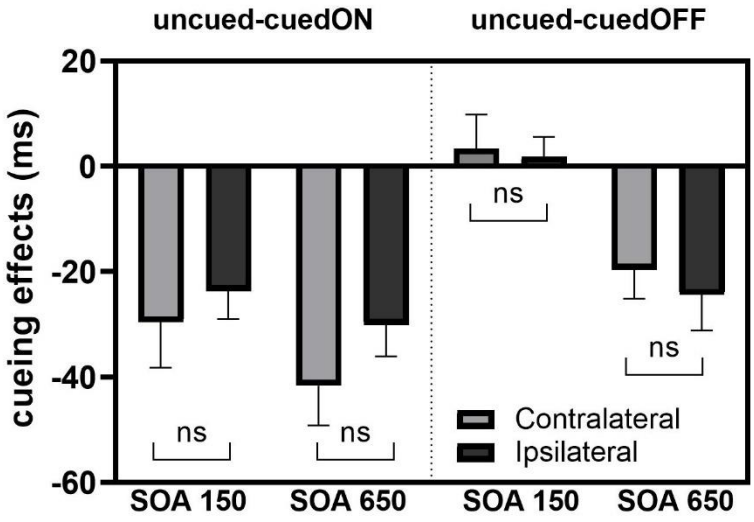


Figure 10. Mean cueing effect (uncued – cued RT) and standard error for each condition. Positive values indicate facilitation and negative values indicate inhibition. There was no difference between contralateral and ipsilateral conditions. Additionally, whereas the inhibitory effect is pervasive across contralateral and ipsilateral conditions, at short SOA no inhibition was observed for cuedOFF targets (i.e., targets appearing at the same side but different location as a cue).

3.4.2. Ipsilateral validity effects across blocks

To explore whether participants strategically allocated attention spatially only once it was apparent that cuedOFF targets could appear only at the same side as the preceding cue, the analysis by blocks was conducted (ipsilateral condition only). Table 6 shows RTs and cueing effects in ipsilateral condition in blocks 1 and 2. Crucially, no main effect of the block, $F(1, 19) = 0.42$, $p = .53$, $\eta_p^2 = .04$ nor any interaction with block was observed. There were significant main effects of validity, $F(2, 38) = 27.84$, $p < .001$, $\eta_p^2 = .59$, and a significant Validity × SOA interaction, $F(2, 38) = 6.91$, $p = .003$, $\eta_p^2 = .27$. RTs were longer for cuedON

targets than cuedOFF (p = .001) or uncued targets (p < .001), and for cuedOFF than uncued targets (p = .010). Participants produced slower responses after short than long SOA in uncued trials (p = .035) but not in cuedON (p = .15) or cuedOFF (p = .40) trials. Again, RTs to cuedOFF targets were slower than to uncued targets but only at SOA 650 (p < .001), whereas SOA 150 cancelled out the inhibitory effects (p = 1.00).

Figure 11 shows mean cuing effects (uncued-cued trials). No significant differences in cueing effects were observed between Block 1 and Block 2 for any of the conditions.

Table 6

Mean (and standard error) reaction times in ipsilateral condition presented for two blocks separately

	Block 1		Block 2	
Validity	SOA 150	SOA 650	SOA 150	SOA 650
CuedON	391 (15)	378 (14)	384 (12)	373 (12)
CuedOFF	366(14)	367 (13)	358 (13)	372 (13)
Uncued	367 (15)	348 (13)	360 (14)	342 (14)

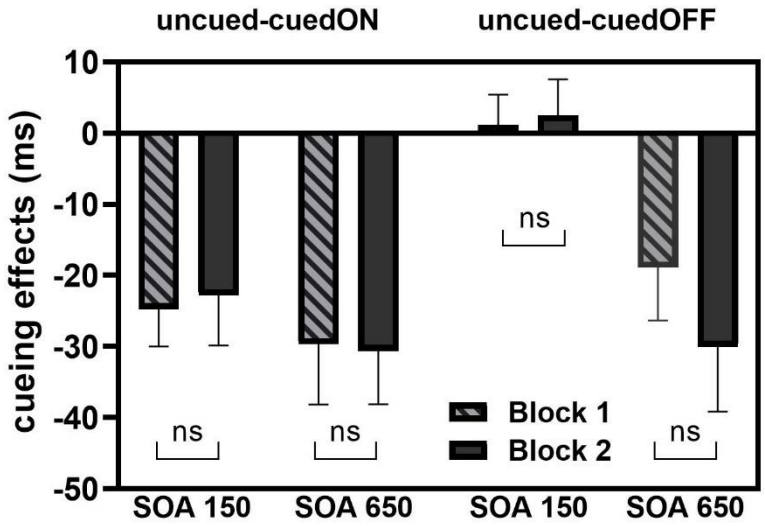


Figure 11. Mean cueing effect (uncued – cued RT) and standard error for SOA 150 and 650 in blocks 1 and 2 in the ipsilateral condition only. There was no difference in response times between blocks. Inhibition was observed throughout the experimental conditions except for cuedOFF trials, in which response times were not slower than to uncued trials at short SOA.

3.4. Discussion

The goal of this study was to elucidate the relative contribution of bottom-up and top-down processes on spatiotemporal distribution of attention using an adapted version of the Posner cueing paradigm. Whereas the paradigm itself is considered to elicit exogenous reflexive attentional orienting by presenting a nonpredictive cue followed by a target, we manipulated the probability of target locations and consequently introduced a top-down factor that could potentially affect the allocation of attentional resources. Specifically, we compared response times to targets that were more likely to appear at the same side of the display as a cue (ipsilateral condition) to response times to targets that appeared equally at two sides of the display (contralateral condition). Further, we increased the number of possible target locations in order to obtain a more comprehensive picture of attentional distribution.

Although we hypothesised that increasing the probability of target occurrence on one side of the display would modulate cueing effects by increasing the IOR, we obtained a different pattern of results. Intriguingly, we did not observe any significant differences between probability conditions. Moreover, even a direct comparison across consecutive blocks of trials in a high probability condition did not reveal any learning effects, further confirming that prior knowledge about target locations leaves attentional guidance unaffected. Yet, spatial inhibitory effects prevailed throughout most of the time course (except for targets appearing after short SOA on the same side but different location as a cue, i.e., cuedOFF condition), as demonstrated by slower response times to cued (both at the same locations as a cue or on the same side as a cue) than uncued targets. Taken together, these results suggest that expectations about the probability of target location does not modulate the spatiotemporal distribution of inhibition. This fact also suggests that that the probability cueing effect cannot be explained in the

framework of a Bayesian ideal observer that weights sensory evidence from possible target locations based on statistical regularities to maximise overall performance.

In the context of previous reports, our study further confirmed that IOR magnitude appears to be unaffected by the changes in target location probability in an adapted spatial cueing paradigm. These findings are consistent with several studies demonstrating that IOR is generally resistant to different experimental manipulations such as variations in temporal expectancies (Gabay & Henik, 2008; Los, 2004; although see Tipper & Kingstone, 2005). Consequently, IOR elicited by the onset of a spatially nonpredictive peripheral cue, and thus reflexive in nature is not modulated by top-down processes as evidenced by no difference in cueing effects between high and low probability of target occurrence at particular locations.

Finally, although we found that inhibition was reliable across most experimental conditions, the data show that no inhibitory effects were present after short SOA in the cuedOFF conditions, namely when targets appeared on the same side but at different locations as a preceding cue. In parallel, IOR was present in cuedOFF conditions after long SOA. This might suggest that inhibition that is triggered at the cued location dispersed across space over time but did not yet reach the cuedOFF locations at the short SOA (hence no inhibitory effect). In other words, this pattern of results, observed in both contralateral and ipsilateral conditions, clearly indicates a spatiotemporal distribution of inhibition.

Similarly to our previous experiments, we did not observe facilitatory effects of a cue typically associated with the spatial cueing paradigm, wherein presenting a target shortly after a cue in the same location is considered to lead to faster RT. Instead, an early and prolonged inhibition was present even when a short cue-target interval was used. Indeed, facilitatory effects appear to be particularly sensitive to experimental parameters (Chica et al., 2014) and

are generally found in discrimination rather than detection tasks as the one used here (Van der Lubbe, Vogel, & Postma, 2005), and in low versus high target frequency across trials. Thus, whereas the observed time course of orienting was shifted with IOR emerging earlier, the cueing effects were robust yielding strong inhibition across two SOAs.

Motivated by sparse reports investigating the role of top-down processes such as statistical regularities of the task in modulating IOR, we aimed to elucidate the contributing role of the target location possibility on attentional distribution in the spatial cueing paradigm. First, we found that the inhibitory effect was pervasive across experimental conditions. Although we hypothesised that inhibition would be increased for appearing more frequently in certain locations, it was not the case. Regardless of whether a target location was more predictable (high certainty manipulation in the ipsilateral condition) or nonpredictable (low certainty manipulation in the contralateral condition) probabilities did not guide target selection (i.e., evidenced by no benefit for the statistically biased location). These results suggest that even with high spatial certainty, behaviour is guided by involuntary processes present in the time course of the task rather than top-down processes such as statistical learning. Finally, whereas the probability cueing did not affect the IOR, inhibitory strength was attenuated as a function of the cue-target distance. Collectively, our results indicate that IOR is resistant to changes in target location probability and its magnitude disperses across space and time.

CHAPTER IV

Object-based versus space-based attention elicits stronger inhibition of return: an ERP study

4.1. Introduction

Efficient sampling of the environment requires not only facilitative processing of relevant locations, but equally importantly, inhibition of previously attended locations in the service of adaptive behaviour. A mechanism proposed to underlie selective suppression of already examined places is known as inhibition of return (IOR), and empirically translates into slower response time to previously attended locations. IOR is typically studied in a spatial cueing paradigm (Posner & Cohen, 1984; Posner et al., 1980), in which attention is attracted to a given location by an onset of a peripheral cue, and draws attention away from the cued location. If attention is then summoned back to the original cued location, its processing (e.g., detection) is relatively suppressed (Klein, 2000; Posner & Cohen, 1984). This phenomenon is thought to reflect an adaptive (evolutionary) mechanism that inhibits the inspection of already attended locations for a time of several eye-movements (Posner et al., 1985). Indeed, the IOR has been linked to both overt and covert orienting of attention (Posner et al., 1985) and its neural basis involve the midbrain saccade systems, with a central role of the colliculus (Sapir, Soroker, Berger, & Henik, 1999), which plays a crucial role in directing responses towards specific locations by means of informed eye movements (Posner et al., 1985; Sereno, Briand, Amador, & Szapiel, 2006).

IOR has been extensively examined in electrophysiological investigations. Studies using event-related potentials (ERPs) have revealed that the P1 component, which a first positive peak around 100 ms after a stimulus presentation reflecting perceptual processing generated in multiple areas of extrastriate cortex can be modulated by attending (or not) to a visual stimulus (Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002; Luck et al., 1994). In an exogenous spatial cueing paradigm, in which participants are required to maintain a central fixation, slower response times to previously cued locations (i.e., behavioural IOR) are paralleled by a reduced P1 amplitude for cued as compared to uncued targets (Prime & Ward, 2004; Prime et al., 2006; Wascher & Tipper, 2004; Van der Lubbe et al., 2005). Indeed, using correlational analysis, Martín-Arévalo and colleagues (2016) demonstrated based on 23 experimental studies that the greater magnitude of IOR was associated with the decrease in the P1 component to cued targets. Yet, it is not always the case that P1 deflection is accompanied by behavioural IOR (Hopfinger & Mangun, 1998) or vice versa (Gutiérrez-Domínguez et al., 2014; Hopfinger & Mangun, 2001; McDonald, Hickey, Green, & Whitman, 2009). Different possible factors such as the orientation of stimuli used in an experimental paradigm, as well as SOA and target duration manipulation, might contribute to these apparent discrepancies of results (Martín-Arévalo et al., 2013), and therefore, more investigations are needed to fully determine the extent to which a decrease in P1 component truly reflects the IOR mechanism.

In addition to modulatory effects on the P1 component, IOR has been also linked to N1 negativity, which is involved in perceptual processing, possibly by integrating activations across multiple visual areas (Di Russo et al., 2002). Like the P1 component, decrease in N1 amplitude following cued versus uncued targets was found to reflect IOR, which was also supported by the behavioural effect in a wide range of experimental tasks (Gutiérrez-Domínguez et al., 2014; Prime & Jolicœur, 2009; Prime et al., 2006; Prime & Ward, 2004;

Satel, Hilchey, Wang, Reiss, & Klein, 2014). It is important to note, however, that other studies did not reveal the modulatory effect of IOR on N1 amplitude in (Martín-Arévalo, Chica, & Lupiáñez, 2014; McDonald, Ward, & Kiehl, 1999; Van der Lubbe et al., 2005; Wascher & Tipper, 2004). Nevertheless, in their correlational analysis, Martín-Arévalo and colleagues (2016) did find a significant relationship between N1 reduction for cued targets along with stronger behavioural IOR, suggesting that IOR is indeed accompanied by an N1 decrease.

Yet, the effects of IOR on electrophysiological modulations have been shown to extend beyond early perceptual processing. One example is an Nd (negative difference) component, which is a negative ERP difference wave between cued and uncued trials in the time window around 220-300 ms since the target, typically measured at occipital sites (Eimer, 2000; McDonald et al., 1999; Prime & Ward, 2006). It has been demonstrated that Nd is related to IOR (Gutiérrez-Domínguez et al., 2014; McDonald et al., 1999; Wascher & Tipper, 2004) and some authors have proposed that Nd might be a marker of IOR which occurs independently of low-level perceptual effects (Satel et al., 2014). In turn, Wascher and Tipper (2004) suggested that Nd, measured at parietal electrodes sites, can instead, reflect the relative facilitation of cued versus uncued targets following an initial perceptual suppression, as they found a negative correlation between the Nd effect and the behavioural IOR. Yet, other studies have implicated the role of Nd in IOR (Eimer, 2000; Gutiérrez-Domínguez et al., 2014; Satel, Hilchey, Wang, Story, & Klein, 2012; Satel, Wang, Hilchey, & Klein, 2012) and therefore, their mutual interactions still need to be examined.

Finally, a later P3 component, likely reflecting decision-related processes (Polich, 2007), was also found to be involved in IOR, whereby stronger behavioural IOR effect was accompanied by more positive P3 amplitude to cued versus uncued targets (McDonald et al.,

1999; Prime & Jolicœur, 2009). However, the vast majority of studies have not tested for or reported the effects of IOR on P3 modulations and further research investigating their relationship would prove particularly informative.

Yet, whereas the aforementioned studies made claims about inhibition of previously attended locations, they mostly used a paradigm in which a target could appear in spatial coordinates occupied by surfaces. Indeed, selective attention operates not only over space-based, but also on object-based representations when prioritising and selecting relevant information in the service of adaptive behaviour (Egly, Driver, & Rafal, 1994; Jordan & Tipper, 1998; Ro & Rafal, 1999; Soto & Blanco, 2004; Tipper et al., 1991, 1999, 1997). As objects occupy spatial locations, the relative contributions of these two representations to attentional guidance is difficult to determine. Nevertheless, their modulatory effects on visual processing were a focus of several studies, including ERP investigations (He, Fan, Zhou, & Chen, 2004; He, Humphreys, Fan, Chen, & Han, 2008; Martínez et al., 2006). For example, Martínez and colleagues (2007), suggested that space- and object-based attention have the common underlying neural mechanisms as they both modulated the N1 component. However different studies found that the effects of spatial and object attentional systems are topographically distinct (He et al., 2004, 2008).

The goal of this study was to elucidate differential modulation of processing elicited by space- versus object-based attention as measured by event-related brain potentials. We contrasted the IOR response bias, by varying cue-target location and cue-target interval (SOA) to estimate sensitivity to object structure. In the space condition, no objects serving as placeholders were present, whereas in the object condition, two placeholders were located on the left and right side of the display. In our paradigm, the target could appear either at the same

location as a preceding cue (cuedON), the opposite location (uncued) or at the same visual field but different location (cuedOFF). Indeed, whereas the inhibition of return effects are strongest at the previously cued location, they spread around the cued location affecting the adjacent locations with a gradual decrease in its strength (Bennett & Pratt, 2001; Pratt, Spalek, & Bradshaw, 1999; Taylor, Chan, Bennett, & Pratt, 2015; Wascher & Tipper, 2004). In their theoretical paper, LaBerge and Brown (1989) have proposed the term 'attentional field' to describe a spatiotemporal distribution of processing resources across the visual field. Yet, the underlying inhibitory processes that determine the topography of the attentional field remain unknown. For instance, Wascher and Tipper (2004) have proposed that a gradual decrease in processing around previously attended locations/objects might stem either from the spatial gradient of inhibition in the proximity of previously cued location, or the existence of two independent inhibitory process, whereby one is linked to the cued object and the other operates in a more general fashion affecting the cued visual field.

In the current study, we aimed to differentiate between inhibitory processes involved in such object versus space attentional mechanisms with the rationale that changes in the mean amplitudes of the ERPs to target onsets across conditions may be used to infer the relative strength of the attentional field at that object/location. More specifically, we looked at the effects of cue-target locations and space/object manipulations on the modulations of well-established ERP components such as P1, N1, Nd and P3. Additionally, we performed mass univariate analyses (Groppe et al., 2011; Guthrie & Buchwald, 1991; Murray et al., 2008). In this kind of analysis, each electrode is used when contrasting conditions for each time point. The rationale behind incorporating MUA was to provide an additional statistical measure, which is more 'bias-free' as it tracks the time course of differences across conditions in all available electrodes and as such, it complements and further supports findings based on

standard waveform analysis.

We formulated the following hypotheses. If inhibition of return operates as low-level sensory process (e.g., perceptual suppression) and there are separate space and object inhibitory mechanisms, we would expect to see differential effects of space and object manipulations on P1 and N1 amplitudes for cuedON and uncued targets. Further, if these inhibitory processes spread around the previously attended location, these ERP components would be also attenuated for the cued visual field (i.e., cuedOFF targets). In turn, if space and/or object inhibition of return mechanisms are generated by other processes (e.g., sensory refractoriness and/or motor execution), different underlying functions of space and object inhibition would be primarily observed in the modulations of amplitude for Nd and P3 components for cuedON versus uncued targets. Again, a dissociable pattern of these modulations across space and object conditions for cuedOFF would be expected. Alternatively, if space and object inhibitory functions modulate cued locations/objects and adjacent locations in a united manner, we should observe no differences in electrophysiological responses for validity levels between space and object conditions. Finally, although we used two SOAs (short: 300 ms and long: 800 ms), based on our previous findings described in Chapters II-III and current literature (Chica et al., 2014; Van der Lubbe et al., 2005), we sought to observe IOR for both time intervals.

4.2. Methods

4.3.1. Participants

Twenty-four students (17 female, M_{age} = 20.83, *SD* = 3.75, 1 left-handed) from the Psychology Department at Bangor University took part in the study for course credit. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). All participants had normal (or corrected-to-normal) vision. The study was conducted under School of Psychology Ethics Protocol.

4.3.2. Apparatus and Stimuli

Data acquisition was conducted using a PC and 1024 x 768 Mitsubishi Diamond Pro 2060u (120 Hz, 40 cm) monitor. The viewing distance was fixed at 57 cm using a chinrest. A standard QWERTY PC keyboard was used for the responses. The SR 1000 eye tracker (1000 Hz) was used to monitor central fixation. A trial was automatically terminated if the fixation point moved outside of a non-visible circular ROI (3 degrees of visual angle) around the fixation point. The experiments were programmed in the Experiment Builder (SR Research Ltd.) synchronised with EEG BioSemi (Biosemi Inc., Amsterdam, The Netherlands) for the EEG data acquisition.

The fixation point was a red cross (RGB: 255, 0, 0) of 13 x 13 pixels which equals 0.5 degrees of visual angle on a 1024 x 786 monitor (of 40 cm horizontal dimension) viewed from 57cm where the vertical and horizontal bars in the cross are each 2 pixels wide. The fixation cross was situated in the centre of the display. The background was grey (RGB: 127,127,127). The display consisted of two cues – a square of 13 x 13 pixels white (RGB 255, 255, 255) which equals 0.5 degrees of visual angle. Cues were positioned on the horizontal line 5 degrees of visual angle from the central fixation on the right or left side. Targets were a square 13 x 13

pixels black (RGB: 0, 0, 0). The target could appear in one of four locations – in the same location as the preceding cue (cuedON), on the same side but different location as a cue (cuedOFF) or at the opposite side as a cue (uncued). Importantly, all locations were kept equidistantly 5 degrees of visual angle from the central fixation.

In the object condition, two black square outlines (RGB: 0, 0, 0) of 39 x 39 pixels which equals 1.5 degrees if visual angle, were present on the right and left side of the display 5 degrees of visual angle from the central fixation. Cues, as well as targets in cuedON and uncued conditions, would appear at the centre of the placeholders. In the space condition, no placeholders were present (Figure 1).

4.3.3. Procedure

Each trial was initiated by the participant by pressing the spacebar after which the blue cross turned red (Fig. 12). The fixation point remained at the centre of the screen for 1,000 ms. Next, a cue appeared randomly at the right or left side for 100 ms. Then, after 300 ms or 800 ms after the cue onset (stimulus onset asynchrony, SOA), a target appeared at one of four possible locations for 1,000 ms which was also a response window. Trials in which a target appeared on the same side and same location as a cue (i.e., cue right/target right) were considered cuedON. Trials in which a target appeared on the same side but different location (either up or down) than a cue were classified as cuedOFF (e.g., cue right/target right up), whereas trials in which a target appeared at the opposite side as a cue (i.e., cue right/target left) were considered uncued. The trial ended with a jittered interval during which a grey display was presented (400 ms-1,000 ms). Participants' task was to detect the target as quickly as possible by pressing the spacebar while minimising errors. Presentation order was randomised within subjects.

Participants were randomly allocated to either the space or object group. There were 12

participants in each group. SOA (short, long) was varied between blocks (Eimer, 2000), with three successive blocks with long SOA and then short SOA, counterbalanced across subjects, presented in randomised order. Six blocks were run with 214 trials in each one, resulting in 1,284 trials altogether. For each condition, 10% of trials were catch trials with no target present. Altogether, there were 144 trials for each of the conditions with the exception of cuedOFF condition with 288 trials for each of the levels. Each block lasted approximately 15 min. A training session was provided with 18 trials to familiarise participants with the task.

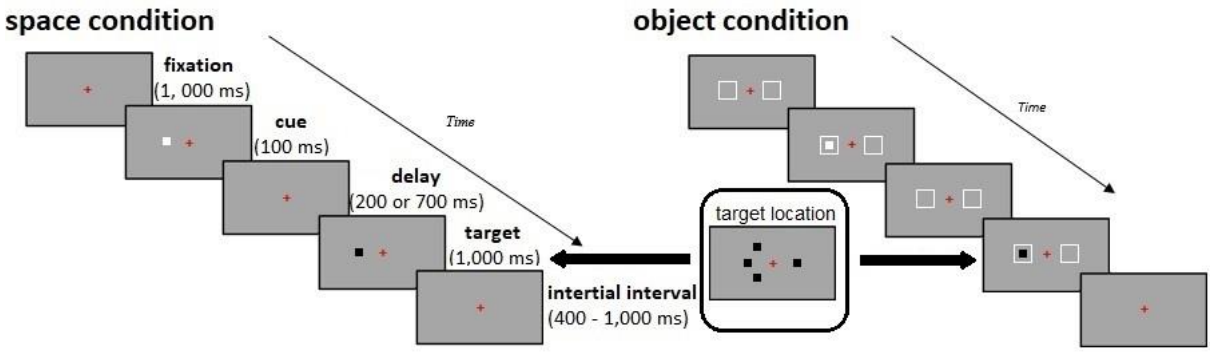


Figure 12. Illustration of trial sequence in space and object conditions. In the object condition, two placeholders were present on the display. A fixation cross appeared for 1,000 ms. Then, a cue was presented randomly either on the left or right side. After a 200 or 700 ms, a target would appear for 1,000 ms. The target would appear in one of four locations: the same location as the cue (cuedON), the opposite side as the cue (uncued), or in the same side as the cue but up or down relative to the cue (cuedOFF). The intertrial interval (ITI) was randomised between 400-1,000 ms. Participants' task was to detect the target as quickly as possible while minimising errors. The figure illustrates a cued trial.

4.3.4. Data analysis

4.2.4.1. Behavioural analysis

The mean response time (RT) in ms was calculated separately for space and object conditions at the 300 and 800 ms SOA and for cuedON, cuedOFF and uncued conditions. Only data from correct trials were included in the analyses; errors (false positives: responses to no-target trials), omissions and trials with RTs less than 100 ms were excluded from the analysis.

A 2 (object presence: space, object) × 3 (validity: cuedON, cuedOFF, uncued) × 2 (SOA: short, long) mixed factorial design was used, with object presence as a between-subjects factor and SOA and validity as within-subjects factors. Bonferroni adjustments were made for pairwise comparisons. Effect sizes were calculated by using partial eta-squared (η_p^2). The Greenhouse–Geisser correction was used if the sphericity assumption was violated (Jennings and Wood, 1976).

4.2.4.2. Electrophysiological recording and processing

The electroencephalograph (EEG) was recorded using the ActiveTwo Biosemi EEG system (Biosemi Inc., Amsterdam, The Netherlands). There were 128 Ag/AgCl electrodes placed on an ECI cap (Electrocap International, Ohio, USA). The electrooculogram (EOG) was recorded using two electrodes lateral to the external canthi in order to measure horizontal eye movements, and by placing electrodes upper and beneath the right eye to measure vertical eye movements and blinks. All activity from all electrodes was sampled at a rate of 1,024 Hz. The signals were re-referenced offline to an average reference. Offline 30 Hz low-pass (filter roll-off: 24 dB/oct) and 0.1 Hz high-pass filters (filter roll-off: 12 dB/oct) were applied to the data. Only correct trials without ocular or muscle artifacts were included in the analyses.

Eye movements and blinks were corrected using the ICA protocol in BrainVision

Analyser 2 software. Following the ICA correction, continuous EEG data was segmented starting from -100 ms prior to target onset to 750 ms after target onset. Segmented data was then visually inspected and trials containing ocular and muscle artifacts were rejected. We used a 100-ms pre-stimulus interval for the baseline correction and the pre-processed data was then used to generate the grand averages.

Separate averaged ERP waveforms were created for each of twelve conditions (space/short/uncued, space/short/cuedON, space/short/cuedOFF, space/long/uncued, space/long/cuedON, space/long/cuedOFF, object/short/uncued, object/short/cuedON, object/short/cuedOFF, object/long/uncued, object/long/cuedON and object/long/cuedOFF). Table 7 presents the mean number of accepted epochs per condition.

Table 7
The mean number of epochs per each condition

	SOA	Uncued	CuedON	CuedOFF
Space	Short	136.17	136.25	170.83
	Long	136.33	136.92	272.75
Object	Short	137	137.50	273.34
	Long	132.83	133.25	265.41

4.2.4.3. EEG analyses

Four early ERP components: P1, N1, Nd and P3, were identified based on the topography and latency characteristics of the grand average ERPs time-locked to target presentation. Specifically, the latency of peak amplitude was used to define epochs for analyses of five components: P1 (100–140 ms; Peak latency (B7) 120 ms; N1 (170-210 ms; Peak latency (A10) 190 ms); Nd (220–260 ms; Peak latency (A7) 240 ms) and P3 (320–450 ms); Peak latency (A1)

385 ms.

Mean amplitudes of standard waveforms for P1, N1, and Nd components were analysed based on averaged activity from symmetrical clusters extracted over nine adjacent posterior electrodes in right: A32, B3, B4, B5, B6, B7, B8, B10, B11 and left hemispheres: A5, A6, A7, A8, A9, A10, A11, D31, D32. These electrode sites correspond to CP2, P4, P6, P8, PO8 and CP1, P3, P5, P7, PO7 of the extended 10–20 system.

The analysis of the P3 component was based on averaged activity from midline and symmetrical clusters extracted over eighteen electrodes spanning frontal to parietal sites: A32, B3, B4, A5, A6, A7, A19, A1, D19, B22, C21, D3, C3, C23, D2, C2, D12 and B31. These electrode sites correspond to F3, F4, Fz, C3, C4, Cz, CP3, CP4, CPz, P3, P4, Pz of the extended 10–20 system.

A mixed-factorial ANOVA was performed to compare mean amplitudes separately for each of the extracted four components' time windows with object presence (space, object) as a between-subject factor and validity (cuedON, cuedOFF, uncued) and SOA (short, long) as within-subject factors.

Bonferroni adjustments were made for pairwise comparisons. Effect sizes were calculated using partial eta-squared (η_p^2).

4.2.4.4. Mass Univariate analyses

In addition to analysing standard ERP components, Mass Univariate analyses (Groppe et al., 2011; Guthrie & Buchwald, 1991; Murray et al., 2008) were conducted to complement the standard waveform analyses. Successive pairwise *t*-tests for each data point between -100 and 750 ms were performed. In order to avoid type I error, *t*-values were found to be reliable if they remained significant for twelve consecutive time frames (≥ 12.29 ms). An a priori

criterion for significance equalled $p < .01$ (two-tailed) in at least five neighbouring electrodes.

The mass univariate analyses were conducted to further contrast cuedON versus uncued and cuedOFF versus uncued conditions across all 128 electrodes for two SOA (short, long) in space and object conditions separately. In order to compare significant differences between experimental manipulations, a time series plot illustrating the frequency distribution of significant contrasts across conditions was plotted. Then, these data were analysed in a non-parametric Friedman test with cueing effects contrasts (cuedON – uncued, cuedOFF – uncued) and SOA (short, long) for each time window of a relevant component (P1, N1, Nd, P3) for space and object conditions separately.

4.3. Results

4.4.1. Behavioural results

Reaction times for all experimental conditions are presented in Table 8. The rate of omission was approximately 4%, whereas the percentage of responses faster than 100 ms was approximately 2%.

There was a main effect of validity on RT, $F(2, 44) = 54.16$, $p < .001$, $\eta_p^2 = .71$. Response times were significantly slower (i.e., stronger IOR) for cuedON versus uncued ($p < .001$), cuedOFF versus uncued ($p = .007$) as well as cuedON versus cuedOFF trials ($p < .001$). There was also a main effect of SOA, $F(1, 22) = 32.18$, $p < .001$, $\eta_p^2 = .59$, with faster response times after short than long interval. Importantly, there was a Validity × Object Presence interaction, $F(2, 44) = 4.89$, $p = .012$, $\eta_p^2 = .18$. Cueing effects were more negative in object versus space condition ($p = .017$). The main effect of object presence was not significant, $F(1, 22) = 1.63$, $p = .22$, $\eta_p^2 = .07$. There was no SOA × Object Presence, $F(1, 22) = 0.18$, $p = .675$, $\eta_p^2 = .01$, Validity × SOA, $F(2, 44) = 1.31$, $p = .281$, $\eta_p^2 = .06$, nor Validity × SOA × Object Presence, $F(2, 44) = 0.15$, $p = .859$, $\eta_p^2 = .01$ interactions.

Figure 13 presents cueing effects in each experimental condition. First, we compared RTs to cued and uncued targets with a t-test separately for space and object as well as short and long SOA conditions. In the space condition, the classic IOR (cuedON versus uncued) was found for short ($p = .014$) and long SOA ($p < .001$). In turn, the IOR to adjacent locations (cuedOFF versus uncued) was found for long ($p = .005$) but not short SOA ($p = .174$). Similarly, in the object condition, the classic IOR (cuedON versus uncued) was observed for short ($p < .001$) and SOA 650 ms ($p < .001$). Again, the IOR for adjacent targets (cuedOFF versus uncued) was found only for long SOA ($p = .007$) with a marginal effect for short SOA ($p = .076$). The magnitude of IOR was computed by subtracting performance on

uncued from cued (i.e., cuedON and cuedOFF) trials. The analysis showed stronger inhibition to object versus space condition when orienting to the same location (i.e., uncued – cuedON) in short (p = .049) and long (p = .025) SOA trials, as well as when orienting to adjacent locations (i.e., uncued – cuedOFF) in short (p = .050) and long (p = .002) trials.

Table 8
Mean reaction time (ms) and standard error

	SOA	Uncued	CuedON	CuedOFF
Space	Short	304 (21)	324 (20)	309 (20)
	Long	336 (16)	356 (16)	348 (16)
Object	Short	323 (15)	360 (13)	331 (15)
	Long	363 (15)	398 (17)	374 (15)

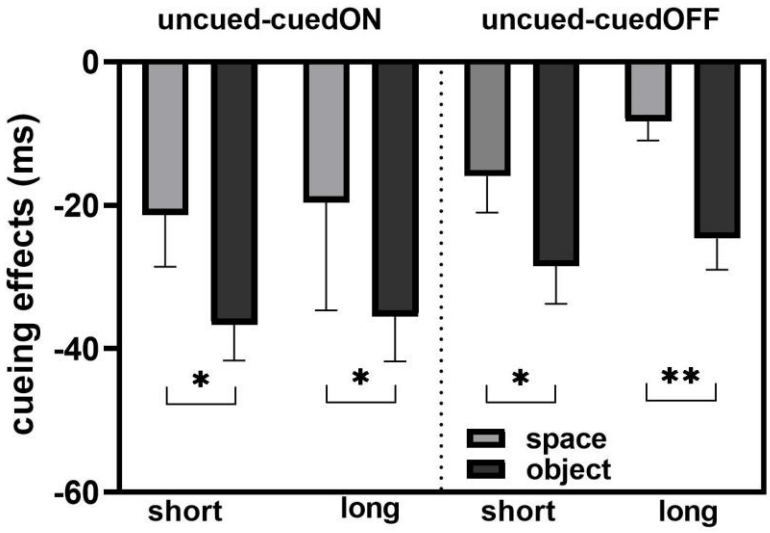


Figure 13. Mean cueing effect (uncued – cued RT) and standard error for SOA 300 and 800 in space and object conditions. The IOR was observed for all conditions with the exception of adjacent targets (uncued-cuedOFF) at short SOA. Importantly, stronger IOR was present for object than space conditions.

4.4.2. ERP results

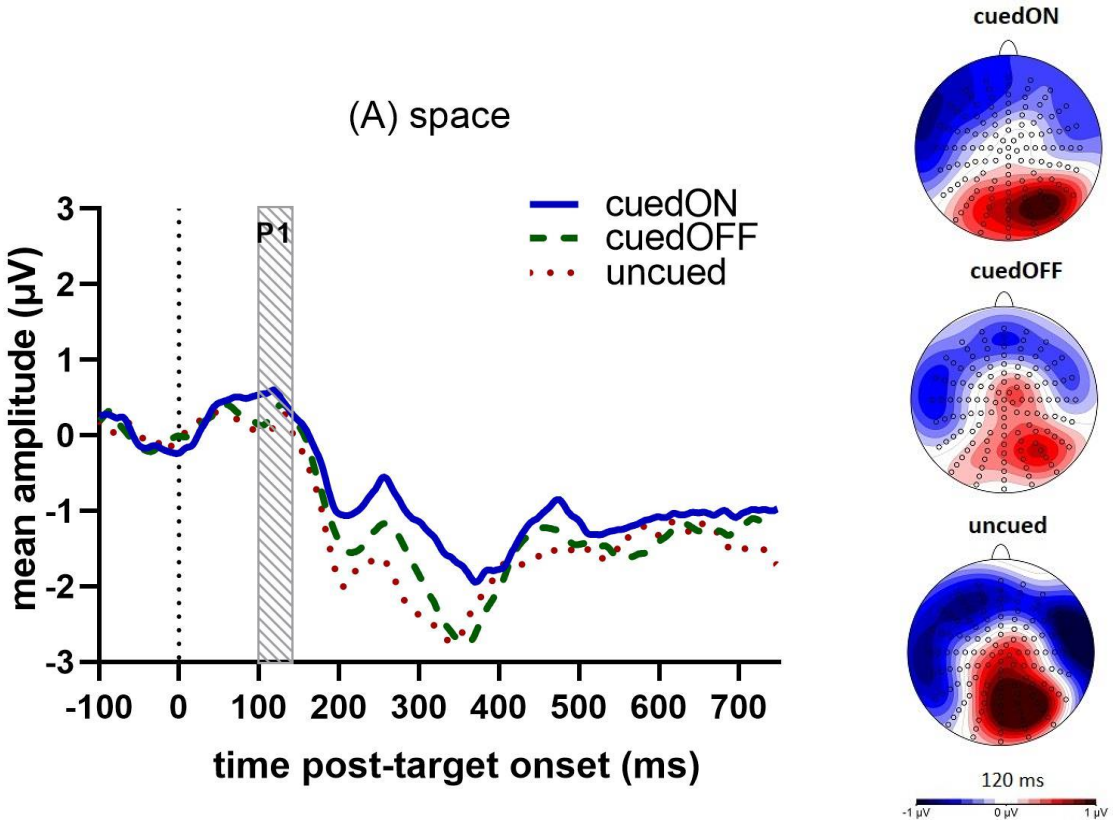
The goals of the ERP analyses were threefold: (1) to establish whether ERPs were differentially modulated by space versus object attentional systems; (2) to determine whether ERPs were sensitive to cueing effects (e.g., event-related brain responses to previously cued and uncued target locations) across different timings; (3) to elucidate whether the ERPs related to cueing effects were further modulated by space versus object attentional deployment.

4.3.2.1. Event-related brain responses to space versus object cueing effects

4.3.2.1.1. Standard Waveform Analyses

P1: 100 to 140 ms time window

Mean ERP amplitudes in the 100 to 140 ms time window were compared for each condition. The analysis showed a marginally significant Validity × Object Presence interaction, $F(2, 44) = 3.13$, $p = .054$, $\eta_p^2 = .12$ (see Figure 14). In object present condition, P1 was significantly reduced in cuedON trials in comparison with uncued ($p = .013$) and cuedOFF trials ($p = .013$). However, no such a pattern of data was present in the space condition. These findings are consistent with behavioural results with faster response times to uncued and cuedOFF versus cuedON trials (i.e., stronger IOR), especially in the object present condition (see Behavioural results section). No other main effects or interactions were observed.


(A) space
cuedON
cuedOFF
uncued
P1
mean amplitude (μV)
3
2
1
0
-1
-2
-3
-100
0
100
200
300
400
500
600
700
time post-target onset (ms)
cuedON
cuedOFF
uncued
120 ms
-1 μV
0 μV
1 μV

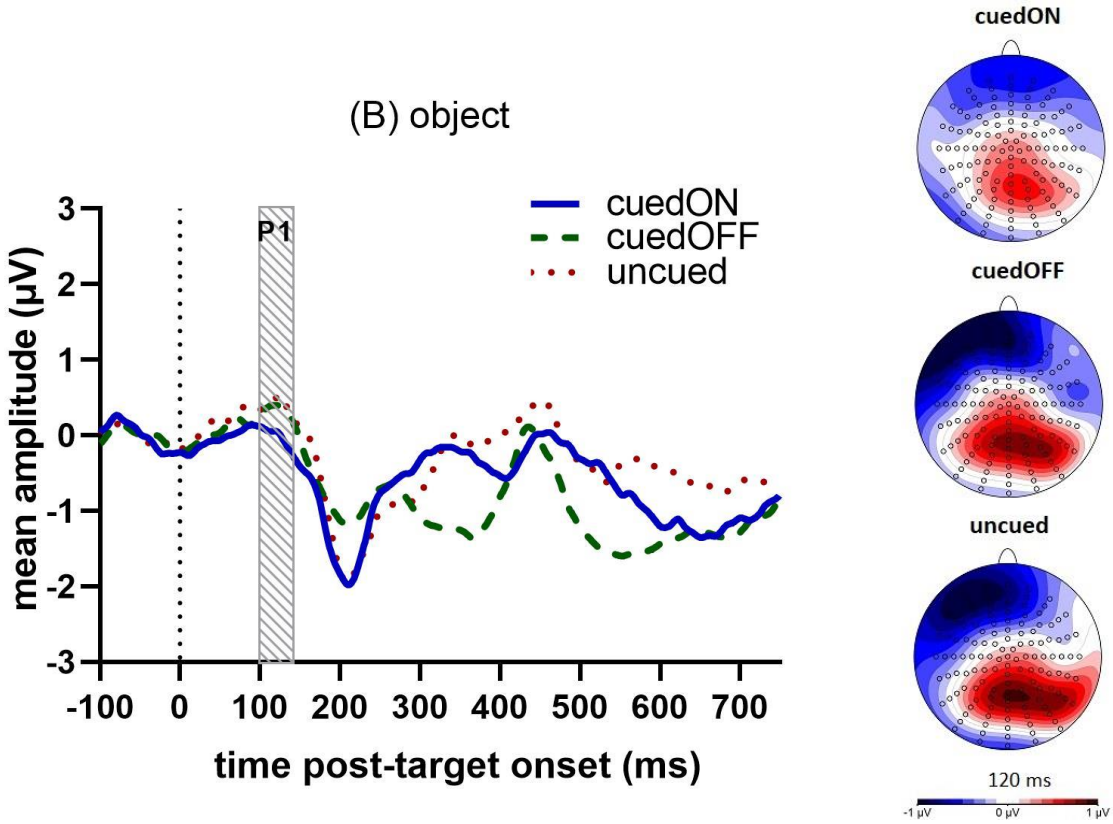
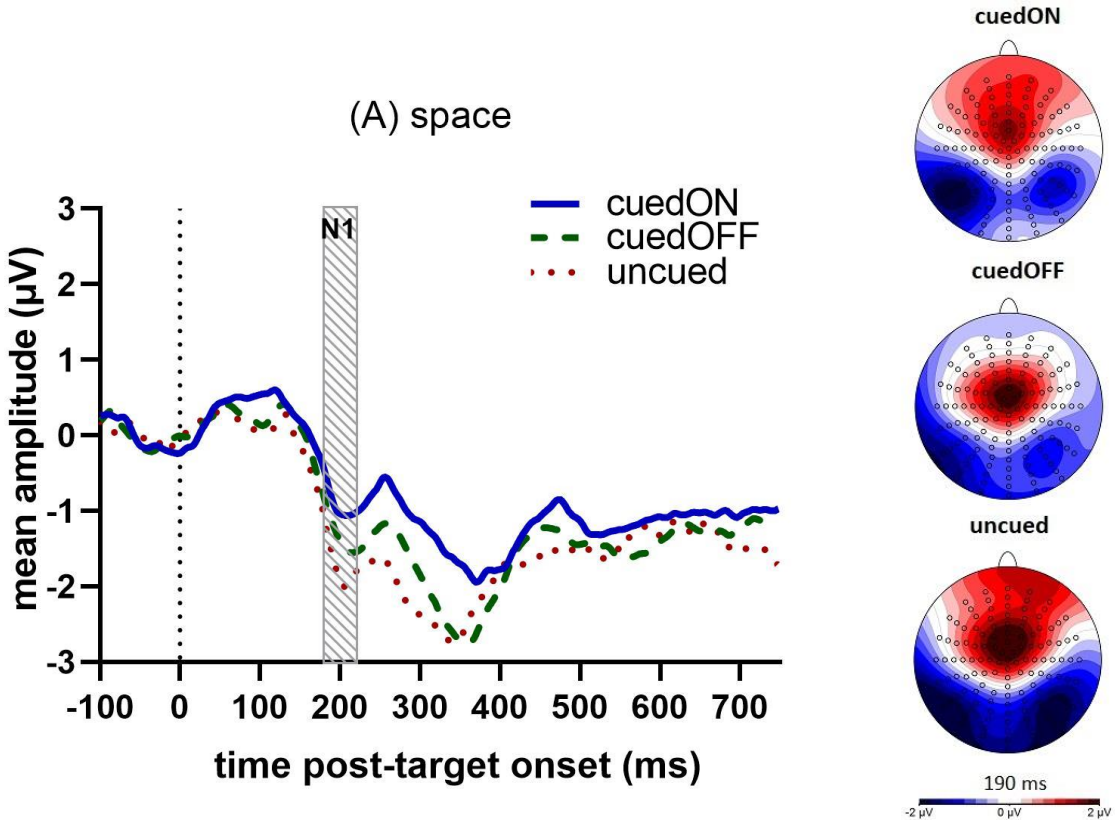
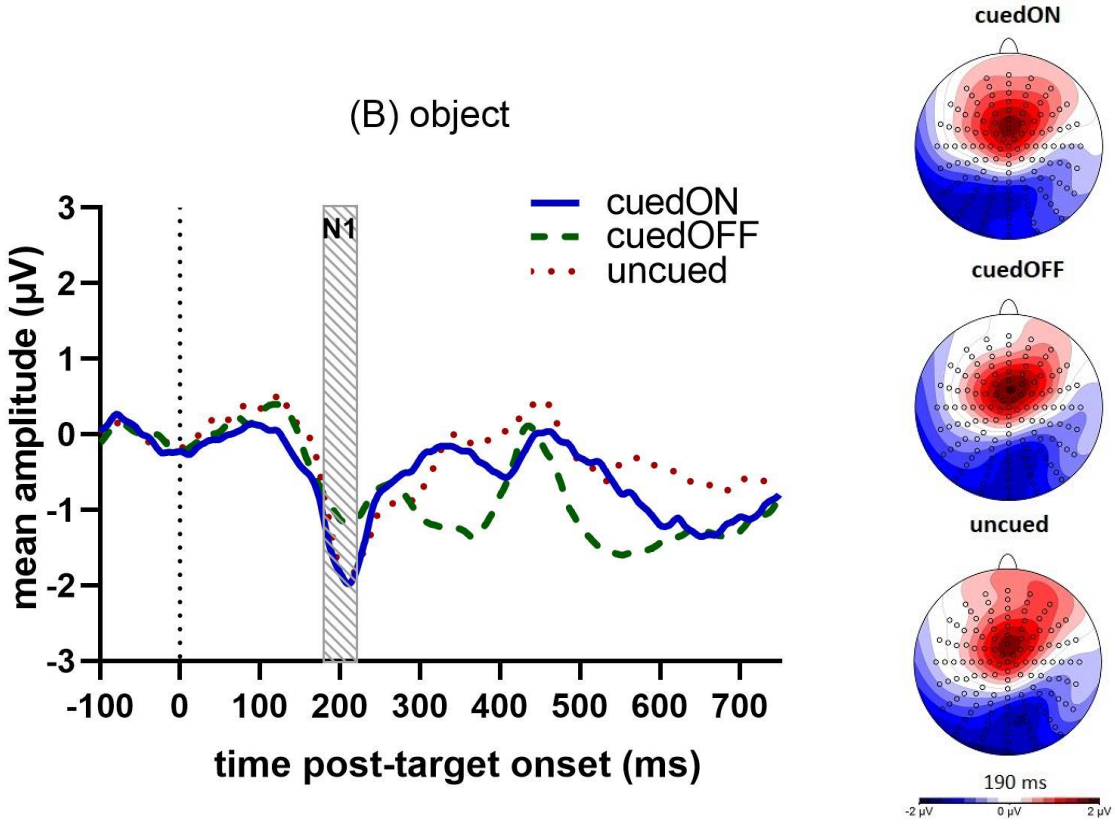


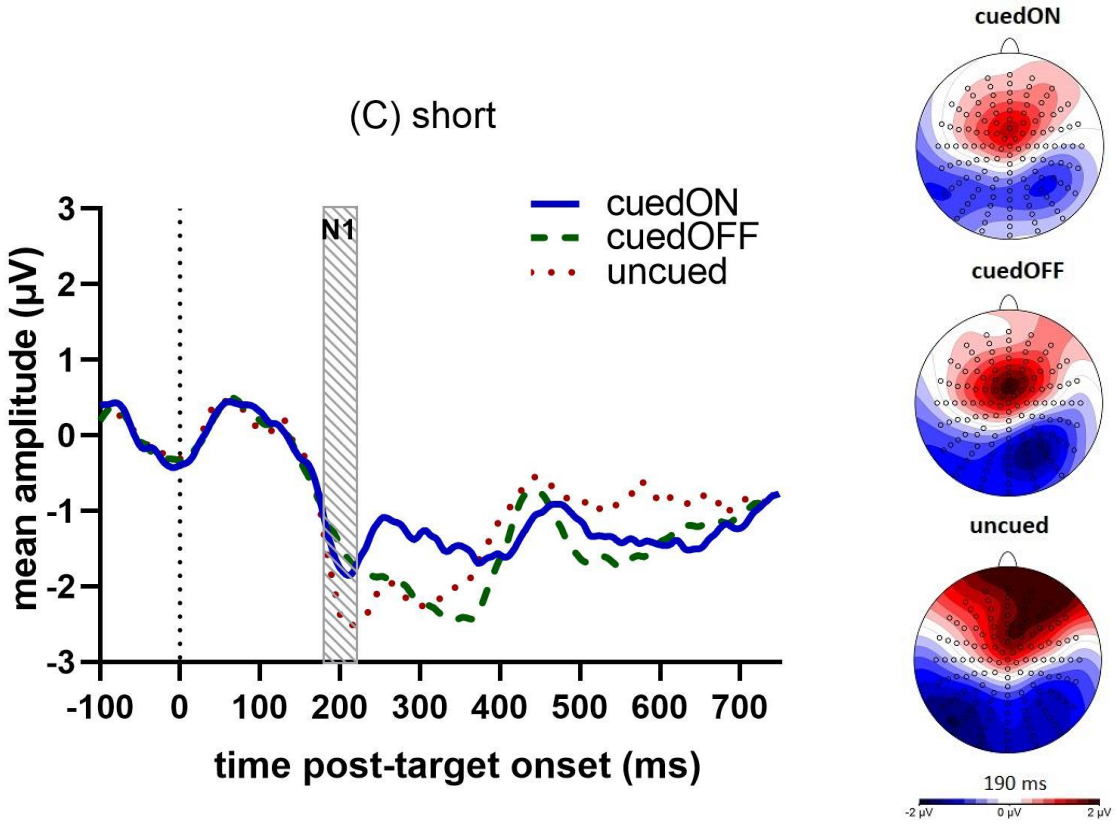
Figure 14. Grand average waveforms for the P1 component (striped area) across validity conditions at the electrode cluster encompassing P7, PO7, P8 and PO8 for (A) space and (B) object groups. Scalp topographies of attentional modulations on P1 (100 – 140 ms) are shown in the right panel (data were referenced to the average of the electrodes). Red reflects positive voltage and blue reflects a negative voltage.

N1: 170 to 210 ms time window

Mean ERP amplitudes in the 170 to 210 ms time window were compared for each condition. Again, the results revealed a significant Validity × Object Presence interaction, $F(2, 44) = 4.17$, $p = .022$, $\eta_p^2 = .16$. N1 negativity was more pronounced for cuedON than cuedOFF trials ($p = .008$) and marginally more pronounced for uncued than cuedOFF trials ($p = .089$) when object was present but it was not the case in space condition for neither cuedON versus cuedOFF trials ($p = .219$) nor uncued versus cuedOFF trials ($p = .850$) (see Figure 15A and 15B). Also, there was a Validity × SOA interaction, $F(2, 44) = 3.74$, $p = .032$, $\eta_p^2 = 15$. For short SOA, the amplitude was more negative in uncued than cuedOFF trials ($p = .011$) but it was not the case for long SOA trials ($p = .762$) (see Figure 15C and 15D). There was no main effect of SOA, $F(1, 22) = 3.28$, $p = .084$, $\eta_p^2 = .13$, validity, $F(2, 44) = 1.04$, $p = .36$, $\eta_p^2 = .05$, or object presence, $F(1, 22) = 0.04$, $p = .842$, $\eta_p^2 = .002$, nor a SOA × Object Presence interaction, $F(1, 22) = 0.02$, $p = .877$, $\eta_p^2 = .001$.


(A) space
cuedON
cuedOFF
uncued
N1
mean amplitude (μV)
time post-target onset (ms)
cuedON
cuedOFF
uncued
190 ms
-2 μV
0 μV
2 μV


(B) object
cuedON
cuedOFF
uncued
N1
mean amplitude (μV)
time post-target onset (ms)
cuedON
cuedOFF
uncued
190 ms
-2 μV
0 μV
2 μV


(C) short
cuedON
cuedOFF
uncued
N1
mean amplitude (μV)
3
2
1
0
-1
-2
-3
-100
0
100
200
300
400
500
600
700
time post-target onset (ms)
cuedON
cuedOFF
uncued
190 ms
-2 μV
0 μV
2 μV

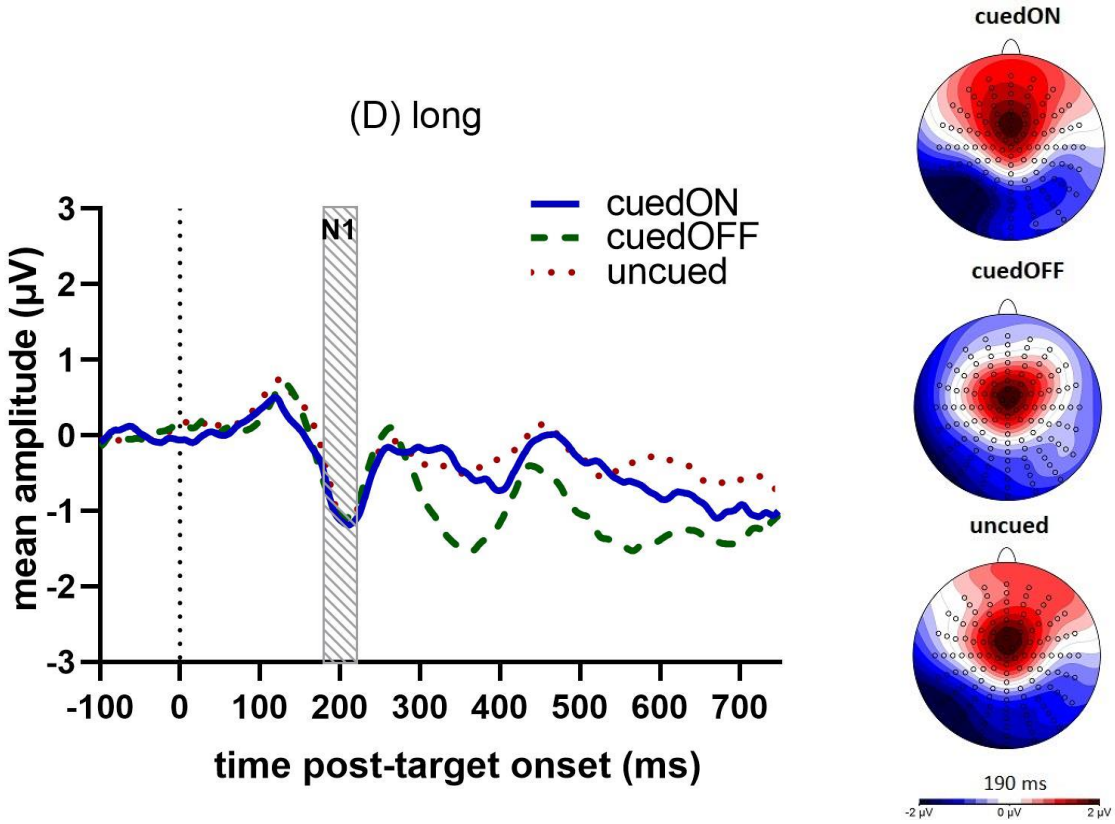
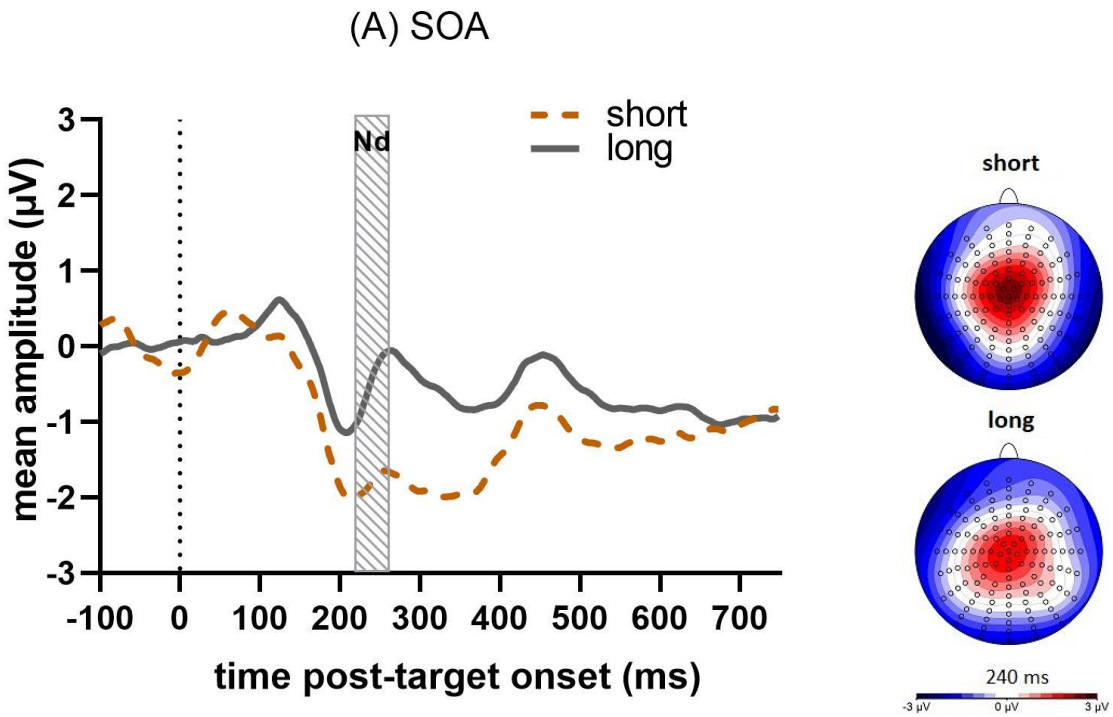
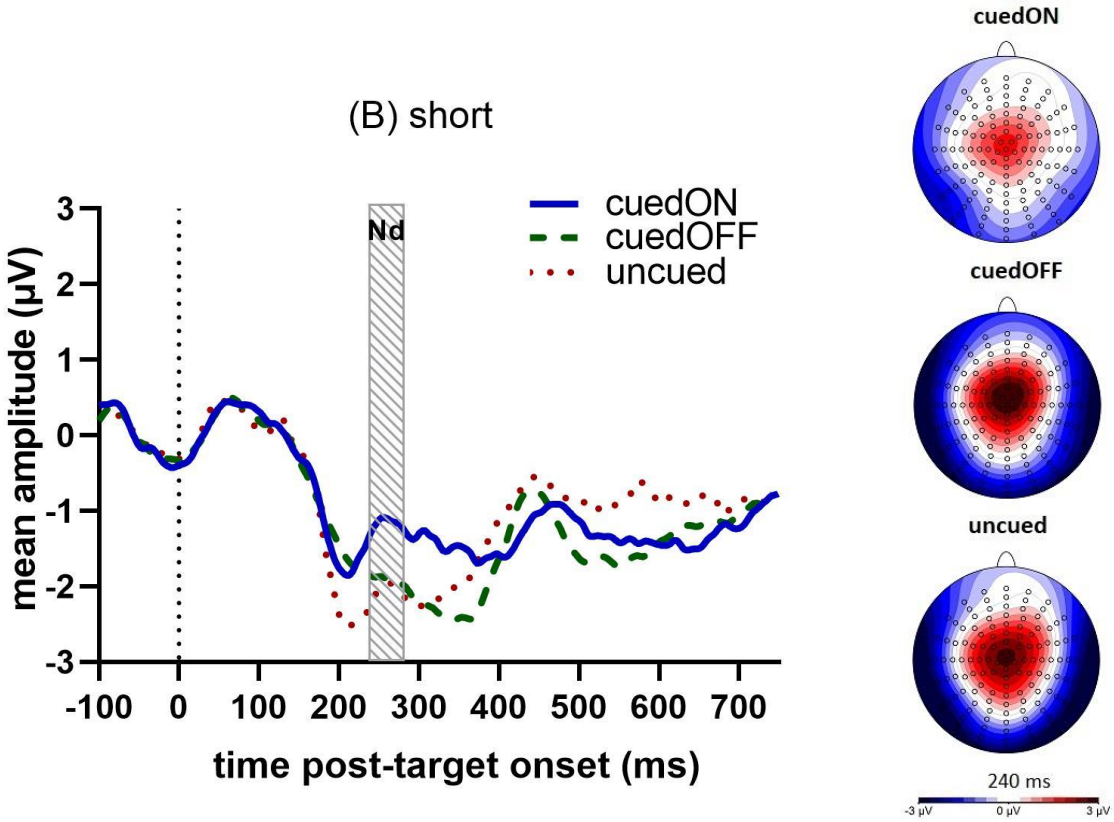


Figure 15. Grand average waveforms for the N1 component (striped area) across validity conditions at the electrode cluster encompassing P7, PO7, P8 and PO8 for (A) space and (B) object groups and short (C) and long (D) SOA. Scalp topographies of N1 modulations (170 – 210 ms) are shown in the right panel (data were referenced to the average of the electrodes). Red reflects positive voltage and blue reflects a negative voltage.

Nd: 220 to 260 ms time window

Mean ERP amplitudes in the 220 to 260 ms time window were compared for each condition. The analysis revealed a main effect of SOA, $F(1, 22) = 10.63$, $p = .004$, $\eta_p^2 = .33$. Nd was more negative in short versus long SOA (Fig.16A). This effect was further explained by Validity × SOA interaction, $F(2, 44) = 4.38$, $p = .018$, $\eta_p^2 = 17$. Nds were larger following uncued versus cuedON targets in short trials ($p = .043$) but not in long trials ($p = .466$) (Fig. 16B and 16C). There was no main effect of validity, $F(2, 44) = 0.57$, $p = .569$, $\eta_p^2 = .03$, object presence, $F(1, 22) = 0.02$, $p = .887$, $\eta_p^2 = .001$, nor a SOA × Object Presence interaction, $F(1, 22) = 0.01$, $p = .999$, $\eta_p^2 = .000$, or Validity × Object Presence interaction, $F(2, 44) = 1.56$, $p = .222$, $\eta_p^2 = .07$.




(B) short
cuedON
cuedOFF
uncued
Nd
mean amplitude (μV)
3
2
1
0
-1
-2
-3
-100
0
100
200
300
400
500
600
700
time post-target onset (ms)
cuedON
cuedOFF
uncued
240 ms
-3 μV
0 μV
3 μV

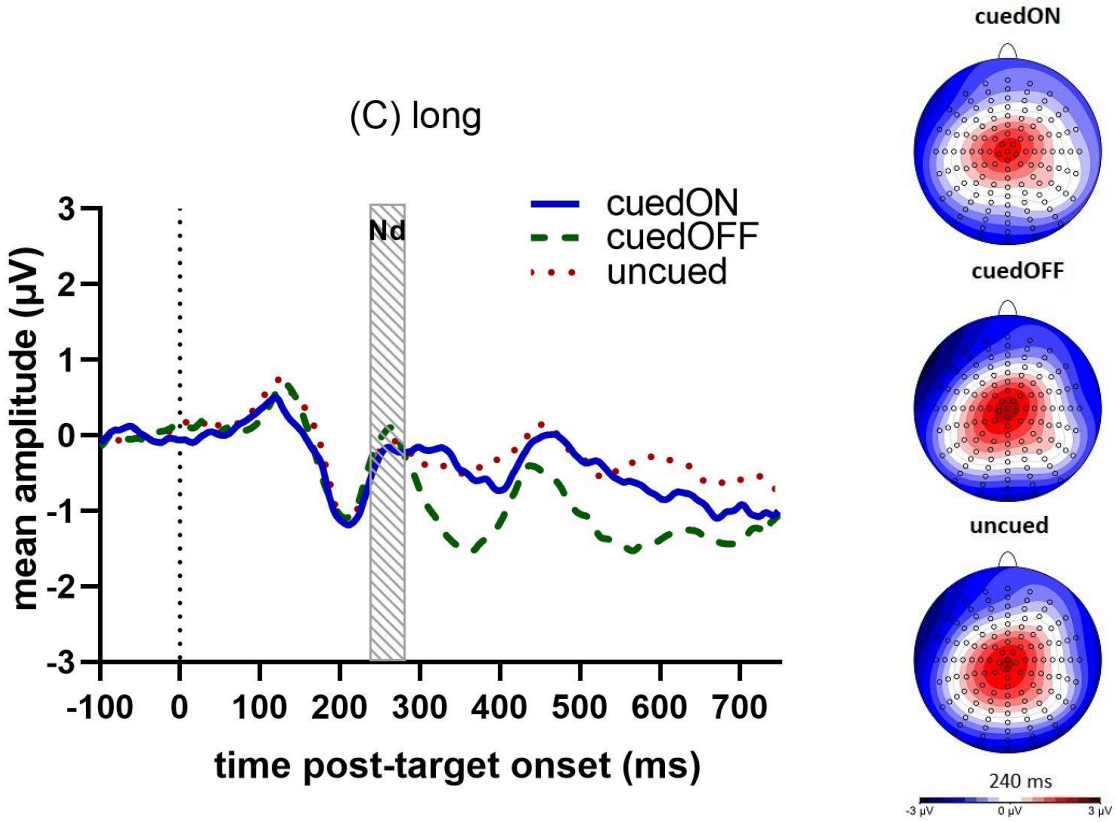
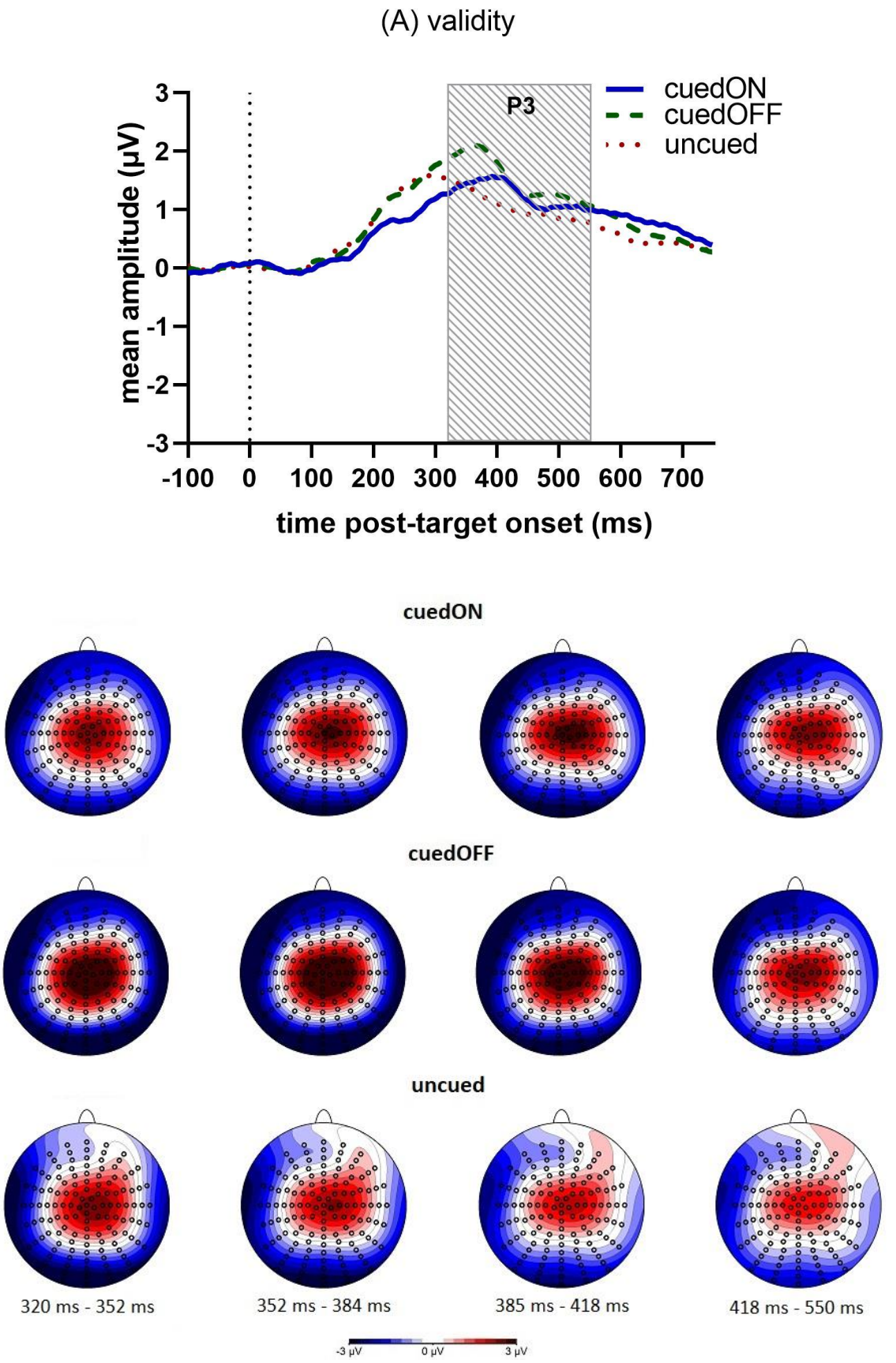
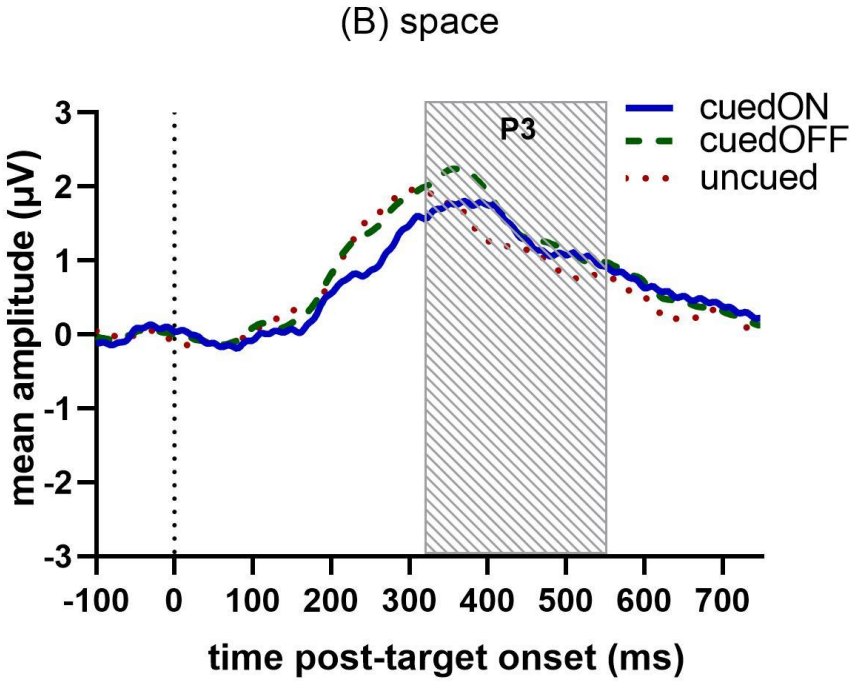


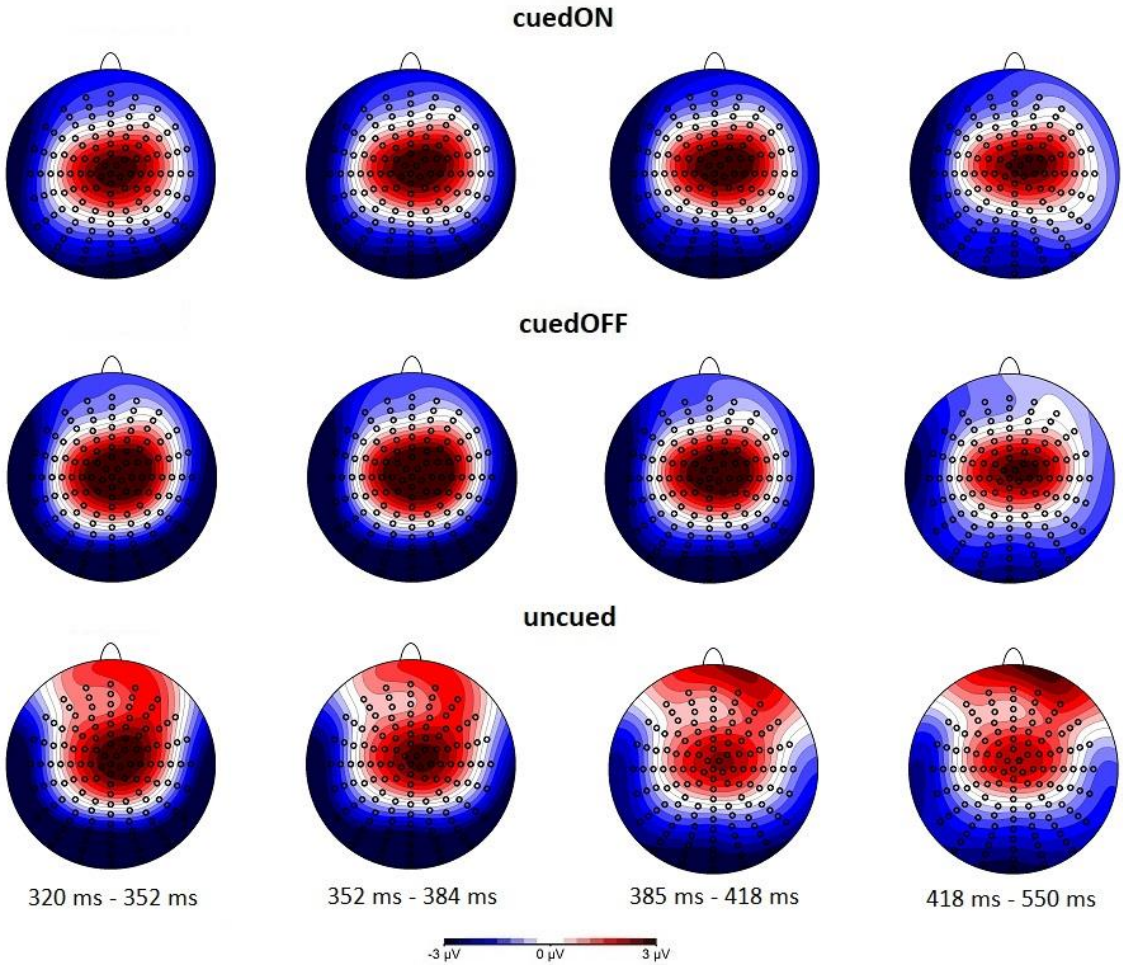
Figure 16. Grand average waveforms for the Nd component (striped area) for two SOA conditions (A) and for each validity level across (B) space and (C) object conditions at the electrode cluster encompassing P7, PO7, P8 and PO8. Scalp topographies of Nd component (220 – 260 ms) are shown in the right panel (data were referenced to the average of the electrodes). Red reflects positive voltage and blue reflects a negative voltage.

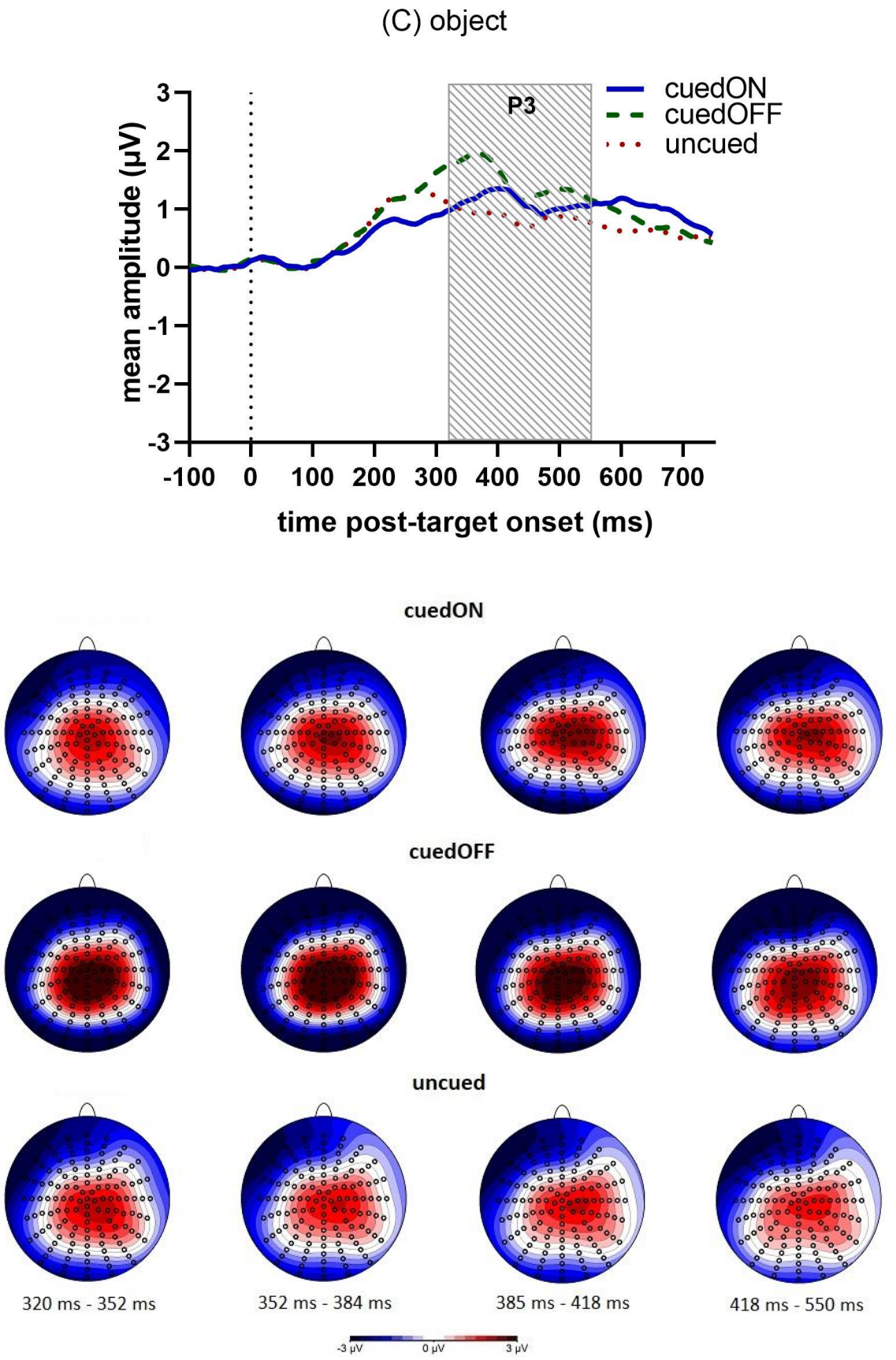
P3: 320 to 450 ms time window

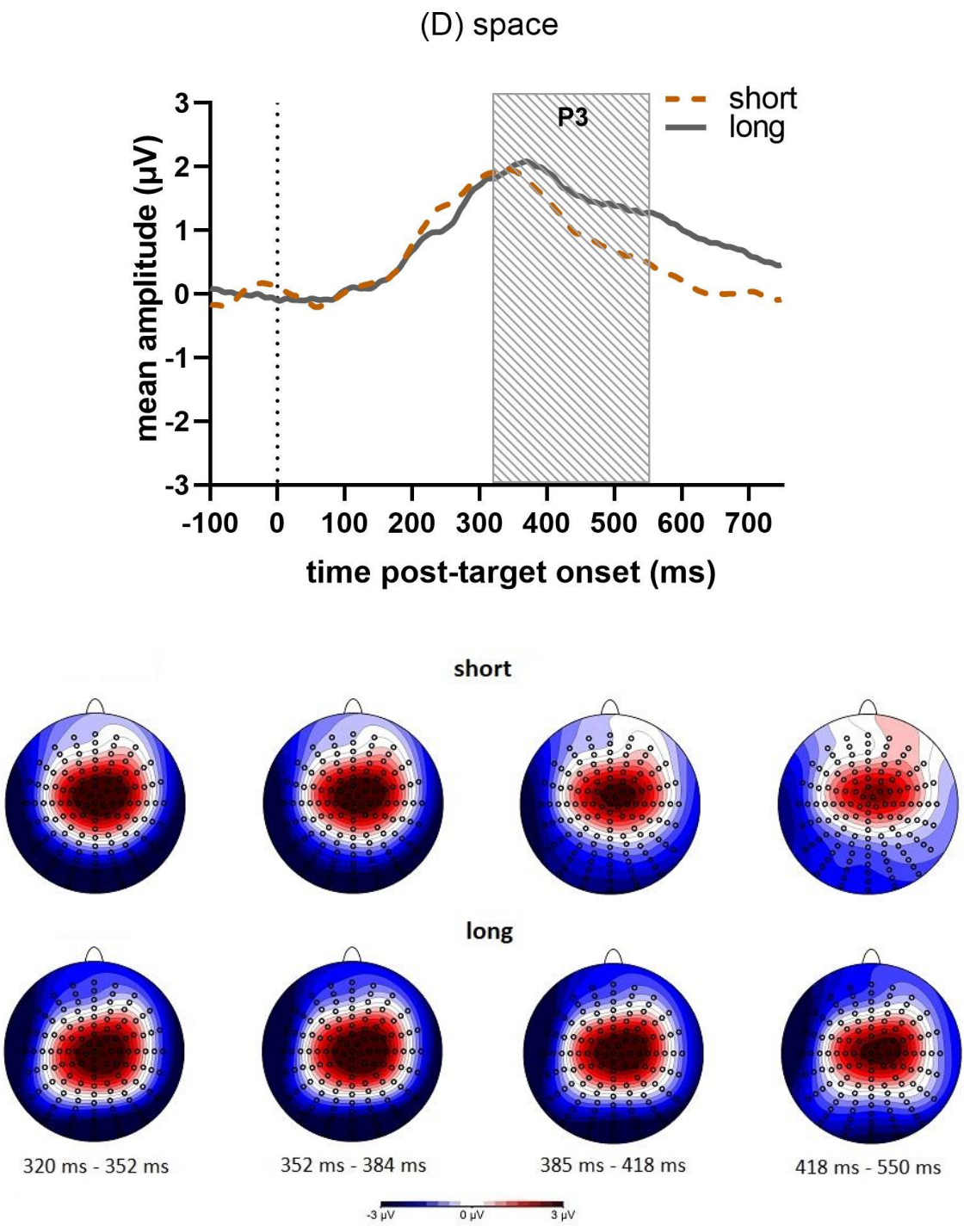
Mean ERP amplitudes in the 320 to 450 ms time window were compared for each condition. The analysis revealed a main effect of validity $F(2, 44) = 19.26$, $p < .001$, $\eta_p^2 = .47$. The amplitude was greater for cuedOFF than cuedON ($p < .001$) and uncued ($p < .001$) conditions. Importantly, there was a Validity × Object Presence interaction, $F(2, 44) = 3.90$, $p = .028$, $\eta_p^2 = .15$. In space condition, P3 positivity was increased for cuedOFF versus cuedON ($p = .052$) as well as cuedOFF versus uncued ($p = .026$) but not in cuedON versus uncued condition ($p = .755$). In turn, in object conditions all above contrasts were statistically significant, with greater positivity for cuedOFF versus cuedON ($p < .001$), cuedOFF versus uncued ($p < .001$) and cuedON versus uncued condition ($p = .026$). There was also a SOA × Object Presence interaction, $F(1, 22) = 13.87$, $p = .001$, $\eta_p^2 = .39$. In space condition, the amplitude was enhanced for long than short trials ($p = .026$), whereas in object condition this pattern reversed yielding more positive amplitudes for short rather than long trials ($p = .009$). There was no main effect of SOA, $F(1, 22) = 0.13$, $p = .725$, $\eta_p^2 = .01$, object presence, $F(1, 22) = 0.66$, $p = .425$, $\eta_p^2 = .03$, nor a SOA × Validity interaction, $F(2, 44) = 0.84$, $p = .437$, $\eta_p^2 = .04$. See Figure 17 for illustration of observed effects.


(A) validity
P3
cuedON
cuedOFF
uncued
mean amplitude (μV)
3
2
1
0
-1
-2
-3
-100
0
100
200
300
400
500
600
700
time post-target onset (ms)
cuedON
cuedOFF
uncued
320 ms - 352 ms
352 ms - 384 ms
385 ms - 418 ms
418 ms - 550 ms
-3 μV
0 μV
3 μV


(B) space
P3
cuedON
cuedOFF
uncued
mean amplitude (μV)
3
2
1
0
-1
-2
-3
-100
0
100
200
300
400
500
600
700
time post-target onset (ms)


cuedON
cuedOFF
uncued
320 ms - 352 ms
352 ms - 384 ms
385 ms - 418 ms
418 ms - 550 ms
-3 μV
0 μV
3 μV


(C) object
P3
cuedON
cuedOFF
uncued
mean amplitude (μV)
3
2
1
0
-1
-2
-3
-100
0
100
200
300
400
500
600
700
time post-target onset (ms)
cuedON
cuedOFF
uncued
320 ms - 352 ms
352 ms - 384 ms
385 ms - 418 ms
418 ms - 550 ms
-3 μV
0 μV
3 μV


(D) space
P3
short
long
mean amplitude (μV)
3
2
1
0
-1
-2
-3
-100
0
100
200
300
400
500
600
700
time post-target onset (ms)
short
long
320 ms - 352 ms
352 ms - 384 ms
385 ms - 418 ms
418 ms - 550 ms
-3 μV
0 μV
3 μV

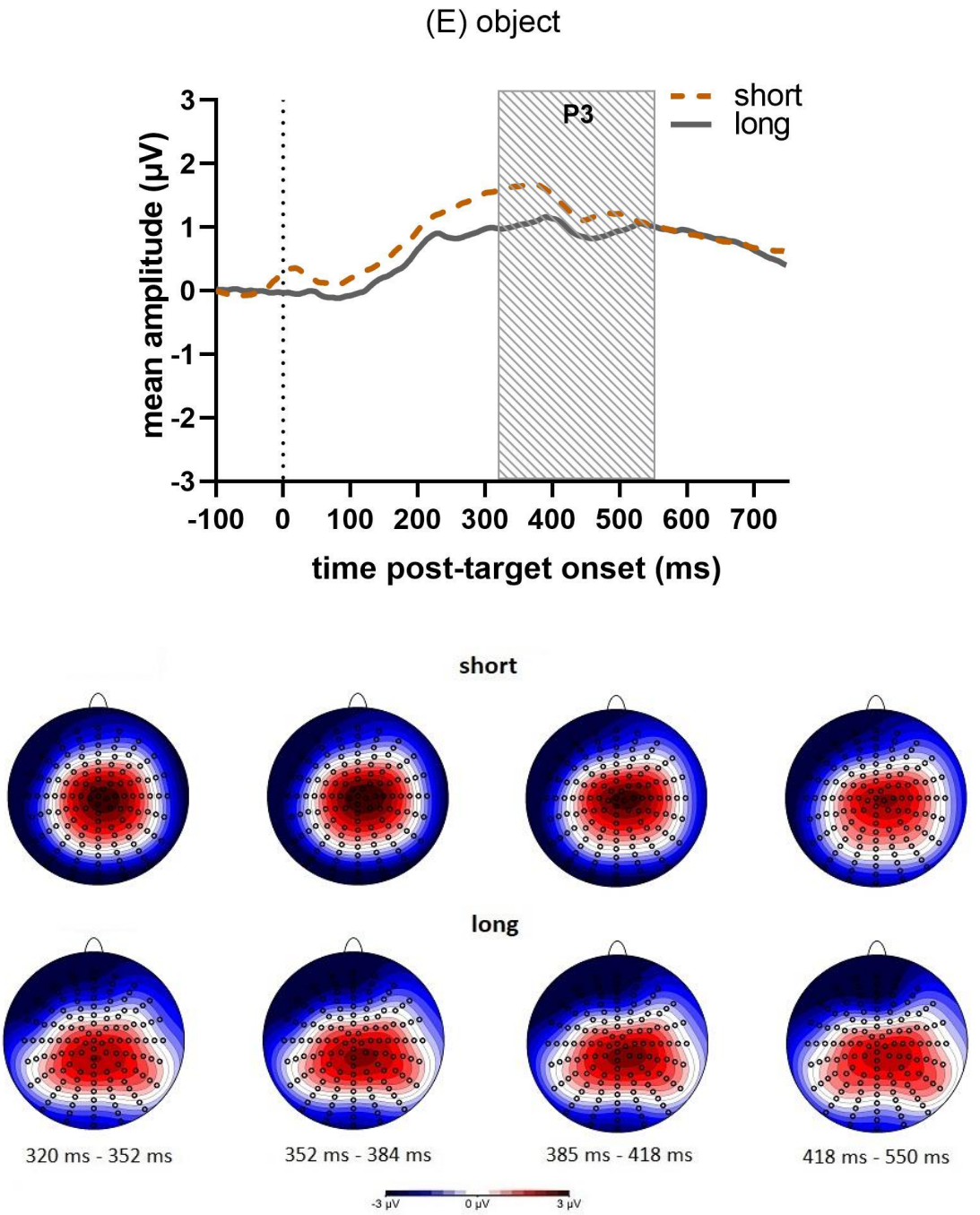
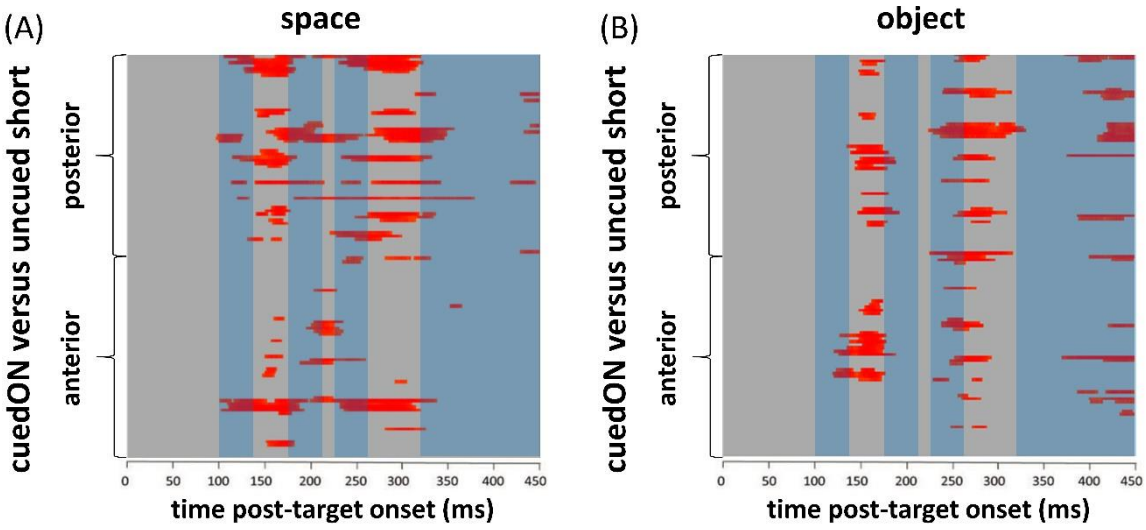


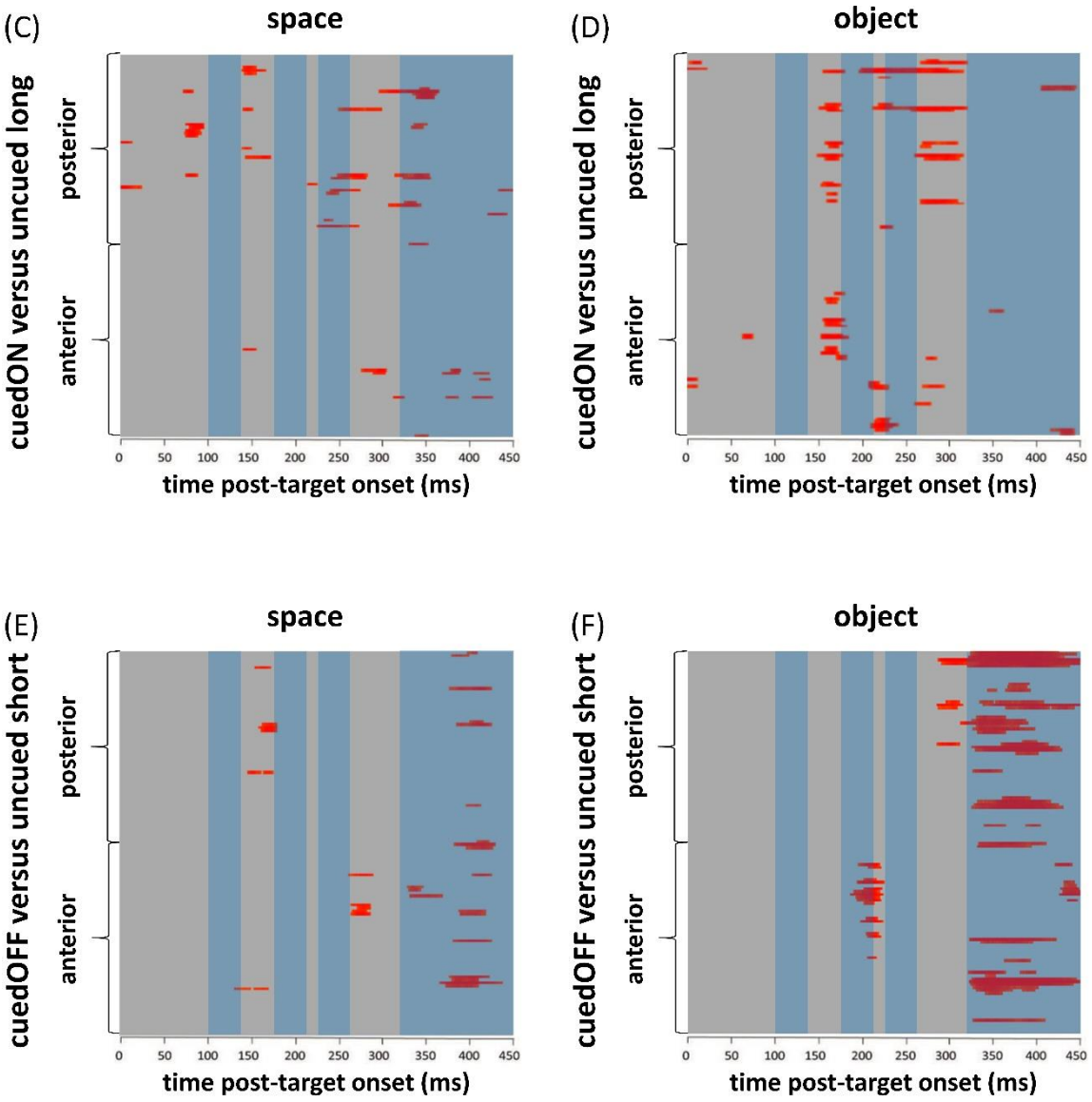
Figure 17. Grand average waveforms for the P3 component (striped area) for two SOA conditions (A) and for each validity level across (B) space and (C) object conditions at the electrode cluster encompassing FC3/ Z/4, C3/Z/4, CP3/Z/4, and P3/Z/4. Scalp topographies of P3 component (320 – 450 ms) are shown in the bottom panel (data were referenced to the

average of the electrodes). Red reflects positive voltage and blue reflects a negative voltage.

4.3.2.1.2. Mass Univariate Contrasts across all 128 electrodes

Mass Univariate analyses were conducted in order to further characterise the effects of space and object attentional mechanisms when directing resources to previously cued (cuedON and cuedOFF) location or side versus uncued locations with varying interval between a cue and a target. The temporal distributions of these contrasts across all 128 electrodes for space and object attentional conditions are shown in Figures 18 A-H.




(C)
space
cuedON versus uncued long
posterior
anterior
0 50 100 150 200 250 300 350 400 450
time post-target onset (ms)
(D)
object
cuedON versus uncued long
posterior
anterior
0 50 100 150 200 250 300 350 400 450
time post-target onset (ms)
(E)
space
cuedOFF versus uncued short
posterior
anterior
0 50 100 150 200 250 300 350 400 450
time post-target onset (ms)
(F)
object
cuedOFF versus uncued short
posterior
anterior
0 50 100 150 200 250 300 350 400 450
time post-target onset (ms)

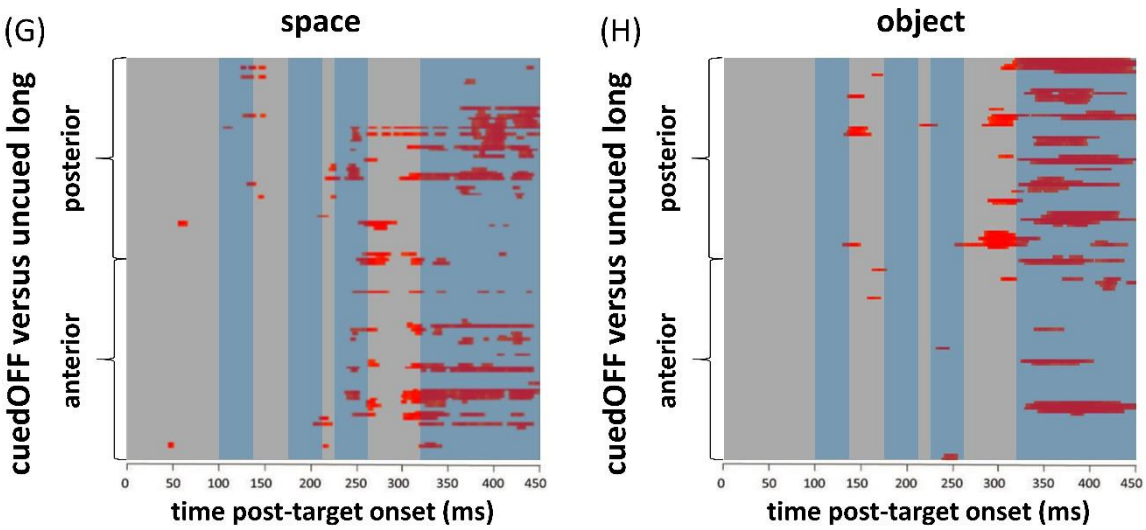


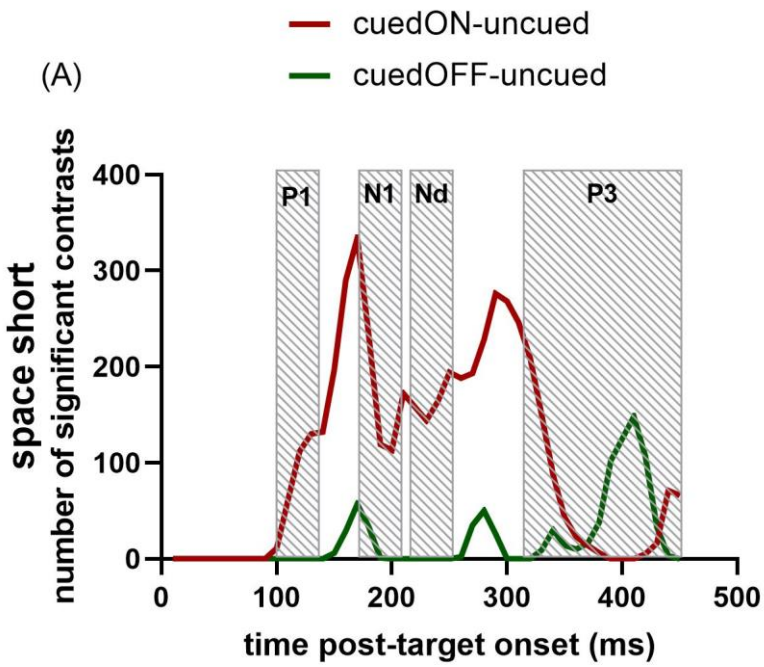
Figure 18. Raster plots of mass univariate contrasts showing significant pairwise contrasts ($p < .01$) for (A) space cuedON-uncued short; (B) object cuedON-uncued short; (C) space cuedON-uncued long; (D) object cuedON-uncued long; (E) space cuedOFF-uncued short; (F) object cuedOFF-uncued short; (G) space cuedOFF-uncued long and (H) object cuedOFF-uncued long. Posterior/anterior electrodes are shown as a function of time (0-450 ms) beginning at the target onset. The blue highlighted areas show the P1, N1, Nd and P3 components.

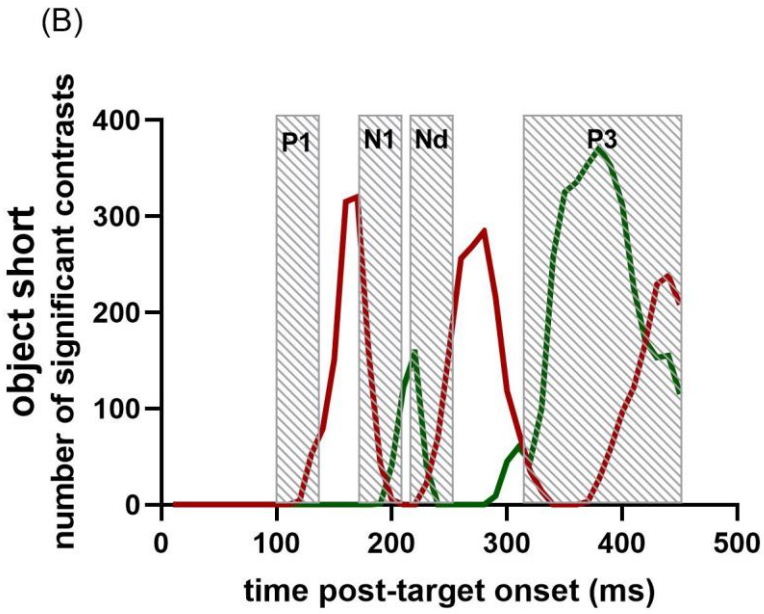
Mass univariate contrasts show the differential sensitivity between space and object conditions and cuedON, cuedOFF and uncued targets in the P1, N1, Nd and P3 components. A time series plot of the frequency distribution of significant differences is depicted in Figure 19. These data were analysed using time series plots of the frequency distribution of significant differences which were submitted as a non-parametric time-series to the Friedman test.

For the P1, during space condition there was a higher frequency of significant differences in cuedON-uncued than cuedOFF-uncued, $\chi^2(1) = 5.00$, $p < .001$ for short SOA,

but it was not the case for long SOA, $\chi^2(1) = 1.80$, p = .180. In the object condition, the frequency of significant differences in cuedON-uncued versus cuedOFF-uncued did not reach significant in neither short SOA, $\chi^2(1) = 3.00$, $p = .083$, nor long SOA trials $\chi^2(1) = 2.00$, $p = .157$. For the N1 during space condition there was again a higher frequency of significant differences between cuedON-uncued than cuedOFF-uncued targets, only in short trials $\chi^2(1) = 5.00$, $p = .025$. In long trials, there was no such difference observed $\chi^2(1) = 0.33$, $p = .564$. In turn, this pattern of results reversed in the object condition, yielding no significant differences between cuedON-uncued and cuedOFF-uncued for short SOA, $\chi^2(1) = 0.20$, $p = .655$ but the frequency of significant differences was higher in cuedON-uncued than cuedOFF-uncued in the long SOA condition, $\chi^2(1) = 5.00$, $p = .025$. The same pattern was also found during Nd, where a frequency of significant differences between cuedON-uncued than cuedOFF-uncued targets in the space condition was higher only in short, $\chi^2(1) = 5.00$, $p = .025$, but not long SOA, $\chi^2(1) = 1.80$, $p = .180$.

In parallel, the opposite results were found in the object condition, in which no significant differences for short SOA were found between cuedON-uncued and cuedOFF-uncued conditions, $\chi^2(1) = 0.20$, $p = .655$, whereas a frequency of significant differences were higher in cuedON-uncued than cuedOFF-uncued conditions for long SOA, $\chi^2(1) = 5.00$, $p = .025$. In turn, during the P3 component, no differences were observed between cuedON-uncued and cuedOFF-uncued for neither short, $\chi^2(1) = 0.00$, $p = .100$ nor long trials $\chi^2(1) = 1.13$, $p = .285$. Conversely, for object short condition, a frequency of significant differences was higher in cuedOFF-uncued than cuedON-uncued, $\chi^2(1) = 4.57$, $p = .033$. Similarly, in object long condition, also a pattern of higher frequency of significant differences in cuedOFF-uncued than cuedON-uncued, $\chi^2(1) = 14.00$, $p < .001$ was found.


cuedON-uncued
cuedOFF-uncued
(A)
space short
number of significant contrasts
P1
N1
Nd
P3
0
100
200
300
400
500
time post-target onset (ms)


(B)
object short
number of significant contrasts
P1
N1
Nd
P3
0
100
200
300
400
500
time post-target onset (ms)

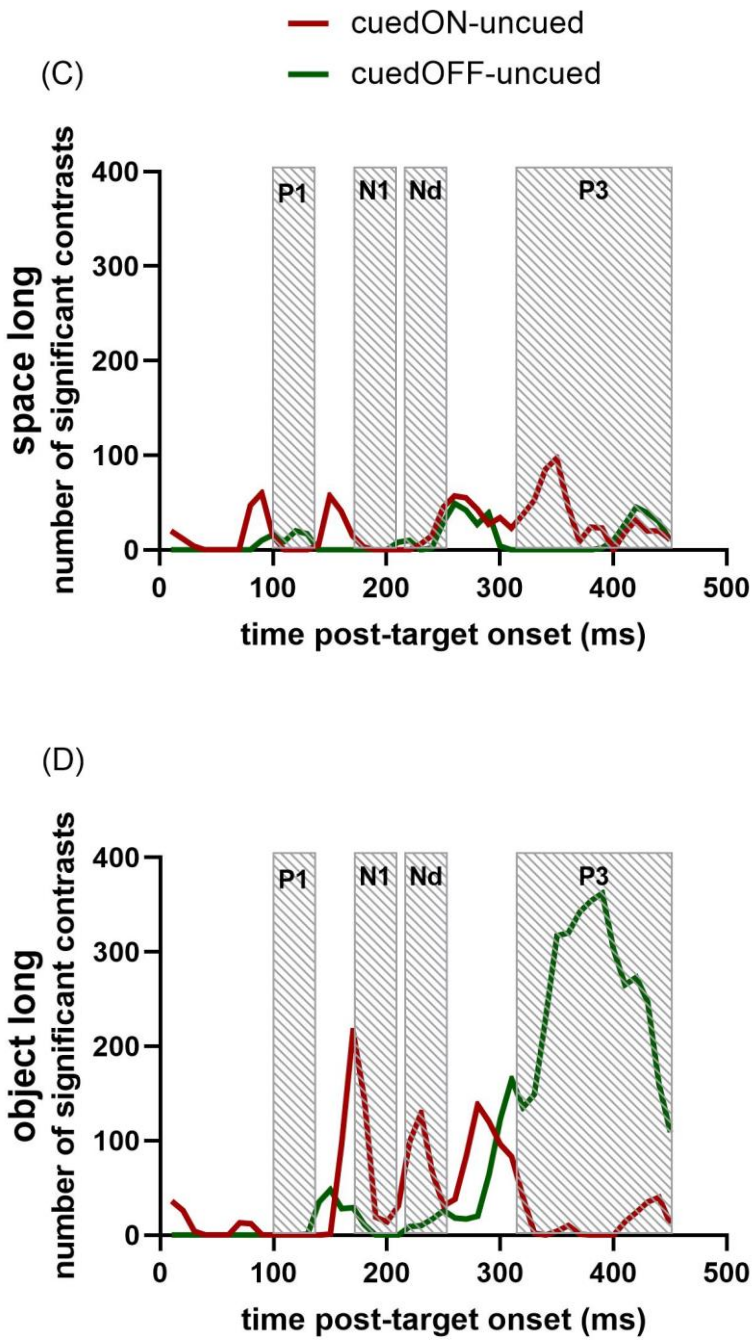


Figure 19. Plots showing the frequency of significant contrasts in each of 128 electrodes in 10 ms time window (max. 1280) from the Mass Univariate analyses between 0 and 450 ms. Contrasts depict the difference between cuedON vs. uncued (red line) and cuedOFF vs. uncued (green line) for (A) space short, (B) object short, (C) space long and (D) object long conditions.

4.4. Discussion

Slower response times to previously attended locations and objects have consistently been demonstrated in a wide range of experimental settings (Chica et al., 2014; Klein, 2000; Posner & Cohen, 1984; Tipper et al., 1991, 1997, 1994; Wang, Satel, & Klein, 2012). Yet, most of the studies used a classic spatial cueing paradigm (Posner & Cohen, 1984; Posner et al., 1980) in which targets appear within placeholders, thereby making it difficult to disentangle spatial and object effects. In our study, we sought to dissociate mechanisms of space- and object-based attentional systems by varying the presence of the placeholders in an adapted spatial cueing paradigm. Furthermore, additionally to presenting a target at the same or opposite location as a preceding cue, we also presented targets at the same visual field as the cue. This experimental manipulation coupled with ERP analysis, allowed us to study how spatiotemporal distribution of inhibition can be modulated by the presence of objects in the visual fields with the assumption that objects can alter the gradients of space-based inhibition at spatial locations outside of object boundaries.

Behavioural results revealed strong IOR effects for both intervals, replicating our previous findings (Chapters II-III). IOR was most pronounced for targets appearing at the same location as a preceding cue. Although weaker in magnitude, inhibition was also present for targets at the same visual field but different location as the preceding cue following long cue-target intervals, which was also reported elsewhere (Wascher & Tipper, 2004). This finding further indicates that inhibition is not spatially restricted to previously inspected places but instead, its effects extend to adjacent locations. Importantly, though, inhibition of return was stronger in object versus space condition, demonstrating that spatiotemporal distribution of inhibition can be indeed modulated by the mere object presence. These results are in line with

previous studies that reported the additive location-based and object-based IOR (Jordan & Tipper, 1998; Leek et al., 2003; Tipper et al., 1999, 1994). Finally, we also observed faster RTs following short versus long SOA. In order to better understand the neural basis of behavioural results, we looked into the EEG data.

The analysis of event-related potentials showed that in the object condition, there was a decrease of P1 amplitude for targets occurring at a previously attended location when compared to targets occurring at opposite locations. These findings are consistent with behavioural results showing stronger IOR in object as compared to space condition. P1 modulations also demonstrate that IOR can be generated at the low sensory level which replicate similar findings on spatial attention (Hopfinger & Mangun, 1998; Satel et al., 2014; Taylor & Klein, 2000; Wang et al., 2012) and extends them to object-based attentional mechanisms. It is important to note that no modulations were observed for adjacent targets. Intriguingly, Wascher and Tipper (2004) did observe P1 reduction (but weaker than at cued object/locations) also for targets occurring at adjacent locations. However, this discrepancy can be potentially explained by differences in paradigms in two studies. In Wascher and Tipper (2004), targets that appeared in adjacent locations were presented within objects (i.e., placeholders), whereas it was not the case in our experiment. Consequently, as demonstrated in the current study, object presence leads to stronger perceptual IOR effects which are also observed at the electrophysiological level. Indeed, our results seem to indicate that early perceptual suppression is restricted to objects and does not occur when only the spatial attentional system is at play. Given the inconsistencies of P1 modulations by cueing effects (Hopfinger & Mangun, 1998; Martín-Arévalo et al., 2016; McDonald et al., 1999), observed P1 decrease which was accompanied by behavioural IOR for object-based attention is a novel

empirical finding suggesting that IOR, at least for object-based attention, acts by affecting early sensory processes.

Yet, P1 is not the only component reflecting perceptual correlates of input amplification. Further analyses showed that when the object attentional system was involved, there was a reduction of the N1 component to targets presented at adjacent locations in the cued visual field as compared to targets presented at the same or opposite location as previously cued. Such selective modulation of adjacent locations only appears to suggest that two separate inhibitory processes might be involved in selective sampling across visual field: one that suppresses an incoming signal at cued object only, and a second one that operates over the whole visual field. In other words, object presence modulated the N1 across space. Interestingly, the analysis also revealed a Validity × SOA interaction, otherwise not detected in the behavioural results. In short trials only, N1 amplitude was more negative to uncued than cuedOFF targets indicating better processing of uninspected locations/objects as compared to adjacent locations. Again, this finding is consistent with behavioural data showing faster response times in uncued and short trials. Such a pattern of data is line with Prime and colleagues' experiments in which they reported N1 reduction to cued as compared to uncued targets paralleled by behavioural IOR effects (Prime & Jolicœur, 2009; Prime & Ward, 2004, 2006).

Besides looking at perceptual effects, we also investigated the modulation of later stages of processing as indicated by the amplitude of negative difference (Nd) and P3 components. Nd component is closely related to selective attention (Eimer, 2000; McDonald et al., 1999; Prime & Ward, 2006; Wascher & Tipper, 2004) and due to its general effects across experimental paradigms, it has been even proposed as a maker of IOR (Satel et al.,

2014). Indeed, this component has been shown to be modulated independently of peripheral or central cueing conditions (Satel et al., 2014) and we have complemented and extended this finding by demonstrating that it can be also modulated independently of space or object conditions. More specifically, the Nd amplitude was significantly more negative to uncued versus cued targets, replicating the results of Satel and colleagues (2014). Such an effect once again suggests that Nd reflects a general mechanism of inhibiting previously attended places. It is noteworthy that akin to Wascher and Tipper's (2004) results, we also did not find Nd modulations for targets at adjacent locations. Thus, this pattern of results indicates that Nd effects are limited to the cued locations/objects and occur independently of early attentional modulation of adjacent locations as observed in the N1 component.

Yet, more pronounced negativity for uncued as compared to cued targets were observed in short interval trials only. One may thus hypothesise that IOR was stronger following a short SOA. However, such an explanation is not supported by the current behavioural data and it is clearly at odds with the theoretical and empirical framework of IOR that finds stronger inhibition after longer cue-target intervals. An alternative explanation takes into account the temporal regularities of the task itself. Here, the cue-target interval was manipulated in a blockwise fashion which is equivalent to a fixed foreperiod (FP) paradigm. In such tasks, temporal preparation is optimal for short rather than long SOA trials which empirically translates into speeded RTs after short versus long intervals (Niemi & Naatanen, 1981; Woodrow, 1914). Indeed, not only did we observe accelerated RTs to short versus long SOA trials, but this effect was also reflected in more negative Nd for short than long SOA. Hence, it is plausible that IOR interacted with temporal preparation leading to enhanced processing of uncued targets when they appeared after short intervals. It is noteworthy that N1 and Nd modulations by temporal preparation seem to contradict previous behavioural reports which

did not observe IOR modulations by temporal expectancy (Gabay & Henik, 2008; Los, 2004). However, these studies have examined the mutual interaction between IOR and temporal information in tasks in which the length of the interval between the cue and the target was manipulated in a blockwise fashion (the variable FP paradigm). In such tasks, different temporal phenomena (e.g., hazard function, sequential effects) underlie behavioural performance (Los et al., 2014; Niemi & Naatanen, 1981; Vallesi & Shallice, 2007) and therefore, its mechanisms cannot be equated to more automatic temporal preparation as observed in a fixed FP paradigm.

Finally, in the context of the P3 component, we observed an increase in amplitude for targets presented at locations adjacent to the previously cued targets. This was particularly apparent in the mass univariate analyses, which showed a higher frequency of significant differences in object versus space condition between cued versus uncued and cuedOFF versus uncued targets. Given that P3 elevation reflects more demanding processing of task-relevant information, and in spatial cueing tasks was found for cued targets along with strong behavioural IOR (McDonald et al., 1999; Prime & Jolicœur, 2009), it likely reflects the neural inhibition of previously attended targets. Therefore, it demonstrates again that inhibitory processes can be selective in nature, affecting already inspected visual fields, but leaving inhibitory processing of attended locations intact. Notwithstanding, this effect was further modulated by object presence. In the object condition, not only was P3 increased for adjacent targets relative to cued and uncued targets but P3 was also more enhanced for cued versus uncued targets. It may be thus reasoned that although P3 modulations primarily reflect inhibition of attended visual field, its effects are also sensitive to object presence and therefore can underlie inhibition of inspected objects during later stages of processing. Indeed, we also observed modulatory effects of object versus space processing when reacting to targets

appearing after short versus long intervals. When spatially orienting to targets, P3 was increased after long rather than short SOA. In turn, this pattern reversed for long SOA trials, yielding a decrease of amplitude for long SOA. This pattern of results seems to suggest that temporal preparation indexed by better stimulus processing after short than long interval, yields dissociable effects depending on whether it interacts with space or object inhibitory systems.

Taken together, our results revealed a picture of the dynamic interplay between neural mechanisms at different stages of processing when deploying spatial and object-based attentional systems. Only when object-based attention was involved, previously cued object and visual field were suppressed as reflected by attenuation of P1 and N1 components, respectively, indicating that IOR affects early perceptual processes (Sapir, Jackson, Butler, Paul, & Abrams, 2013; Taylor & Klein, 2000; Wang et al., 2012). This selective inhibition of object versus spatial attention was mirrored by stronger behavioural IOR in object versus space trials. During later stages of processing, a more general neural mechanism reflected by Nd decrease to uncued versus cued targets was modulated independently of attentional systems (whether space- or object-based), suggesting that they might share, at least to some extent, same neural origins. In turn, P3 amplitude was differentially modulated by space and object-based inhibition of return. Whereas the space condition revealed a P3 increase when processing adjacent locations, suggesting stronger inhibitory signal, the object presence additionally led to a P3 increase at previously inspected objects. Therefore, our results suggest that although space and object-based systems may share some common neural components, they affect stimuli processing in a dissociable manner. Additionally, our results support the existence a separate inhibitory mechanism that directs attentional resources to previously attended visual field, rather than a general inhibitory function that leads to a spatial decline in inhibition around the cued location/object. Finally, our study demonstrates once again that temporal preparation

not only further exacerbates spatial and object-based effects but can act alone to guide attentional mechanisms in the service of adaptive behaviour.

CHAPTER V

The effects of object complexity on spatiotemporal distribution of inhibition: an ERP study

5.1. Introduction

After inspecting a location in space, a separate inhibitory process prevents attention from orienting towards this place again. This suppression process is called inhibition of return (IOR; Posner & Cohen, 1984; Posner et al., 1985). Such inhibition can also be directed to objects (Leek et al., 2003; Possin et al., 2009; Tipper et al., 1991, 1999, 1994). In our previous ERP experiment (Chapter IV), we have demonstrated using an adapted version of the Posner cueing paradigm (Posner 1980) that space- and object-based inhibitory mechanisms are accompanied by generally distinct neuronal processes. Overall, the ERP results were in line with behavioural data which also revealed stronger inhibition in object-based conditions. ERP analysis revealed that object-based inhibition was associated with diminished perceptual processing of cued targets as reflected by a decrease of P1 component. Furthermore, orienting to objects also affected the early processing of targets adjacent to cued objects (i.e., located in the same visual field as a preceding cue) by attenuating N1 component. Yet, a negative difference (Nd) component, which has been proposed as a potential neural marker of IOR (Satel et al., 2014) was not selectively modulated to space versus object attentional processing. Instead, the Nd was more negative to uncued than cued targets regardless of the space/object conditions, suggesting once again that it reflects a more general in nature inhibitory process. Later

processing as demonstrated by P3 component modulations was also differentially affected by space and object processes, whereby objects increased the P3 amplitude to already scanned objects and targets at adjacent locations, and space affected the processing of targets at adjacent locations only. Finally, the spatial and object-based attentional effects were further modulated by temporal preparation (Woodrow, 1914). In fact, optimal temporal preparation alone (i.e., following short rather than long SOA) modulated Nd as demonstrated by more pronounced negative amplitudes after short SOA, which was also accompanied by faster RTs.

Yet, previous studies have demonstrated that inhibition of return is not only differentially modulated by space and objects but is also sensitive to object contours (Leek et al., 2003; Reppa & Leek, 2006; Reppa et al., 2012). It was shown (Leek et al., 2003 Reppa & Leek, 2003) that IOR was stronger for L-shape objects than rectangles. Furthermore, the IOR was more pronounced when cues and targets were separated by a boundary within an object than when they occurred on the same part of the object. These findings appear to suggest that IOR mechanisms can be sensitive to object's internal structure (Leek et al., 2003; Reppa & Leek, 2003, 2006).

IOR modulations by object complexity were also indirectly evidenced by a study by McAuliffe, Pratt and O'Donnell (2001). In their paradigm, targets could appear within a placeholder (object condition) or in the location without a placeholder (space condition). Importantly, space and object conditions were randomly presented within a block *or* presented in separate blocks. Object-based trials led to stronger IOR than space-based trials only when mixed in the same block. Therefore, it seems plausible that repetitive exposure to object contours in a blocked design reduced their effects on attentional processing. Overall, these findings indicate the role of the saliency of object contours in modulating inhibitory effects.

The goal of the current experiment was to extend previous results that differentiated between space and object-based neural mechanisms in the context of static displays (Chapter IV). More specifically, we now aimed to examine the role of object structure in modulating IOR. We varied the complexity of shapes that acted as placeholders in the adapted cueing task based on the stimuli used in the work by Schmidtmann, Jennings, & Kingdom (2015). In the current study, the stimuli were a combination of radial frequency (RF) pattern, with 2-3-4 RFs in the less complex condition and 3-5-8 RFs in the complex condition. Importantly for our research question, the saliency of the shapes was kept high by rotating images on each trial.

Similarly to our previous study (Chapter IV), we manipulated the cue-target location to elicit cueing effects across different SOAs. Building on the concept of "attentional field" (LaBerge & Brown, 1989), which defines attention as a spatiotemporal distribution of resources across the visual field, we examined inhibitory functions to targets appearing at the same (cuedON), opposite (uncued) and adjacent (cuedOFF) locations/objects as the preceding cue. Our previous findings confirmed a well-established finding that IOR is strongest at previously cued locations (Klein, 2000; Posner & Cohen, 1984) and this effect is further increased by the object presence (Jordan & Tipper, 1998; Leek et al., 2003), indicating that separate space- and object-based IOR components might operate in parallel (but see McAuliffe et al., 2001). Still, the IOR is - albeit weaker - also observed at locations adjacent to the ones that have been previously scanned (Bennett & Pratt, 2001; Pratt, Spalek, & Bradshaw, 1999; Taylor, Chan, Bennett, & Pratt, 2015; Wascher & Tipper, 2004). Wascher and Tipper (2004) have suggested that such findings might reflect a single inhibitory mechanism that produces a gradient of inhibition around the cue or, alternatively, two separate mechanisms, one that affects the cued location/object and another one that operates on to a whole cued visual field. Our previous ERP findings supported the latter hypothesis, revealing that processing of

adjacent targets were in general reflected by modulations of different ERP components than processing of cued targets.

In the current experiment, we analysed behavioural and event-ralated brain potentials data to estimate sensitivity to object structure. More specifically, we investigated the modulations of ERP components such as P1, N1, Nd and P3 by cue-target locations and object complexity. To further confirm and extend our standard waveform analysis, we also ran a mass univariate analysis (Groppe et al., 2011; Guthrie & Buchwald, 1991; Murray et al., 2008). By performing MUA which contrasts two conditions for each time point across all electrode sites, we were able to get a more comprehensive and "bias-free" picture of attentional modulations.

Based on previous findings (Leek et al., 2003; McAuliffe et al., 2001; Reppa & Leek, 2003, 2006; Reppa et al., 2012), we expected that IOR mechanisms utilise information about object structure. Therefore, we hypothesised to see differences between less complex and complex conditions, as well as in general between the object conditions and space conditions. More specifically, as object-based IOR affects the perceptual processing by affecting low-level visual components like P1 and N1, we sought to see similar effects with less pronounced P1 to cued targets, and N1 to adjacent targets in complex versus less complex condition. Furthermore, we expected to observe more negative P1 and N1 amplitudes for complex and less complex conditions than in space condition. In turn, in line with our previous results, no differences between space and object conditions were expected for the Nd component. Instead, we hypothesised to see a general inhibition demonstrated as more negative amplitudes to uncued versus cued targets regardless of space/object attentional components. Additionally, more enhanced negativities of Nd component were expected for short versus long SOA trials, accounting for better temporal preparation after a shorter interval. Finally, we expected that

complex objects would elicit higher P3 amplitude to cued locations and visual fields than less complex condition.

5.2. Methods

5.3.1. Participants

Twenty students (8 female, M_{age} = 23.10, *SD* = 3.17, 3 left-handed) from the Psychology Department at Bangor University took part in the study for course credit. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). All participants had normal (or corrected-to-normal) vision. The study was conducted under School of Psychology Ethics Protocol.

5.3.2. Apparatus and Stimuli

Data acquisition was conducted using a PC and 1024 x 768 Mitsubishi Diamond Pro 2060u (120 Hz, 40 cm) monitor. The viewing distance was fixed at 57 cm using a chinrest. A standard QWERTY PC keyboard was used for the responses. The SR 1000 eye tracker (1000 Hz) was used to monitor central fixation. A trial was automatically terminated if the fixation point moved outside of a non-visible circular ROI (3 degrees of visual angle) around the fixation point. The experiments were programmed in the Experiment Builder (SR Research Ltd.) synchronised with EEG BioSemi (Biosemi Inc., Amsterdam, The Netherlands) for the EEG data acquisition.

The fixation point was a red cross (RGB: 255, 0, 0) of 13 x 13 pixels which equals 0.5 degrees of visual angle on a 1024 x 786 monitor (of 40 cm horizontal dimension) viewed from 57cm where the vertical and horizontal bars in the cross are each 2 pixels wide. The fixation cross was situated in the centre of the display. The background was grey (RGB: 127,127,127). The display consisted of two cues – a square of 13 x 13 pixels white (RGB 255, 255, 255) which equals 0.5 degrees of visual angle. Cues were positioned on the horizontal line 5 degrees of visual angle from the central fixation on the right or left side. Targets were a square 13 x 13

pixels black (RGB: 0, 0, 0). The target could appear in one of four locations – in the same location as the preceding cue (cuedON), on the same side but different location as a cue (cuedOFF) or at the opposite side as a cue (uncued). Importantly, all locations were kept equidistantly 5 degrees of visual angle from the central fixation.

In two object conditions two asymmetric black shapes (RGB: 0, 0, 0) of 39 x 39 pixels which equals 1.5 degrees of visual angle, were present on the right and left side of the display 5 degrees of visual angle from the central fixation. They were created following the procedure from Schmidtmann, Jennings, & Kingdom (2015), using the Matlab script shared by the authors. The stimuli were combinations of radial frequency (RF) patterns. We used combinations of simpler (2-3-4) in the less complex condition, and more complex (3-5-8) radial frequencies patterns in the complex condition, to manipulate the complexity of the shapes. Neither of these stimuli had an internal axis of symmetry but they varied in the underlying complexity of the RF pattern. In order to keep the saliency of the shapes on each trial, we introduced variability in the pixel locations of edges for each stimulus by using different versions across trials where we rotated the image by 90 degrees such that there was a 0, 90, 180, and 270 degrees version (orientation was randomly varied across trials).

Cues as well as targets in cuedON and uncued conditions would appear at the centre of the shapes that acted as placeholders. In the space condition, no placeholders were present (see Figure 20).

5.3.3. Procedure

Each trial was initiated by the participant by pressing the spacebar after which the blue cross turned red. The fixation point remained at the centre of the screen for 1,000 ms (Fig. 20). Next, a cue appeared randomly at the right or left side for 100 ms. Then, after 300 ms or 800 ms after the cue onset (stimulus onset asynchrony, SOA), a target appeared at one of four

possible locations for 1,000 ms which was also a response window. Trials in which a target appeared on the same side and same location as a cue (i.e., cue right/target right) were considered cuedON. Trials in which a target appeared on the same side but different location (either up or down) than a cue were classified as cuedOFF (e.g., cue right/target right up), whereas trials in which a target appeared at the opposite side as a cue (i.e., cue right/target left) were considered uncued. The trial ended with a jittered interval during which a grey display was presented (400 ms-1,000 ms). In the complex and less complex object conditions, two objects appeared in the left and right locations at the start of each trial always at the same locations. The objects remained on the screen during the whole trial (from initial central fixation to subject's response). Then they were removed during the intertrial interval and a new object set was shown at the start of the following trial. Participants' task was to detect the target as quickly as possible by pressing the spacebar while minimising errors. Presentation order was randomised within subjects.

Object complexity and validity were counterbalanced within a block, whereas SOA (short, long) was varied between blocks (Eimer, 2000), with two successive blocks with short and then long SOA (counterbalanced across subjects), presented in randomised order. Four blocks were run with 318 trials in each block (including 10% of catch trials for each condition), resulting in 1,272 trials altogether. There were 48 trials for each of the experimental conditions except for cuedOFF conditions which comprised 96 trials for each of the factors. Each block lasted approximately 15 min. A training session was provided with 18 trials to familiarise participants with the task.

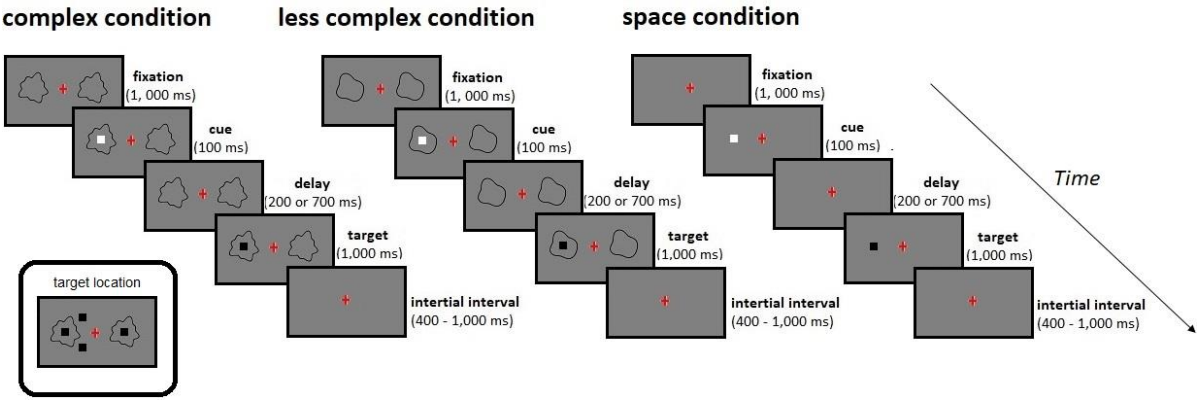


Figure 20. Illustration of trial sequence in complex, less complex object and space conditions. In both object conditions, two placeholders that varied in the level of complexity were present on the display. A fixation cross appeared for 1,000 ms. Then, a cue was presented randomly either on the left or right side. After a 200 or 700 ms, a target would appear for 1,000 ms. The target would appear in one of four locations: the same location as the cue (cuedON), the opposite side as the cue (uncued), or in the same side as the cue but up or down relative to the cue (cuedOFF). The intertrial interval (ITI) was randomised between 400-1,000 ms. Participants' task was to detect the target as quickly as possible while minimising errors. The figure illustrates a cued trial.

5.3.4. Data analysis

5.2.4.1. Behavioural analysis

The mean response time (RT) in ms was calculated separately for complex, less complex and object conditions at the 300 and 800 ms SOA and for cuedON, cuedOFF and uncued conditions. Only data from correct trials were included in the analyses; errors (false positives: responses to no-target trials), omissions and trials with RTs less than 100 ms were excluded from the analysis.

A 3 (object presence: complex, less complex, space) × 3 (validity: cuedON, cuedOFF, uncued) × 2 (SOA: short, long) repeated-measures ANOVA was performed. Bonferroni adjustments were made for pairwise comparisons. Effect sizes were calculated by using partial eta-squared (η_p^2). The Greenhouse–Geisser correction was used if the sphericity assumption was violated (Jennings and Wood, 1976).

5.2.4.2. Electrophysiological recording and processing

The electroencephalograph (EEG) was recorded using the ActiveTwo Biosemi EEG system (Biosemi Inc., Amsterdam, The Netherlands). There were 128 Ag/AgCl electrodes placed on an ECI cap (Electrocap International, Ohio, USA). The electrooculogram (EOG) was recorded using two electrodes lateral to the external canthi in order to measure horizontal eye movements, and by placing electrodes upper and beneath the right eye to measure vertical eye movements and blinks. All activity from all electrodes was sampled at a rate of 1,024 Hz. The signals were re-referenced offline to an average reference. Offline 30 Hz low-pass (filter roll-off: 24 dB/oct) and 0.1 Hz high-pass filters (filter roll-off: 12 dB/oct) were applied to the data. Only correct trials without ocular or muscle artifacts were included in the analyses.

Eye movements and blinks were corrected using the ICA protocol in BrainVision Analyser 2 software. Following the ICA correction, continuous EEG data was segmented starting from -100 ms prior to target onset to 750 ms after target onset. Segmented data was then visually inspected and trials containing ocular and muscle artifacts were rejected. We used a 100-ms pre-stimulus interval for the baseline correction and the pre-processed data was then used to generate the grand averages.

Separate averaged ERP waveforms were created for each of eighteen conditions produced by the full crossing of the levels of the factors. In order to achieve a sufficient power in the ERP waveforms, a criterion of 40 trials per each condition was set (not a single participant was excluded based on that criterion).

5.2.4.3. EEG analyses

Four early ERP components: P1, N1, Nd and P3, were identified based on the topography and latency characteristics of the grand average ERPs time-locked to stimulus presentation. Specifically, the latency of peak amplitude was used to define epochs for analyses of five components: P1 (100–140 ms; Peak latency (A10) 120 ms; N1 (170-210 ms; Peak latency (A10) 190 ms); Nd (220–260 ms; Peak latency (B7) 240 ms) and P3 (320–450 ms); Peak latency (A1) 385 ms.

Mean amplitudes of standard waveforms for P1, N1, and Nd components were analysed based on averaged activity from symmetrical clusters extracted over nine adjacent posterior electrodes in right: A32, B3, B4, B5, B6, B7, B8, B10, B11 and left hemispheres: A5, A6, A7, A8, A9, A10, A11, D31, D32. These electrode sites correspond to CP2, P4, P6, P8, PO8 and CP1, P3, P5, P7, PO7 of the extended 10–20 system.

The analysis of the P3 component was based on averaged activity from midline and

symmetrical clusters extracted over eighteen electrodes spanning frontal to parietal sites: A32, B3, B4, A5, A6, A7, A19, A1, D19, B22, C21, D3, C3, C23, D2, D2, C2, D12 and B31. These electrode sites correspond to F3, F4, Fz, C3, C4, Cz, CP3, CP4, CPz, P3, P4, Pz of the extended 10–20 system.

A repeated-measures ANOVA was performed to compare mean amplitudes separately for each of extracted four time windows corresponding to P1, N1, Nd and P3 components with object complexity (complex, less complex, space), validity (cuedON, cuedOFF, uncued) and SOA (short, long) as within-subject factors.

Bonferroni adjustments were made for pairwise comparisons. Effect sizes were calculated using partial eta-squared (η_p^2).

5.2.4.4. Mass Univariate analyses

Mass Univariate analyses (Groppe et al., 2011; Guthrie & Buchwald, 1991; Murray et al., 2008) complemented the analysis of standard ERP components. Successive pairwise *t*-tests for each data point between -100 and 750 ms were performed to contrast cuedON versus uncued as well as cuedOFF versus uncued across all 128 electrodes for each combination of object complexity and SOA (less complex short, less complex long, complex short, complex long). *T*-values were found to be reliable if they remained significant for twelve consecutive time frames (≥ 12.29 ms). An a priori criterion for significance equalled $p < .01$ (two-tailed) in at least five neighbouring electrodes.

The mass univariate analyses were conducted to further contrast across all 128 electrodes cuedON versus uncued and cuedOFF versus uncued conditions, critical for establishing IOR effects, across all 128 electrodes for two SOA (short, long) for less complex and complex conditions separately. In order to compare significant differences between

experimental manipulations, a time series plot of the frequency distribution of significant contrasts across conditions was plotted. Then, these time series data were analysed in a non-parametric Friedman test with cueing effects contrasts (cuedON – uncued, cuedOFF – uncued) and SOA (short, long) for each time window of a relevant component (P1, N1, Nd, P3) for less complex and complex conditions separately.

5.3. Results

5.4.1. Behavioural results

Reaction times for all experimental conditions are presented in Table 9. The rate of omission was approximately 3%, whereas the percentage of responses faster than 100 ms was approximately 1%.

There was a main effect of validity on RT, $F(2, 34) = 13.44$, $p < .001$, $\eta_p^2 = .44$. Response times were significantly slower (i.e., stronger IOR) for cuedON versus uncued ($p < .001$), cuedON versus cuedOFF ($p = .011$) but not for cuedOFF versus uncued trials ($p = .159$). There was a main effect of SOA, $F(1, 17) = 25.58$, $p < .001$, $\eta_p^2 = .60$, with faster response times after short than long interval. The analysis also showed a Validity × SOA interaction, $F(2, 34) = 5.07$, $p = .012$, $\eta_p^2 = .23$. In the short SOA condition, the IOR was observed for cuedON versus uncued trials ($p = .003$) but not for cuedOFF versus uncued trials ($p = 1.00$). In contrast, in the long SOA condition, cueing effects were observed for both cuedON versus uncued trials ($p < .001$) as well as cuedOFF than uncued trials ($p = .054$). Importantly, there was a Validity × Object Complexity interaction, $F(2, 34) = 6.85$, $p = .012$, $\eta_p^2 = .29$. In the space condition, there was no IOR observed neither for cuedON versus uncued trials ($p = 0.583$) nor cuedOFF versus uncued trials ($p = 1.00$). However, IOR was observed for cuedON versus uncued trials in both complex ($p < .001$) and less complex condition ($p < .001$). Yet, no IOR was present for cuedOFF versus uncued targets in neither complex ($p = 1.00$) nor less complex ($p = 1.00$) conditions. There was no main effect of object complexity, $F(2, 34) = 0.96$, $p = .392$, $\eta_p^2 = .05$, nor an Object Complexity × SOA, $F(2, 34) = 0.51$, $p = .607$, $\eta_p^2 = .03$, or Validity × SOA × Object Complexity, $F(4, 68) = 1.13$, $p = .350$, $\eta_p^2 = .06$ interactions.

Figure 21 presents cueing effects in each experimental condition. We compared RTs

to cued and uncued targets with a t-test separately for complex, less complex and space, as well as short and long SOA conditions. In the complex condition, the classic IOR (cuedON versus uncued) was found for short ($p = .007$) and long SOA ($p < .001$). In contrast, the IOR to adjacent locations (cuedOFF versus uncued) was found only for long ($p = .006$) SOA with no such effect short SOA ($p = .633$). Similarly, in the less complex condition, the classic IOR (cuedON versus uncued) was observed for SOA 150 ms ($p = .003$) and SOA 650 ms ($p < .001$). Again, the IOR for adjacent targets (cuedOFF versus uncued) was found for long SOA ($p = .004$) but not for short SOA ($p = .376$). In contrast, no IOR was present in the space condition. Inhibitory costs were further computed by subtracting performance on uncued from cued (i.e., cuedON and cuedOFF) trials separately for complex, less complex and space, as well as short and long SOA. The IOR was stronger in less complex ($p = .011$) and complex ($p < .001$) object conditions than in space condition when orienting to the same location (i.e., uncued – cuedON) in long interval trials. No other significant simple effects contrasts were significant.

Table 9
Mean reaction time (ms) and standard error

	SOA	Uncued	CuedON	CuedOFF
Complex	Short	316 (17)	340 (13)	319 (15)
	Long	344 (13)	378 (14)	361 (13)
Less complex	Short	315 (16)	345 (13)	320 (15)
	Long	343 (13)	386 (13)	362 (13)
Space	Short	319 (17)	334 (13)	322 (15)
	Long	350 (15)	363 (12)	364 (14)

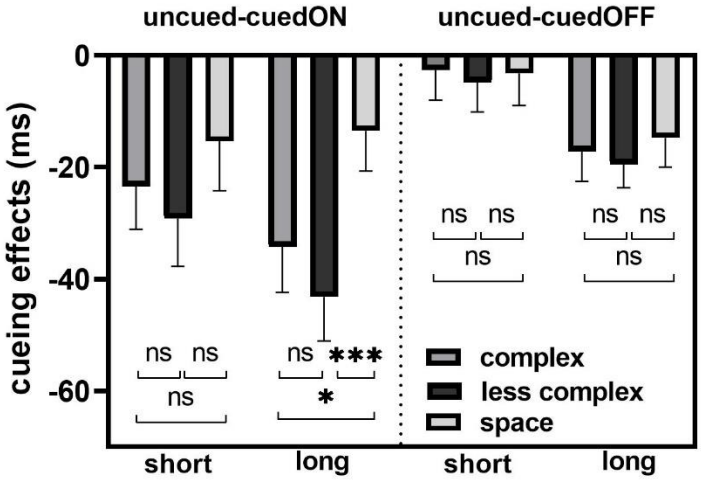


Figure 21. Mean cueing effect (uncued – cued RT) and standard error for short and long SOA in complex and less complex object conditions as well as in space conditions. IOR was observed in complex and less complex trials for uncued-cuedON targets as well as for adjacent targets (uncued-cuedOFF) following a long SOA.

5.4.2. ERP results

The goals of the ERP analyses were threefold: (1) to establish whether ERPs were differentially modulated by object complexity (i.e., the placeholders); (2) to determine whether ERPs were sensitive to cueing effects (e.g., event-related brain responses to previously cued and uncued target locations) across different timings; (3) to elucidate whether the ERPs to cueing effects were further modulated by object complexity.

5.3.2.1. Event-related brain responses to space versus object cueing effects

5.3.2.1.1. Standard Waveform Analyses

P1: 100 to 140 ms time window

Amplitude. Mean ERP amplitudes in the 100 to 140 ms time window were compared for each condition. As expected, there was a main effect of object complexity, $F(2, 34) = 11.77$, $p < .001$, $\eta_p^2 = .41$. P1 was greater for space versus complex object ($p < .001$) and less complex object ($p < .001$). However, the amplitude did not differ between complex and less complex object conditions ($p = .592$) (Fig. 22). No main effect of validity, $F(2, 34) = 0.36$, $p = .702$, $\eta_p^2 = .02$, SOA, $F(1, 17) = 3.39$, $p = .083$, $\eta_p^2 = .17$, nor Object Complexity × Validity $F(4, 68) = 1.22$, $p = .309$, $\eta_p^2 = .07$, Object Complexity × SOA interactions, $F(2, 34) = 0.19$, $p = .832$, $\eta_p^2 = .01$, or Validity × SOA interaction, $F(2, 34) = 0.61$, $p = .552$, $\eta_p^2 = .03$, were found.

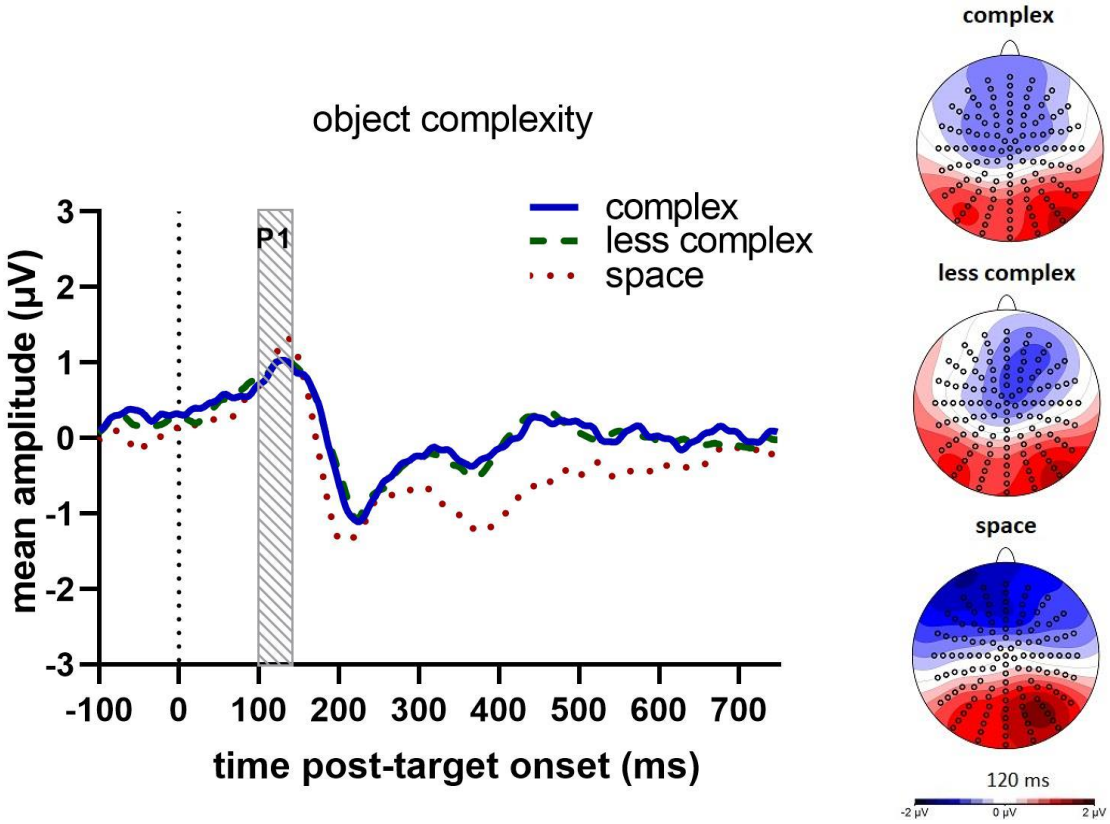


Figure 22. Grand average waveforms for the P1 component (striped area) across validity conditions at the electrode cluster encompassing P7, PO7, P8 and PO8 for object complexity. Scalp topographies of attentional modulations on P1 (100 – 140 ms) are shown in the right panel (data were referenced to the average of the electrodes). Red reflects positive voltage and blue reflects a negative voltage.

N1: 170 to 210 ms time window

Amplitude. Mean ERP amplitudes in the 170 to 210 ms time window were compared for each condition. There was a significant validity main effect, $F(2, 34) = 5.92$, $p = .006$, $\eta_p^2 = .26$. N1 amplitude was more negative for uncued than cuedON ($p = .012$) and cuedOFF ($p = .003$) trials (Fig. 23). No other main effects or interactions were observed.

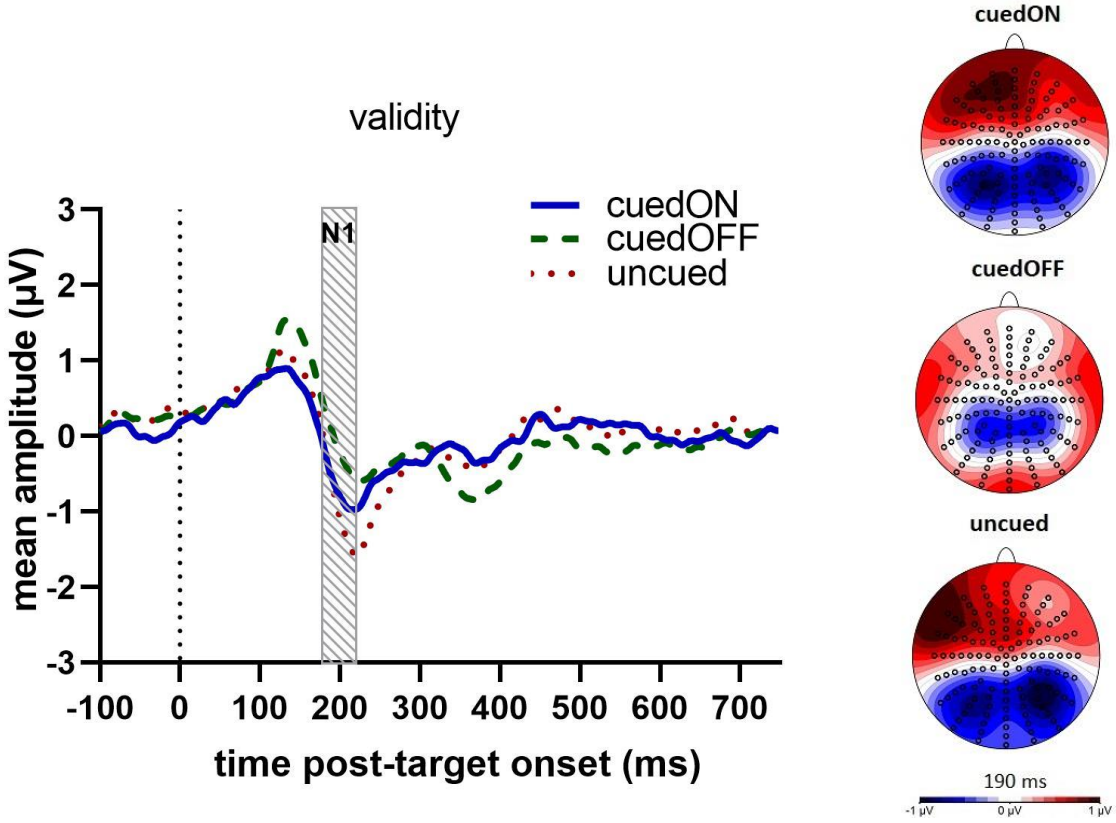
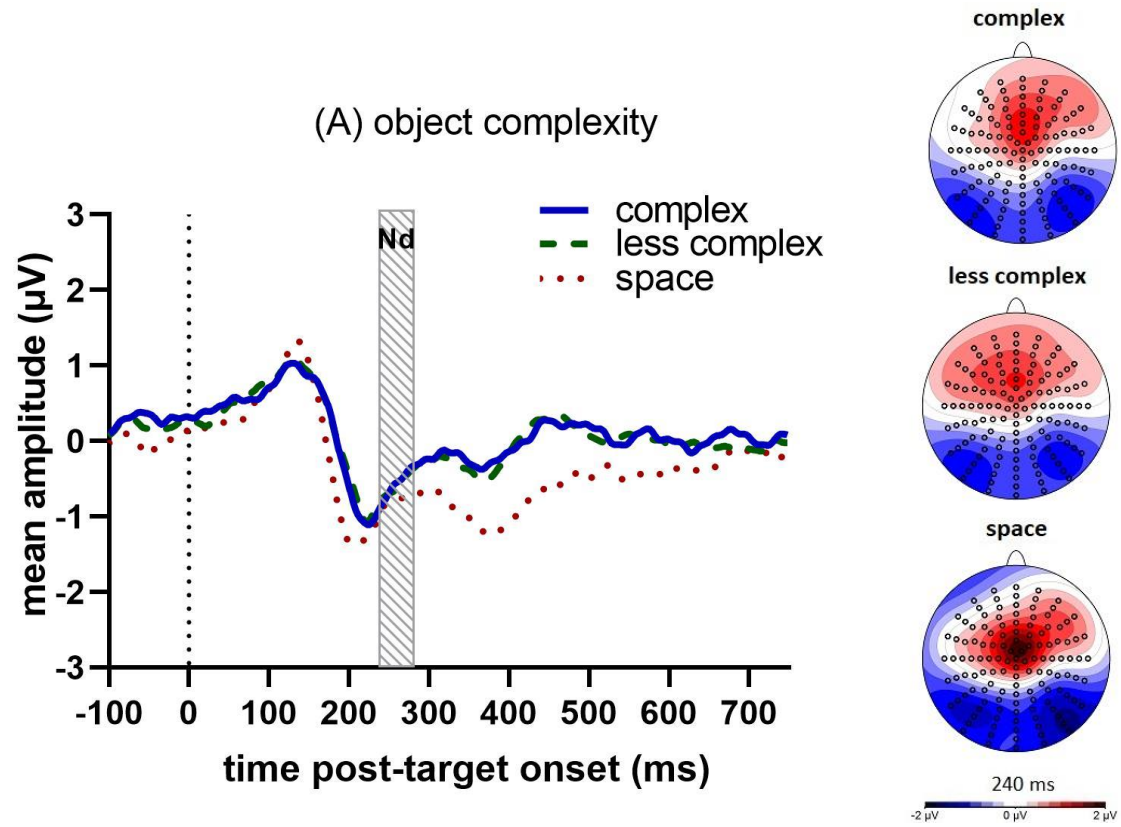
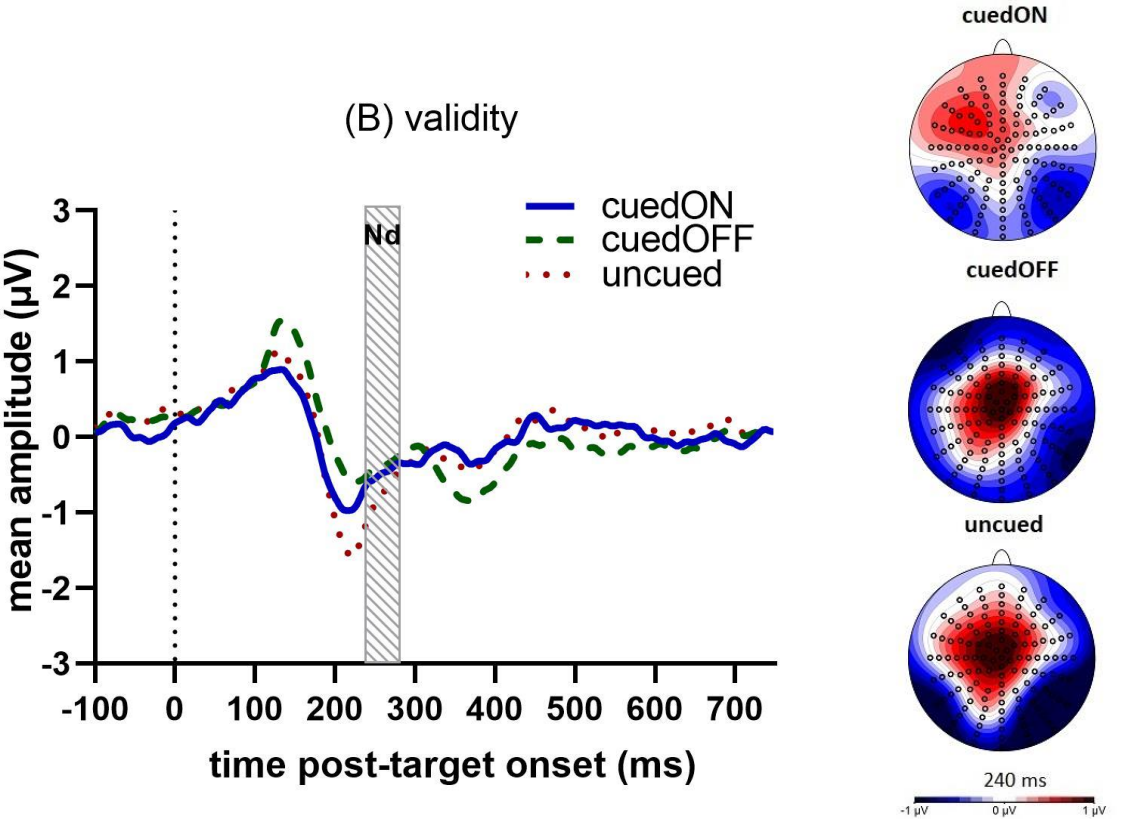


Figure 23. Grand average waveforms for the N1 component (striped area) across validity conditions at the electrode cluster encompassing P7, PO7, P8 and PO8. Scalp topographies of N1 modulations (170 – 210 ms) are shown in the right panel (data were referenced to the average of the electrodes). Red reflects positive voltage and blue reflects a negative voltage.

Nd: 220 to 260 ms time window

Amplitude. Mean ERP amplitudes in the 220 to 260 ms time window were compared for each condition. The analysis revealed a main effect of object complexity, $F(2, 34) = 6.41$, $p = .004$, $\eta_p^2 = .27$, with more negative amplitudes for space than complex ($p = .002$) and less complex ($p = .007$) object conditions (see Figure 24A). There was also a validity main effect, $F(2, 34) = 12.97$, $p < .001$, $\eta_p^2 = .43$. Nd was more negative to uncued than cuedOFF targets ($p < .001$). Also, the amplitude was more negative to cuedON than cuedOFF targets ($p = .001$). However, no difference in amplitude was observed between uncued and cuedON targets ($p = .140$) (see Figure 24B). Replicating our previous results (see: Chapter IV), there was a SOA main effect, $F(1, 17) = 17.00$, $p < .001$, $\eta_p^2 = .50$. Again, Nd was more negative in short versus long SOA (see Figure 24C). There was no Validity × Object Complexity interaction, $F(4, 68) = 1.45$, $p = .228$, $\eta_p^2 = .08$, Object Complexity × SOA interaction, $F(2, 34) = 1.40$, $p = .259$, $\eta_p^2 = .08$ or Validity × SOA interaction, $F(2, 34) = 0.66$, $p = .525$, $\eta_p^2 = .04$.


(A) object complexity
complex
less complex
space
Nd
mean amplitude (μV)
time post-target onset (ms)
3
2
1
0
-1
-2
-3
-100
0
100
200
300
400
500
600
700
complex
less complex
space
240 ms
-2 μV
0 μV
2 μV


(B) validity
cuedON
cuedOFF
uncued
Nd
mean amplitude (μV)
time post-target onset (ms)
3
2
1
0
-1
-2
-3
-100
0
100
200
300
400
500
600
700
cuedON
cuedOFF
uncued
240 ms
-1 μV
0 μV
1 μV

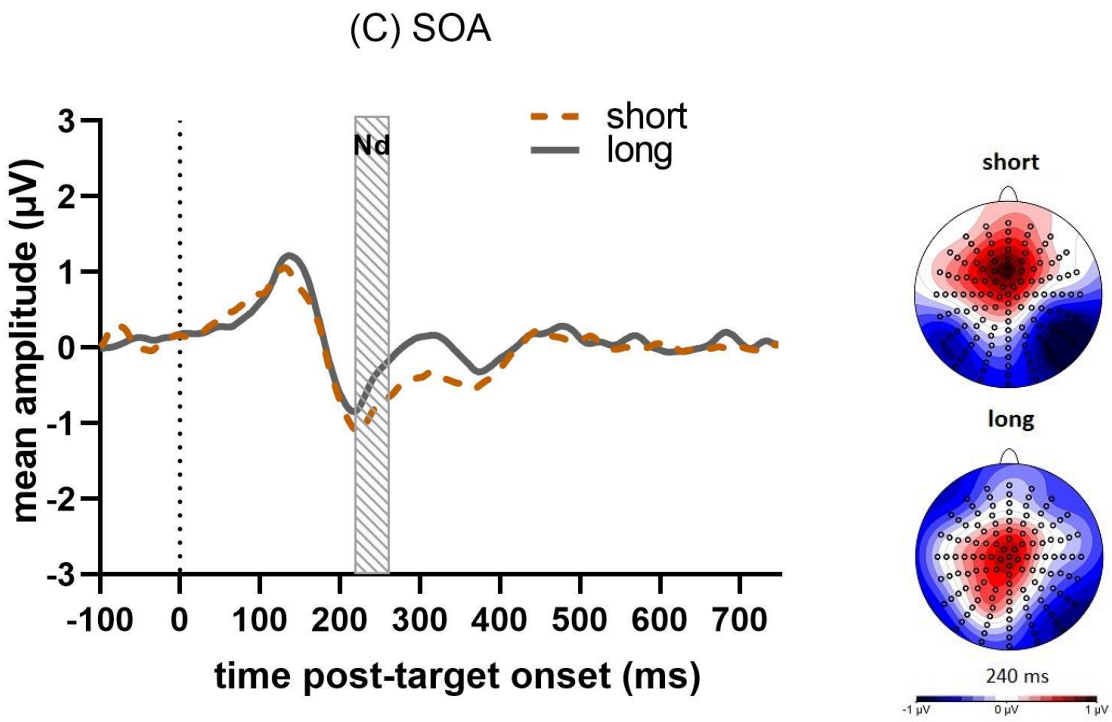
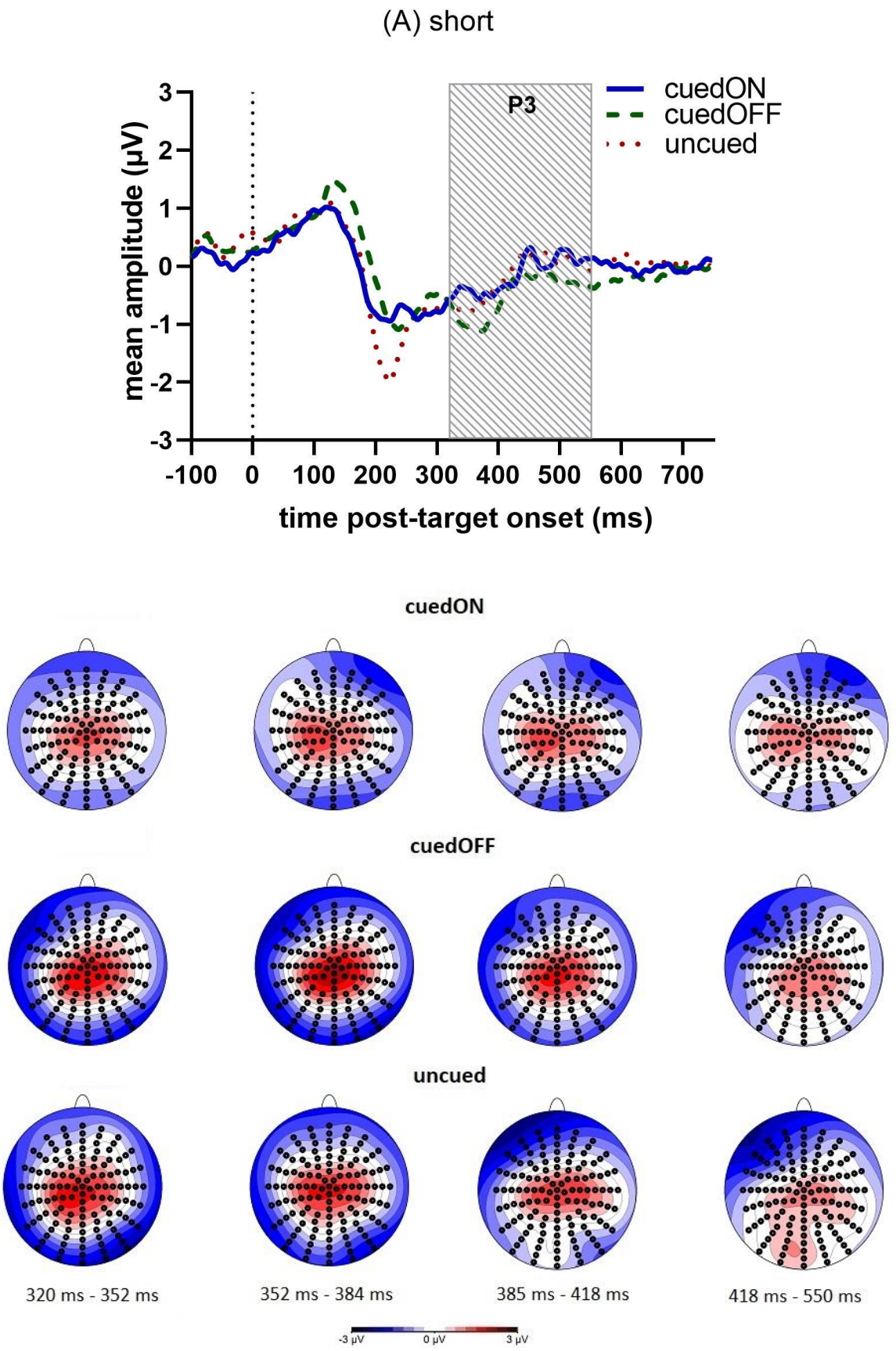
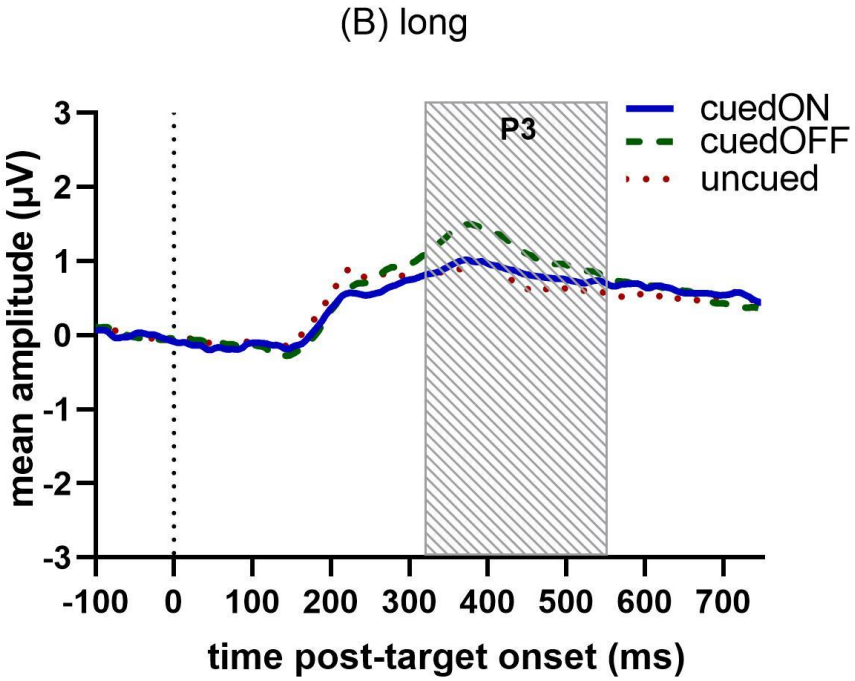


Figure 24. Grand average waveforms for the Nd component (striped area) for object complexity conditions (A) and for each validity (B) and SOA (C) levels at the electrode cluster encompassing P7, PO7, P8 and PO8. Scalp topographies of Nd component (220 – 260 ms) are shown in the right panel (data were referenced to the average of the electrodes). Red reflects positive voltage and blue reflects a negative voltage.

P3: 320 to 450 ms time window

Amplitude. Mean ERP amplitudes in the 320 to 450 ms time window were compared for each condition. The analysis revealed a Validity × SOA interaction, $F(2, 34) = 11.77$, $p < .001$, $\eta_p^2 = .41$. In short trials, P3 positivity was significantly smaller in cuedOFF than cuedON ($p = .039$) and marginally smaller than in uncued trials ($p = .060$) (Fig. 25), which is in line with the behavioural lack of the IOR for cuedOFF targets. In turn, in long SOA trials, P3 positivity was greater for cuedOFF than for cuedON ($p < .001$) and uncued ($p < .001$) conditions, which parallels behavioural IOR for cuedOFF targets following long SOA. No other main effects or interactions were observed.


(A) short
P3
cuedON
cuedOFF
uncued
mean amplitude (μV)
3
2
1
0
-1
-2
-3
-100
0
100
200
300
400
500
600
700
time post-target onset (ms)
cuedON
cuedOFF
uncued
320 ms - 352 ms
352 ms - 384 ms
385 ms - 418 ms
418 ms - 550 ms
-3 μV
0 μV
3 μV


(B) long
P3
cuedON
cuedOFF
uncued
mean amplitude (µV)
3
2
1
0
-1
-2
-3
-100
0
100
200
300
400
500
600
700
time post-target onset (ms)

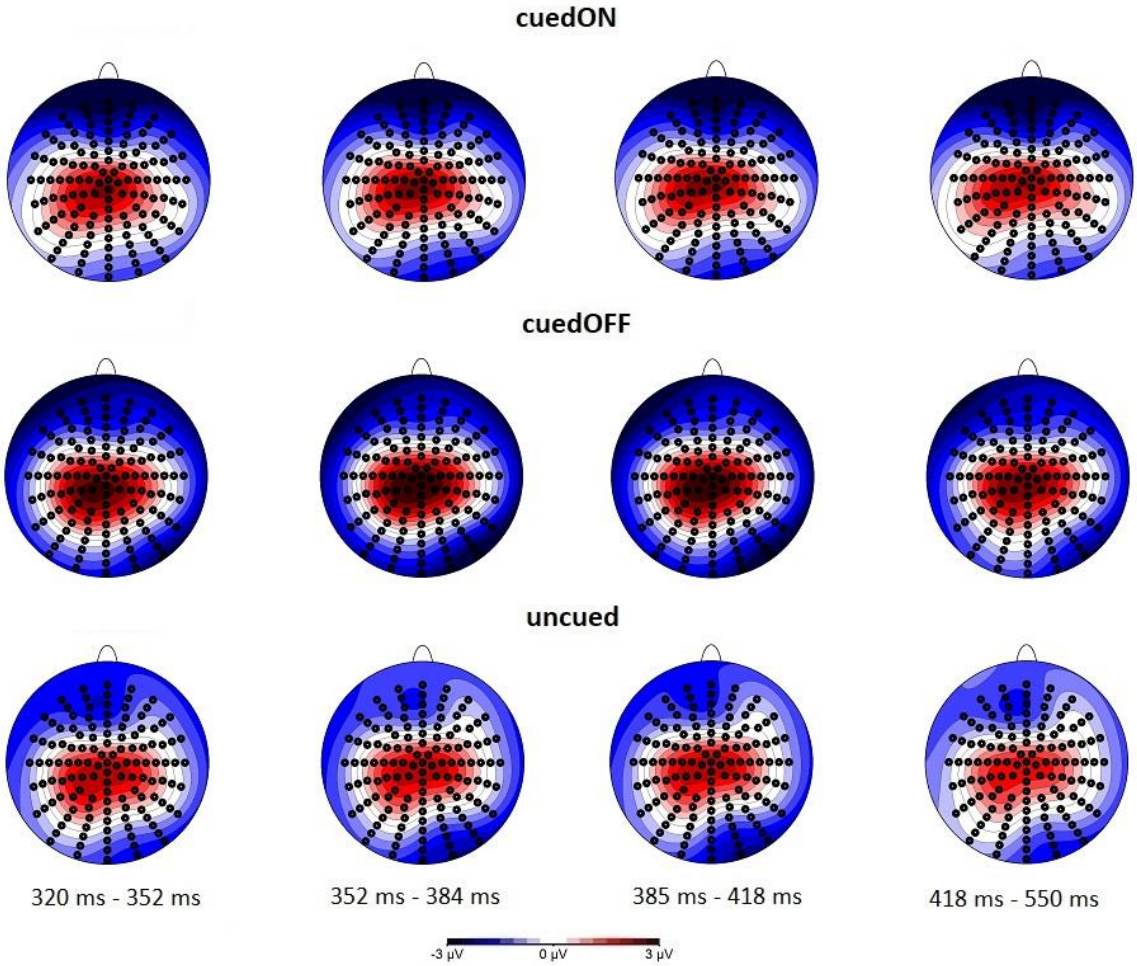
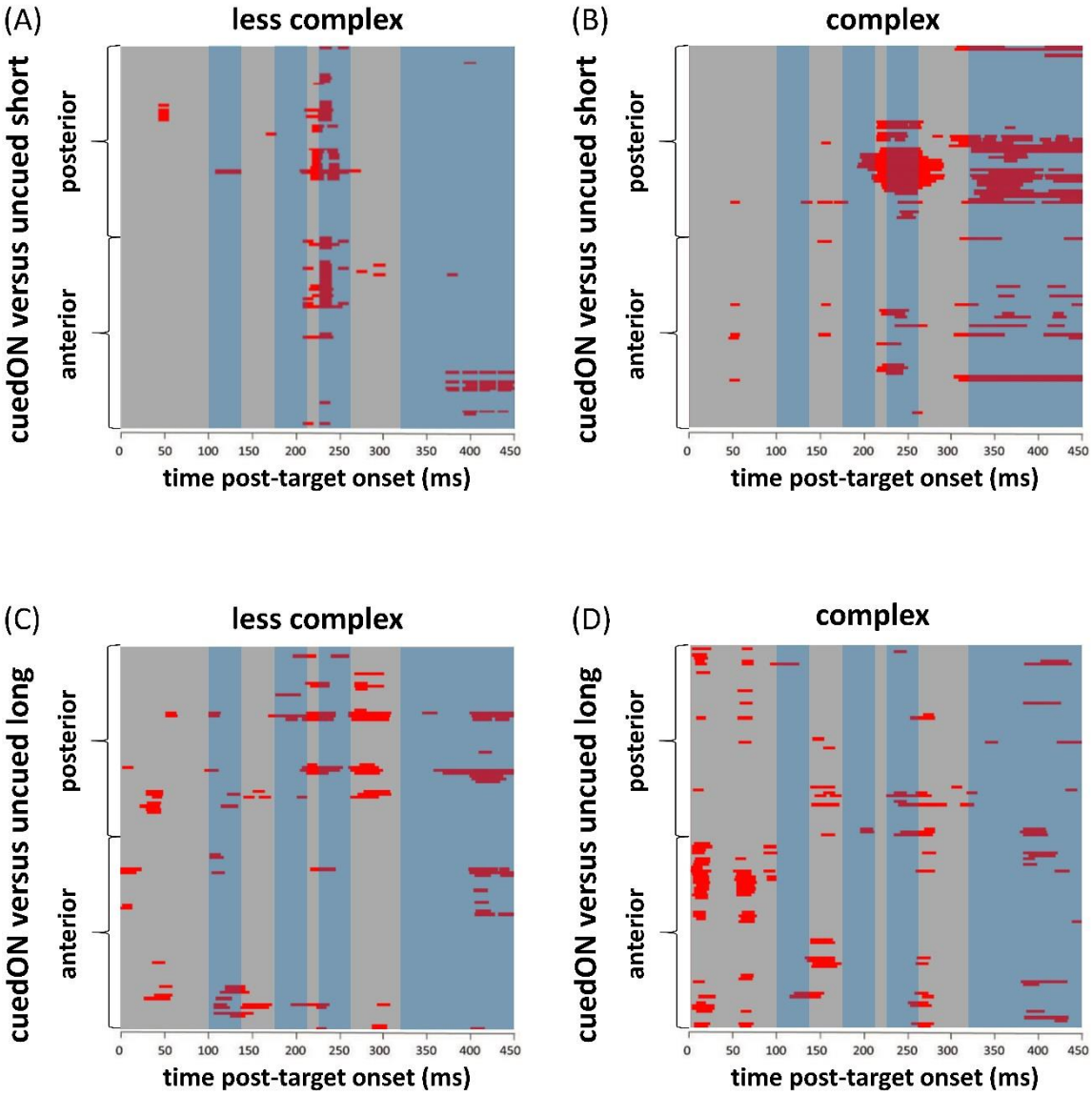


Figure 25. Grand average waveforms for the P3 component (striped area) for each of validity conditions across (A) short and (B) long SOA conditions at the electrode cluster encompassing FC3/ Z/4, C3/Z/4, CP3/Z/4, and P3/Z/4. Scalp topographies of P3 component (320 – 450 ms) are shown in the bottom panel (data were referenced to the average of the electrodes). Red reflects positive voltage and blue reflects a negative voltage.

5.3.2.1.2. Mass Univariate Contrasts across all 128 electrodes

Mass Univariate analyses were conducted in order to further characterise the effects of object complexity on attentional modulations across validity (cuedON, cuedOFF, uncued) and SOA (short, long) levels. The contrasts for each time point across all 128 electrodes for less

complex and complex object conditions are shown in Figure 26 A-H.



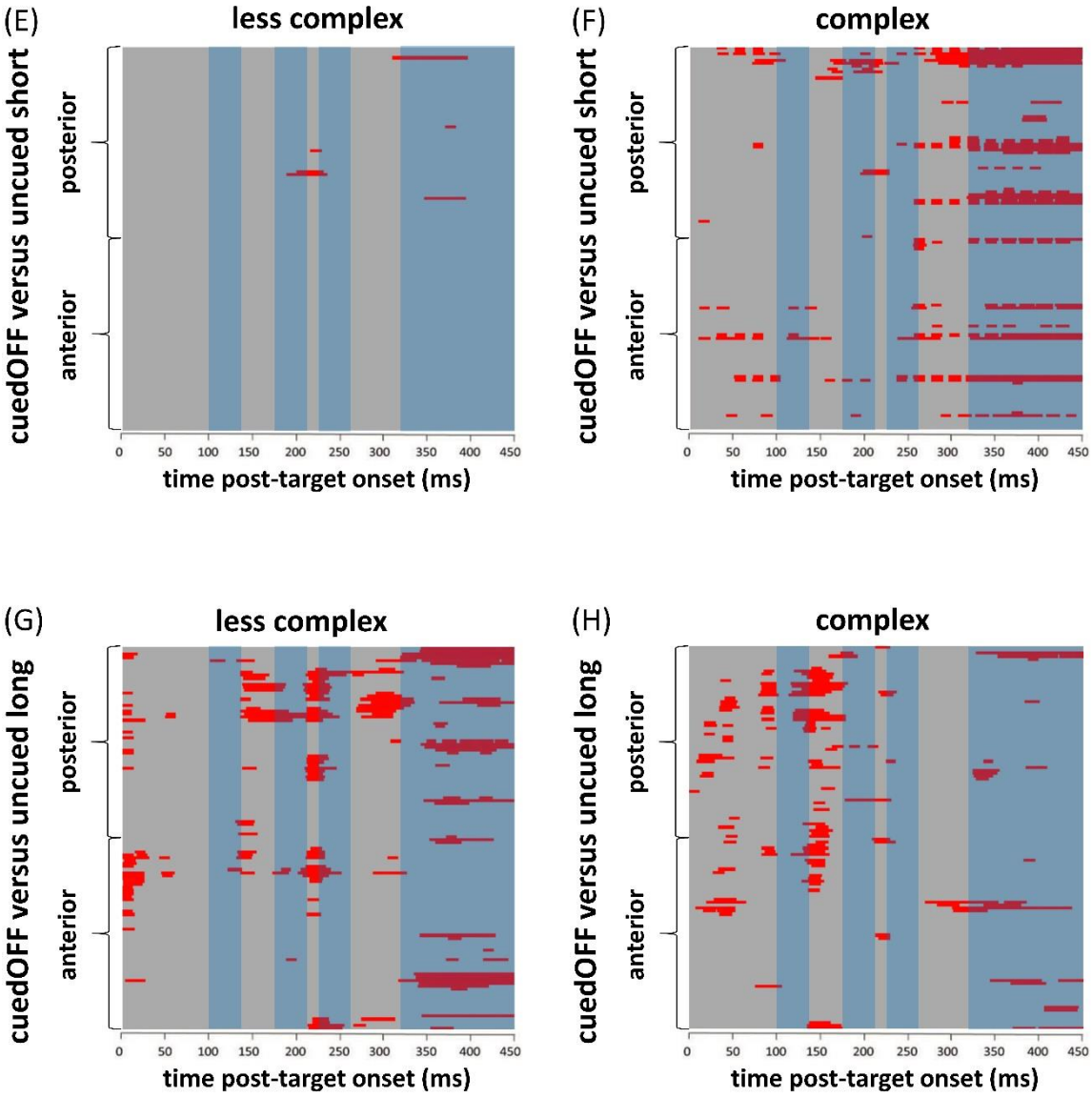
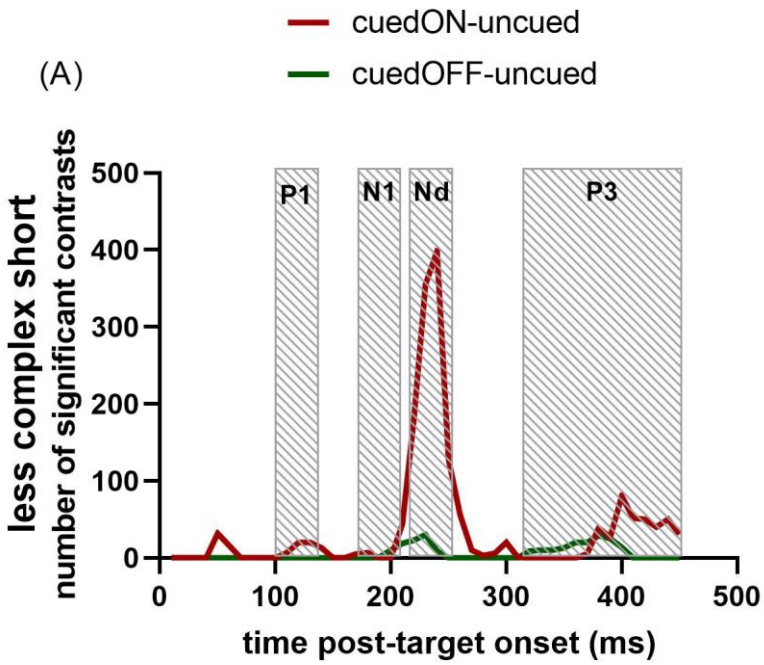


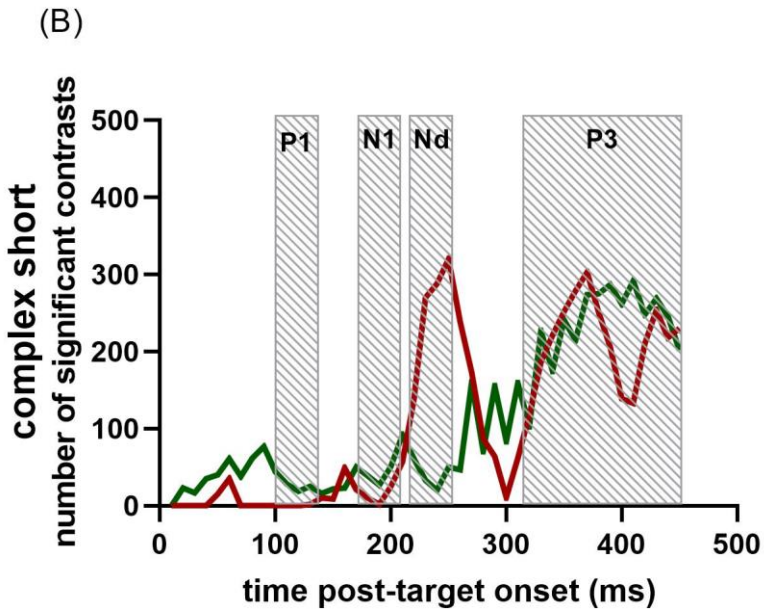
Figure 26. Raster plots of mass univariate contrasts showing significant pairwise contrasts ($p < .01$) for (A) less complex cuedON-uncued short; (B) complex cuedON-uncued short; (C) less complex cuedON-uncued long; (D) complex cuedON-uncued long; (E) less complex cuedOFF-uncued short; (F) complex cuedOFF-uncued short; (G) less complex cuedOFF-uncued long and (H) complex cuedOFF-uncued long. Posterior/anterior electrodes are shown as a function of time (0-450 ms) beginning at the target onset. The blue highlighted areas show the P1, N1, Nd and P3 components.

Mass univariate contrasts showed the differential sensitivity between less complex and complex conditions and cuedON, cuedOFF and uncued targets in the P1, N1, Nd and P3 components. A time series plot of the frequency distribution of significant differences is shown in Figure 27. These data were further analysed as a non-parametric time-series in the Friedman test.

For the P1, during less complex condition there was a higher frequency of significant differences in cuedON-uncued than cuedOFF-uncued, $\chi^2(1) = 4.00$, $p = .046$ for short SOA, but it was not the case for long SOA, $\chi^2(1) = 1.80$, $p = .180$. Similarly, in the complex condition, the frequency of significant differences in cuedON-uncued versus cuedOFF-uncued was higher in short SOA, $\chi^2(1) = 5.00$, $p = .025$, but not in long SOA trials $\chi^2(1) = 1.80$, $p = .180$. For the N1, in the less complex condition there was no difference between cuedON-uncued versus cuedOFF-uncued targets neither in short trials $\chi^2(1) = 0.20$, $p = .655$ nor in long trials $\chi^2(1) = 1.80$, $p = .180$. In turn, in the complex condition, the frequency of significant differences was higher in cuedOFF-uncued than cuedON-uncued condition in the short SOA trials, $\chi^2(1) = 5.00$, $p = .025$, but not in the long SOA trials $\chi^2(1) = 1.80$, $p = .180$. During Nd, a frequency of significant differences was higher for cuedON-uncued than cuedOFF-uncued targets in the less complex condition in short SOA, $\chi^2(1) = 5.00$, $p = .025$. On contrary, in long SOA trials, a frequency of significant differences was higher for cuedOFF-uncued versus cuedON-uncued trials, $\chi^2(1) = 5.00$, $p = .025$. In turn, in the complex condition, a higher frequency of significant differences was found in cuedON-uncued versus cuedOFF-uncued conditions for short SOA only, $\chi^2(1) = 5.00$, $p = .025$, whereas long SOA cancelled out this effect yielding no significant differences between cuedON-uncued and cuedOFF-uncued conditions, $\chi^2(1) = 0.20$, $p = .655$, During the P3 component, in less complex condition, no differences were observed between cuedON-uncued and cuedOFF-uncued for short trials $\chi^2(1) = 0.286$, $p = .593$. In turn, in long

trials, a frequency of significant differences was higher in cuedOFF-uncued than cuedON-uncued condition $\chi^2(1) = 14.13$, $p < .001$. For complex condition, no differences between cuedOFF-uncued and cuedON-uncued were observed in neither short, $\chi^2(1) = 0.286$, $p = .593$, nor long SOA trials, $\chi^2(1) = 1.14$, $p = .285$.


cuedON-uncued
cuedOFF-uncued
(A)
less complex short
number of significant contrasts
P1
N1
Nd
P3
500
400
300
200
100
0
0
100
200
300
400
500
time post-target onset (ms)


(B)
complex short
number of significant contrasts
P1
N1
Nd
P3
500
400
300
200
100
0
0
100
200
300
400
500
time post-target onset (ms)

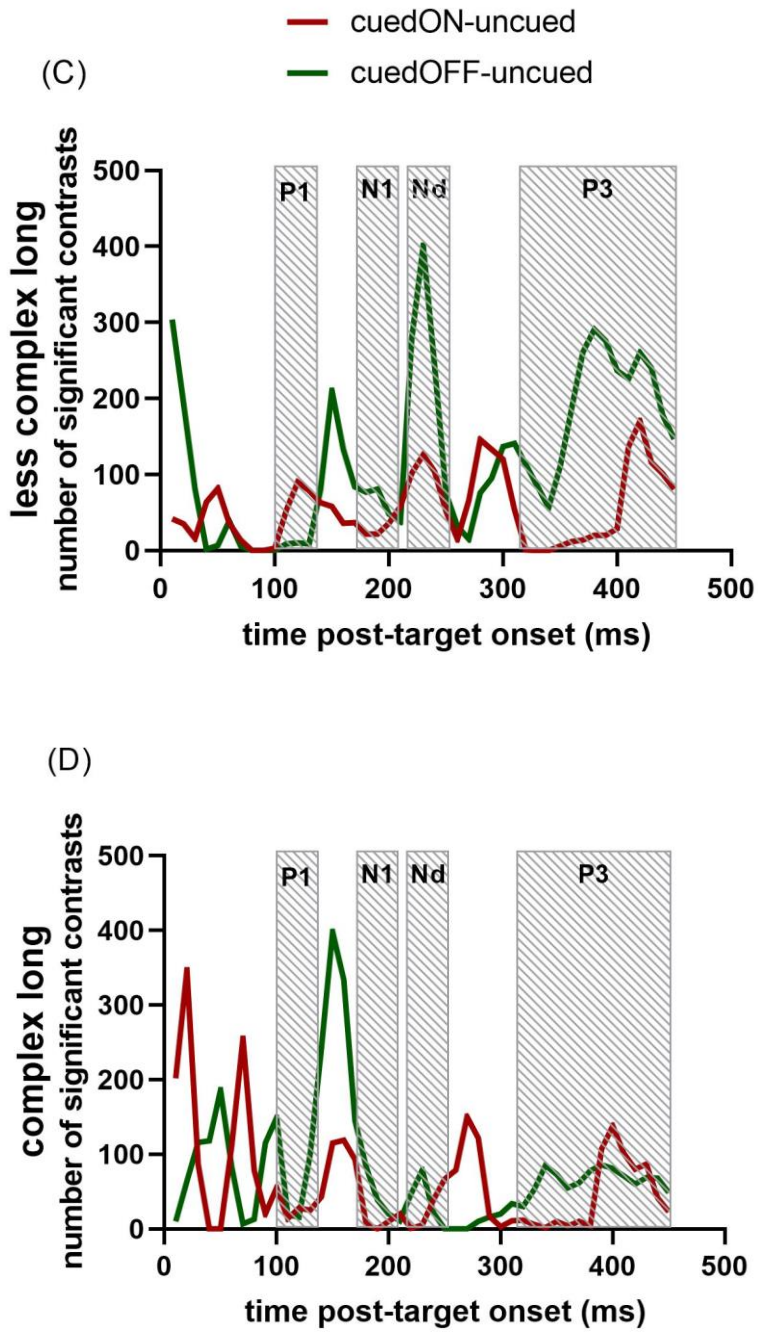


Figure 27. Plots showing the frequency of significant contrasts in each of 128 electrodes in 10 ms time window (max. 1280) from the Mass Univariate analyses between 0 and 450 ms. Contrasts depict the difference between cuedON vs. uncued (red line) and cuedOFF vs. uncued (green line) for (A) less complex short, (B) complex short, (C) less complex long and (D) complex long conditions.

5.4. Discussion

Spatial IOR is enhanced by the presence of objects in static displays (Jordan & Tipper, 1998; Tipper et al., 1999). The origin of this effect has been attributed to the existence of separate inhibitory mechanisms of space- and object-based attention that act in parallel, leading to greater IOR. Yet, studies have shown that inhibition is also modulated by the salience of object contours (Leek et al., 2003; Reppa & Leek, 2006; Reppa et al., 2012), but the underlying neural mechanisms of this effect remain uncertain. In the present study, we aimed to characterise the effects of object complexity on behavioural and neurophysiological IOR. In our adapted Posner cueing paradigm (Posner, 1980), non-informative cues were presented, followed by targets that could appear at the same (cuedON), opposite (uncued) or adjacent (cuedOFF) location relative to the cue. In the object conditions, cues and targets (cued and uncued) were located in two placeholders that varied as a function of shape complexity (complex and less complex).

The behavioural results showed IOR only in object conditions (both complex and less complex), but not in the space condition. Importantly, however, no differences were observed between complex and less complex objects. Furthermore, although in short interval trials IOR was found for previously attended places only, in long interval trials the IOR was present for both previously attended and – albeit weaker - adjacent locations. Hence, it suggests that although inhibition is most pronounced within the location of the previous cue, it spreads out to the visual field and also affects adjacent locations (Wascher & Tipper, 2004). Additionally, replicating our previous findings (Chapter IV), response times were accelerated following short versus long SOA, indicating better temporal preparation after short intervals (Woodrow, 1914). To summarise, although we found differences across space and objects conditions, there were no differences between complex and less complex object conditions. These findings suggest

that the manipulation of object complexity in our experiment did not give rise to behavioural changes in the magnitude of IOR.

The ERP data revealed that P1 amplitude was reduced for both complex and less complex object conditions relative to space condition. This modulation was independent of cueing effects and therefore it possibly reflects a purely perceptual process that did not vary as a function of the attentional orienting. One may presume that processing objects elicited smaller P1 activation to target onset because of the mere perceptual difference between the space and object conditions in which placeholders were present on the display at all times. Previous studies examining P1 modulations in attentional cueing are generally inconsistent with some studies reporting the link between IOR and P1 (Hopfinger & Mangun, 1998; Satel et al., 2014; Taylor & Klein, 2000; Wang et al., 2012), and other ones failing to find the effects of IOR on P1 modulations (Martín-Arévalo et al., 2014; McDonald et al., 1999; Van der Lubbe et al., 2005; Wascher & Tipper, 2004). Intriguingly, though, our previous study (Chapter IV) in fact demonstrated smaller P1 activity to cued versus uncued targets selectively in object condition, which was also accompanied by stronger behavioural IOR in object versus space condition. Therefore, object complexity manipulation appears to cancel out this effect.

In contrast, low-level perceptual effects elicited by N1 activation were modulated by cueing as indexed by the more negative N1 to uncued versus cued and adjacent targets. However, no differences between space and object conditions were observed, suggesting that this pattern of data was due to a more general inhibitory mechanism that did not vary between space- and object-based frames of reference. Again, it appears to contradict our previous N1 activity results that did show the dissociable effects of validity depending upon the object presence/absence.

The analysis of Nd component revealed more pronounced negativity for space than object conditions as well as for uncued targets in relative to targets that occurred in adjacent locations. Such selective inhibition of adjacent locations provides further support for a separate mechanism that operates over the visual field rather than a single inhibitory function that generates a gradient around the previously attended locations/objects. We have also replicated findings from our previous experiment, which showed more negative Nd component in short than long SOA trials (Chapter IV), demonstrating again that optimal temporal preparation is reflected at the neural level.

Finally, P3 activation to cued, uncued and adjacent targets was differentially modulated by SOA. Whereas in long trials, a greater P3 activity was observed for adjacent targets relative to cued and uncued targets, which is generally consistent with our previous results (Chapter IV), short trials yielded the opposite effect with smaller P3 amplitude for adjacent targets when compared to cued and uncued targets. As P3 increase to cued when compared to uncued targets has been linked stronger behavioural IOR effect (McDonald et al., 1999; Prime & Jolicœur, 2009), one may presume that elevated P3 to adjacent locations in long trials can reflect a greater IOR, whereas a reduced P3 to adjacent locations in short trials can reflect weaker inhibition after short SOA. Such a double dissociation of SOA effects is indeed nicely mirrored by behavioural results that revealed slower response times to adjacent targets in long but not short interval trials. Consequently, we have shown again that inhibition can act selectively affecting the visual field only and is further sensitive to the cue-target interval. Nevertheless, this effect was not modulated by object complexity.

Therefore, our results demonstrated neural modulations of cueing effects during the time course of the target processing. As early as approximately 200 ms after the target onset,

negative visual potentials in N1 component were more pronounced for uncued than cued and adjacent targets. This effect indicates that the IOR affects early perceptual modulation, which is in line with our results (Chapter IV) and previous reports (Sapir et al., 2013; Taylor & Klein, 2000; Wang et al., 2012). However, object complexity did not interact with this effect which suggests that, at least at neural level, IOR is not differentially modulated by object complexity. Nd component was more negative to uncued than adjacent targets, indicating a selective suppression of the cued visual field and intriguingly, of space locations rather than locations occupied by complex and less complex objects. We have also replicated our previous results of more pronounced Nd component following short versus long SOA, which points to the beneficial role of temporal preparation (i.e., performance is better after short than long intervals) when SOA is manipulated in a blockwise fashion (Woodrow, 1914). Finally, P3 analysis revealed a double dissociation of cueing effects depending on the SOA: in long trials P3 amplitude was greater to adjacent targets, but in short trials this pattern reversed yielding smaller P3 to adjacent targets. Again, this effect was also indifferent to object complexity manipulation.

Taken together, our results showed differential modulation of inhibitory effects at the neural level, but we failed to observe any differences between less complex and complex object conditions. Therefore, although our previous and current results support the differential role of space and object-based inhibitory systems in generating the IOR, object complexity does not appear to modulate the inhibitory strength at previously cued and adjacent locations. Alternatively, it is also plausible that we were not able to capture any differences due to an inadequate experimental manipulation (e.g., less complex and complex conditions did not sufficiently vary in their “complexity”). Nonetheless, more studies are required to draw definitive conclusions regarding the role of object complexity in IOR modulation.

CHAPTER VI

GENERAL DISCUSSION

Studies on covert attention have started over a century ago with Helmholtz's discovery (1867) that we can selectively process visual information in particular locations without actually directing our eyes towards this place. Since then, we have vastly expanded our knowledge about cognitive and neural mechanisms that prioritise and select relevant visual information to guide adaptive behaviour. For instance, we now know that attention can operate over multiple frames of reference such as locations, objects, features as well as temporal structure (Chelazzi et al., 1993; Coull & Nobre, 1998; Desimone & Duncan, 1995; Moran & Desimone, 1985; Posner & Cohen, 1984; Tipper et al., 1991) and that overt and covert attentional systems share overlapping neural substrates (Beauchamp et al., 2001; Corbetta et al., 1998; Nobre et al., 2000, 1997; Rizzolatti et al., 1987). Furthermore, we have come to understand neural mechanisms of selective attending to the sensory environment which include facilitation of relevant information and inhibition of irrelevant one by the means of lowering the noise, modulation of firing rates or neural entrainment (Desimone & Duncan, 1995; Fries, 2015; Reynolds & Chelazzi, 2004).

The goal of this thesis was to further characterise the function of the inhibitory mechanisms in selective covert attention. We identified and aimed to answer the following

theoretical problems: (1) how inhibitory mechanisms are utilised to bring covert and overt selection systems into spatial alignment; (2) the extent to which the distribution of inhibition is permeable to top-down modulations; (3) whether spatial distributions of inhibition and their neural basis are modulated by objects in the visual field.

In the current chapter, I will first outline the summary of empirical results from Chapters II, III, IV and V. Next, I will provide an in-depth discussion of the findings, present the broader implications of the results and suggest possible directions for future research.

6.1. Summary of findings

In Chapter II, we investigated the functional role of the effect of slower response times to already scanned locations – known as the inhibition of return (IOR; Klein, 2000; Posner & Cohen, 1984; Posner et al., 1985), in realigning covert and overt attentional systems. Reorienting cue was varied as a function of its location: it could appear at the centre, whereby it overlapped with the central ocular fixation, or unlike any previous study, at the periphery. We demonstrated that the IOR was stronger when the reorienting event occurred at the centre, which was also the current fixation point, suggesting a central realignment of covert and overt attention. Therefore, we propose that the IOR might act to realign overt and covert attention by biasing attention shifts towards the current (central) fixation.

In Chapter III, we aimed at elucidating whether top-down factors such as statistical priors can modulate the exogenous attentional orienting elicited by the presentation of the nonpredictive spatial cues. Based on previous reports, we hypothesised that increasing the probability of target locations at one visual hemifield would affect the allocation of attentional

resources by exacerbating the IOR magnitude relative to a condition in which targets appeared with equal probability on both sides. However, there was no difference in response times to targets between two probability conditions. Further, a direct comparison of two consecutive blocks in a high probability condition failed to reveal significant learning effects, indicating that statistical priors does not modulate inhibition. Such findings demonstrate that exogenous attention is relatively impermeable to top-down processes. We additionally probed attention to targets adjacent to previously cued locations and also found IOR following long cue-target intervals, indicating that inhibition disperses across space affecting targets in the same visual field.

In Chapter IV, we investigated the neural basis of modulations of space-based IOR by object presence. We contrasted behavioural and electrophysiological responses to targets in object present versus absent static displays. Importantly, targets could appear at the same or opposite place as previously cued or at the adjacent locations in the same visual field. Behavioural results showed two main findings: (1) the IOR was stronger in object versus space condition; and (2) the IOR was most pronounced at previously attended places but it also spread out – albeit weaker in magnitude – to affect nearby locations. The ERP analysis revealed that target processing encompasses the modulation of several neural components. Object-based attention involved the modulation of early perceptual processes in response to targets. However, the IOR to previously cued locations was primarily reflected at a decrease of P1 component, whereas inhibition of locations adjacent to previously visited ones was observed as the N1 attenuation. In turn, a decrease of later Nd component to uncued versus cued targets was independent of space and object manipulations, suggesting the existence of a more general neural inhibitory mechanism. Finally, when objects were present, an elevated P3 component, suggesting stronger inhibition, was found when processing inspected places and locations

adjacent to them. In turn, space condition yielded stronger P3 component only for the adjacent locations. Therefore, findings from this experiment suggest that objects indeed modulate spatial distributions by leading to stronger IOR which is reflected at the neural level across multiple stages of target processing.

Chapter V used experimental findings from Chapter IV to further characterise behavioural and electrophysiological modulations induced by object complexity when orienting attentional resources to locations in space. Our hypothesis was that more complex shapes would elicit stronger inhibitory signal to both attended and adjacent locations. On the contrary, we did not observe any significant differences between complex and less complex experimental manipulations neither at the behavioural nor at the electrophysiological level. Such null findings suggest that the IOR is not modulated by object contours. Alternatively, it is also plausible that our complexity manipulation was not successful, i.e., the objects did not vary in their complexity sufficiently to reveal behavioural and ERP differences.

Taken together, results from all four empirical chapters revealed a picture of robust inhibitory effects across a wide range of cue-target intervals. Such inhibition was demonstrated to be impermeable to top-down processes such as statistical priors of target locations. Furthermore, we showed that the IOR acts to realign covert and overt attentional systems by biasing attention to the current (central) fixation as demonstrated by stronger IOR following central rather than peripheral reorienting event. Yet, as our visual field is full of objects, we aimed to elucidate neural underpinnings of space- and object-based inhibitory mechanisms. The results demonstrated that object-based inhibition elicits a decline in perceptual processing of already attended places as well as locations adjacent to them. Similarly, object presence leads to inhibition of previously inspected and adjacent locations at the later stage of processing

that reflects more demanding processing of task-relevant information, whereas space-based inhibition targets selectively inspected locations. In turn, both space- and object-based inhibitory mechanisms appear also to share, at least partly, a common neural basis as demonstrated by enhanced processing of new locations in relative to the ones that have been already visited around 220-260 ms after exposed to a target. Finally, although we hypothesised that the saliency of object contours would also modulate underlying inhibitory mechanisms, we failed to observe such findings. Theoretical implications of results as well as limitations and future research directions are discussed in the following sections of this chapter.

6.2. The role of inhibition in spatial orienting of attention

Selective attention is conceptualised as the set of mechanisms that guide our perception and action by prioritising and selecting relevant information and suppressing irrelevant one. These two mechanisms, facilitation and inhibition are the core components of attention. The top-down signal is generated in the frontal eye fields and parietal cortex which bias the receptive field in the visual cortex (Georgia, Stephen, Huihui, & Robert, 2009; Moore & Armstrong, 2003). Theoretical and empirical work has emphasised the role that facilitation plays in biasing relevant locations through neural synchronisation, filtering and fire rates regulation (Baldauf & Desimone, 2014; Chelazzi et al., 1993; Desimone & Duncan, 1995; Fries, 2015).

Yet, the second facet of selective attention is the suppression of unattended locations. In line with this framework, attention would allow for adaptive behaviour by assigning high gain to relevant items and low gain to distractors (Houghton & Tipper, 1994). For example, neurophysiological studies have demonstrated that activity in the receptive field of ignored target was suppressed in relative to the one of attended item (Moran & Desimone, 1985). In

the spatial cueing paradigm (Posner, 1980), suppression is applied to previously inspected items in order to prevent searching this location again and therefore, to enhance processing of the visual field (Bennett & Pratt, 2001; Klein, 2000, 1988; Lupiáñez et al., 2001; Posner & Cohen, 1984; Posner et al., 1985; Prime & Ward, 2006b; Reppa et al., 2012; Taylor & Klein, 1998). Such a phenomenon, known as inhibition of return (IOR) is empirically observed as slower response times to previously cued locations. At the neural level, the IOR has been linked to the superior colliculus (Dorris, Klein, Everling, & Munoz, 2002; Sapir et al., 1999) and the lateral intraparietal sulcus (Robinson, Bowman, & Kertzman, 1995).

In order to allow for the build-up of inhibitory signal at the previously attended place, a reorienting event is usually presented at the centre of the display between a peripheral initial cue and a target to move attention away from the original cue location. In the current thesis (Chapter II), we manipulated the position of the reorienting event to further probe the role of inhibition of return in spatial orienting. We presented the reorienting cue at the centre of the screen, which was also the fixation point or at the periphery. Consequently, a central reorienting cue summoned covert and overt attention, whereas a peripheral cue reoriented covert attention only. Beginning with Helmholtz's seminal work (1867), covert (independent of eye movements) and overt (accompanied by eye movements) attentional systems have been studied in a wide range of experimental settings (Beauchamp et al., 2001; Itti & Koch, 2000; Kulke, Atkinson, & Braddick, 2016; Mccoy & Theeuwes, 2017; Nobre et al., 2000; Satel, Wang, et al., 2012). Our study aimed to examine whether the IOR can be utilised to realign covert and overt attention as demonstrated by stronger inhibition following central versus peripheral reorienting. Indeed, this is exactly the pattern that we found: response times were slower to attended than unattended locations after central in relative to peripheral reorienting cue. These findings have shed new light on the rules that govern mechanisms of spatial

orienting. More specifically, we demonstrated that in addition to a temporal component (i.e., IOR is stronger after longer cue-target intervals), the spatial position of the reorienting cue also plays an important role in generating inhibitory signals at the previously scanned locations. These novel findings also yield important consequences for understanding the interplay between covert and overt attentional systems. In this context, the inhibition of return acts to realign covert and overt mechanisms and such results suggest a fundamental bias of covert attention towards the (central) ocular fixation.

Although the IOR is affected by bottom-up factors such as the location of the abrupt onset of the reorienting cue, its sensitivity to top-down modulations is still being probed. Some studies have reported that the magnitude of the IOR can indeed be reduced by more intention-driven processes such as temporal expectations (Tipper & Kingstone, 2005). However, other studies have demonstrated that inhibition is relatively impermeable to top-down factors (Gabay & Henik, 2008; Los, 2004). In the current thesis, we provided further evidence that the IOR is not modulated by prior expectations such as the probability of target occurrence (Chapter III). Although previous studies have demonstrated that we detect targets faster when they are more likely to occur in certain locations – so-called the "probability cueing effect", they studied this phenomenon in the context of visual search tasks (Druker & Anderson, 2010; Fecteau et al., 2009; Geng & Behrmann, 2002, 2005; Hoffmann & Kunde, 1999; Kabata & Matsumoto, 2012; Maljkovic & Nakayama, 1996; Sayim et al., 2010; Shaw & Shaw, 1977). In contrast, we used a new methodological approach by investigating the attentional deployment when one target only is present in the visual field by the means of the spatial cueing paradigm. Our results suggest a relative resistance of the IOR to top-down factors such as statistical priors inherent in the task structure. Therefore, it suggests that inhibitory mechanisms in space are indeed impermeable to top-down modulations.

In sum, our findings (Chapters II and III) are particularly informative in providing a better understanding of the role inhibition in spatial orienting of attention. We demonstrated that the IOR is stronger following a central (overlapping with ocular fixation) versus peripheral nonpredictive cue which suggests that it plays an instrumental role in realigning covert and overt attention by a fundamental bias towards the ocular fixation. In parallel, the inhibition of return appears to be impermeable to top-down factors such as statistical probabilities of targets locations. Thus, such dissociable effects of bottom-up and top-down components on the IOR suggest that it is predominantly a reflexive phenomenon that boosts the efficiency of the target search in the environment.

6.3. Electrophysiological basis of space- and object-based modulation of inhibition

Whereas two first empirical chapters of this thesis (Chapter II and III) examined the role of inhibition in space-based orienting, the visual field often contains objects. It has been well-documented that separate inhibitory mechanisms can be deployed to process particular objects (Abrams & Dobkin, 1994; Egly et al., 1994; Jordan & Tipper, 1998; Leek et al., 2003; Possin et al., 2009; Ro & Rafal, 1999; Tipper et al., 1991, 1999, 1994; Weaver, Lupiáñez, & Watson, 1998). Such object-based IOR can track an object that moves to a new location (Tipper et al., 1991) or can exacerbate the inhibitory signal at the given location in static displays (Jordan & Tipper, 1998; Leek et al., 2003). Our current investigation (Chapters IV and V) aimed to characterise the electrophysiological basis of object-based modulations of spatial distributions of inhibition in static displays.

Although the event-related potential (ERP) studies have not linked the IOR to a single electrophysiological marker, several components have been proposed to underlie the

behavioural effect of slower responses to previously attended places. More specifically, the reports have pointed to P1 (Prime & Ward, 2004; Prime et al., 2006; Van der Lubbe et al., 2005; Wascher & Tipper, 2004), N1 (Gutiérrez-Domínguez et al., 2014; Prime & Jolicœur, 2009; Prime et al., 2006; Prime & Ward, 2004; Satel et al., 2014), Nd (Gutiérrez-Domínguez et al., 2014; McDonald et al., 1999; Wascher & Tipper, 2004) and P3 (McDonald et al., 1999; Prime & Jolicœur, 2009) modulations that accompany the behavioural IOR. Yet, the results of the studies are fairly inconsistent, with some studies reporting the aforementioned modulations, and other ones failing to find effects of the IOR on a given component.

In Chapter IV we investigated the influence of space- versus object-based inhibition on processing targets located in different locations by combining behavioural and ERP measures. First, we provided further evidence of stronger IOR for combined space- and object-based frames of reference. Importantly, this effect was observed at the behavioural and neural level. A decrease of P1 component was observed to cued items for object-based attention, suggesting that IOR can act by affecting early perception. At later stage of perceptual processing, targets adjacent to previously cued ones are also inhibited selectively for object-based system suggesting that a separate inhibitory function is applied to a given visual field. In the context of the debate on a possible electrophysiological marker of the IOR, our results point to an Nd component, which shows a decrease for cued in relative to uncued targets irrespectively of involvement of space and object attentional systems. As such, this finding offers new insight into the neural correlates of the IOR and provides further support to accounts proposing an Nd component as a good candidate for an electrophysiological markers of the inhibition of return (Satel et al., 2014).

It is important to note that an Nd attenuation for cued rather that uncued items were found for short cue-target interval trials only. Given that in a fixed foreperiod paradigm, in

which the cue-target interval is manipulated in a blockwise fashion (like in our study) and optimal temporal preparation is reached following short than long interval (Niemi & Naatanen, 1981; Woodrow, 1914), it is plausible that the IOR effect further interacts with temporal preparation. At first glimpse, such possibility appears to contradict previous studies which reported the relative resistance of IOR to modulations by temporal expectancies (Gabay & Henik, 2008; Los, 2004). However, these studies manipulated the cue-target interval within blocks, which results in the opposite pattern of data, i.e., faster response times after *long* rather than short intervals and is underlined by more explicit in nature temporal expectations (Niemi & Naatanen, 1981). N1 and Nd modulations by temporal preparation reflect the interplay between IOR mechanisms and temporal dimension inherent in the task itself. Furthermore, temporal preparation per se (i.e., independent of the IOR effects) was also observed in faster response times after short than long intervals and more negative Nd component in short versus long interval trials. Overall, our results show that temporal dimension can further modulate inhibition and that its role in cognitive processes cannot be underestimated.

In turn, most studies have not examined the later evaluative stage reflected in the P3 component in the context of the IOR (Gutiérrez-Domínguez et al., 2014; Prime & Ward, 2004, 2006a; Satel et al., 2014; Wascher & Tipper, 2004). Yet, a few investigations have linked more pronounced P3 activity with inhibition of already attended places (McDonald et al., 1999; Prime & Jolicœur, 2009). Similarly, we found P3 enhancement for targets adjacent to previously cued items and, in case of the object-based attentional manipulation, also for the previously cued items. Therefore, these findings provide evidence that IOR is indeed accompanied by an increase of P3 to already attended targets. Furthermore, our results shed new light on the nature of proactive attentional mechanisms that operate following a transient nonpredictive event. Specifically, they further support the existence of two inhibitory

mechanisms, one operating on previously scanned items and a second one that suppresses already attended visual field.

In Chapter V we aimed to further characterise the effects of object contours saliency on the strength of the IOR by comparing behavioural and event-related responses elicited by objects that varied in a complexity level. Intriguingly, we did not observe any differences between complex and less complex conditions behaviourally, nor at the neural level. As such, our results contradict previous findings (Leek et al., 2003; McAuliffe et al., 2001; Reppa & Leek, 2003, 2006; Reppa et al., 2012) that reported the IOR modulation by object shape. However, it is also probable that we did not find significant differences due to inadequate complexity manipulation. In other words, objects in less complex and complex experimental conditions did not contrast sufficiently to allow for potential differences to be observed.

Nonetheless, the cueing effects modulated brain responses across the time course of target processing. First, negative visual potentials as reflected in the N1 component appear to be more negative to uncued in relative to cued and adjacent targets, suggesting a general inhibitory mechanism operating at already attended places. Such perceptual modulation by the IOR further validates our previous findings (Chapter IV) as well as other empirical work (Sapir et al., 2013; Taylor & Klein, 2000; Wang et al., 2012). In turn, inhibition of locations close to previously scanned targets was demonstrated by less pronounced Nd to adjacent than novel locations. Again, it supports the account assuming the existence of two separate inhibitory mechanisms (i.e., one targeting a cued location and a second one affecting the visual field), rather than one general inhibitory signal that spreads around the cued location (Wascher & Tipper, 2004). Finally, more negative Nd amplitudes for short than long interval trials, accompanied by faster response times following short than long cue-target intervals demonstrate again that temporal preparation effects are robust and play an important role in

attentional orienting.

In turn, behavioural IOR to adjacent targets in long but not short trials was mirrored by a similar double dissociation of P3 effects, showing an increase of P3 amplitude following long trials, and a decrease of P3 amplitude for adjacent locations. In the context of electrophysiological basis of inhibition, these findings visibly demonstrate that P3 component is indeed involved in the IOR (McDonald et al., 1999; Prime & Jolicœur, 2009).

6.4. Limitations and future research directions

Previous sections of this chapter summarised the obtained findings and discussed results in relation to current literature. In this section, possible limitations and methodological considerations, as well as future research directions, will be presented.

In Chapter II, we presented empirical work examining the role of a reorienting cue location in eliciting stronger inhibitory signal when overlapping with current fixation point and consequently, supporting the realignment of covert and overt attentional systems. Indeed, our results showed a more pronounced IOR following central (overlapping with the fixation point) than peripheral intervening event. However, in the deployed paradigm, it is impossible to rule out the possibility that rather than supporting the realignment of covert and overt attention, a reorienting cue exacerbates the bias of attention towards a *central* location. In other words, it is challenging to disentangle the effect of reorienting cue position due to the fact, that the fixation point was always central. Therefore, it would prove particularly informative if future studies would use non-central ocular fixation (e.g., by monitoring fixation within the region of interest on each trial with an eye-tracker).

Another issue that should be discussed is the absence of facilitatory effects throughout the series of the experiments. Indeed, we did not observe faster response times to targets following short cue-target intervals in any of 6 experiments that used an adapted version of the cueing paradigm. It is important to note that we used an SOA as short as 150 ms, so the lack of facilitative effects cannot be explained by prolonged cue-target intervals that are found to lead to inhibition of previously cued locations and a result, longer responses to already attended places. On the contrary, in our tasks, we found the IOR effect for a range of SOAs spanning from 150 ms to 1,725 ms. Such puzzling results with no facilitative effects for short SOA in detection tasks have been also observed in other experiments (Chica et al., 2014; Collie et al., 2000; Klein, 2000; Van der Lubbe et al., 2005). Indeed, facilitation has started to be recognised as a phenomenon that occurs under a restrained set of conditions, and it appears plausible that its effects are even more fragile to experimental parameters than previously assumed. For instance, a temporal overlap between a cue and target appears to be necessary to observe an early facilitation (Collie et al., 2000). Importantly, the type of task at hand is an important factor in generating attentional effects (Klein, 2000; Lupiáñez et al., 1997). More specifically, whereas facilitative effects are pretty robust when discrimination is required, they are often absent or transient in detection tasks (Maylor & Hockey, 1987). To better understand mechanisms underlying this dissociative effects, Van der Lubbe and colleagues (2005) aimed to differentiate between two hypotheses that have been proposed to account for a given data. The delayed attention withdrawal hypothesis assumes that attention needs more time when discriminating among targets, which is why facilitation lasts longer than in simple detection tasks. The other one called the speeded motor hypothesis puts the emphasis on enhanced motor preparation when detecting a target which subsequently leads to faster IOR at previously cued location. Interestingly, the results suggested that both mechanisms play a role in generating

differential cueing effects in detection and discrimination tasks (Van der Lubbe et al., 2005). In all our experiments, we used a detection task and found the inhibitory effects only. Although in our work, we used relatively consistent parameters to allow for comparisons across experiments, it is pertinent to also consider the spatiotemporal distribution of facilitation. Future studies could thus utilise discrimination paradigms with no temporal cue-target overlap to study the effects of top-down modulations and object presence on the distribution of facilitation. Such approach would provide a more comprehensive understanding of attentional processes.

In turn, in Chapter V we describe a null effect of inhibitory modulations by object complexity. Although one possibility remains that objects did not vary in their complexity sufficiently, hence no significant differences, there is also another possibility. Namely, as the design of the experiment was complex with a total of 18 experimental conditions, there was approximately 50 trials per each condition. Although it is generally a satisfactory number when investigating a large component (e.g., P3 wave), some ERP researchers suggest that several hundred trials per condition are necessary when investigating smaller components like the P1 (Luck, 2005). In other words, it might be the case that our experiment lacked power and therefore, we did not observe modulatory effects of object complexity. Consequently, future studies examining the role of object complexity on the distribution of inhibition could use larger samples, which was demonstrated to represent the population more accurately (Maxwell, Kelley, & Rausch, 2008) and/or increase the number of trials per condition to allow for drawing conclusions with more confidence.

Indeed, power analysis (Faul, Erdfelder, Lang, & Buchner, 2007) revealed that in order to obtain 80% power to detect a small to medium effect size in complex within-subjects and

mixed designs as ones used in our experiments, a sample size of up to 70 subjects would be required. Therefore, to provide reasonable confidence in detecting effect sizes of interest, future studies should increase the number of subjects. Furthermore, in order to be able to confidently interpret the null effect, the data can be also examined by the means of Bayesian analysis (Dienes, 2014). Future studies could thus use this approach to allow for accepting the null hypothesis with a high degree of certainty.

6.5. Final conclusions

To conclude, this thesis provides novel insights into inhibitory mechanisms of selective visual attention. Overall, our findings suggest that the IOR acts to realign covert and overt attentional systems by eliciting stronger inhibition following events that are overlapping with the fixation point and that it is relatively impermeable to top-down modulations such as statistical priors of target locations. Furthermore, our results show that the IOR is stronger when objects occupy scanned locations and that it can also disperse to affect nearby items. The electrophysiological data further revealed that the object-based modulation of inhibition is implemented by the means of a dynamic process encompassing perceptual and evaluation-related stages of the target processing. In turn, inhibition applied to adjacent targets is likely generated by a separate neural function. Finally, although in general objects modulate the spatial distribution of attention, our results suggest that object complexity does not affect the inhibitory signal. Taken together, findings from this thesis further support the role of inhibition in selective attention and have important implications for a wide variety of cognitive fields that aim to understand how the human brain is able to selectively attend to visual information.

REFERENCES

Abrams, R. A., & Dobkin, R. S. (1994). Inhibition of Return: Effects of Attentional Cueing on Eye Movement Latencies. *Journal of Experimental Psychology: Human Perception and Performance*, *20*(3), 467–477.

Anton-Erxleben, K., & Carrasco, M. (2013). Attentional enhancement of spatial resolution: linking behavioural and neurophysiological evidence. *Nature Reviews. Neuroscience*, *14*(3), 188–200. https://doi.org/10.1038/nrn3443

Averbach, E. and Coriell, A. S. (1961). Short-term memory in vision. *Bell System Technical Journal*, *40*, 309-328. doi:10.1002/j.1538-7305.1961.tb03987.x

Baldauf, D., & Desimone, R. (2014). Neural mechanisms of object-based attention. *Science*, *344*(6182), 424–427. https://doi.org/10.1126/science.1247003

Baylis, G. C., & Driver, J. (1993). Visual attention and objects: Evidence for hierarchical coding of location. *Journal of Experimental Psychology: Human Perception and Performance*, *19*(3), 451–470. https://doi.org/10.1037/0096-1523.19.3.451

Bayliss, A. P., Pellegrino, G. Di, & Tipper, S. P. (2005). Sex differences in eye gaze and symbolic cueing of attention. *Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology*, *58*(4), 631–650. https://doi.org/10.1080/02724980443000124

Beauchamp, M. S., Petit, L., Ellmore, T. M., Ingeholm, J., & Haxby, J. V. (2001). A parametric fMRI study of overt and covert shifts of visuospatial attention. *NeuroImage*, *14*(2), 310–321. https://doi.org/10.1006/nimg.2001.0788

Beech, A., Agar, K., & Baylis, G. C. (1989). Reversing priming while maintaining

interference. *Bulletin of the Psychonomic Society 27: 553*. https://doi.org/10.3758/BF03334667

Bennett, P. J., & Pratt, J. (2001). The spatial distribution of inhibition of return. *Psychological Science*, *12*(1), 76–80. https://doi.org/10.1111/1467-9280.00313

Brass, M., & Haggard, P. (2008). The What, When, Whether Model of Intentional Action. *The Neuroscientist*, *14*(4), 319–325. https://doi.org/10.1177/1073858408317417

Bundesen, C. (1990). A theory of visual attention. *Psychological Rev*iew *97*(4), 523–547. https://doi.org/10.1037/0033-295X.97.4.523

Bundesen, C., Habekost, T., & Kyllingsbæk, S. (2005). A neural theory of visual attention: Bridging cognition and neurophysiology. *Psychological Review*, *112*(2), 291–328. https://doi.org/10.1037/0033-295X.112.2.291

Bundesen, C., Habekost, T., & Kyllingsbæk, S. (2011). A neural theory of visual attention and short-term memory (NTVA). *Neuropsychologia*, *49*(6), 1446–1457. https://doi.org/10.1016/j.neuropsychologia.2010.12.006

Burle, B., Vidal, F., Tandonnet, C., & Hasbroucq, T. (2004). Physiological evidence for response inhibition in choice reaction time tasks. *Brain and Cognition, 56*, 153–164. http://dx.doi.org/10.1016/j.bandc.2004.06.004

Chelazzi, L., Miller, E. K., Duncan, J., & Desimone, R. (1993). A neural basis for visual search in inferior temporal cortex. *Nature, 363*(6427), 345–347. https://doi.org/10.1038/363345a0

Chica, A. B., Martín-Arévalo, E., Botta, F., & Lupiáñez, J. (2014). The Spatial Orienting paradigm: How to design and interpret spatial attention experiments. *Neuroscience and Biobehavioural Reviews, 40*, 35–51. https://doi.org/10.1016/j.neubiorev.2014.01.002

Chun, M. M. (2000). Contextual cueing of visual attention. *Trends in Cognitive Sciences*, *4*,

170-178. 10.1016/S1364-6613(00)01476-5.

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*(6), 1733–1745. https://doi.org/10.1037/0096-1523.26.6.1733

Corbetta, M. (1998). Frontoparietal cortical networks for directing attention and the eye to visual locations: Identical, independent, or overlapping neural systems? *Proceedings of the National Academy of Sciences*, *95*(3), 831–838. https://doi.org/10.1073/pnas.95.3.831

Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., … Shulman, G. L. (1998). A common network of functional areas for attention and eye movements. *Neuron*, *21*(4), 761-773. https://doi.org/10.1016/S0896-6273(00)80593-0

Coull, J.T. (1998). Neural correlates of attention and arousal: insights from electrophysiology, functional neuroimaging and psychopharmacology. *Progress in Neurobiology*, *55*, 343-361. https://doi.org/10.1016/s0301-0082(98)00011-2

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. *The Journal of Neuroscience*, *18*(18), 7426–7435. https://doi.org/10.1523/jneurosci.18-18-07426.1998

D'Angelo, M. C., Thomson, D. R., Tipper, S. P., & Milliken, B. (2016). Negative priming 1985 to 2015: a measure of inhibition, the emergence of alternative accounts, and the multiple process challenge. *The Quarterly Journal of Experimental Psychology*, *69*(10), 1890–1909. https://doi.org/10.1080/17470218.2016.1173077

Davranche, K., Tandonnet, C., Burle, B., Meynier, C., Vidal, F., & Hasbroucq, T. (2007).

The dual nature of time preparation: Neural activation and suppression revealed by transcranial magnetic stimulation of the motor cortex. *European Journal of Neuroscience*, *25*(12), 3766–3774. https://doi.org/10.1111/j.1460-9568.2007.05588.x

Desimone, R., & Duncan, J. (1995). Neural Mechanisms of Selective Visual. *Annual Review of Neuroscience*, *18*(1), 193–222. https://doi.org/10.1146/annurev.ne.18.030195.001205

Dienes, Z. (2014). Using Bayes to get the most out of non-significant results. *Frontiers in Psychology*, *5*, 781. https://doi.org/10.3389/fpsyg.2014.00781

Di Russo, F., Martínez, A., Sereno, M. I., Pitzalis, S., & Hillyard, S. A. (2002). Cortical sources of the early components of the visual evoked potential. Human Brain Mapping, 15(2), 95–111.

Dorris, M. C., Klein, R. M., Everling, S., & Munoz, D. P. (2002). Contribution of the primate superior colliculus to inhibition of return. *Journal of Cognitive Neuroscience*, *14*(8), 1256–1263. https://doi.org/10.1162/089892902760807249

Druker, M., & Anderson, B. (2010). Spatial probability aids visual stimulus discrimination. *Frontiers in Human Neuroscience*, *4*, 63. https://doi.org/10.3389/fnhum.2010.00063

Duncan, J. (1984) Selective attention and the organization of visual information. *Journal of Experimental Psychology: General*, *113*(4), 501–517. https://doi.org/10.1037/0096-3445.113.4.501

Duque, J., Labruna, L., Verset, S., Olivier, E., & Ivry, R. B. (2012). Dissociating the role of prefrontal and premotor cortices in controlling inhibitory mechanisms during motor preparation. *Journal of Neuroscience*, *32*(3), 806–816. https://doi.org/10.1523/JNEUROSCI.4299-12.2012

Egly, R., Driver, J., & Rafal, R. D. (1994). Shifting visual attention between objects and locations: evidence from normal and parietal lesion subjects. *Journal of Experimental*

Psychology: General, *123*(2), 161–177. https://doi.org/10.1037//0096-3445.123.2.161

Eimer, M. (2000). The time course of spatial orienting elicited by central and peripheral cues: evidence from event-related brain potentials. *Biological Psychology*, *53*(2-3), 253–258. https://doi.org/10.1016/S0301-0511(00)00049-1

Eriksen, C. W., Pan, K., & Botella, J. (1993). Attentional distribution in visual space. *Psychological Research*, *56*: *5*. https://doi.org/10.1007/BF00572128

Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception & Psychophysics*, *16*(1), 143-149. https://doi.org/10.3758/BF03203267

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*, 175-191. https://doi.org/10.3758/bf03193146

Fecteau, J. H., Korjoukov, I., & Roelfsema, P. R. (2009). Location and color biases have different influences on selective attention. *Vision Research*, *49*(9), 996–1005. https://doi.org/10.1016/j.visres.2009.03.013

Filoteo, J. V., Maddox, W. T., Ing, A. D., & Song, D. D. (2007). Characterizing rule-based category learning deficits in patients with Parkinson's disease. *Neuropsychologia*, *45*(2), 305–320. https://doi.org/10.1016/j.neuropsychologia.2006.06.034

Filoteo, J. V, Delis, D. C., Salmon, D. P., Demadura, T., Roman, M. J., & Shults, C. W. (1997). An examination of the nature of attentional deficits in patients with Parkinson's disease: evidence from a spatial orienting task. *Journal of the International Neuropsychological Society : JINS*, *3*(4), 337–347.

Fries, P. (2015). Rhythms for Cognition: Communication through Coherence. *Neuron*, *88*(1), 220–235. https://doi.org/10.1016/j.neuron.2015.09.034

Fuentes, L. J., & Tudela, P. (1992). *Semantic processing of foveally and parafoveally presented words in a lexical decision task. The Quarterly Journal of Experimental Psychology*, *45*, 299-322. https://doi.org/10.1080/14640749208401328.

Gabay, S., & Henik, A. (2010). Temporal expectancy modulates inhibition of return in a discrimination task. *Psychonomic Bulletin & Review*, *17*(1), 47–51. https://doi.org/10.3758/PBR.17.1.47

Gabay, S., & Henik, A. (2008). The effects of expectancy on inhibition of return. *Cognition*, *106*(3), 1478–1486. https://doi.org/10.1016/j.cognition.2007.05.007

Geng, J. J., & Behrmann, M. (2002). Probability cuing of target location facilitates visual search implicitly in normal participants and patients with hemispatial neglect. *Psychological Science*, *13*(6), 520–525. https://doi.org/10.1111/1467-9280.00491

Geng, J. J., & Behrmann, M. (2005). Spatial probability as attentional cue. *Perception & Psychophysics*, *67*(7), 1252–1268. https://doi.org/10.3758/BF03193557

Geng, J. J., Eger, E., Ruff, C. C., Kristjánsson, A., Rotshtein, P., & Driver, J. (2006). On-line attentional selection from competing stimuli in opposite visual fields: effects on human visual cortex and control processes. *Journal of Neurophysiology*, *96*, 2601–2612. https://doi.org/10.1152/jn.01245.2005

Gernsbacher, M. A., & Faust, M. E. (1991). The mechanism of suppression: a component of general comprehension skill. *Journal of experimental psychology. Learning, memory, and cognition*, *17*(2), 245–262. doi:10.1037//0278-7393.17.2.245

Gregoriou, G.G., Gotts, S.J., Zhou, H., Desimone, R., 2009. High-frequency, long-range coupling between prefrontal and visual cortex during attention. *Science*, *324*, 1207–1210. https://doi.org/ 10.1126/science.1171402

Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its

role in object recognition. *Vision Research*, *41*(10–11), 1409–1422. https://doi.org/10.1016/S0042-6989(01)00073-6

Groppe, D. M., Urbach, T. P., & Kutas, M. (2011). Mass univariate analysis of event-related brain potentials/fields I: A critical tutorial review. *Psychophysiology*, *48*(12), 1711–1725. https://doi.org/10.1111/j.1469-8986.2011.01273.x

Gurvich, C., Georgiou-Karistianis, N., Fitzgerald, P. B., Millist, L., & White, O. B. (2007). Inhibitory control and spatial working memory in Parkinson's disease. *Movement Disorders*, *22*(10), 1444–1450. https://doi.org/10.1002/mds.21510

Guthrie, D., & Buchwald, J. S. (1991). Significance testing of difference potentials. *Psychophysiology*, *28*(2), 240–244. https://doi.org/10.1111/j.1469-8986.1991.tb00417.x

Gutiérrez-Domínguez, F.-J., Pazo-Álvarez, P., Doallo, S., Fuentes, L. J., Lorenzo-López, L., & Amenedo, E. (2014). Vertical asymmetries and inhibition of return: Effects of spatial and non-spatial cueing on behaviour and visual ERPs. *International Journal of Psychophysiology*, *91*(2), 121–131. https://doi.org/10.1016/J.IJPSYCHO.2013.12.004

Harmening, W. M., Tuten, W. S., Roorda, A., & Sincich, L. C. (2014). Mapping the perceptual grain of the human retina. *Journal of Neuroscience*, *34*(16), 5667–5677. https://doi.org/10.1523/JNEUROSCI.5191-13.2014

Hayward, D. A., & Ristic, J. (2013). Measuring attention using the Posner cuing paradigm: the role of across and within trial target probabilities. *Frontiers in Human Neuroscience*, *7*, 205. https://doi.org/10.3389/fnhum.2013.00205

He, X., Fan, S., Zhou, K., & Chen, L. (2004). Cue validity and object-based attention. *Journal of Cognitive Neuroscience*, *16*(6), 1085–1097. https://doi.org/10.1162/0898929041502689

He, X., Humphreys, G., Fan, S., Chen, L., & Han, S. (2008). Differentiating spatial and

object-based effects on attention: An event-related brain potential study with peripheral cueing. *Brain Research, 1245*, 116–125. https://doi.org/10.1016/j.brainres.2008.09.092

Hebb, D. O. (1949). *The organization of behaviour: A neuropsychological theory*. New York: Wiley.

Von Helmholtz, Hermann (1867). Handbuch der physiologischen Optik. 3. Leipzig: Voss. Quotations are from the English translation produced by Optical Society of America (1924–25): Treatise on Physiological Optics.

Hillstrom, A. P. (2000). Repetition effects in visual search. *Perception & Psychophysics*, *62*, 800-817. https://doi.org/10.3758/BF03206924

Hoffmann, J., & Kunde, W. (1999). Location-specific target expectancies in visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(4), 1127–1141. https://doi.org/10.1037/0096-1523.25.4.1127

Hommel, B., Pratt, J., Colzato, L., & Godijn, R. (2001). *Symbolic control of visual attention. Psychological Science*, *12*(5), 360–365. https://doi.org/10.1111/1467-9280.00367

Hopfinger, J., Luck, S., & Hillyard, S. (2004). *Selective attention: electrophysiological and neuromagnetic studies*. In M. S. Gazzaniga (Ed.), The cognitive neurosciences (Vol. 3, pp. 561-574). Cambridge, MA: MIT Press.

Hopfinger, J.B., & Mangun, G. R. (2001). Tracking the influence of reflexive attention on sensory and cognitive processing. *Cognitive, Affective & Behavioural Neuroscience*, *1*(1), 56–65. https://doi.org/10.3758/cabn.1.1.56

Hopfinger, J.B., & Mangun, G. R. (1998). Reflexive attention modulates processing of visual stimuli in human extrastriate cortex. *Psychological Science*, *9*(6), 441–446. https://doi.org/10.1111/1467-9280.00083

Houghton, G., & Tipper, S. P. (1994). A model of inhibitory mechanisms in selective

attention. In D. Dagenbach & T. H. Carr (Eds.), *Inhibitory Processes in Attention, Memory and Language.* (pp. 53-112). Florida: Academic Press.

Itti, L., & Koch, C. (2000). A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Research, 40*, 1489–1506. https://doi.org/10.1016/s0042-6989(99)00163-7

James, W. (1890). *The Principles of Psychology*. New York: H. Holt and Company.

Jordan, H., & Tipper, S. P. (1998). Object-based inhibition of return in static displays. *Psychonomic Bulletin and Review*, *5*(3), 504–509. https://doi.org/10.3758/BF03208829

Kabata, T., & Matsumoto, E. (2012). Cueing effects of target location probability and repetition. *Vision Research, 73*, 23–29. https://doi.org/10.1016/J.VISRES.2012.09.014

Kam, J. W. Y., Solbakk, A.-K., Endestad, T., Meling, T. R., & Knight, R. T. (2018). Lateral prefrontal cortex lesion impairs regulation of internally and externally directed attention. *NeuroImage, 175*, 91–99. https://doi.org/10.1016/j.neuroimage.2018.03.063

Klein, P. A., Petitjean, C., Olivier, E., & Duque, J. (2014). Top-down suppression of incompatible motor activations during response selection under conflict. *NeuroImage, 86*, 138-149. https://doi.org/10.1016/j.neuroimage.2013.08.005

Klein, R. M. (2000). Inhibition of return. *Trends in Cognitive Sciences, 4*(4), 138–147. https://doi.org/10.1016/S1364-6613(00)01452-2

Klein, R. M. (1988). Inhibitory tagging system facilitates visual search. *Nature*, *334*(6181), 430–431. https://doi.org/10.1038/334430a0

Kolling, N., & O'Reilly, J. X. (2018). State-change decisions and dorsomedial prefrontal cortex: the importance of time. *Current Opinion in Behavioural Sciences, 22*, 152–160. https://doi.org/10.1016/j.cobeha.2018.06.017

Kulke, L. V, Atkinson, J., & Braddick, O. (2016). Neural differences between covert and

overt attention studied using EEG with simultaneous remote eye tracking. *Frontiers in Human Neuroscience*, *10*, 592. https://doi.org/10.3389/fnhum.2016.00592

LaBerge, D., & Brown, V. (1989). Theory of attentional operations in shape identification. *Psychological Review*, *96*(1), 101–124. https://doi.org/10.1037/0033-295X.96.1.101

Leek, E. C., Reppa, I., & Tipper, S. P. (2003). Inhibition of return for objects and locations in static displays. *Perception and Psychophysics*, *65*(3), 388–395. https://doi.org/10.3758/BF03194570

List, A., & Robertson, L. C. (2008). Inhibition of return and object-based attentional selection. *Journal of Experimental Psychology*, *33*(6), 1322–1334. https://doi.org/10.1037/0096-1523.33.6.1322.Inhibition

Los, S. A. (2004). Inhibition of return and nonspecific preparation: separable inhibitory control mechanisms in space and time. *Perception & Psychophysics*, *66*(1), 119–130. https://doi.org/10.3758/BF03194866

Los, S. A. (2013). The role of response inhibition in temporal preparation: Evidence from a go/no-go task. *Cognition*, *129*(2), 328–344. https://doi.org/10.1016/j.cognition.2013.07.013

Los, S. A., Kruijne, W., & Meeter, M. (2014). Outlines of a multiple trace theory of temporal preparation. *Frontiers in Psychology*, *5*, 1058. https://doi.org/10.3389/fpsyg.2014.01058

Luck, S. J., Hillyard, S. A., Mouloua, M., Woldorff, M. G., Clark, V. P., & Hawkins, H. L. (1994). Effects of spatial cuing on luminance detectability: Psychophysical and electrophysiological evidence for early selection. *Journal of Experimental Psychology: Human Perception and Performance*, *20*(4), 887–904. https://doi.org/10.1037/0096-1523.20.4.887

Luck, S. J. (2005). Ten simple rules for designing ERP experiments. In T. C. Handy (Ed.),

Event-related potentials: A methods handbook (pp. 17–32). Cambridge, MA: MIT Press.

Lupiáñez, J., Milán, E. G., Tornay, F. J., Madrid, E., & Tudela, P. (1997). Does IOR occur in discrimination tasks? Yes, it does, but later. *Perception and Psychophysics*, *59*(8), 1241–1254. https://doi.org/10.3758/BF03214211

Lupiáñez, J., Milliken, B., Solano, C., Weaver, B., & Tipper, S. P. (2001). On the strategic modulation of the time course of facilitation and inhibition of return. *The Quarterly Journal of Experimental Psychology*, *54*(3), 753–773. https://doi.org/10.1080/713755990

Macquistan, A. D., & Macquistan, A. D. (1997). Object-based allocation of visual attention in response to exogenous, but not endogenous, spatial precues. *Psychonomic Bulletin & Review*, *4*(4), 512–515. http://dx.doi.org/10.3758/BF03214341

Maljkovic, V., & Nakayama, K. (1996). Priming of pop-out: II. The role of position. *Perception & Psychophysics*, *58*, 977–991. https://doi.org/10.3758/BF03206826

Marí-Beffa, P., Hayes, A. E., Machado, L., & Hindle, J. V. (2005). Lack of inhibition in Parkinson's disease: Evidence from a lexical decision task. *Neuropsychologia*, *43*(4), 638–646. https://doi.org/10.1016/j.neuropsychologia.2004.07.006

Martín-Arévalo, E., Chica, A. B., & Lupiáñez, J. (2016). No single electrophysiological marker for facilitation and inhibition of return: A review. *Behavioural Brain Research*, *300*, 1–10. https://doi.org/10.1016/j.bbr.2015.11.030

Martín-Arévalo, E., Chica, A. B., & Lupiáñez, J. (2014). Electrophysiological modulations of exogenous attention by intervening events. *Brain and Cognition*, *85*(1), 239–250. https://doi.org/10.1016/j.bandc.2013.12.012

Martín-Arévalo, E., Kingstone, A., & Lupiáñez, J. (2013). Is "Inhibition of Return" due to the inhibition of the return of attention? *Quarterly Journal of Experimental Psychology*,

66(2), 347–359. https://doi.org/10.1080/17470218.2012.711844

Martínez, A., Teder-Sälejärvi, W., Vazquez, M., Molholm, S., Foxe, J. J., Javitt, D. C., … Hillyard, S. A. (2006). Objects are highlighted by spatial attention. *Journal of Cognitive Neuroscience*, *18*(2), 298–310. https://doi.org/10.1162/jocn.2006.18.2.298

Martínez, A., Teder-Salejarvi, W., & Hillyard, S. A. (2007). Spatial attention facilitates selection of illusory objects: Evidence from event-related brain potentials. *Brain Research*, *1139*(1), 143–152. https://doi.org/10.1016/j.brainres.2006.12.056

Martínez, A., DiRusso, F., Anllo-Vento, L., Sereno, M. I., Buxton, R. B., & Hillyard, S. A. (2001). Putting spatial attention on the map: timing and localization of stimulus selection processes in striate and extrastriate visual areas. *Vision Research*, *41*(10), 1437–1457. https://doi.org/10.1016/S0042-6989(00)00267-4

Maxwell, S. E., Kelley, K., & Rausch, J. R. (2008). Sample size planning for statistical power and accuracy in parameter estimation. *Annual Review of Psychology*, *59*, 537-563. https://doi.org/10.1146/annurev.psych.59.103006.093735

Maylor, E. A., & Hockey, R. (1987). Effects of repetition on the facilitatory and inhibitory components of orienting in visual space. *Neuropsychologia*, *25*(1A), 41–54. https://doi.org/10.1016/0028-3932(87)90042-X

McAuliffe, J., Pratt, J., & O'Donnell, C. (2001). Examining location-based and object-based components of inhibition of return in static displays. *Perception and Psychophysics*, *63*(6), 1072–1082. https://doi.org/10.3758/BF03194525

Mccoy, B., & Theeuwes, J. (2017). Overt and covert attention to location-based reward. *Vision Research*, *142*, 27–39. https://doi.org/10.1016/j.visres.2017.10.003

McDonald, J. J., Hickey, C., Green, J. J., & Whitman, J. C. (2009). Inhibition of return in the covert deployment of attention: Evidence from human electrophysiology. *Journal of*

Cognitive Neuroscience, *21*(4), 725–733. https://doi.org/10.1162/jocn.2009.21042

McDonald, J. J., Ward, L. M., & Kiehl, K. A. (1999). An event-related brain potential study of inhibition of return. *Perception and Psychophysics*, *61*(7), 1411–1423. https://doi.org/10.3758/BF03206190

Moore, T., & Armstrong, K. M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. *Nature*, *421*(6921), 370–373. https://doi.org/10.1038/nature01341

Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science*, *229*(4715), 782–784. https://doi.org/10.1126/science.4023713

Mostofsky, S., & Simmonds, D. (2008). Response inhibition and response selection: two sides of the same coin. *Journal of Cognitive Neuroscience*, *20*(5), 751–761. https://doi.org/10.1162/jocn.2008.20500

Müller, N. G., Mollenhauer, M., Rösler, A., & Kleinschmidt, A. (2005). The attentional field has a Mexican hat distribution. *Vision Research*, *45*(9), 1129–1137. https://doi.org/10.1016/j.visres.2004.11.003

Murray, M. M., Brunet, D., & Michel, C. M. (2008). Topographic ERP analyses: A step-by-step tutorial review. *Brain Topography*, *20*(4), 249–264. https://doi.org/10.1007/s10548-008-0054-5

Neisser, U. & Becklen, P. (1975). Selective looking: Attending to visually specified events. *Cognitive Psychology*, *7*, 480-494. https://doi.org/10.1016/0010-0285(75)90019-5

Niemi, P., & Naatanen, R. (1981). Foreperiod and simple reaction time. *Psychological Bulletin*, *89*(1), 133–162. https://doi.org/10.1037/0033-2909.89.1.133

Niklaus, M., Nobre, A. C., & van Ede, F. (2017). Feature-based attentional weighting and

spreading in visual working memory. *Scientific reports*, *7*, 42384. doi:10.1038/srep42384

Nobre, A. C., Gitelman, D. R., Dias, E. C., & Mesulam, M. M. (2000). Covert visual spatial orienting and saccades: Overlapping neural systems. *NeuroImage*, *11*(3), 210–216. https://doi.org/10.1006/nimg.2000.0539

Nobre, A. C., Sebestyen, G. N., Gitelman, D. R., Mesulam, M. M., Frackowiak, R. S. J., & Frith, C. D. (1997). Functional localization of the system for visuospatial attention using positron emission tomography. *Brain*, *120*(3), 515–533. https://doi.org/10.1093/brain/120.3.515

Pavlov, I. P. (1927) Conditioned reflexes: an investigation of the physiological activity of the cerebral cortex. Translated and edited by G. V. Anrep. London: Oxford University Press.

Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*(10), 2128–2148. https://doi.org/10.1016/j.clinph.2007.04.019

Posner, M. I. (1980). Orienting of attention. *The Quarterly Journal of Experimental Psychology*, *32*(1), 3–25. https://doi.org/10.1080/00335558008248231

Posner, M. I., & Cohen, Y. (1984). *Components of Visual Orienting*. In H. Bouma, & D. Bowhuis (Eds.), Attention and Performance X (pp. 531-556). Hillsdale, NJ: Erlbaum.

Posner, M. I., Rafal, R. D., Choate, L. S., & Vaughan, J. (1985). Inhibition of return: Neural basis and function. *Cognitive Neuropsychology*, *2*(3), 211–228. https://doi.org/10.1080/02643298508252866

Posner, M. I., Snyder, C. R. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology: General*, *109*(2), 160–174. https://doi.org/10.1037/0096-3445.109.2.160

Possin, K. L., Filoteo, J. V., Song, D. D., & Salmon, D. P. (2009). Space-based but not object-based inhibition of return is impaired in Parkinson's disease. *Neuropsychologia*, *47*(7), 1694–1700. https://doi.org/10.1016/j.neuropsychologia.2009.02.006

Pratt, J., Hillis, J., & Gold, J. M. (2001). The effect of the physical charasteristics of cues and targets on facilitation and inhibition. *Psychonomic Bulletin & Review*, *8*(3), 489–495. https://doi.org/10.3758/bf03196183

Pratt, J., & Fischer, M. H. (2002). Examining the role of the fixation cue in inhibition of return. *Canadian Journal of Experimental Psychology*, *56*(4), 294–301. https://doi.org/10.1037/h0087405

Pratt, J., Spalek, T. M., & Bradshaw, F. (1999). The time to detect targets at inhibited and noninhibited locations: Preliminary evidence for attentional momentum. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(3), 730–746. https://doi.org/10.1037/0096-1523.25.3.730

Prime, D. J., & Jolicœur, P. (2009). On the relationship between occipital cortex activity and inhibition of return. *Psychophysiology*, *46*(6), 1278–1287. https://doi.org/10.1111/j.1469-8986.2009.00858.x

Prime, D. J., Visser, T. A. W., & Ward, L. M. (2006). Reorienting attention and inhibition of return. *Perception & Psychophysics*, *68*(8), 1310–1323. https://doi.org/10.3758/BF03193730

Prime, D. J., & Ward, L. M. (2004). Inhibition of return from stimulus to response. *Psychological Science*, *15*(4), 272–276. https://doi.org/10.1111/j.0956-7976.2004.00665.x

Prime, D. J., & Ward, L. M. (2006). Cortical expressions of inhibition of return. *Brain Research*, *1072*(1), 161–174. https://doi.org/10.1016/j.brainres.2005.11.081

Quoilin, C., & Derosiere, G. (2015). Global and specific motor inhibitory mechanisms during action preparation. *Journal of Neuroscience*, *35*(50), 16297–16299. https://doi.org/10.1523/JNEUROSCI.3664-15.2015

Reppa, I., & Leek, E. C. (2003). The modulation of inhibition of return by object- internal structure : Implications for theories of object-based attentional selection. *Psychonomic Bulletin & Review*, *10*(2), 493–502. https://doi.org/10.3758/BF03196512

Reppa, I., & Leek, E. C. (2006). Structure-based modulation of inhibition of return is triggered by object-internal but not occluding shape features. *Quarterly Journal of Experimental Psychology*, *59*(11), 1857–1866. https://doi.org/10.1080/17470210600872113

Reppa, I., Schmidt, W. C., & Leek, E. C. (2012). Successes and failures in producing attentional object-based cueing effects. *Attention, Perception, & Psychophysics*, *74*(1), 43–69. https://doi.org/10.3758/s13414-011-0211-x

Reynolds, J. H., & Chelazzi, L. (2004). Attentional modulation of visual processing. *Annual Review of Neuroscience*, *27*(1), 611–647. https://doi.org/10.1146/annurev.neuro.26.041002.131039

Ristic, J., Friesen, C. K., & Kingstone, A. (2002). Are eyes special? It depends on how you look at it. *Psychonomic Bulletin and Review*, *9*(3), 507–513. https://doi.org/10.3758/BF03196306

Rizzolatti, G., Riggio, L., Dascola, I., & Umiltá, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, *25*(1A), 31–40. https://doi.org/10.1016/0028-3932(87)90041-8

Ro, T., & Rafal, R. D. (1999). Components of reflexive visual orienting to moving objects. *Perception and Psychophysics*, *61*(5), 826–836. https://doi.org/10.3758/BF03206900

Robinson, D. L., Bowman, E. M., & Kertzman, C. (1995). Covert orienting of attention in macaques: II. Contributions of parietal cortex. *Journal of Neurophysiology*, *74*(2), 698–712. https://doi.org/10.1152/jn.1995.74.2.698

Samuel, A. G., & Kat, D. (2003). Inhibition of return: a graphical meta-analysis of its time course and an empirical test of its temporal and spatial properties. *Psychonomic Bulletin & Review*, *10*(4), 897–906. https://doi.org/10.3758/BF03196550

Sapir, A., Jackson, K., Butler, J., Paul, M. A., & Abrams, R. A. (2013). Inhibition of return affects contrast sensitivity. *Quarterly Journal of Experimental Psychology*, *67*(7), 1305-1316. https://doi.org/10.1080/17470218.2013.859282

Sapir, A., Soroker, N., Berger, A., & Henik, A. (1999). Inhibition of return in spatial attention: Direct evidence for collicular generation. *Nature Neuroscience*, *2*(12), 1053–1054. https://doi.org/10.1038/15977

Satel, J., Hilchey, M. D., Wang, Z., Reiss, C. S., & Klein, R. M. (2014). In search of a reliable electrophysiological marker of oculomotor inhibition of return. *Psychophysiology*, *51*(10), 1037–1045. https://doi.org/10.1111/psyp.12245

Satel, J., Hilchey, M. D., Wang, Z., Story, R., & Klein, R. M. (2012). The effects of ignored versus foveated cues upon inhibition of return: An event-related potential study. *Attention, Perception, and Psychophysics*, *75*(1), 29–40. https://doi.org/10.3758/s13414-012-0381-1

Satel, J., Wang, Z., Hilchey, M. D., & Klein, R. M. (2012). Examining the dissociation of retinotopic and spatiotopic inhibition of return with event-related potentials. *Neuroscience Letters*, *524*(1), 40–44. https://doi.org/10.1016/j.neulet.2012.07.003

Sayim, B., Grubert, A., Herzog, M. H., & Krummenacher, J. (2010). Display probability modulates attentional capture by onset distractors. *Journal of Vision*, *10*(3), 1–8.

https://doi.org/10.1167/10.3.10

Schmidtmann, G., Jennings, B. J., & Kingdom, F. A. A. (2015). Shape recognition: Convexities, concavities and things in between. *Scientific Reports*, *5*, 1–11. https://doi.org/10.1038/srep17142

Sereno, A. B., Briand, K. A., Amador, S. C., & Szapiel, S. V. (2006). Disruption of reflexive attention and eye movements in an individual with a collicular lesion. *Journal of Clinical and Experimental Neuropsychology*, *28*(1), 145–166. https://doi.org/10.1080/13803390590929298

Shaw, M. L., & Shaw, P. (1977). Optimal allocation of cognitive resources to spatial locations. *Journal of Experimental Psychology: Human Perception and Performance*, *3*(2), 201–211. https://doi.org/10.1037/0096-1523.3.2.201

Smith, D. T., & Schenk, T. (2012). The Premotor theory of attention: Time to move on? *Neuropsychologia*, *50*(6), 1104–1114. https://doi.org/10.1016/j.neuropsychologia.2012.01.025

Sohn, W., Papathomas, T. V., Blaser, E., & Vidnyánszky, Z. (2004). Object-based cross-feature attentional modulation from color to motion. *Vision Research*, *44*(12), 1437–1443. https://doi.org/10.1016/j.visres.2003.12.010

Soto, D., & Blanco, M. J. (2004). Spatial attention and object-based attention: a comparison within a single task. *Vision Research*, *44*, 69–81. https://doi.org/10.1016/j.visres.2003.08.013

Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs*, *74*, 1-29. http://dx.doi.org/10.1037/h0093759

Tandonnet, C., Garry, M. I., & Summers, J. J. (2011). Selective suppression of the incorrect response implementation in choice behaviour assessed by transcranial magnetic

stimulation. *Psychophysiology*, *48*(4), 462–469. https://doi.org/10.1111/j.1469-8986.2010.01121.x

Taylor, J. E. T., Chan, D., Bennett, P. J., & Pratt, J. (2015). Attentional cartography: mapping the distribution of attention across time and space. *Attention, Perception, & Psychophysics*, *77*(7), 2240–2246. https://doi.org/10.3758/s13414-015-0943-0

Taylor, T. L., & Klein, R. M. (1998). On the causes and effects of inhibition of return. *Psychonomic Bulletin and Review*, *5*(4), 625–643. https://doi.org/10.3758/BF03208839

Taylor, T. L., & Klein, R. M. (2000). Visual and motor effects in inhibition of return. *Journal of Experimental Psychology: Human Perception and Performance*, *26*(5), 1639–1656. https://doi.org/10.1037/0096-1523.26.5.1639

Tipper, C., & Kingstone, A. (2005). Is inhibition of return a reflexive effect? *Cognition*, *97*(3), B55–B62. https://doi.org/10.1016/j.cognition.2005.02.003

Tipper, S. P. (1985). The negative priming effect: Inhibitory priming by ignored objects. *The Quarterly Journal of Experimental Psychology*, *37*(4), 571-590. https://doi.org/10.1080/14640748508400920

Tipper, S. P., & Driver, J. (1987). Negative priming between pictures and words in a selective attention task: Evidence for semantic processing of ignored stimuli. *Memory & Cognition*, *16*(1), 64–70. https://doi.org/10.3758/BF03197746

Tipper, S. P., Driver, J., & Weaver, B. (1991). Short Report: Object-centred Inhibition of Return of Visual Attention. *The Quarterly Journal of Experimental Psychology*, *43*(2), 289–298. https://doi.org/10.1080/14640749108400971

Tipper, S. P., Jordan, H., & Weaver, B. (1999). Scene-based and object-centred inhibition of return: Evidence for dual orienting mechanisms. *Perception and Psychophysics*, *61*(1), 50–60. https://doi.org/10.3758/BF03211948

Tipper, S. P., Reuter-Lorenz, P. A., Rafal, R., Starrveldt, Y., Ro, T., Egly, R., … Weaver, B. (1997). Object-based facilitation and inhibition from visual orienting in the human split-brain. *Journal of Experimental Psychology: Human Perception and Performance*, *23*(5), 1522–1532. https://doi.org/10.1037/0096-1523.23.5.1522

Tipper, S. P., Weaver, B., Jerreat, L. M., & Burak, A. L. (1994). Object-based and environment-based inhibition of return of visual attention. *Journal of Experimental Psychology: Human Perception and Performance*, *20*(3), 478–499. https://doi.org/10.1037/0096-1523.20.3.478

Tipples, J. (2002). Eye gaze is not unique: Automatic orienting in response to uninformative arrows. *Psychonomic Bulletin and Review*, *9*(2), 314–318. https://doi.org/10.3758/BF03196287

Titchener, E. B. (1908). Lectures on the Elementary Psychology of Feeling and Attention. New York: Macmillan. doi:10.1037/10867-000

Treisman, A. (1986). Features and objects in visual processing. *Scientific American*, *255*(5), 114–125. https://doi.org/10.1038/scientificamerican1186-114B

Vallesi, A., & Shallice, T. (2007). Developmental dissociations of preparation over time: Deconstructing the variable foreperiod phenomena. *Journal of Experimental Psychology: Human Perception and Performance*, *33*(6), 1377–1388. https://doi.org/10.1037/0096-1523.33.6.1377

Van der Lubbe, R. H. J., Vogel, R. O., & Postma, A. (2005). Different effects of exogenous cues in a visual detection and discrimination task: Delayed attention withdrawal and/or speeded motor inhibition? *Journal of Cognitive Neuroscience*, *17*(12), 1829–1840. https://doi.org/10.1162/089892905775008634

Van der Stigchel, S., & Theeuwes, J. (2007). The relationship between covert and overt

attention in endogenous cuing. *Perception and Psychophysics*, *69*(5), 719–731. https://doi.org/10.3758/BF03193774

Van Ede, F., Chekroud, S. R., Stokes, M. G., & Nobre, A. C. (2018). Decoding the influence of anticipatory states on visual perception in the presence of temporal distractors. *Nature Communications*, *9*(1), 1449. https://doi.org/10.1038/s41467-018-03960-z

Vecera, S., & Farah, M. (1994). Does visual attention select objects or locations? J*ournal of Experimental Psychology: Human Perception and Performance*, *23*, 1-14. http://dx.doi.org/10.1037/0096-3445.123.2.146

Walthew, C., & Gilchrist, I. D. (2006). Target location probability effects in visual search: An effect of sequential dependencies. *Journal of Experimental Psychology: Human Perception and Performance*, *32*(5), 1294–1301. https://doi.org/10.1037/0096-1523.32.5.1294

Wang, Z., Satel, J., & Klein, R. M. (2012). Sensory and motor mechanisms of oculomotor inhibition of return. *Experimental Brain Research*, *218*(3), 441–453. https://doi.org/10.1007/s00221-012-3033-8

Wascher, E., & Tipper, S. P. (2004). Revealing effects of noninformative spatial cues: An EEG study of inhibition of return. *Psychophysiology*, *41*(5), 716–728. https://doi.org/10.1111/j.1469-8986.2004.00198.x

Weaver, B., Lupiáñez, J., & Watson, F. L. (1998). The effects of practice on object-based, location-based, and static-display inhibition of return. *Perception and Psychophysics*, *60*(6), 993–1003. https://doi.org/10.3758/BF03211934

Weinbach, N., & Henik, A. (2012). Temporal orienting and alerting - the same or different? *Frontiers in psychology*, *3*, 236. https://doi.org/10.3389/fpsyg.2012.00236

Woodrow, H. (1914). The measurement of attention. *The Psychological Monographs*, *17*(5),

1–158. https://doi.org/10.1037/h0093087

Wurtz, R. H., Goldberg, M. E., & Robinson, D. L. (1982). Brain mechanims of visual attention. *Scientific American*, *246*(6), 124–135. https://doi.org/10.1038/scientificamerican0682-124