Investigating Inhibition of Return with Converging Interdisciplinary Methods

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for mom, 阿林 aunty and uncle

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Abstract

This dissertation investigates inhibition of return (IOR) as two forms of inhibitory cueing effects operating on spatially uninformative visual stimuli (i.e., cues): an output form of IOR that is generated when saccades are permitted, and an input form of IOR that arises when saccades are not allowed. Using paradigms adapted from Posner's (1980) spatial cueing task, our first set of experiments in Chapter 2 attempts to dissociate the two forms of IOR by incorporating an incompatible response paradigm that requires either saccadic or manual keypress responses to targets. This design allowed us to examine separately the input form of IOR at the stimulus level versus the output form that is response related. The event-related potential (ERP) study in Chapter 3 builds upon the previous paradigm but uses saccades to cues to activate the oculomotor system. The activation of the oculomotor system allowed us to probe the neural mechanisms underlying the inhibitory cueing effects that are usually exhibited and studied in terms of behavioural response times. By manipulating stimulus-response compatibility in combination with activation or suppression of the oculomotor system in Chapters 2 and 3, we showed that the input form of IOR can be observed behaviourally when the oculomotor system is supressed. However, since we are ultimately looking for evidence of output-based IOR, which we have not been able to show with the anti-localisation paradigm, we decided that a change in direction was necessary. Chapters 4 and 5 present a shift in focus towards investigating modulations of behavioural cueing effects associated with the inclusion of non-targets (i.e., distractors) in a discrimination-localisation task. Our time-course study laid out the development of IOR in a distractor paradigm, and the results indicate that when distractors are present, oculomotor IOR starts early and slowly decays, whereas sensory-based IOR emerges later but decays relatively faster. The visually balanced ERP experiment in Chapter 6 allowed us to study

the N2pc component as a neurophysiological marker of the output form of IOR while the oculomotor system is activated. We provide convincing evidence for behavioural IOR despite the presence of distractors, although ERP results are less clear cut. This dissertation provides converging evidence in support of an input based sensory/attentional IOR that is distinct from output based oculomotor IOR.

Glossary of Terms

The following table shows a summary of definitions for various technical terms used throughout this thesis.

Term	Definition
Bottom-up processing	Information processing that rely primarily on sensory input (bottom), building upward from the smaller, finer details to form a more complete representation (Neisser, 1967).
Covert attention	Fixation that is maintained at one location while spatial attention is directed towards a different location / Allocation of attention to an item or location that is not foveated (i.e., in the periphery).
Cueing effect	The difference in reaction time (RT) between cued and uncued targets. Where differences exist, it could be facilitatory (cued RT < uncued RT) or inhibitory (uncued RT < cued RT). Sometimes spelled "cuing" in the literature.
Endogenous stimuli	Visual stimuli that are symbolic of a cue or target location, typically a central arrow that directs attention to the location of the cue or target.
Endogenous orienting	Shift of attention that is voluntarily directed towards stimuli.
Event-related potential	Averaged brain potentials in response to a specific cognitive event or stimulus.

Exogenous stimuli	Visual stimuli that is directly indicative of the cue or target location, in this thesis referring to peripheral stimuli.
Exogenous orienting	Shift of attention that is automatic and reflexively drawn towards stimuli.
Inhibition of return	A behaviour characterised by slowed reaction to recently attended stimuli.
N1	An ERP component characterised as the first negative-going deflection that peaks around 150 to 200 ms post-stimulus. The component can be modulated by selective visual attention processes.
N2pc	An ERP component that appears over posterior electrode sites contralateral to the attended location around 200 ms post-stimulus. The component may be modulated by selective visual attention processes.
Nd	An ERP component derived from the negative difference of attended vs. unattended waveforms. The component can be modulated by selective visual attention processes.
Overt attention	Fixation that is maintained at the same location that spatial attention is directed towards. / Allocation of attention to an item or location by foveating it.
P1	An ERP component characterised as the first positive-going deflection that peaks around 100 ms post-stimulus. The component can be modulated by selective visual attention processes.

Retinotopic	An “eye-centred” representation of space in the visual system based on a topographic map that constantly updates to account for each saccade.
Saccade	Rapid eye movement between two points.
Sensory adaptation	Decrease in receptor sensitivity after exposure to a stimulus.
Spatiotopic	A “world-centred” representation of space in the visual system based on a topographic map that is invariant to fixation.
Top-down processing	Information processing that is contingent on higher level cognition (top) at the neocortical level, which flows down to influence sensory-based mechanisms (Broadbent, 1977; Gilbert & Li, 2013). Examples include goal directed or memory-related responses.

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List of Abbreviations

The following table describes the significance of various abbreviations and acronyms used throughout this thesis.

Abbreviation	Word/Phrase
2-AFC	Two-alternative forced choice
ANOVA	Analysis of variance
CTOA	Cue-target onset asynchrony
EEG	Electro-encephalography
ERP	Event-related potentials
ERL	Event-related lateralisations
FLSD	Fisher's Least Significant Difference
IOR	Inhibition of return
ISI	Inter-stimulus interval
MAD	Median absolute deviation
MSE	Mean squared error
MRT	Manual response time
N1	First negative peak
N2pc	Second negative peak over posterior electrode sites contralateral to the attended location

Nd	Negative difference
P1	First positive peak
RT	Response time
SD	Standard deviation
SRT	Saccadic response time
TMS	Transcranial magnetic stimulation

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Chapter 1 : Introduction

1.1 Visual Attention

Human beings are highly visual creatures, with millions of neurons devoted to visual processing (Levy, Hasson, & Malach, 2004). In the prehistoric era, an effective search could be the key to survival in a life-or-death situation. You want to be able to track and kill wildlife for nourishment, and, more importantly, spot a predator before they could get to you. Nowadays, one still spends most of their waking moment looking, watching, scanning, searching; for a book on the shelf, keys in the living room, a bird in the sky, a familiar face in a crowd, et cetera (Eckstein, 2011). All of these functions rely, in one way or another, on efficient visual data processing because the amount of data at any one point can overwhelm the system should there not exist some sort of mechanism to prioritise certain functions over others.

Other than psychologists and neurobiologists, visual attention research has drawn considerable attention from computer scientists now that computational neuroscience has become more accessible than ever. As we attempt to approach human-level artificial intelligence, modern technical systems struggle with similar issues where computational resources are limited. Without a thorough understanding of the neurophysiology of human vision, machine vision algorithms can be painstakingly inefficient as the machine is put to work processing thousands of raw images. However, if the various mechanisms underlying visual search (e.g., tuning out irrelevant stimuli) can be implemented into those algorithms, object search and recognition can be optimised, thus freeing up valuable processing power.

That being said, fundamental research like the experiments delineated in this dissertation, contribute to the understanding of nature itself. A process as ubiquitous as visual search, although it has the potential to inform and contribute to the development of advanced technologies, is also

justifiably a topic of interest purely for its scientific value alone. The questions that we aim to address come down to: How does visual search work? What are the attentional mechanisms that regulate an efficient search?

Visual attention involves brain processes that integrate visual information from external sources (exogenous) and internal, volitional sources (endogenous) (e.g., Coull, Frith, Büchel, & Nobre, 2000; Hopfinger & West, 2006; Theeuwes, 1991). However, its capacity is inherently limited when it comes to processing visual information. Due to these limitations, attention is selectively focused. Selective visual attention involves orienting one's attention to an object or location in space (Koch & Ullman, 1985), whether it is to find a set of keys in a purse or to locate a source of water in a vast desert. Land, Mennie, and Rusted (1999) for example, examined how our visual system fixates on different elements in a natural setting when making tea. Because humans have finite capacity for processing information at any one time, selectivity in visual attention allows us to narrow things down to a more manageable amount of visual input to be processed and thus helps us to determine where to look next.

Generally, the allocation of attention is first regulated by bottom-up stimulus-driven factors and modulated almost immediately by top-down user-driven factors (Theeuwes, 2010a, 2010b). Where bottom-up processing is concerned, visual perception begins at the sensory input (i.e., stimulus), where the most basic information (e.g., saliency, luminosity, colour, motion) is processed. Exogenous orienting relies heavily on bottom-up processing, as the shifting of attention to the stimuli is automatic and reflexive. Top-down processing, on the other hand, relies on the goals of the perceiver. This stage is where endogenous orienting comes in, when one is given explicit (peripheral target) or implicit (central target) instructions to direct their attention to a specific location. Working in tandem, the two processes determine the selection of some

information and the inhibition of other information. Attentional modulation of the selected information, also referred to as attentional effects, can involve either overt (attending to a location or an object with eye movements) or covert (no eye movements) orienting. Either exogenous (stimulus-driven attentional capture, such as onset of a salient peripheral stimulus) and/or endogenous (voluntary control in orienting of attention, such as expecting where stimulus will appear) mechanisms are at play during the overt or covert orienting of attention.

1.2 Inhibition of Return

"Inhibition of return" (IOR) is an inhibitory phenomenon in visual attention that was first described by Posner and Cohen (1984) and later termed as such by Posner, Rafal, Choate, and Vaughan (1985). IOR is described as a slowed response to a cued target (caused by inhibition) when the target appears at a location that has been recently attended, given that sufficient time has passed between cue and target onset (approximately 200 ms). This inhibitory process is important in conducting effective visual searches to prevent one's attention from returning to the most salient locations over and over again. Proposed as a mechanism of novelty seeking (Posner et al., 1985) or foraging facilitation (Klein, 1988), IOR is of particular interest to vision scientists due to its role in making visual searches efficient (Danziger, Kingstone, & Snyder, 1998; Posner & Cohen, 1984; Posner et al., 1985; Taylor & Klein, 1998; Wang & Klein, 2010). To function in such roles, IOR must be relatively long lasting (see Samuel & Kat, 2003, for a review), and be represented in spatiotopic coordinates following each successive eye movement (Hilchey, Klein, Satel, & Wang, 2012). Spatiotopically coded visual inputs give rise to a perceptual experience of the world that is anchored and stable whilst saccades are made, unlike a retinotopic system where the map changes completely with each eye movement. The idea that IOR must be spatiotopic

comes from early research (Posner et al., 1985) where participants saccade to targets following peripheral cues, showing that inhibition is tied to previously stimulated locations on a display, instead of the stimulated retinal location.

In the typical cue-target paradigm (Posner, 1980) used to investigate IOR, a trial begins with participants fixating at a central location on a computer monitor, with two placeholders arranged at equal distances to the left and right of the central location, as depicted in Figure 1.1a. Presentation of the first stimulus (S1) follows, which can be either a central cue in the form of a left- or right-pointing arrow or a peripheral cue appearing as a highlighted or thickened border around the left or right placeholder. Note that auditory cues, such as pure tones presented as if the source came from one side or another, can also produce IOR (Mondor, Breau, & Milliken, 1998; Spence & Driver, 1998a, 1998b; Tassinari, Campara, Benedetti, & Berlucchi, 2002), but this thesis will focus on visual spatial orienting. After the cue disappears, there is an interval during which no stimulus is presented (inter-trial stimulus interval; ISI) before the response stimulus (S2), often referred to as the target, appears. Participants then respond as accurately and quickly as possible, either by making an eye movement or saccade to the response stimulus (or target) or by manually pressing a key that represents one of the two locations. Studies specifically looking at response modality in the context of IOR suggests that activation of the oculomotor system when making saccadic responses may elicit output-based IOR, whereas a suppressed oculomotor system during manual localisation responses elicits input-based IOR (Kingstone & Pratt, 1999).

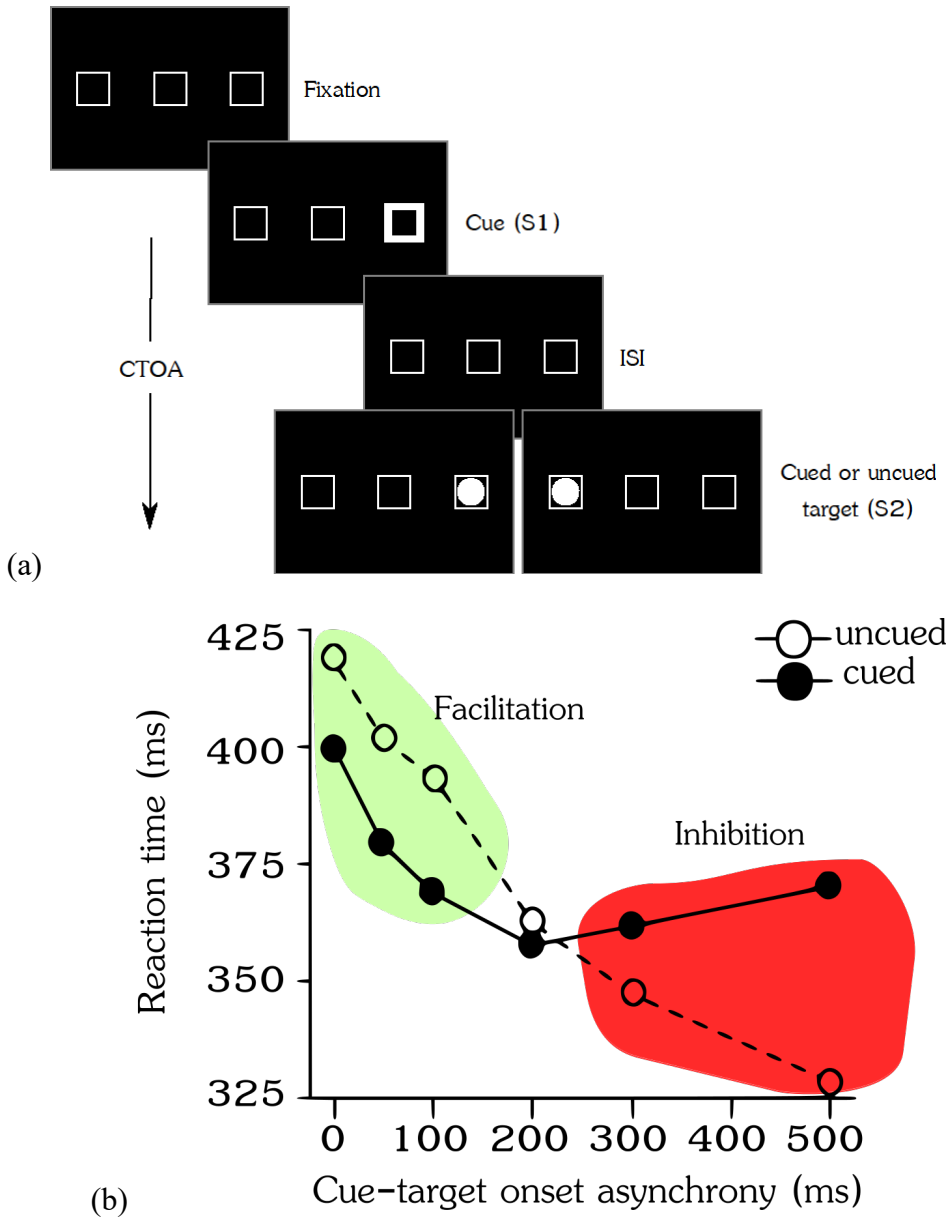

Figure 1.1. (a) A typical cue-target paradigm begins with a fixation screen followed by a non-predictive cue (S1; pictured is a peripheral cue), an inter-stimulus interval (ISI) and a target (S2; pictured is a peripheral target in the form of a filled circle) that could be either cued (presented in the right location) or uncued (presented in the left location). Varying cue-target onset asynchrony (CTOA) allows for observation of facilitated or inhibited responses to the target. (b) Responses are faster to cued (filled circles) compared to uncued (unfilled circles) targets when CTOA is less than ~200 ms. At longer CTOAs, IOR is observed when the opposite is true such that responses to uncued targets are faster (adapted from Klein, 2000, based on data from Posner and Cohen, 1984).

To *observe* IOR, enough time must have elapsed between the onset of S1 and S2, which is also referred to as the cue-target onset asynchrony (CTOA). IOR is typically observed at CTOAs of 300 ms and above and has been shown to last for up to 3 seconds (Samuel & Kat, 2003). We consider a trial to be "cued" if S1 was presented at the same location to which attention was later directed during S2. Likewise, a trial is "uncued" if S1 appeared at one location and attention was later directed to an opposite location during S2. IOR is then measured by comparing the difference between cued and uncued trials, the idea being that cognitive process underlying IOR contributes to the delay in response. Figure 1.1b illustrates findings from Posner and Cohen's (1984) seminal study, whereby a marked improvement in performance can be seen in cued trials compared to uncued trials at CTOAs less than 200 ms. This process is also known as facilitation. IOR is apparent when the opposite is true at later CTOAs, as response latencies to cued trials become slower than response latencies to uncued trials.

Although this thesis is concerned with non-informative cues only (i.e., there is a 50-50 chance that a target appears in the same location as the cue in each trial), some researchers have introduced predictability of the target as a factor (e.g., Chica & Lupiáñez, 2009; Chica, Lupiáñez, & Bartolomeo, 2006; Lupiáñez et al., 2004) in studying endogenous and exogenous cueing in IOR. Chica et al. (2006) showed IOR in a peripheral cueing paradigm at 75% predictability, whereas Lupiáñez et al. (2004) obtained IOR where there is an 80% chance that targets are likely to occur at the endogenously attended location. If there is a greater chance for a target to be cued rather than uncued, the higher predictability would presumably increase the strength of endogenous signals. By removing predictability as an element in our experimental design, we can be more confident that any such inhibitory cueing effects come from our manipulations and not the predictability variable.

1.3 Input/Output-based IOR

IOR, as it was defined by Posner and colleagues (1985), requires (a) oculomotor activation that (b) causes a motor response bias that is relatively long lasting (up to 3,000 ms; Samuel & Kat, 2003). However, there is also evidence of an input form of IOR that is generated when the oculomotor system is actively suppressed (Hilchey, Klein, & Satel, 2014; Klein & Hilchey, 2011; Posner & Cohen, 1984; Taylor & Klein, 2000). This input form of IOR has been observed even at long CTOAs but, without oculomotor activation triggered by explicit eye movements, does not satisfy Posner et al.'s (1985) IOR prerequisites.

Input and output-based IOR receive their names from the brain-computer analogy popular in cognitive psychology. To understand brain and behaviour, the idea is that information processing in the brain takes sensory input and produces an output (the observable behaviour). The input and output forms of IOR therefore refer to inhibitory cueing mechanisms that operate either on sensory processing when taking in information, or on oculomotor processing at the response end. In both cases, the basic assumption is that IOR is generated at cue onset and measured via responses to target onset in a spatial orienting experimental paradigm.

The proposed functional significance of IOR is novelty seeking (Posner & Cohen, 1984), or foraging facilitation (Klein, 1988). To accommodate this function, IOR must therefore be relatively long lasting, coded in spatiotopic coordinates, and present during the execution of eye movements (Hilchey, Klein, & Satel, 2014; Posner et al., 1985). Later work suggested that there were two distinct forms of inhibition: i) an input-based form of IOR that primarily affects early sensory processes, and ii) an output-based form of IOR that primarily affects later motor processes (Taylor & Klein, 2000). Sensory IOR is thought to be generated exclusively when the

oculomotor system is actively inhibited, whereas motor IOR occurs when the eyes are free to move in response to either cues or targets, regardless of whether the cues and targets are endogenous or exogenous in nature in the form of central or peripheral stimuli (e.g., Hilchey, Klein, & Satel, 2014; Rafal, Calabresi, Brennan, & Sciolto, 1989; Taylor & Klein, 2000). The importance of eye movements in determining whether input-based or output-based IOR is causing the delayed responses (e.g., Hilchey, Hashish et al., 2014; Pratt & Abrams, 1999) is key throughout this dissertation.

Not to be confused with input-based IOR, sensory adaptation is also input-based, but it is actually an early sensory inhibitory cueing mechanism distinct from IOR (Hilchey, Klein, & Satel, 2014). Observed at CTOAs shorter than about 500 ms, sensory adaptation is relatively short-lasting at cued locations (Fecteau & Munoz, 2005, 2006), whereby sensory responses to a sustained stimulus decay to negligible levels less than 500 ms after stimulus presentation. The relevance of sensory adaptation is backed up by neurophysiological evidence from single unit recordings of the superior colliculus (SC) in non-human primate studies (Dorris, Klein, Everling, & Munoz, 2002; Fecteau & Munoz, 2005; Ignashchenkova, Dicke, Haarmeier, & Thier, 2004; Sapir, Soroker, Berger, & Henik, 1999). The SC is part of the retinotectal visual system located in the midbrain that connects the occipital lobe and parietal cortex to the brainstem. The upper layers of the SC receive information from the retina, whereas the deeper layers of the SC process signals from visual as well as other parts of the brain and have been implicated in coordinating hand-eye movements (Lünenburger, Kleiser, Stuphorn, Miller, & Hoffmann, 2001), head orientation (Klier, Wang, Constantin, & Crawford, 2002; Klier, Wang, & Crawford, 2003; Stryker & Schiller, 1975), and shifts in visual attention (Kustov & Robinson, 1996).

Intermediate layers of the SC (iSC) have been linked to the preparation of saccades, whether it be overt or covert shifts of attention (Ignashchenkova et al., 2004). The saccade generation process requires visual (i.e., sensory) information from the retina and neural inputs from the cortex that are both exogenous and endogenous in nature to activate a population of neurons that, when the level of neural activity reaches a threshold, generate a saccadic eye movement. The iSC is made up of topologically arranged neurons that encode information in retinotopic coordinates. The sensory pathway reflects bottom-up processing whilst the motor pathway reflects top-down processing that together forms the basis of input- and output-based IOR (Taylor & Klein, 2000).

Oculomotor IOR, as first described by Posner et al. (1985) and espoused by Hilchey, Klein, and Satel (2014), is markedly distinct from sensory IOR. In Satel, Story, Hilchey, Wang, and Klein's (2013) model of IOR (also see Satel, Wang, Trappenberg, & Klein, 2011), both sensory adaptation and oculomotor IOR (that they referred to as direct inhibition) were implemented. Using a dynamic neural field model (DNF) – a mathematical model that describes the spatio-temporal evolution of a population of neurons (in this case in response to visual stimuli) – as a theoretical framework for describing IOR, one can simulate existing data sets and make predictions to direct future experiments. As demonstrated behaviourally in Hilchey, Klein, and Satel (2014) and simulated in Satel, Story et al. (2013), we do not see the effects of sensory adaptation when S1 is a central stimulus rather than a peripheral stimulus, because there is no repeated stimulation of cells representing the location of the target.

1.4 Compatible and Incompatible Responses With or Without Saccades

The idea that an activated oculomotor system is involved in generating an output-based form of IOR has been challenged by several studies that used the anti-saccade task and found IOR with both pro- and anti-saccades (Abegg, Sharma, & Barton, 2012; Barton, Goff, & Manoach, 2006; Fecteau, Au, Armstrong, & Munoz, 2004; Khatoon, Briand, & Sereno, 2002; Rafal, Egly, & Rhodes, 1994). In an anti-saccade task, as exemplified by Figure 1.2, observers perform an eye movement to the opposite location of a peripheral target (i.e., an anti-saccade) instead of making an eye movement to the location of the target (i.e., a pro-saccade). There is an exogenous component involved in pro-saccades, because attention is drawn directly towards a stimulus location, and an endogenous component during anti-saccades, because, while eye movements are directed towards a location opposite to that of the target, one must still covertly register the location of the target before inverting the response. Should IOR be input/sensory based rather than output/motor-based, the anti-saccade task should elicit similar IOR effects as pro-saccades, because slowed reaction is tied to attention towards the target appearing at the location of the cue (a sensory component) regardless of response.

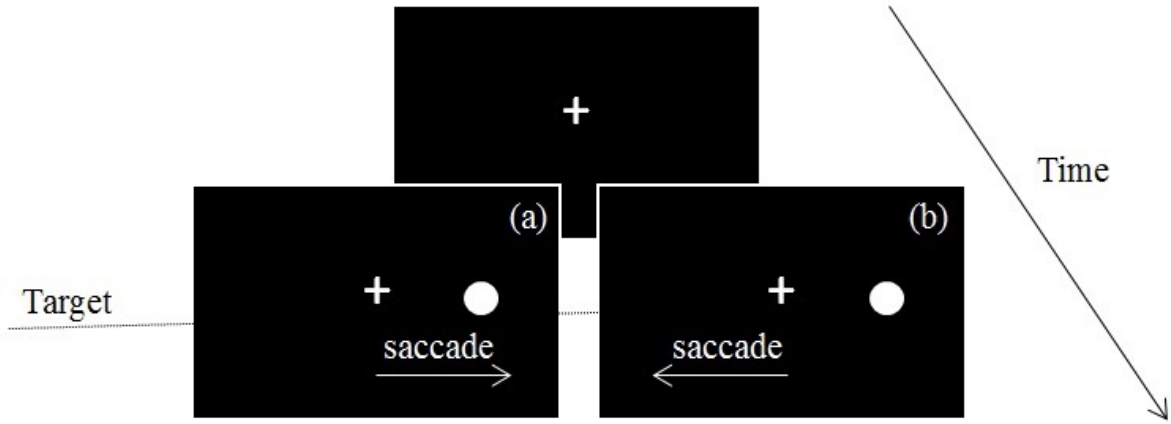

Figure 1.2. An illustration of pro- and anti-saccade tasks. Participants fixate at the centre '+' and either (a) respond towards the location of the target in a pro-saccade task or (b) respond to the location opposite of the target in an anti-saccade task.

In a series of experiments, Rafal et al. (1994) examined combinations of fixations or saccades to central and peripheral cues followed by pro- and anti-saccades in response to central arrow or peripheral targets. A consistent IOR effect when the target appears at a cued location, regardless of where the response is made, would imply that the inhibition was sensory based. On the other hand, the motor bias that is characteristic of oculomotor IOR, as theorised by Posner et al. (1985), would generate IOR when a response was made towards a location that was recently cued, whether or not the target appeared at that same cued location. Results from Rafal et al. (1994) showed the former pattern, and they argued that the IOR effect is more input-based when participants perform anti-saccade tasks. Later studies involving anti-saccades and IOR generally provided corroborating evidence (e.g., Abegg et al., 2012; Fecteau et al., 2004; Khatoon et al., 2002). For instance, Khatoon et al. (2002; Exp. 2) found IOR with both pro- and anti-saccades at a 1,000 ms CTOA. Similarly, Fecteau et al. (2004; Exp. 3) demonstrated an "alternation advantage", evident in slowed RTs in both pro- and anti-saccade responses where there was repetition in the presented trials (much like IOR in a target-target paradigm where participants respond to both the cue and target). Thus, the occurrence of eye movements is not the only determining factor underlying which form of IOR is observed. Instead, there is also a sensory component whereby the suppression of reflexive saccades (involuntary saccades in response to an exogenous stimuli) contributes to an input form of IOR (Klein & Hilchey, 2011).

Besides the type of task, researchers have also used manual response times (MRTs) (e.g., Posner & Cohen, 1984) or saccadic response times (SRTs) (e.g., Abrams & Dobkin, 1994) as a response variable in investigating IOR. Manual responses typically involve participants pushing a button or making a simple keypress upon target onset, whereas saccadic responses call for an eye movement towards the target. It thus follows that the act of a saccadic response itself

inherently requires spatial localisation of the target (overt attention) to make a successful response. A manual detection task, on the other hand, does not necessarily involve localisation of the target as the task only entails making a keypress upon detection of the target, requiring localisation only when one is asked to respond with left or right keypresses that correspond to target location. Manual responses can occur either overtly (e.g., manual responses accompanied by eye movements to the target) or covertly (e.g., manual responses while eye movements to the target are suppressed). With regards to manual responses, the process boils down to detection requiring processing of the target, localisation requiring processing of the target location, and discrimination requiring processing of the target features. When the response is saccadic, localisation is requisite, whereas discrimination adds another layer of processing as one needs to both localise and distinguish perceptual or sensory stimuli. It is important to make the distinction between manual and saccadic responses, so that attentional (input/sensory-based) and oculomotor (output/motor-based) components of IOR can be dissociated.

In addition to replicating the literature on IOR with pro- and anti-saccadic tasks, we describe in Chapter 2 experiments that incorporate responding to an opposite location with manual localisation tasks, essentially pro- and anti-localisation, in an effort to dissociate input-based and output-based IOR. A methodological combination of both pro-/anti-saccades and pro-/anti-localisation where saccades are either explicitly required or actively discouraged (monitored by an eye-tracker) could provide converging evidence for the understanding of input/output based IOR. We expect to find response times to be slower for anti-saccades and anti-localisation tasks compared to pro-saccades and pro-localisation tasks, because the oculomotor system must be actively suppressed to perform an anti-task correctly (Briand, Larrison, & Sereno, 2000; Munoz & Everling, 2004). We also expect cueing effects with pro-

saccades and pro-localisation trials, as well as greater IOR effects when saccades instead of manual responses are made. Chapter 3 follows up this behavioural study with an electroencephalographic study that investigates neurophysiological mechanisms underlying IOR that we will elaborate upon in the following section.

1.5 Distractors and IOR

Regardless of oculomotor activation state, it is also clear that the type of task can influence the time at which behavioural inhibition is observed, especially when task demands are different between task sets (Berger, Henik, & Rafal, 2005; Lupiáñez, Milán, Tornay, Madrid, & Tudela, 1997; Lupiáñez & Milliken, 1999; Terry, Valdes, & Neill, 1994). Simple detection tasks are the most straightforward, involving just a simple manual key press upon detection of the target. Discrimination or two-alternative force choice (2-AFC) tasks can be either feature-based (e.g., press X if the target is red, press O if the target is blue) or location-based (e.g., press the left button if the target appears on the left, press the right button if the target appears on the right). In addition, these discrimination tasks can be presented either with single targets, or with a target and a distractor at the opposite location.

Early work comparing detection and discrimination responses showed that inhibition did not occur when a discrimination response was required. Terry et al. (1994, Exp. 1), using a target-target paradigm, asked participants to respond to targets appearing to the left or right of fixation with a simple manual key press (i.e., feature discrimination without localisation). They further presented a paradigm in which participants completed a single target localisation task or a discrimination task with a distractor at the location opposite of the target (Exp. 2). In both the detection task and the localisation task, there was a slowed response to repeated targets, but

facilitation occurred in the discrimination task. However, although Terry et al. (1994) found no inhibition with their discrimination task, it was later discovered that inhibition can indeed be elicited in discrimination tasks despite the presence of distractors along with target stimuli given a long enough CTOA (Lupiáñez, Milliken, Solano, Weaver, & Tipper, 2001; Pratt, 1995; Pratt & Abrams, 1999; Pratt et al., 1997).

Besides the CTOA and task type, the presence of output-based IOR also seems to depend on attentional processes. Whether IOR and attention are inherently linked has been a constant debate in the literature. Rafal et al. (1989) investigated whether attention is truly inhibited in IOR by manipulating the way participants allocated attention via two forms of orienting, either reflexive or voluntary. Reflexive or exogenous orienting was manipulated by a peripheral stimulus that elicited an automatic orienting of attention to the area of interest, whereas voluntary or endogenous orienting was brought about by a symbolic representation of a spatial location (i.e., by using central arrows rather than peripheral stimuli) and viewers were required to deliberately allocate their attention to the location of interest. Their study found that the observation of IOR depended on the type of orienting. Specifically, IOR was only observed on trials in which reflexive orienting took place, despite cues and targets appearing at the same location. With this finding, Rafal et al. (1989) challenged the idea of IOR as an attentional allocation mechanism and proposed that IOR is merely an oculomotor bias that affects the output end rather than the input end of processing.

Nonetheless, other researchers (e.g., Taylor & Klein, 1998) were able to find support for the attentional account of IOR. They argued that if IOR reflects the inhibition of attention, then the factors that would affect the magnitude of attention would also affect the magnitude of IOR, in turn affecting performance on perceptual tasks regardless of response modality (Taylor &

Klein, 1998). Indeed, Spence and Driver (1998a, 1998b) observed IOR using auditory cueing (but see Reuter-Lorenz & Rosenquist, 1996, for counterevidence).

To investigate the role of attention in IOR, researchers have noted the importance of observing IOR in a discrimination task rather than in just detection and localisation tasks. Pratt, Kingstone, and Khoe (1997) noted that if IOR reflected more of a motor bias that delays responses to previously cued locations, IOR should be elicited only in localisation tasks because these were spatially directed manual responses. Otherwise, if IOR was elicited in both detection and localisation tasks, then an attentional bias that inhibits the allocation of attention to previously cued locations would be more likely, because inhibition could be observed behaviourally regardless of response. Similarly, when comparing discrimination and localisation tasks, if IOR is more input-based, we should see IOR affected by sensory processing in discrimination tasks, whereas output-based IOR should be elicited in both discrimination and localisation tasks.

1.6 Electrophysiological Markers of IOR

Behaviourally, experimental findings pointing toward both input and output forms of IOR can seem impossible to reconcile given that multiple mechanisms – both input and output processes – are engaged with overlapping effects. However, electrophysiological experiments provide a promising avenue for dissociating those two processes, given the temporal sensitivity of the technique.

On top of examining the neural underpinnings of IOR, ERPs can be used in determining whether input-based or output-based IOR is involved in a certain experimental paradigm. Generally, in attention and cognition, well established early ERP components, such as the P1 and

N1, are useful for indexing perceptual/attentional processing. On the other hand, higher order cognitive processes, like memory encoding and semantic processing, are reflected in modulations of later ERP components, such as the P300 and N400. ERP components that are sensitive to specific experimental manipulations, for example components known to be modulated by perceptual processes, can therefore become invaluable tools for studying input-based IOR, separate from output-based IOR.

The P1 component in ERP literature has long been established as an index of early sensory processing in both the visual and auditory systems. Recorded at parieto-occipital regions on the scalp when behavioural responses are made to transiently presented visual stimuli, P1 is a positivity that typically peaks at around 100 ms after stimulus onset followed by a negative going waveform called the N1 (Luck, Heinze, Mangun, & Hillyard, 1990). In the context of IOR, we look at P1 cueing effects (the difference between cued and uncued P1 mean peak amplitudes) whereupon attenuated P1 amplitudes have been associated with inhibited perceptual processing at cued locations (e.g., Prime & Ward, 2004, 2006). An ERP study by Satel, Hilchey, Wang, Story, and Klein (2013), using a typical cue-target spatial orienting paradigm, in one condition engaged the oculomotor system by requiring saccades to a peripheral cue followed by a manual localisation response to a peripheral target. In another condition, they actively suppressed oculomotor activation by having participants fixate at the centre throughout each trial instead of making a saccade to the cues. Behavioural IOR was observed in both conditions, as were P1 cueing effects (posterior P1 and N1 amplitudes were reduced on cued relative to uncued trials), although behavioural IOR was greater when saccades were required.

Indeed, Satel, Hilchey et al. (2013) demonstrated that P1 cueing effects were apparent both with and without oculomotor activation. However, their meta-analysis on a range of

published experiments (19 experiments from 9 articles: Hopfinger & Mangun, 1998, 2001; McDonald, Ward, & Kiehl, 1999; Prime & Jolicœur, 2009a, 2009b; Prime & Ward, 2004, 2006; Tian & Yao, 2008; Van der Lubbe, Vogel, & Postma, 2005) where cues were ignored and a localisation response to the target was made showed that P1 cueing effects are correlated with behavioural IOR, but only if eye movements are suppressed. Given that Satel, Hilchey et al. (2013) found no correlation between P1 cueing effects and behavioural IOR when eye movements were made, it thus seems unlikely that the P1 modulation is a good index for output-based IOR, as was previously assumed (Chica & Lupiáñez, 2009; Martín-Arévalo, Chica, & Lupiáñez, 2014; Prime & Jolicœur, 2009a; Prime & Ward, 2006; Satel, Hilchey, Wang, Reiss, & Klein, 2014; Satel, Hilchey et al., 2013; Tian & Yao, 2008; Van der Lubbe et al., 2005; Wascher & Tipper, 2004). Instead, P1 cueing effects could reflect either input-based IOR or sensory adaptation, depending on the CTOA used. Where relatively short CTOAs are concerned, repeated stimulation at the cued location (i.e., peripheral cues followed by peripheral targets) suggests that the inhibitory effect elicited is really sensory adaptation (e.g., Dorris et al., 2002; Lim, Eng, Janssen, & Satel, 2018). Because sensory adaptation (appearing as an early input-based cueing effect) decays over time, any persistent inhibitory effect observed at late CTOAs can no longer be explained by sensory adaptation, but instead as a result of differential modulations caused by input-based IOR. Either way, it could not be output-based IOR when eye movements were suppressed.

Later components that have been implicated in IOR include the Nd and the N2pc (e.g., McDonald, Hickey, Green, & Whitman, 2009). The Nd effect is an observed cued minus uncued negative difference that is greatest at occipital and parietal areas around 220-300 ms after the onset of a target stimulus. There have been a number of IOR-ERP studies that have shown the

Nd effect in visual spatial paradigms (Eimer, 1994; Prime & Ward, 2006; Satel, Wang, Hilchey, & Klein, 2012; but see McDonald et al., 1999) albeit less consistently than the P1 effect (see Martín-Arévalo, Chica, & Lupiáñez, 2016, for a review). For instance, Prime and Jolicœur (2009a) reported an inverse relationship between Nd and the magnitude of IOR, whereas McDonald et al. (1999, Exp. 2) showed no Nd modulation despite significant behavioural IOR, leading to their argument that perhaps modulations of Nd found in previous studies reflect a form of sensory adaptation.

First discovered in a visual search paradigm (Luck, Fan, & Hillyard, 1993), the N2pc component has been implicated as an index of spatially selective visual attention (Luck & Hillyard, 1994a, 1994b) in the context of distractor-suppression (Eimer, 1996; but see Mazza, Turatto, & Caramazza, 2009, for a counter-argument) that originates from the occipito-temporal cortex (Hopf, Boelmans, Schoenfeld, Luck, & Heinze, 2004; Hopf et al., 2000). In Luck and Hillyard (1994a), using homogenous and non-homogenous pop-out search arrays to compare feature search/parallel processing with conjunction search/serial processing, participants were asked to fixate at the centre, then make a manual response with one button when they saw a salient target, and another button when the target was not present. In a traditional visual search experiment, participants are instructed to identify a pre-specified target within an array of visual stimuli. Parallel processing occurs when a search array is made up of mostly identical stimuli elements except for one that has a distinguishing feature compared to the other elements. In such a scenario, it is relatively easy to detect the one that does not belong as it would appear to "pop-out" from the rest of the stimuli. In contrast to that is serial processing, when a search array consists of elements possessing subtler differences, such that no one element "pops out". Participants must check each element in the search array sequentially until they find the target.

Luck and Hillyard (1994b) found the N2pc component to be more prominent for target pop-outs than for non-target pop-outs (i.e., distractors). They also observed that the N2pc component is only elicited when distractors are present, but not if distractors provide relevant information for target selection.

Although there is much to be gleaned from behavioural data by manipulating key components of an experimental paradigm, ultimately, to understand the underlying processes that contribute to IOR, it is only reasonable to investigate brain activity for more direct evidence on cueing effects. ERP studies provide a bridge between single-neuron recordings in nonhuman primate physiology research and human behavioural research. Additionally, if we could link IOR to an ERP component that has been established to reflect certain cognitive processes, for example, one that reflects attentional processing or oculomotor processing, it would help clarify and resolve debates on distinct forms of IOR observed in behavioural performance.

1.7 Research Questions

The focus of this dissertation is on late inhibitory cueing effects, where we investigate how late oculomotor IOR differs from input-based IOR. Since IOR was first described in the literature (Posner et al., 1985; Posner & Cohen, 1984), the past couple of decades of research have refined what we know about IOR, allowing researchers to narrow down key components in studying IOR. One such component is the CTOA, whereas another is oculomotor activation. Using two different approaches, we investigate the two forms of IOR at CTOAs long enough that early inhibitory cueing effects (i.e., sensory adaptation) should no longer be relevant and therefore do not affect our results. We manipulate stimulus-response (S-R) compatibility in the first two experimental chapters, then the presence of distractors in the following three chapters,

the main premise being to separate stimuli-level differences from response-level effects. However, the anti-localization paradigm in Chapters 2 and 3 is not easily comparable with visual search studies, and does not allow us to examine certain ERP components. To address that limitation in experimental design, Chapters 4, 5, and 6 follow a distractor paradigm that makes it possible to examine IOR involving non-target stimuli.

We therefore planned and report in Chapter 4, 5, and 6 a visually balanced paradigm much like Satel, Hilchey et al. (2013), except with one crucial difference: S2 is a discrimination task with a target and a non-target (i.e., a distractor) displayed on either side of the fixation point, where participants must localise and respond to the appropriate target. Chapter 4 is our first foray into investigating the neurophysiological indices of IOR with ERP analyses, where participants stayed fixated on the centre of the screen throughout Experiment 1, eliciting input-based IOR. Experiment 2 is a behavioural study where participants saccade to targets. However, we could not investigate the N2pc component as a neurophysiological index of output-based IOR without oculomotor activation in the experimental paradigm. Following a time course behavioural study in Chapter 5, we returned to search for the elusive N2pc component in Chapter 6, this time engaging the oculomotor system by requiring saccade to the cues. A potential drawback to a distractor-spatial cueing paradigm is that, with a distractor stimulus, the N2pc could reflect more than a single attentional process and thus cannot be directly associated with IOR either. This issue will be addressed in the discussion section of the thesis (i.e., Chapter 7).

Chapter 2 : Manual and Saccadic Anti-localisation[1]

Numerous variations to the basic non-informative cue-target paradigm have been explored over the years, showing IOR to be an extremely robust cognitive phenomenon measured using, for example, detection (e.g., Maylor & Hockey, 1985), discrimination (e.g., Lupiáñez et al., 1997), localisation (e.g., Taylor & Ivanoff, 2005), or a combination of tasks (e.g., Chica et al., 2006). Simple detection tasks are the most straightforward, involving just a simple manual key press upon detection of the target (regardless of the location of the target). Because attentional orienting is supposed to facilitate both detection and discrimination, other IOR researchers have turned to discrimination tasks where participants are asked to make a two-alternative forced choice (2-AFC) response upon detecting and *distinguishing* target features (Lupiáñez et al., 2001; Pratt, 1995; Pratt & Abrams, 1999; Taylor & Ivanoff, 2005). Discrimination or 2-AFC tasks can be either feature-based (e.g., press X if the target is red, press O if the target is blue) or location-based (e.g., press the left button if the target appears on the left, press the right button if the target appears on the right), the latter of which also involves localisation. In addition, these discrimination tasks can be presented either with single targets only, or with a target and a non-target (i.e., distractor) at the opposite location. Lupiáñez et al. (2001) showed that IOR can be measured in a colour discrimination task, albeit at later CTOAs than in a detection task. Similar observations were also made with shape (Cheal, Chastain, &

[1] A modified version of this chapter and parts of the discussion chapter have been published in: Eng, V., Kwon, S. M., Gan, S. R., Jamaluddin, S. A., Lim, A., Janssen, S. M. J., & Satel, J. (2017). Stimulus-response incompatibility eliminates inhibitory cueing effects with saccadic but not manual responses. *Attention, Perception, and Psychophysics, 79*, 1097-1106. doi:10.3758/s13414-017-1295-8

Lyon, 1998; Pratt, Kingstone, & Khoe, 1997) and size (Handy, Jha, & Mangun, 1999) discrimination. Lupiáñez et al. (2001) suggested that increased task demands when making discrimination responses led to the delayed emergence of IOR in discrimination tasks.

Sensory processes, in the world of vision research, often involve low-level processing, such as discerning motion, luminosity or brightness, and contrast in stimuli. In the visual cortex, for example, the excitatory and inhibitory activity in a cortical cell determines how bright or dark visual stimuli is at the perceptual level (Barlow, 1972; Wiesel & Hubel, 1963). Because this activity occurs closer to the input stage, sensory IOR is often also referred to as input-based IOR. Further along the processing line is a decision-making component involving motor feedback to certain stimuli, known as output-based IOR because it is closer to the response stage (Klein & Hilchey, 2011). This output-based IOR has been theorised to be modulated by tasks requiring eye movements to either the cue or the target (Chica, Taylor, Lupiáñez, & Klein, 2010; Hilchey, Klein, & Satel, 2014; Satel, Hilchey, et al., 2013; Smith, Schenk, & Rorden, 2012; Sumner, Nachev, Vora, Husain, & Kennard, 2004; Taylor & Klein, 2000; Wang, Satel, & Klein, 2012).

Reuter-Lorenz, Jha, and Rosenquist (1996) compared both manual and saccadic responses at 1,000 and 1,300 ms CTOAs but found equivalent IOR with both response modalities. A similar observation was made by Taylor and Klein (2000), who manipulated the response modality to S1 and S2 in their attempt to investigate the input and output forms of IOR. Participants could either ignore the cue (fixate at centre during S1) or respond to S1 by indicating the location (left or right) at which the cue appeared or where the central arrow was pointing towards. Responses could be in the form of a keypress (manual localisation) or an eye movement (saccadic localisation). Likewise, with S2, either manual or saccadic localisation was required. The study found inhibition to peripheral and central stimuli with saccadic responses, whereas

inhibition was only present when making manual responses to peripheral stimuli while fixation was maintained at the centre. Their interpretation of the results was that there is not one, but two, mutually exclusive forms of IOR – an output-based, oculomotor form of IOR when saccades are required and an input-based, sensory form of IOR when eye movements are suppressed (Taylor & Klein, 2000).

Taylor and Klein (2000) tested various combinations of fixation at the centre, manual or saccadic responses to central and peripheral cues, followed by manual and saccadic responses to central and peripheral targets. Because peripheral targets are exogenous and capture attention reflexively, responses to these targets must be sensitive to inhibitory effects at the sensory/perceptual level. The output-form of IOR, on the other hand, is a delay in motor response to targets. Ivanoff and Klein (2006) interpreted these two flavours of IOR as a speed-accuracy tradeoff, where slower responses correspond with greater accuracy. This speed-accuracy tradeoff was apparent for motor-based IOR but not for sensory-based IOR.

By comparing manual versus saccadic responses, we can investigate this two-forms theory of IOR: input and output (Chica et al., 2010; Hilchey, Klein, & Satel, 2014; Hunt & Kingstone, 2003; Kingstone & Pratt, 1999; Sereno, Jeter, Pariyadath, & Briand, 2006; Taylor & Klein, 2000; Wang et al., 2012), by pitting the condition where the sensory-based input form of IOR is measured with manual responses against the condition where the motor-based output form of IOR is measured with saccadic responses. If IOR were only reported in saccadic localisation tasks, one could surmise that IOR reflects an oculomotor bias against the recently cued location rather than being evidence of attentional effects in processing perceptual properties of the target. Note that input-based IOR should not be confused with sensory adaptation or habituation, both potentially modulated by sensory differences in the stimuli. Unlike habituation,

a learned behaviour observable when irrelevant stimuli elicit decreased responses upon repeated stimulus presentations, sensory adaptation describes fatigue in neuronal activity due to repeated stimulation (Kohn, 2007).

If suppressing saccades is involved in eliciting input-based IOR, then the input/output dissociation of IOR depends on whether the oculomotor mechanisms responsible for generating reflexive saccades are actively suppressed. However, many IOR studies use manual detection or discrimination tasks where observers respond by making a keypress without strict monitoring and control over eye movements during the experiments, allowing for a possible mix of both covert and overt attention and ambiguity in whether saccades are activated or suppressed (e.g., Lupiáñez et al., 1997; Zhao, Heinke, Ivanoff, Klein, & Humphreys, 2011).

The goal of the present chapter was to tease apart further differential effects of pro- and anti-localisations with manual and saccadic responses to investigate how sensory (input) and oculomotor (output) processes contribute to IOR. In this study, participants made either manual or saccadic responses to targets in cued and uncued trials of a pro- or anti-localisation task. However, because it is unclear whether manual "localisation" responses are equivalent to saccadic localisation responses, we will from here on use the terms *compatible* and *incompatible* to refer to pro-localisation and anti-localisation, respectively (as in Wascher, Schneider, & Hoffmann, 2015). Participants in all conditions completed a spatial cueing task (peripheral cue: maintain fixation, peripheral target: manual or saccadic response), in which they had to respond to targets with either a compatible or incompatible action, depending on instructions presented during each trial. The incompatible stimulus-response mapping task is thus able to dissociate sensory and motor processes, by separating the locations of the stimulus and the response. By removing repeated peripheral stimulation at the target location in the incompatible tasks, we can

be more confident that any IOR observed is more likely due to oculomotor processing rather than sensory processing.

Furthermore, because manual response trials required an actively inhibited oculomotor system – whereas eye movements were required on every trial in the saccadic response tasks – we can test the two-forms theory of IOR as well as examine the effects of response modality to further clarify discrepancies found in previous studies. For instance, Briand et al. (2000) found differences in the development of IOR followed by the decay of facilitation effects in a standard cue-target paradigm with saccadic and manual responses, with the amount of IOR reported as equivalent with both response modalities. Hunt and Kingstone (2003), on the other hand, found a dissociation in IOR results following manual and saccadic responses, with only saccadic responses interacting with luminance and fixation offset, which indicates that IOR can involve both attentional and oculomotor components. In addition, using a standard cue-target paradigm requiring manual responses, Wascher et al. (2015), for example, did not find any difference between compatible and incompatible tasks, nor did Olk and Kingstone (2003) when saccadic responses were involved.

In line with previous work, saccadic responses should overall be faster than manual responses (Briand et al., 2000), as should compatible compared to incompatible tasks (Massen, 2004; Olk & Kingstone, 2003). We also expect to find IOR in all compatible tasks, regardless of the response modality (Briand et al., 2000; Hunt & Kingstone, 2003). Whether the IOR effects are input-based or output-based depends on the interaction between task and response modality. If IOR is largely input-based, we would expect to find equivalent IOR effects in both compatible and incompatible tasks with manual responses. Similarly, with saccadic responses, we would

expect to reproduce previous findings that IOR effects affect the target stimulus location, not the unstimulated location to which a response is made.

To investigate how the strength of input and output forms of IOR is affected by response modality, we designed an experiment with four conditions to dissociate manual and saccadic responses in a spatial cueing paradigm. For each response modality, the location of the target stimulus must be encoded (i.e., localisation must occur) before a correct manual or saccadic response can be executed. A secondary objective of this chapter is to use an incompatible task in addition to a compatible task to examine how sensory input-based and motoric output-based processes contribute to IOR. Participants completed a spatial cueing task with peripheral cues in which they were asked to maintain fixation, followed by a cue-back stimulus that signalled them whether to respond towards (compatible) or away from (incompatible) the target, just before the peripheral targets were displayed.

We expected to find response times to be slower for incompatible tasks compared to compatible tasks, because the oculomotor system must be actively suppressed to perform the task correctly (Briand et al., 2000; also see Munoz & Everling, 2004, for a review). We also expected to find cueing effects in all the compatible conditions (in line with previous work), but not necessarily in the incompatible conditions, with greater IOR effects when saccades instead of manual responses are made.

2.1 Method

Four sets of experiments were conducted: i) mixed design with manual responses, ii) mixed design with saccadic responses, iii) blocked design with manual responses, and iv) blocked design with saccadic responses. This study had a 2 (Experimental Design: mixed vs.

blocked) x 2 (Response Type: manual vs. saccade) x 2 (Cueing: cued vs. uncued) x 2 (Compatibility: compatible vs. incompatible) mixed factorial design. Experimental design and Response Type were manipulated between subjects, whereas Cueing and Compatibility were manipulated within-subjects.

2.1.1 Participants.

Of all 58 undergraduate students from University of Nottingham Malaysia who participated in this experiment in exchange for course credit or non-monetary compensation, data from three participants who completed less than ¾ of the experiment were excluded from the analyses. Data from four participants were removed due to error rates exceeding 10%, and two others were removed because their mean RTs were +/- 3 SDs beyond the overall mean. Pruning left 12 datasets in each experiment, with the exception of the blocked design with saccadic responses, which had 13 datasets. Mean age of the remaining 49 participants (29 females, 45 right-handed) was 21.0 years (age ranging between 19 and 30 years old, *SD* = 2.06). All reported normal or corrected-to-normal vision and no known neurological or psychiatric illness. The experiment was approved by the Science and Engineering Research Ethics Committee.

2.1.2 Stimuli and apparatus.

Participants were seated in a dimly lit room during testing with their head positioned on a chin-rest 57 cm away from the display monitor. A 64-bit Windows 7 computer with a 3.4 GHz CPU and 8 GB of RAM running Python scripts was used for stimulus presentation and recording of behavioural data. Stimuli were presented on a 24-inch BenQ gaming monitor, whereas participants made the manual responses on a standard QWERTY keyboard. A desktop-mounted

eye-tracking system (EyeLink 1000 Plus) from SR Research was used to monitor participants' eye movements throughout the experiment at a sampling rate of 1000 Hz. In the saccadic response conditions, SRTs to targets were recorded using the eye-tracker. If participants ever made incorrect eye movements (i.e., leaving fixation when it was not appropriate to do so), then an error message was presented ('incorrect eye movement') and the trial was randomly recycled and completed again later.

Except for the 'cue-back' fixation crosses, all stimuli were presented in white against a black background, with two peripheral boxes (4.5° x 4.5°, visual angle) as placeholders 8.7° to the left and right of the centre along the horizontal meridian and a fixation cross (0.8° x 0.8°) that appeared at the centre of the screen. Cues were presented as a highlighting (increased border thickness) of one of the peripheral boxes, whereas cue-backs appeared as either a green or red fixation cross (0.8° x 0.8°), with the colours indicating whether the current trial was a compatible or incompatible trial, respectively. The cue-back also serves as a central reorienting event (Pratt & Fischer, 2002). Participants responded to targets that were filled circles (2.4° in diameter) inside either one of the peripheral boxes. A five-point calibration and validation procedure was performed on every participant prior to the experiment to ensure that the eye-tracking precision was within one degree of visual angle.

2.1.3 Design and procedure.

Figure 2.1 illustrates the sequence of events of a trial. In all 4 conditions, each trial began with a drift correction in which participants fixated on a small circle at the centre of the screen, followed by a fixation cross that appeared on the screen for 500 ms. An uninformative cue came on immediately after and stayed on the screen for 300 ms to allow sufficient time for attention to

shift to the cue location. After a 400 ms delay, a green or red cue-back fixation cross flashed for 300 ms, indicating whether a compatible or incompatible response should be made to the upcoming target. There was another 500 ms delay prior to displaying the target, to which participants were instructed to respond as quickly and accurately as possible. Trials ended as soon as a response was made or after 3,000 ms had elapsed, whichever came first. A randomly selected inter-trial interval ranging between 1,000 and 1,500 ms elapsed before the start of the next trial.

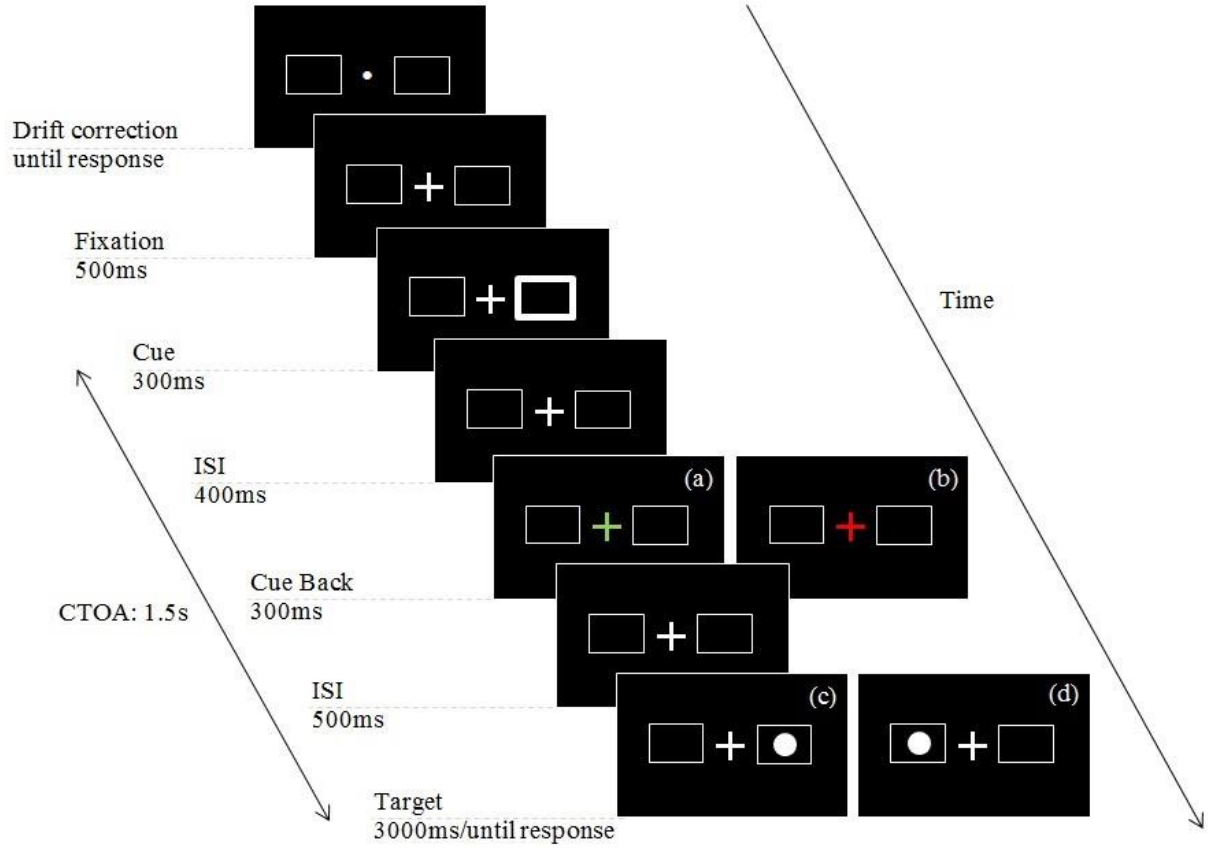

Figure 2.1. Illustration of the experimental paradigm used. Cues were non-informative of the subsequent location at which targets appeared. A green cue-back called for (a) a compatible response to the target, whereas a red cue-back called for (b) an incompatible response. Trials were considered (c) cued if the cue and response were in the same location and (d) uncued when the cue and response were in opposite locations.

In the two mixed design conditions (with either manual or saccadic responses), 600 intermixed compatible and incompatible trials were presented per participant, separated into four blocks of 150 trials, with short breaks between the blocks and a five-point calibration preceding each block. Seventy-five compatible trials were cued to the left and 75 more cued to the right, making up 150 cued compatible trials. Similarly, 75 compatible trials were uncued with left targets and 75 more were uncued with right targets, making up 150 uncued compatible trials. The same ratios applied to incompatible trials. Trials were considered cued trials when cues and targets appeared at the same location and uncued when they appeared on opposite sides, regardless of the localisation task required.

The two blocked design conditions (with either manual or saccadic responses) were identical to the mixed conditions, with the following exceptions: 1) the number of trials was reduced to a total of 320 trials split into four blocks of 80 trials to facilitate data collection, and 2) compatible and incompatible trials were blocked separately and counterbalanced, such that half of the participants completed two blocks of compatible trials followed by two blocks of incompatible trials whereas the other half performed the same blocks in the opposite order.

The manual response conditions required participants to stay fixated throughout each trial and make a manual keyboard response (‘Z’ for left, ‘/’ for right) when the target appeared. The saccadic response conditions required participants to maintain central fixation until the target appeared, then make a saccade in response to the target. The eye-tracker was set to detect saccades based on velocity (22°/s), acceleration thresholds (5000°/s^2), and motion (0.15°). Trials were abruptly terminated (with an error message presented on the screen) and randomly recycled if the participant’s gaze position deviated by more than 3° from the fixation stimulus at any point during a trial. However, in the saccadic response conditions, saccades were allowed to valid

response locations (target's location or the opposite side, depending on localisation task) within a 3° visual angle region centred in placeholders upon a target's appearance, and any incorrect responses after target appearance were counted as errors.

2.2 Results

Trials with incorrect responses (3.65%), anticipatory responses (RTs faster than 2.5 Median Absolute Deviation; MAD[2] below the median of each participant for each factor level; 0.45%), and slow responses (RTs slower than 2.5 MAD above the median of each participant for each factor level; 6.74%) were removed prior to statistical analyses. Mixed design ANOVAs and planned comparisons were then performed. Planned comparisons rather than post-hoc tests were used, because we had a specific prediction about the nature of the difference. In other words, we have strong theoretical reasons to examine cueing effects to evaluate whether there was inhibition or facilitation. This approach allows us to conduct comparisons for the Cueing factor regardless of whether there are any significant interactions, which is usually the basis for running post-hoc tests.

The mean RTs for each level of within-subjects factors Cueing (cued vs. uncued) and Task Condition (compatible vs. incompatible), as well as between-subjects factors Experimental Design (mixed vs. blocked) and Response Type (manual vs. saccade) can be found in Table 2.1. Cueing effects were calculated as the difference between RTs to cued and uncued targets (cued - uncued), with positive values representing inhibition, and are plotted in Figure 2.3.

[2] MAD is used instead of SD because response time data is presumably skewed by outlying data points and thus the use of mean/SD is unreliable as it is particularly sensitive to outliers. See Leys (2013) for evidence demonstrating the robustness of MAD compared to SD for outlier removal.

Table 2.1. Mean manual response time (MRT) and saccadic response time (SRT) in ms for cued and uncued targets for each level of each factor (with SDs in parentheses), as well as the corresponding cueing effect (cued - uncued).

Task	Mixed			Blocked		
	Cued	Uncued	Cueing effect	Cued	Uncued	Cueing effect
Manual responses (ms)						
Compatible	331 (28)	323 (27)	9**	356 (45)	330 (36)	26***
Incompatible	378 (36)	360 (37)	18***	401 (64)	384 (56)	17*
Saccadic responses (ms)						
Compatible	225 (31)	201 (22)	25***	286 (61)	237 (36)	50***
Incompatible	255 (25)	268 (26)	-13**	325 (81)	328 (78)	-3

(*$p < .05$, **$p < .01$, ***$p < .001$)

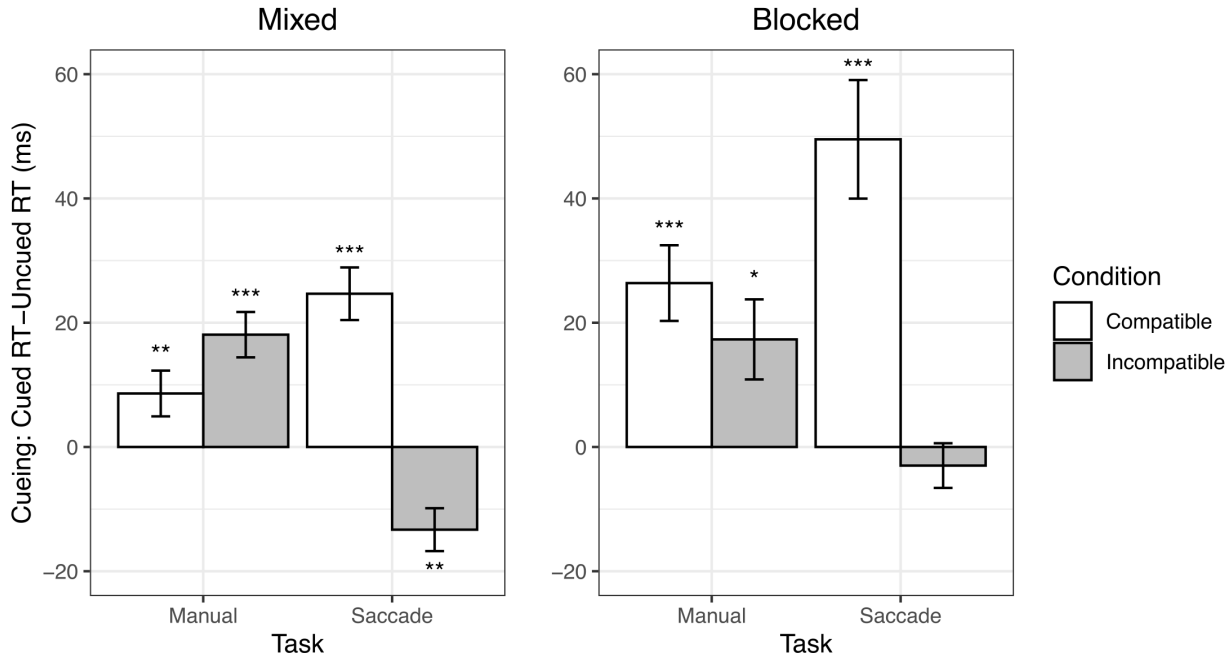

Figure 2.2. Cueing effects (cued - uncued MRT/SRT) plotted as a function of Task Condition and Cueing in both mixed- and blocked-design conditions. Asterisks indicate significant differences between cued and uncued trials (*$p < .05$, **$p < .01$, ***$p < .001$), error bars represent standard errors.

2.2.1 Examining cueing effects for mixed vs. blocked designs for each modality.

Four 2x2 ANOVAs with factors of Experimental Design and Cueing were also conducted on mean MRTs and SRTs for compatible and incompatible task conditions respectively, revealing a main effect of Cueing when no eye movements occurred (manual responses) in compatible trials [$F(1, 22) = 24.17$, $MSE = 151.93$, $p < .001$, $\eta^2 = .52$] due to faster MRTs to uncued trials compared to cued trials. There was no main effect of Experimental Design [$F(1, 22) = 1.36$, $MSE = 2289.94$, $p = .257$, $\eta^2 = .06$]. Because uncued trials when blocked were faster than when mixed, but cued trials when blocked were slower than when mixed, the interaction between

Experimental Design and Cueing was significant [$F(1, 22) = 6.23$, $MSE = 151.93$, $p = .021$, $\eta^2 = .22$]. Results of planned comparisons for each ANOVA are presented in section 2.2.2.

For incompatible tasks, only the main effect of Cueing was significant [$F(1, 22) = 22.83$, $MSE = 164.60$, $p < .001$, $\eta^2 = .51$], where facilitation occurred in both mixed and blocked trials. There was no main effect of Experimental Design [$F(1, 22) = 1.39$, $MSE = 4767.93$, $p = .250$, $\eta^2 = .06$], nor any interaction between Experimental Design and Cueing [$F(1, 22) = 0.01$, $MSE = 164.60$, $p = .919$, $\eta^2 < .01$].

When saccades were made to the target, the Experimental Design x Cueing ANOVA on pro-saccades showed significant main effects of Experimental Design [$F(1, 23) = 9.85$, $MSE = 2978.91$, $p = .005$, $\eta^2 = .30$] and Cueing [$F(1, 23) = 49.01$, $MSE = 360.31$, $p < .001$, $\eta^2 = .68$]. The former occurred because blocked trials had overall faster SRTs than mixed trials, and the latter because strong IOR cueing effects were apparent in both blocked and mixed trials. There was also a significant interaction [$F(1, 23) = 5.35$, $MSE = 360.31$, $p = .030$, $\eta^2 = .19$] where participants' responses to uncued targets were faster in blocked compared to mixed trials but SRTs to cued targets were slower in blocked compared to mixed trials.

For the anti-saccade tasks, there were also main effects of Experimental Design [$F(1, 23) = 7.44$, $MSE = 7096.99$, $p = .012$, $\eta^2 = .24$] and Cueing [$F(1, 23) = 10.12$, $MSE = 77.96$, $p = .004$, $\eta^2 = .31$], in which blocked trials had overall slower SRTs than those of mixed trials, whereas facilitatory effects were observed in both blocked and mixed trials. However, the Experimental Design x Cueing [$F(1, 23) = 4.26$, $MSE = 77.96$ $p = .051$, $\eta^2 = .16$] interaction was only marginally significant.

2.2.2 Planned comparison t-tests to examine cueing effects separately for each condition.

Planned comparisons (two-tailed, paired-samples t-tests) revealed that in the mixed-design compatible task, there were significant differences between cued and uncued trials in both the manual response condition (9 ms) [$t(11) = 2.34$, $p = .040$, Cohen's $d = 0.68$] and the saccadic response condition (25 ms) [$t(11) = 5.82$, $p < .001$, Cohen's $d = 1.68$], demonstrating an IOR effect regardless of response modality when the task was compatible. In the blocked conditions, these planned comparisons also revealed that responses to uncued trials were significantly faster than cued trials when manual responses were made (26 ms) [$t(11) = 4.33$, $p = .001$, Cohen's $d = 1.25$] and when saccadic responses were made (50 ms) [$t(12) = 5.19$, $p < .001$, Cohen's $d = 1.44$], further demonstrating an IOR effect regardless of response modality when the task was compatible (regardless of whether the task was mixed or blocked, manual or saccadic).

For incompatible tasks, participants were still significantly faster to respond to uncued trials with manual responses in mixed (18 ms) [$t(11) = 4.95$, $p < .001$, Cohen's $d = 1.43$] and blocked (17 ms) [$t(11) = 2.69$, $p = .021$, Cohen's $d = 0.78$] designs, both showing robust IOR whether the task was mixed or blocked. However, when saccades were made to the target in mixed (-13 ms) [$t(11) = -3.86$, $p = .001$, Cohen's $d = 1.11$] and blocked (-3 ms) [$t(12) = -0.83$, $p = .421$, Cohen's $d = 0.23$] designs, facilitation was observed in the former and there were no inhibitory cueing effect in the latter.

Taken together, our results demonstrate an IOR effect regardless of response modality when the task was compatible. For incompatible tasks, an IOR effect also occurred for manual responses regardless of whether the task was mixed or blocked, but there was no IOR effect when saccadic responses were made. Instead, for anti-saccades, we found facilitation in the

mixed design condition and no cueing effect in the blocked design condition.

2.3 Discussion

Three primary findings emerge from this study. First, our study replicated previous findings: manual responses were consistently slower than saccadic responses (Briand et al., 2000), incompatible responses were slower than compatible responses whether they were manual or saccadic (Massen, 2004; Olk & Kingstone, 2003), and, in all of the compatible conditions, our results replicated many past studies that have shown the presence of IOR with both manual and saccadic responses (Briand et al., 2000; Hunt & Kingstone, 2003). These results serve to validate our distractor spatial cueing experimental paradigm prior to assessing differences between manual and saccadic incompatible responses.

Second, the results in the blocked condition with manual responses replicate and expand upon those observed by Wascher et al. (2015) who found equivalent magnitudes of IOR with manual responses for both compatible and incompatible trials when the two conditions were blocked. We found similar IOR for manual incompatible responses, even when the trials were randomly intermixed. Our study also used longer cue and target onsets than Wascher et al. (2015) did, which allowed more time for early inhibitory effects, such as sensory adaptation, to dissipate, leaving only late inhibitory effects to be measured. We used a fixed CTOA of 1,500 ms versus their time course design (with CTOAs ranging from 80 to 1,240 ms), and a cue-back colouration to indicate response type whereas Wascher et al. (2015) used a simple central fixation, providing further validation that IOR is observed with incompatible manual responses.

Third, the results in the blocked condition with saccadic responses failed to replicate those of previous studies where IOR was observed with anti-saccades (Fecteau et al., 2004;

Khatoon et al., 2002; Rafal et al., 1994). However, these conditions were sufficiently different methodologically to suggest that different cueing effects could have been generated. Fecteau et al. (2004) used a target-target paradigm with a longer time interval between each target's appearance (3,700 ms), where participants made either pro- or anti-saccades in response to targets depending on the colour of the fixation point. Although they also observed IOR for anti-saccades, this paradigm is quite different from our own in these respects.

In Rafal et al. (1994), where pro- and anti-saccade trials were blocked, IOR was generated even with inhibition of the reflexive oculomotor system when no eye movements were allowed. Although there was an overall cueing effect where saccade latencies to cued targets were slower than those to uncued targets, Rafal et al. (1994) found no interaction between task condition and cueing. In other words, both pro- and anti-saccades were slowest when the target appeared at cued locations, implying that IOR acted only by inhibiting detection of targets at tagged locations, thereby lending support to an input/sensory form of IOR being activated in this task. Our results contradict those findings, because we found IOR with pro-saccades but not with anti-saccades, consistent with an output/oculomotor form of IOR being generated (Hilchey, Klein, & Satel, 2014) whereby a motor bias favours saccades directed away from the previously cued location. One potential explanation for these conflicting results lies in a difference in RT calculation across studies; whereas we analysed mean RTs in a traditional manner, Rafal et al. (1994) did not report any RTs, nor the results of tests directly comparing cued and uncued conditions. Instead, they first determined the median for each participant and then analysed the means of the median RTs.

Khatoon et al. (2002) also only blocked their conditions, and furthermore included a third condition that used an indirect vertical eye-movement response. This study examined the time

course of IOR, wherein a very short onset cue (27 ms) was followed by a range of five CTOAs between 67 to 1,000 ms, resulting in only 12 trials per cell. Although IOR was observed at the longest CTOA for anti-saccades (16 ms), it was substantially smaller than that for pro-saccades (31 ms).

As for the absence of IOR in the saccadic incompatible condition, we suspect that may have to do with motoric IOR. In light of recent studies that have brought unique evidence to the scholarship of IOR by challenging existing theories of attentional and oculomotor IOR, a "new" form of late IOR has been shown to emerge from reaching movements (Chang & Ro, 2005; Cowper-Smith, Eskes, & Westwood, 2013; Cowper-Smith & Westwood, 2013; Fischer, Pratt, & Neggers, 2003; Howard, Lupiáñez, & Tipper, 1999; Neyedli & Welsh, 2012). Cowper-Smith and Westwood (2013) conducted a test of purely motoric IOR by presenting targets on either the horizontal or vertical meridian in a target-target paradigm. Participants were required to use their index finger to point to the targets while maintaining fixation at a central location throughout each trial (to eliminate the contribution of oculomotor IOR) and were given sufficiently long intervals to prepare for making a response (to remove the contribution of early sensory IOR). Consistent with the idea of a separate motoric IOR effect, the authors observed longer RTs to cued targets than to uncued targets. This alternative motor form of IOR could potentially be contributing to the late inhibitory cueing effect observed in our incompatible task where manual responses were made by pressing spatially congruent and incongruent keys.

Taken together, findings from this chapter support the two-forms theory of IOR (Hilchey, Klein, & Ivanoff, 2012; Klein & Redden, 2018). Our results with manual responses showed evidence for input-based IOR because, although the oculomotor system was suppressed in both compatible and incompatible trials, there were still delayed responses to cued targets. Responses

were slowest when the target occupied the same location as the cue, implying that inhibition is related to sensory processing. On the other hand, when the oculomotor system was activated, delayed saccadic responses were only observed to compatible targets suggesting that the output-form of IOR was also at play, because this type of inhibition is tied to the eye movement response. In the following chapter, we continue our efforts to dissociate input-based sensory and output-based oculomotor IOR using the incompatible response task, with a few changes. Participants made a saccade to the cue to activate the oculomotor system, then – instead of making a saccade to or away from the target – we required them to make manual responses while fixating a central point. In addition, we sought to incorporate EEG in our experimental design to investigate the neural mechanisms underlying these inhibitory cueing effects that are more commonly measured using behavioural response times.

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Chapter 3 : EEG Study of IOR with the Anti-localisation Task

A number of electroencephalographic (EEG) studies have attempted to probe the neurophysiological underpinnings of IOR (e.g., McDonald et al., 2009; Prime & Jolicœur, 2009a, 2009b; Prime & Ward, 2006). EEG electrodes on the scalp measure summations of synchronously generated inhibitory and excitatory postsynaptic potentials originating from neuronal populations within the underlying cortex. Event-locked segments of the EEG recordings are then averaged across participants to obtain event-related potential (ERP) waveforms, the peaks and troughs of which are identified as ERP components (Luck & Kappenman, 2011). Because behavioural IOR is typically observed in the 250 ms to 3,000 ms time range, ERPs have become a particularly useful tool to capture the temporal dynamics of inhibitory cueing effects within that time window due to the technique's high temporal resolution. ERP data, when presented alongside behavioural data, allows us to paint a better picture of the neural underpinnings of IOR.

Input and output-based IOR have been conflated in the literature for decades, with little consensus on the causes and effects of IOR (Dukewich & Klein, 2015). The two forms of IOR consist of: i) an input-based form that is generated when the oculomotor system is actively inhibited, and ii) an output-based form that occurs with oculomotor activation (Klein & Redden, 2018; Taylor & Klein, 2000). The input-form corresponds with the IOR found in Posner and Cohen (1984), whereas the output-form was likely observed by Posner and colleagues (1985), despite both simply being referred to as IOR. The jury is still out on the neural dynamics of input vs. output IOR, however.

Having established that behavioural inhibitory cueing effects can indeed be elicited with manual but not saccadic responses in incompatible tasks in Chapter 2, the present chapter sought first to clarify the relative role of output-based oculomotor effects in behavioural IOR. To clarify the role of output-based oculomotor effects, we conducted a pilot study (Experiment 1 of this chapter) that is a behavioural-only experiment where no EEG is involved. In this pilot experiment, we asked participants to make eye movements to the cue and back to central fixation before target onset, making sure that the oculomotor system was engaged, thus eliciting output-based behavioural IOR. Where behavioural responses are concerned, if oculomotor IOR is output-based, we should observe a delay in making compatible responses on cued trials but not when responses are incompatible. We also expected to find faster RTs in response to compatible responses compared to incompatible responses, because the latter requires active suppression of an automatic response towards the target.

Experiment 2 of this chapter builds upon the same behavioural experimental paradigm as Experiment 1 but includes electrophysiological recording while participants complete the tasks, with trials requiring compatible and incompatible responses that are either intermixed or blocked. Blocking rather than intermixing trials of different conditions could create a spatial attentional control setting that encourages participants to better filter irrelevant cues, subsequently eliminating IOR at late CTOAs (Hilchey, Klein, & Ivanoff, 2012). For example, using spatially non-informative cues followed by central and peripheral targets in trials that were either blocked or intermixed, attentional capture at the cued location can vary depending on the target type (Hilchey, Klein, & Ivanoff, 2012). Simply put, trials of different conditions that are blocked allow participants to apply certain mental strategies to perform most efficiently in that blocked condition. Trials that are randomly intermixed prevent participants from strategizing the

same way, because the selection of the next trial is unpredictable (Folk & Anderson, 2010). That being said, despite potential confounds from strategic differences, we used blocked trials in Experiment 1 due to the complexity of our task. In Experiment 2, we examined both blocked and intermixed trials, under the presumption that intermixed trials discourage participants from using different strategies to perform compatible versus incompatible tasks.

Our experimental design allows us to investigate the neural patterns of output-based IOR because the oculomotor system is activated. Using ERPs to examine the relationship between IOR and oculomotor-based processes here, we measured P1 and Nd modulations that were time-locked to target onset. If oculomotor processes contribute to IOR, a reduction in the amplitude of the P1 and Nd components over the parietal-occipital cortex should be observed for both compatible and incompatible tasks when targets were cued, because the oculomotor system was activated in both conditions.

3.1 Experiment 1 (Behavioural Only, Blocked Trials)

3.1.1 Method.

Participants. Eleven students from the University of Nottingham Malaysia (6 females, 10 right-handed), with age ranging between 19 and 26 years old (M = 21.3, SD = 2.28), participated in this experiment. All reported normal or corrected-to-normal vision and no known neurological or psychiatric illness. The experiment was approved by the Science and Engineering Research Ethics Committee.

Stimuli and apparatus. Stimuli were written in Python and presented on a 24-inch BenQ gaming monitor (1920x1080 pixels resolution), whereas participants made manual responses to targets on a standard QWERTY keyboard. Participants sat in an electromagnetically shielded

room with their heads stabilised by a chin rest positioned 65 cm away from the screen. Eye movements were monitored using the EyeLink 1000 Plus eye tracking system at a sampling rate of 250 Hz. Consistent to our previous experiments (see Chapter 2), all stimuli were presented in white on a black background, except for the cue-back fixation cross that turned green for compatible trials and red for incompatible trials. Two peripheral boxes (4.5° x 4.5° of visual angle) were used as placeholders at 8.7° to the left and right from the centre. This experimental setup is identical to the one described in Chapter 2.

Design and procedure. The current experiment used a 2 (Cueing: cued vs. uncued) x 2 (Task condition: compatible vs. incompatible response) within-subjects design. Participants underwent 24 practice trials prior to completing 320 experimental trials in 4 blocks of 80 trials each, with breaks between each block. Task condition was blocked and counter-balanced across participants, such that half of the participants began with 2 blocks of compatible trials followed by 2 blocks of incompatible trials and vice versa for the other half. Cueing was randomised throughout.

We followed the paradigm in Figure 2.1 closely, the only difference being that participants were instructed to saccade to cues, then quickly return their gaze to the central fixation before target onset, maintaining fixation throughout the rest of the trial. In anticipation of Experiment 2 where we would be extracting ERPs, we extended the ISI between cue-back and target onset by 100 ms (i.e., the ISI was 500 ms in Chapter 2 and extended to 600 ms in this chapter) as an attempt to reduce residual eye movement artefacts in the ERP data. The CTOA was thus 1,600 ms (instead of the 1,500 ms in Chapter 2) in all experiments presented in Chapter 3.

3.1.2 Results and discussion.

We excluded incorrect trials (2.48%), anticipatory responses (MRT < 2.5 MAD; 0.09%), long outliers (MRT > 2.5 MAD; 4.27%), and trials contaminated with eye movements (0.31%) prior to statistical analyses. Means of MRTs are shown in Table 3.1 below.

Table 3.1. Mean MRTs in ms for cued and uncued targets for each level of each factor (with SDs in parentheses) as well as the corresponding cueing effect (cued - uncued).

Task Condition	*Cued*	*Uncued*	*Cueing Effects*
Compatible	379 (72)	345 (79)	34**
Incompatible	434 (78)	402 (57)	32*

(*$p < .05$, **$p < .01$)

A two-way ANOVA with Cueing (cued vs. uncued) and Task Condition (compatible vs. incompatible) as within-subjects factors revealed no interaction effects [$F(1, 10) = 0.04$, $MSE = 464.18$, $p = .837$, $\eta^2 = .63$], which indicated that IOR was not different for compatible and incompatible responses. We did, however, find main effects of Cueing [$F(1, 10) = 16.86$, $MSE = 716.42$, $p = .002$, $\eta^2 = .63$] and Task Condition [$F(1, 10) = 14.79$, $MSE = 2306.03$, $p = .003$, $\eta^2 = .60$], in which responses on uncued trials were faster than cued trials and compatible trials were overall faster than incompatible trials. Planned comparisons confirmed that inhibitory effects were indeed statistically significant in both compatible (34 ms) [$t(10) = 4.02$, $p = .002$, Cohen's $d = 1.21$] and incompatible (32 ms) [$t(10) = 2.68$, $p = .023$, Cohen's $d = 0.81$] trials.

Our findings show that the inhibitory cueing effect that is caused by saccades to the cues and measured with manual responses occurs not only in compatible trials but also persists in

incompatible trials. In incompatible trials, responses are made to the opposite location, such that overt shifts of attention to the cue do not correspond to the same target location. This pattern of results is consistent with Rafal et al. (1994; Exp 1), who measured saccadic responses, Khatoon et al. (2002), who measured both saccadic and manual responses, and Wascher et al. (2015), who found IOR with both compatible and incompatible manual responses at late CTOAs.

3.2 Experiment 2 (ERP and Behavioural, Mixed and Blocked Trials)

3.2.1 Method.

Participants. Thirty-seven participants (21 males, 34 right-handed) with age ranging between 18 and 64 years old (M = 23.59, SD = 8.75) were recruited from the University of Nottingham Malaysia. All reported normal or corrected-to-normal vision and no known neurological or psychiatric illness. Of the 37 volunteers, 18 participated in the condition where compatible and incompatible trials were mixed and 19 participated in the condition where trials were blocked. The experiment was approved by the Science and Engineering Research Ethics Committee.

Stimuli and apparatus. Our experimental setup here was identical to Experiment 1, where participants' eye movements were monitored with an eye-tracker, with the addition of EEG recording equipment consisting of 128-channel EGI HydroCel Geodesic Sensor Nets that were connected to an amplifier. For an EEG recording net montage, see Appendix Figure 1. NetStation software (Version 4.5.4; Electrical Geodesics, Inc., Eugene, OR) was used to record EEG data at a sampling rate of 250 Hz. Codes for presenting stimuli and sending event markers were written in the Python 2.7 programming language. All offline pre-processing of the EEG

data were performed using EEGLAB (Delorme & Makeig, 2004), a Matlab® toolbox (The MathWorks, Inc., Natick, MA).

Design and procedure. This study used a 2 (Cueing: cued vs. uncued; within-subjects) x 2 (Task condition: compatible vs. incompatible response; within-subjects) x 2 (Experimental Design: mixed vs. blocked; between-subjects) mixed factorial design. When trials were mixed, participants underwent 24 practice trials prior to completing 600 experimental trials divided over 4 blocks of 150 trials each, with breaks between each block. Where the experiment called for a blocked design, task condition was blocked and counter-balanced across participants, such that half of the participants began with 2 blocks of compatible trials followed by 2 blocks of incompatible trials, and vice versa for the other half. Participants in the blocked experimental design condition were presented with 24 practice trials followed by 400 experimental trials divided over 4 blocks of 100 trials each. Cueing was randomised throughout. The increased number of trials compared to Experiment 1 was necessary to obtain sufficient power, as we anticipated discarding a number of trials during EEG pre-processing. With the exception of EEG net application, all other experimental procedures were identical to those described in Chapter 2 and Chapter 3, Experiment 1.

After giving their consent, the participants' head sizes were measured to select the appropriate sized net. The net was then soaked for 5 minutes in an electrolyte solution consisting of 2 litres of water mixed with 2 spoonful of potassium chloride and 1 spoonful of baby shampoo, as per Geodesic Sensor Net Technical Manual. To maintain consistency for net placement, we then located the vertex of each participant's head. Using a measuring tape and erasable chalk, we identified and drew a small line on the mid-point between the nasion and inion of the participant's head, as well as the mid-point of the periauricular line. The intersection

of those two lines is known as the vertex, that we used to align the EEG net such that the Cz electrode would lie directly above the vertex during net application. Once the net was placed over the participant's head, we adjusted and tightened the net's chin straps, so that they were snug but not uncomfortably tight. We then proceeded to measure the electrode sensor's impedance, adding electrolyte to each electrode sponge where impedances were above 50kΩ. Impedances were checked and corrected as needed during each break time.

EEG pre-processing. During EEG recording, all electrodes were referenced to the vertex (Cz) by default. EEG data was then imported into EEGLAB and corrected for latency delays caused by the EGI system. Based on our sampling rate of 250 Hz, an 8 ms correction was applied (Electrical Geodesics, Inc., Nov 26, 2014). We filtered the data offline by using a highpass filter of 1 Hz followed by a lowpass filter at 30 Hz. Bad channels were removed based on flatline, channel, and line noise criteria using the Clean Rawdata EEGLAB plug-in. Channels with flatlines longer than 5 seconds, that were poorly correlated (less than 0.75 correlation) relative to their reconstruction based on neighbouring channels, or with noise more than 4 standard deviations from the signal means were rejected. Participants who had parietal-occipital electrode sites PO7 or PO8 (corresponding to EGI channels 65 and 90) identified as bad channels were excluded from the analysis. Electrodes PO7 and PO8 sit over the parieto-occipital scalp areas, which we singled out to analyse for comparison with previous studies that also used these two electrodes (e.g., Prime & Jolicœur, 2009a; Prime & Ward, 2006; Satel, Hilchey et al., 2013; Van der Stigchel, Heslenfeld, & Theeuwes, 2006). Other bad channels removed were interpolated using spherical spline interpolation and re-referenced to the average.

EEG data were then segmented from 200 ms prior to the onset of the target to 900 ms post-target. Epochs time-locked to target onset in which an eye blink occurred or fixation

deviated from centre during the fixation period were discarded. An independent component analysis (ICA) was performed on the remaining EEG data using EEGLAB (Delorme & Makeig, 2004). The weights were calculated using the information-maximisation ICA algorithm of Bell and Sejnowski (1995). The ICA analysis resulted in component weights and activations for each component. ICA components to be removed were determined by the joint use of spatial and temporal features using the ADJUST EEGLAB plug-in (Mognon, Jovicich, Bruzzone, & Buiatti, 2011). Independent components representing eye blinks and horizontal eye movements were removed from the EEG data. Epochs were baseline corrected by subtracting the average signal activity across the 100 ms prior to target onset. Epochs in which amplitudes exceeded ±75 μV during the -100 ms to 400 ms interval were also rejected from further analyses.

3.2.2 Results and discussion.

Behavioural performance. Before we analysed the electrophysiological data, we first analysed the behavioural data. Trials with incorrect responses (3.24%), anticipatory responses (RTs faster than 2.5 MAD below the median of each participant for each factor level; 0.21%), and slow responses (RTs slower than 2.5 MAD above the median of each participant for each factor level; 5.31%) were removed prior to the behavioural statistical analyses. Mean RTs for each level of the between-subjects factor, Experimental Design (mixed vs. blocked), as well as within-subjects factors, Cueing (cued vs. uncued) and Task Condition (compatible vs. incompatible), can be found in Table 3.2.

An omnibus three-way ANOVA (Experimental Design x Cueing x Task Condition) was first conducted to examine interaction effects between the three factors. Results showed main effects of Cueing [$F(1, 35) = 11.04$, $MSE = 436.26$, $p = .002$, $\eta^2 = .24$] and Task Condition [$F(1,$

35) = 19.46, *MSE* = 2065.89, $p < .001$, $\eta^2 = .36$], as cued trials were overall responded to slower than uncued trials, whereas compatible trials were responded to faster than incompatible trials. The main effect of Experimental Design was not significant ($F(1, 35) = 0.12$, *MSE* = 26571.70, $p = .731$, $\eta^2 = .00$). There was also a significant Cueing x Task Condition interaction [$F(1, 35) = 7.20$, *MSE* = 226.71, $p = .002$, $\eta^2 = .17$], where the difference between cued and uncued trials was larger in the compatible condition compared to the incompatible condition when collapsed between mixed and blocked trials. The other two-way and the three-way interactions were not significant.

We also conducted two-way ANOVAs separately for mixed and blocked designs. When trials were mixed, we found only a main effect of Task Condition [$F(1, 17) = 17.56$, *MSE* = 1146.43, $p < .001$, $\eta^2 = .51$], with no main effect of Cueing ($F(1, 17) = 0.84$, *MSE* = 516.97, $p = .373$, $\eta^2 = .05$) and no interaction effect ($F(1, 17) = 0.20$, *MSE* = 331.96, $p = .663$, $\eta^2 = .01$). When trials were blocked, however, both main effects of Cueing [$F(1, 18) = 16.29$, *MSE* = 360.03, $p < .001$, $\eta^2 = .48$] and Task Condition [$F(1, 18) = 6.84$, *MSE* = 2934.27, $p = .017$, $\eta^2 = .28$] were significant. The interaction effect between Cueing and Task Condition was significant as well [$F(1, 35) = 18.48$, *MSE* = 127.31, $p < .001$, $\eta^2 = .51$].

Planned comparisons were two-tailed paired-sampled t-tests that revealed no cueing effects for either compatible (7 ms) [$t(17) = 1.04$, $p = .314$, Cohen's $d = 0.24$] or incompatible (3 ms) [$t(17) = 0.42$, $p = .680$, Cohen's $d = 0.10$] responses when trials were mixed. When trials were blocked, however, a robust inhibitory cueing effect emerged in the compatible condition (29 ms) [$t(18) = 5.80$, $p < .001$, Cohen's $d = 1.33$], but this inhibitory cueing effect was not observed in the incompatible condition (6 ms) [$t(18) = 1.24$, $p = .230$, Cohen's $d = 0.29$].

Table 3.2. Mean MRTs in ms for cued and uncued targets for each level of each factor (with SDs in parentheses) as well as the corresponding cueing effect (cued - uncued).

Task	Mixed			Blocked		
	Cued	Uncued	Cueing effect	Cued	Uncued	Cueing effect
Compatible	375 (77)	369 (85)	7	378 (90)	349 (91)	29***
Incompatible	407 (90)	404 (90)	3	399 (82)	392 (77)	6

(***$p < .001$)

In Chapter 3, Experiment 2, we failed to replicate the behavioural cueing effect observed in Experiment 1 with both compatible and incompatible responses when trials were mixed. Additionally, although we still observed behavioural IOR with compatible responses when trials were blocked, there was no behavioural IOR measured with incompatible responses.

Electrophysiological analyses.

During pre-processing of the electrophysiological data, we discarded one dataset (out of 18) in the mixed condition that had PO7/PO8 electrodes identified by the interpolation algorithm as bad channels. Data from two other participants were rejected because there were insufficient trials (< 50%) left after pre-processing. One other additional dataset was excluded because of excessive noise remaining in the ERPs. These exclusions left 14 datasets that were subjected to statistical analyses. Of the 14 datasets, participants made incorrect responses on 8.48% of all trials, which were excluded from further analyses. We also filtered our data to exclude anticipatory responses (individual mean RT < 2.5 MAD; 1.16%) and slow responses (individual mean RT > 2.5 MAD; 11.61%). A further 5.86% of trials that were identified as noisy

(amplitudes > ±75 μV between -100~400 ms) were removed. Statistical analyses were performed on the remaining 72.89% of all trials.

Similarly, in the blocked condition, we discarded one dataset (out of 22) that had PO7/PO8 electrodes identified by the interpolation algorithm as bad channels. Data from three other participants were excluded from further analyses because more than 16% of channels were identified as bad channels, which points to overall excessively noisy datasets. Data from an additional three participants were rejected because there were insufficient trials left after pre-processing. These exclusions left 15 datasets that were subjected to statistical analyses. Of the 15 datasets, participants made incorrect responses on 4.86% of all trials, which were excluded from further analyses. The error rate for blocked trials was lower than mixed trials presumably because the task was easier without constantly having to switch between compatible and incompatible trials. We also filtered our data to exclude anticipatory responses (individual mean RT < 2.5 MAD; 1.47%) and slow responses (individual mean RT > 2.5 MAD; 9.07%). A further 12.10% of trials that were identified as noisy (amplitudes > ±75 μV between -100~400 ms) was removed. Statistical analyses were performed on the remaining 72.50% of all trials.

To investigate the effects of cueing on visual processing, we first examined the ERPs elicited by cued and uncued targets when making compatible and incompatible manual responses. Grand average waveforms for mixed trials were plotted at posterior-occipital electrode sites PO7/PO8 in response to cued and uncued targets for both compatible and incompatible condition at electrodes ipsilateral and contralateral to the visual stimuli (see Figure 3.1). Figure 3.2 shows the blocked design counterpart. Statistical analyses were performed on electrodes that were either ipsilateral or contralateral to the presented target stimuli.

For data when compatible and incompatible trials were intermixed, the positive polarity ERP at ipsilateral electrodes, beginning at around 200 ms and peaking at 230 ms (210~250 ms) after target onset, appeared more pronounced for uncued trials compared to cued trials when responses were incompatible to target locations. When we blocked compatible and incompatible trials, however, we observed attenuated amplitudes at contralateral electrodes for cued trials relative to uncued trials when responses were incompatible in the 250~350 ms time window which resemble an Nd effect.

The time windows for our ERP components were identified through visual inspection of the grand averaged ERP data, taking into account the typical time windows for the components from existing studies. In the mixed trials condition, the ipsilateral P1 peak for compatible responses was defined as the most positive point between 100 ms and 300 ms after the target stimulus onset (232 ± 20 ms), and the N1 peak average was at 288 ± 20 ms. The Nd peak was identified to be between 220 ms and 300 ms after the target stimulus onset based on precedence in the literature. Mean amplitude for P1, N1, and Nd peaks in these windows were extracted from each dataset and subjected to statistical analyses (see Table 3.3).

We performed planned comparisons on ERP amplitudes in compatible and incompatible tasks for responses both ipsilateral and contralateral to targets. Where trials were mixed, paired-samples t-tests did not show any significant difference between cued and uncued trials for all [p = .113 ~ .892] but one condition: cueing difference in mean P1 peak where incompatible responses were ipsilateral to the targets [$t(13) = -1.96$, $p = .072$, $d = 0.52$] were marginally significant. Specifically, P1 mean amplitudes in cued trials ($M = 2.58$ μV, $SD = 1.65$ μV) were more attenuated than uncued trials ($M = 3.16$ μV, $SD = 1.88$ μV). Where trials were blocked, only the cueing effect in Nd amplitudes contralateral to targets during incompatible responses

approached significance [$t(14) = -1.91$, $p = .077$, $d = 0.49$], with cued trials ($M = 1.48$ μV, $SD = 3.70$ μV) reduced in amplitude compared to uncued trials ($M = 2.10$ μV, $SD = 3.34$ μV). All other tests were not significant [$p = .170 \sim .852$].

Table 3.3. Mean amplitudes (in μV) for cued and uncued targets for each level of each factor (with SDs in parentheses) as well as the corresponding cueing effect (cued - uncued).

		Mixed			Blocked		
		Cued	*Uncued*	*Cueing effect*	*Cued*	*Uncued*	*Cueing effect*
P1	Compatible						
	Ipsi	2.96 (1.74)	3.04 (1.47)	-0.09	1.85 (2.12)	1.57 (2.21)	0.28
	Contra	2.52 (1.82)	2.37 (1.55)	0.15	2.04 (2.46)	1.75 (1.54)	0.29
	Incompatible						
	Ipsi	2.58 (1.65)	3.16 (1.88)	-0.59†	1.26 (1.31)	1.37 (2.32)	-0.11
	Contra	2.18 (1.32)	2.52 (1.76)	-0.34	1.45 (2.34)	1.63 (1.70)	-0.18
N1	Compatible						
	Ipsi	0.22 (1.91)	0.40 (1.89)	-0.18	0.60 (1.63)	0.49 (1.33)	0.11
	Contra	-0.10 (1.69)	-0.38 (1.54)	0.28	-0.78 (3.50)	-0.97 (3.64)	0.19
	Incompatible						
	Ipsi	-0.27 (1.77)	-0.19 (2.11)	-0.08	-0.53 (2.45)	-0.62 (2.77)	0.09
	Contra	0.07 (1.50)	0.12 (1.63)	-0.05	-1.07 (3.82)	-0.57 (3.17)	-0.50
Nd	Compatible						
	Ipsi	1.65 (1.22)	1.87 (1.34)	-0.21	1.48 (2.35)	1.29 (2.70)	0.19
	Contra	0.69 (1.56)	0.36 (1.34)	0.33	2.20 (3.05)	2.35 (3.47)	-0.15
	Incompatible						
	Ipsi	1.48 (1.22)	1.78 (1.59)	-0.30	0.63 (2.61)	0.50 (2.65)	0.12
	Contra	0.65 (1.24)	0.68 (1.39)	-0.04	1.48 (3.70)	2.10 (3.34)	-0.61†

($^{\dagger}p < .1$)

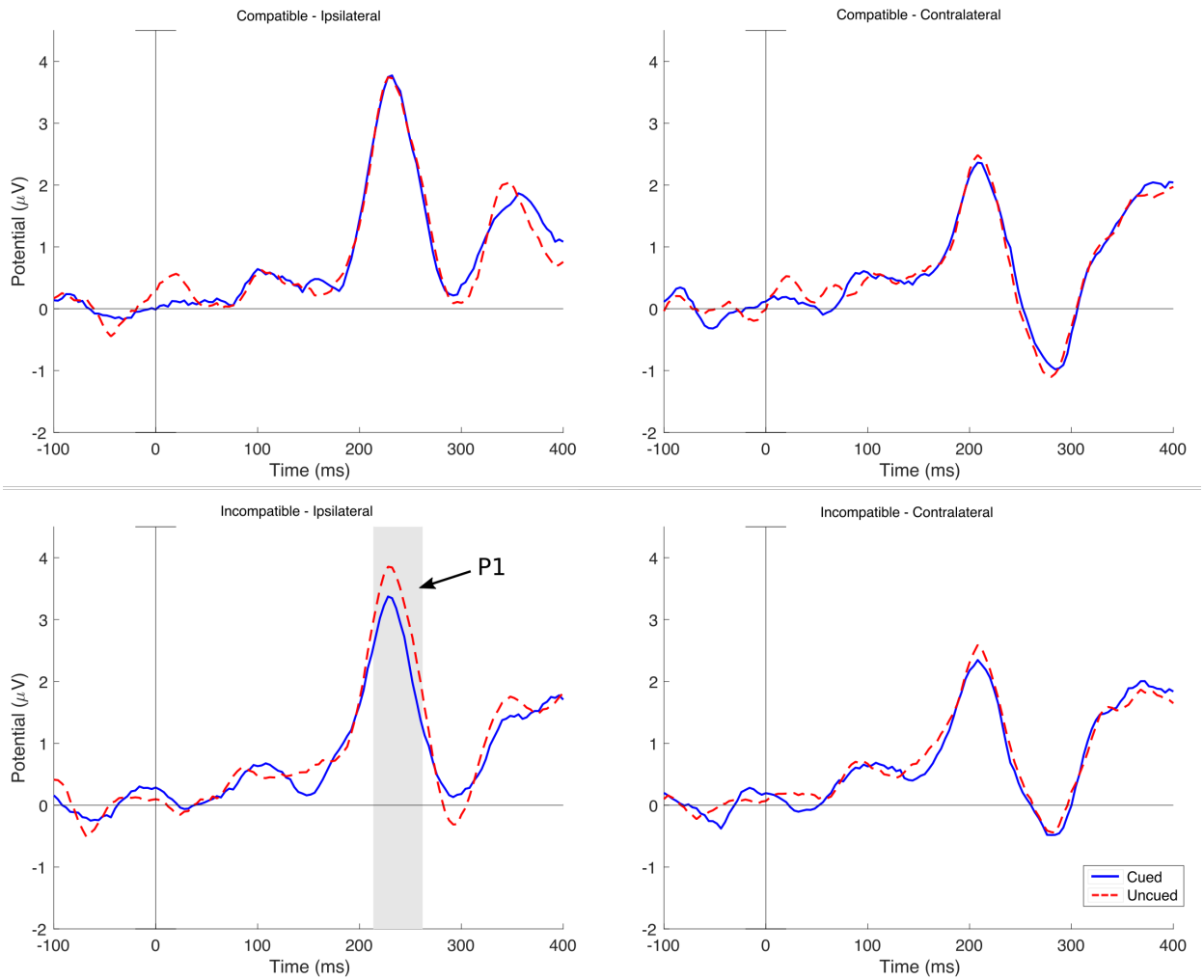

Figure 3.1. Grand average ERPs elicited at posterior electrode sites PO7/PO8 in response to cued (solid line) and uncued (dashed line) targets when compatible and incompatible trials were intermixed. The gray shaded area in the incompatible-ipsilateral panel represents the 210-250 ms time window where there was a marginally significant difference between cued and uncued trials. Waveforms were collapsed across left and right hemifield target stimuli at scalp sites ipsilateral and contralateral to the side of stimulation.

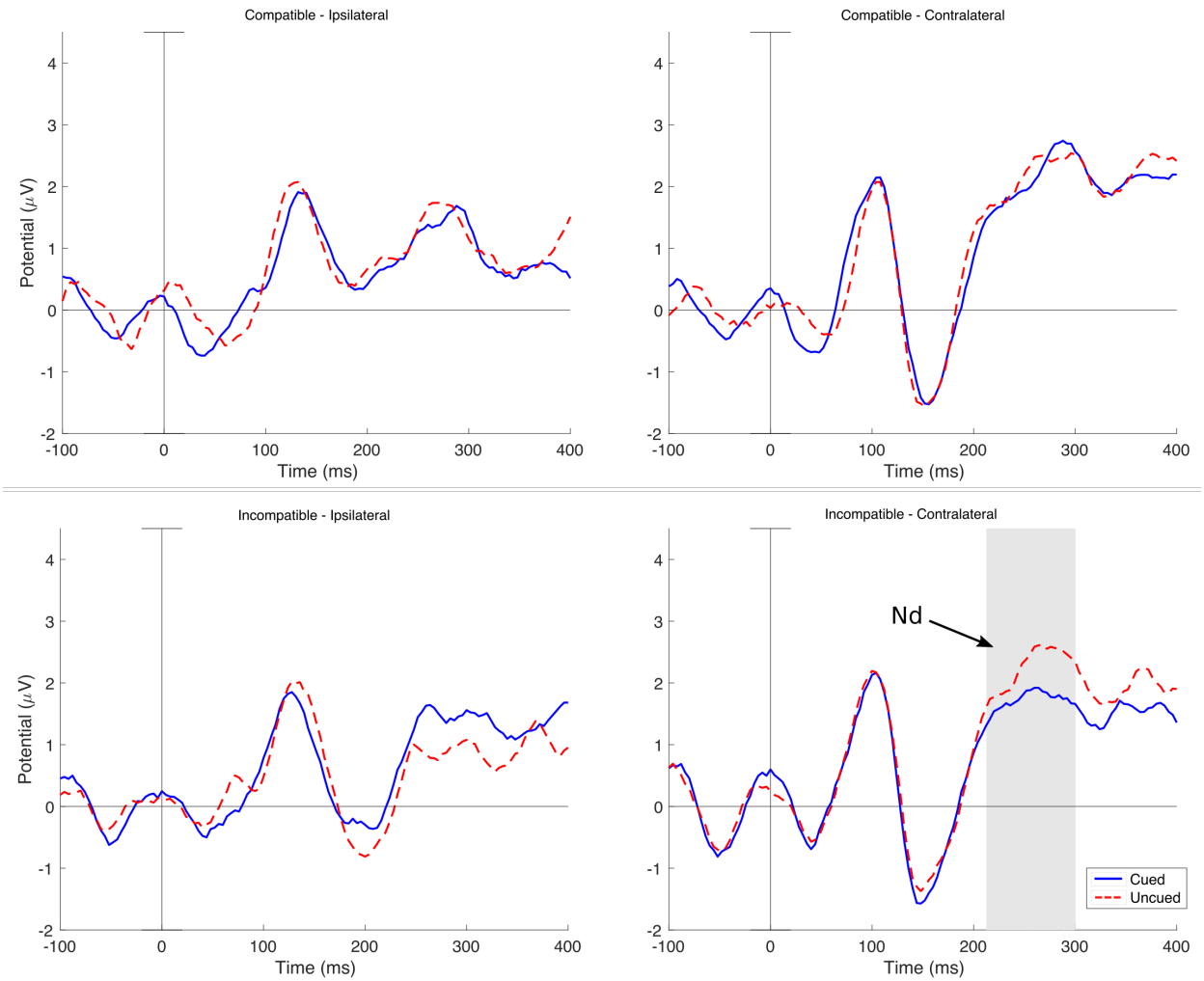

Figure 3.2. Grand average ERPs elicited at posterior electrode sites PO7/PO8 in response to cued (solid line) and uncued (dashed line) targets when compatible and incompatible trials were blocked. The gray shaded area in the incompatible-contralateral panel represents the 220-300 ms time window where there was a marginally significant difference between cued and uncued trials. Waveforms were collapsed across left and right hemifield target stimuli at scalp sites ipsilateral and contralateral to the side of stimulation.

3.3 General Discussion

Using compatible and incompatible responses in a spatial cueing task, we aimed to establish whether we could elicit the output form of IOR, and how that behavioural effect would be reflected in ERPs. In the present chapter, we therefore examined inhibitory cueing effects

when making compatible or incompatible responses in terms of behavioural and electrophysiological measures. The behavioural results from compatible trials in Experiment 1, where IOR was observed, are consistent with those observed by Taylor and Klein (2000). We also found behavioural IOR in the incompatible response task, consistent with Wascher et al. (2015) who also found that IOR did not differ between compatible and incompatible responses (~15 to 20 ms of IOR in both). Their experiment, however, required fixation throughout and thus did not engage the oculomotor system.

The presence of behavioural IOR in both tasks seems to suggest that saccades to the cues did engage the oculomotor system, thereby producing an output-based motor bias that slowed participants' reaction to the cued targets, regardless of stimulus-response compatibility. The present findings replicate our results in Chapter 2, in which fixation was maintained throughout and input-based IOR was found in both compatible and incompatible blocked trials. IOR was much larger in the present experiment (34 ms and 32 ms) compared to 26 ms and 17 ms in Chapter 2, when only input-based IOR was involved. The larger cueing effect in Experiment 1 of Chapter 3 could be due to summation of input-based and output-based IOR contributing to an overall larger IOR effect (Satel & Wang, 2012).

In Experiment 2, our behavioural results tell a somewhat inconsistent story. Prior experiments have shown that IOR can be elicited by compatible responses whether manual (Khatoon et al., 2002; Wascher et al., 2015) or saccadic (Rafal et al., 1994), just like what we found when trials were blocked. However, there was no IOR observed in incompatible blocked trials (effect size, $d = 0.29$) despite an activated oculomotor system, where we were expecting to find output-based IOR. With incompatible responses, the difference in RT between cued and uncued trials that we found in Experiment 1, with an effect size of 0.81, is certainly not trivial.

Either Experiment 1 was a Type I error, where we chanced upon the 5 percent possibility of finding a strong effect when none exists in nature, or Experiment 2 was a Type II error. Given that we have increased the number of trials for ERP analysis in Experiment 2, and thus have more trials for the behavioural analysis, a Type II error in Experiment 2 is less likely. Everything else being equal, greater sampling size typically reduces overall variability. However, our distribution of data in Experiment 2, despite the increased number of trials, showed increased variability, which reduces our ability to detect statistical significance. The absence of IOR in Experiment 2 is therefore likely due to the greater variability in the data, as evident in the larger SDs (77~82 ms) for both cued and uncued trials in the blocked-incompatible condition of Experiment 2 (versus 57~78 ms in Experiment 1). This increased variability is perhaps due to contextual differences or hidden moderators between Experiment 1 and 2, such as fatigue in participants from participating in a longer experiment due to not only more trials but also extra time involved in EEG application or distraction of participants due to wearing the EEG cap. Our "failed replication", although remaining a close replication rather than being a conceptual replication, does yield effects in the same direction, just with insufficient power to be statistically significant.

Alternatively, the absence of a delayed response where incompatible responses were required to targets that were cued is consistent with at least one comparable study by Rafal and colleagues (1994; Exp. 2). The authors of the study asked participants to saccade to an endogenous S1, followed by an auditory cue-back, and then pro- and anti-saccadic responses to an exogenous S2. Their pattern of results mimics ours in the blocked condition of Experiment 2, where IOR was found with compatible but not incompatible responses, which suggests that the

IOR elicited is output-based rather than input-based because the delayed response was due to an oculomotor bias rather than sensory bias.

The mixed-design counterpart of Experiment 2 also revealed no behavioural IOR. Because previous studies have only used blocked designs (e.g., Rafal et al., 1994; Wascher et al., 2015), we suspect that the differences between mixed and blocked trials may lie in participants employing distinct attentional control settings that could have interfered with IOR. It is entirely possible that when trials were blocked, the strategy or mental set for completing the task differ according to the demands of the current task block, which in turn changes the manual response times on cued and uncued trials. Mixed trials prevent the use of such strategies and are thus spared of a potential experimental confound. Hilchey, Klein, and Ivanoff (2012) discussed extensively the implications of using blocked versus mixed paradigms with central arrow targets. Although our experiment uses peripheral targets, the key takeaway is that different strategies could affect the allocation of attention, but further research is necessary to confirm this assertion.

Electrophysiological responses.

The ERP results from Experiment 2 were mostly inconclusive, with a P1 cueing effect being only marginally significant in mixed-incompatible-ipsilateral trials, whereas the Nd component was similarly only marginally significant between cued and uncued blocked-incompatible-contralateral trials. Effect sizes for both tests were in the medium range ($d = 0.52$ for the former, $d = 0.49$ for the latter), which suggests that with increased power, we may have found significant differences.

Even though our results are not comparable statistically, it is worth highlighting that the occipital-parietal P1 component was noticeably delayed (occurring at 180~300 ms) in all of the

mixed trials conditions of Experiment 2, relative to the 80~130 ms time range where P1 typically shows up in spatial selective attention paradigms. With intermixed trials, the colour of the cue-back indicated which task-set/behavioural response was required on each trial: green for compatible responses and red for incompatible responses. In addition to responding as quickly and as accurately as possible, making the correct response also required keeping the colour of the cue-back in one's working memory until a response was made. We suspect that the constant random task switching (see Monsell, 2003, for a review) may have contributed to a delayed P1, much like how IOR onset can be delayed when task difficulty increases (Folk, Remington, & Johnston, 1992; Klein, 2000). In an earlier study, we did establish that there were significantly higher error rates in mixed design trials compared to blocked trials (Eng et al., 2017). However, our data cannot definitively determine the effect of task difficulty because error rates were not analysed, but the ANOVA showed no difference between mixed and blocked trials, which means RT, as a proxy for task difficulty, was not significantly greater for mixed relative to blocked trials.

Compatible and incompatible trials were blocked in a time-course study by Wascher et al. (2015), who generated ERPs at late CTOAs (collapsed between 550, 750, 980, and 1,240 ms). They found no effects of S-R compatibility on IOR. Instead, they observed cueing effects at the Pz electrode (Nd1: 145-175 ms; Nd2: 270-300 ms). At electrodes PO7/PO8, there was a difference between cued and uncued trials at contralateral electrodes around 265 ms after target onset (Nd2-pc: 250-280 ms), whereas ipsilateral sites showed differences around 175 ms (Nd1-pi: 160-190 ms) and again around 285 ms (Nd2-pi: 270-300 ms). Additionally, although statistical differences were not reported, an attenuated P1 component for cued trials could be seen in ipsilateral electrodes. Without eye movement monitoring to ensure participants were

maintaining fixation like they were supposed to, shifts of attention could have changed between trials, making it difficult to determine whether input-based or output-based IOR was ultimately measured (Hilchey, Klein, & Satel, 2014).

Should there be different mechanisms (an input-based or an output-based one) mediating inhibitory cueing effects, we should have observed qualitatively different target-elicited ERP waveforms. However, overall, we did not find any reliable effect of cueing. The absence of a reduced P1 component with cued trials has been previously reported without behavioural IOR (Gutiérrez-Domínguez et al., 2014; Satel et al., 2012), despite repeated stimulation with cues and targets at the same location. Our lack of a P1 effect elsewhere is consistent with Gutiérrez-Domínguez and colleagues (2014), who suggested that P1 effects could disappear at longer CTOAs. McDonald et al. (2009) also observed a lack of P1 effects in an ERP study that included a neutral condition (display containing non-targets) in addition to repeat (cued) and change (uncued) conditions, essentially demonstrating that P1 effects could be eliminated when sensory differences between conditions were accounted for.

If we consider that the one mixed-incompatible-ipsilateral condition, where P1 for cued is somewhat attenuated compared to uncued, is statistically underpowered, our result is also not without precedence in the literature. Using a discrimination task, Hopfinger and Mangun (1998) reported no behavioural IOR, but a significant P1 effect where amplitude for cued trials was reduced compared to uncued trials. Given that our p-values did not reach the conventional significance threshold, the author's preferred interpretation is to treat the P1 effect as spurious. Similarly, we did not find significant differences in N1 and Nd components due to various limitations to our study that we will discuss in the next section.

ERP limitations.

The lack of IOR cueing effects in our ERP data could be due to a Type I error, essentially a false negative, because of low signal-to-noise ratio. Based on experience, Luck (2005) recommended 400~800 artefact-free trials per condition for relatively "small" ERP components like the P1; Woodman (2010) suggested 300~1,000 trials. Boudewyn, Luck, Farrens, and Kappenman (2018) systematically looked at error-related negativity (ERN) and lateralised readiness potential (LRP) ERP components to examine the effect of number of trials on statistical power, but to the best of our knowledge, there are no equivalent studies for the P1 component. Other than the component of interest, factors involved in estimating the number of trials required to produce a significant ERP effect (using averaging methods) include participant sample size, data quality, background electrical noise level, participant alertness, and effect magnitude. For comparison, we have 6,045 total remaining trials across 14 participants in the condition where trials were intermixed and did our best at data quality control. Dividing 6,045 by the 4 conditions (compatible/incompatible and cued/uncued) within intermixed trials gives us approximately 1,500 good trials per condition, suggesting that our study had sufficient trials.

However, the amount of noise affecting raw EEG data can increase the number of trials/subjects required to elicit an ERP component in a given experiment substantially (Luck, 2005), such that 1,500 may not be good enough after all. For example, convenience sampling of mostly undergraduate participants does not allow us to control for participant alertness, the lack of sleep having been reported by 75% of survey respondents in an unrelated study among undergraduate students at a different university in Malaysia (Elias, Wong, & Abdullah, 2011). Noticeable differences at our pre-stimulus baseline of 100 ms (which ideally should be as close

to zero as possible), even after baseline correction, points to either poor signal-to-noise ratio of the averages or the presence of some unidentified confound. Noise in the alpha frequency band (8~13 Hz) is notoriously difficult to remove during pre-processing because of brain-related waves that also occur in the same frequency band. This alpha wave noise increases when participants are relaxed, tired, or drowsy (Boksem, Meijman, & Lorist, 2005; Eoh, Chung, & Kim, 2005). We attempted to reduce alpha noise during data acquisition by randomly jittering the inter-trial interval to minimise the potential for participants' alpha waves to be phase-locked with stimulus presentation. Budgetary issues notwithstanding, caffeinated beverages could in future studies be offered to participants before or during the experiment to improve attentiveness, although that may introduce yet another confound by potentially changing attention-related brain activity.

In addition, we did not jitter the interval between presentation of the cue-back and target stimuli. This may have led to overlapping components originating from the cue-back stimuli, especially ones that emerge around 800 ms (duration between cue-back and target stimuli). Future ERP studies following a paradigm like ours should consider introducing a randomized jitter between cue-back and target stimuli, so that ERPs elicited by the cue-back can be averaged out during pre-processing of the data.

The present chapter sought to dissociate perceptual/attentional processing (i.e., input-based IOR) with that of oculomotor processing of cued and uncued targets (i.e., output-based IOR). Our null effects in the ERPs indicate that neither low-level sensory nor oculomotor mechanisms were affected by peripheral cueing. Alternatively, effects may have been obscured by poor signal-to-noise ratio. In the following chapters, we used a different approach to explore

IOR, first introducing distractors into a spatial cue-target paradigm, then studying the neural mechanisms of input-based and output-based IOR using ERPs in the distractor paradigm.

Chapter 4 : IOR with Distractors[3]

4.1 Introduction

Having investigated input and output-based IOR by manipulating S-R compatibility, we next explored the two types of IOR in a distractor paradigm. If input-based IOR is sensory/attentional and linked to stimulus-driven exogenous attentional processing, whereas output-based IOR is oculomotor and more likely to affect the response stage of the information processing line, how would a non-target stimulus (hereafter referred to as a distractor) presented alongside a target tell us more about these two forms of IOR? In the present and following two chapters, we will first investigate the presence of IOR with distractors (Chapter 4), explore the temporal dynamics of IOR with distractors (Chapter 5), and, finally, attempt to associate our behavioural results with ERP data (Chapter 6).

Some studies have proposed that oculomotor activation is the primary criterion in determining whether an input-based IOR or output-based IOR is generated (Taylor & Klein, 2000; see Klein & Hilchey, 2011, for a review), in large part because an equivalent amount of inhibition was observed whether central arrow or peripheral stimuli were used when eye movements were allowed to either cues or targets, but not when eye movements were forbidden. However, Taylor and Klein (2000) only investigated a static CTOA of 1,500 ms. A similar pattern was observed in a subsequent time course design (Hilchey, Klein, & Satel, 2014), where equivalent inhibition was observed behaviourally regardless of target type at a CTOA of 1,050

[3] Parts of this chapter and the discussion have been published in Eng, V., Gan, S. R., Kwon, S. M., Lim, A., Jamaluddin, S. A., & Satel, J. (2016). Influence of distractors on inhibition of return in a spatial orienting paradigm. Proceedings from *The 2016 International Conference on Cognitive and Behavioral Psychology*. doi:10.5176/2251-1865_CBP16.49

ms, but no inhibition was observed for central targets with peripheral cueing at CTOAs of 450 ms or less, suggesting that output-based IOR arises at some point between 450 and 1,050 ms post-cue when a saccadic localisation task is used in the spatial cueing paradigm.

4.1.1 Discrimination tasks.

Other than detection and localisation tasks that provide empirical support for both input and output forms of IOR, discrimination tasks have also been used to explore cueing effects. Following a peripheral cue, Pratt (1995) presented either a single target (requiring detection and localisation) or a target and a distractor (requiring discrimination and localisation) on either side of the central fixation during S2 and found that both conditions elicited equivalent amounts of IOR when the task was saccadic localisation of the target. When saccades were not allowed and fixation was maintained at central fixation (manual localisation to target) during S2 with the presence of a distractor, however, IOR was reduced (Kingstone & Pratt, 1999). In a similar spatial cueing paradigm where six instead of just two placeholders were used, Theeuwes and Godijn (2004) found that a distractor presented at an inhibited location is, in effect, less distracting, because IOR reduced input from the distractor. A discrimination task could also be conducted by introducing distractors alongside the target in a common spatial cueing task. An example of such a task can be found in Kingstone and Pratt (1999), where researchers presented distractors within the placeholder that were opposite the target. Participants were then required to discriminate between the distractor and the target to make an accurate response. The researchers also manipulated the appearance of the distractor – it could either be present or absent, depending on the trial. The study found that when distractors were introduced into this spatial cueing task, IOR was still present at a 960 ms CTOA, further supporting the attentional account

of IOR. That study identified eye movements as a key component in modulating behavioural IOR. Specifically, oculomotor activation led to larger (output-based) IOR, but when eye movements were supressed, distractors diminished the magnitude of (input-based) IOR, suggesting that both input-based and output-based IOR were in play.

4.1.2 Response modality.

Using saccadic instead of manual responses, Pratt (1995) observed behavioural inhibition when participants made an eye movement localisation response to the target upon simultaneous presentation of both a target and a distractor. With a CTOA of 960 ms following the onset of a non-informative peripheral cue, Pratt (1995) presented either a single target (detection) or a target and a distractor (discrimination) on either side of the central fixation point – the target and distractor being a diamond and a square that were counterbalanced across participants. Results showed that both conditions elicited equivalent amounts of inhibition upon localisation of the target with saccades. When fixation was maintained during target onset with the presence of a distractor, however, inhibition persisted but was reduced (Kingstone & Pratt, 1999). Pratt and Abrams (1999) later replicated their experiments with manual responses at a long CTOA (1,160 ms), finding similar evidence for an inhibitory cueing effect that is, however, inconsistent with the output form of IOR. They reported no inhibitory cueing effects despite oculomotor activation, although suppressed eye movements were associated with input-based IOR.

Using peripheral cues followed by peripheral targets (“X”s and “O”s) at CTOAs ranging from 100 to 1,000 ms, Lupiáñez et al. (2001, Exp. 2) introduced a distractor at the location directly opposite to the target, which led to a behavioural IOR emerging at an earlier CTOA (400 ms) compared to when there were no distractors present. However, increasing task difficulty by

requiring participants to discriminate between “M” and “N” rather than “X” and “O” (Lupiáñez et al., 2001, Exp. 3) revealed no behavioural IOR when distractors were absent. Inhibition appeared only with the presence of distractors at later CTOAs of 700 ms and 1,000 ms. Taken together, Lupiáñez et al. (2001) made the distinction between target discrimination and target selection (with the presence of a distractor), concluding that the former delays whereas the latter hastens the emergence of behavioural inhibition.

It is important to further investigate IOR in a cue-target paradigm involving distractors, because allocating attention while conducting a visual search rarely ever involves only simple detection-like tasks. That is, humans are unlikely to be looking and searching for a target stimulus that is at the same time devoid of distractors. A much more common task in the real world would be akin to finding an eraser in a pencil box where one would need to discriminate between a target (e.g., an eraser) and distractor stimuli (e.g., pencils). Although a spatially non-predictive cue-target paradigm (Posner, 1980) is simpler than that of visual search in which one performs a succession of saccades in a more complex visual array in search of a target, the mechanisms underlying such processes are thought to be similar (Klein, 1988) when eye movements are allowed.

4.1.3 Visual search.

Outside of experiments using Posner’s (1980) spatial cueing paradigm, distractors and IOR have been more commonly explored in studies of visual search. For example, Klein (1988) used a serial search task to induce the inhibitory tagging mechanism, as well as a parallel search task as a baseline to account for potential non-IOR explanations. A probe was placed at a location where an item was previously displayed (referred to as an on-probe, much like a cued

target in Posnerian paradigms), which was detected more slowly than off-probes. This observation of reduced RTs to on-probes, only apparent in the serial but not parallel search paradigm, is reminiscent of IOR where RTs to cued trials are slower compared to uncued trials. It thus follows that IOR has been observed when distractors were present in visual search paradigms when observers executed saccades to targets that were either presented alone or along with a distractor (e.g., Müller & von Mühlenen, 2000; Theeuwes & Godijn, 2004). Müller and von Mühlenen (2000) extended upon Klein's (1988) serial search task in search of IOR by performing a series of experiments requiring saccades during serial visual search prior to presenting probes at either potentially inhibited search distractor locations or at previously empty location (again, akin to cued and uncued trials). They reported evidence of object-based IOR so long as the search array remained on screen, further supporting the idea that IOR operates on recently attended locations to increase efficiency in conducting a visual search.

Evidence of IOR with distractors is further supported by electrophysiological studies of visual search (Eimer, 1996; Hickey, Di Lollo, & McDonald, 2009), but rarely examined together, because traditional IOR paradigms do not include distractors whilst traditional visual search paradigms always include distractors. Hickey et al. (2009), for example, studied the N2pc component using a search array where stimuli could be presented in one of six locations on the screen. Similarly, Müller and von Mühlenen (2000) used a serial-search array consisting of a target surrounded by five distractor stimuli. They found behavioural IOR when cues were non-predictive of target locations. This gap in the literature occurs in spite of IOR having been found in visual search paradigms (Müller & von Mühlenen, 2000; Takeda & Yagi, 2000) as well as investigations of its role in facilitating visual search (Danziger et al., 1998; Klein, 1988; Klein & MacInnes, 1999; Wang & Klein, 2010).

4.1.4 The current study.

The main objective of the current study was to investigate input-based IOR by introducing distractors. When distractors are introduced into a spatial cueing paradigm with peripheral cues and targets (instead of just one target appearing inside one placeholder or the other), two different stimuli are presented in the placeholders and participants are asked to respond to one of them. Having two stimuli presented on the screen involves more than simple localisation, as participants need to discriminate between the two stimuli before making a manual or saccadic localisation response – a process that could conceivably carry greater attentional cost due to the addition of target selection processing that increases the task difficulty (Braun & Julesz, 1998).

Two experiments were conducted to examine the role of distractors in spatial cueing tasks: the first requiring manual localisation (with EEG, specifically to examine the P1 component as a neurophysiological index of inhibitory cueing effects), and the second requiring saccadic localisation of the targets. Similar to the EEG experiments described in Chapter 3, manual responses were necessary in Experiment 1 to obtain clean ERP signals by minimizing eye movement artefacts. Should saccadic responses in Experiment 2 elicit the same patterns in RTs, there would be more reason to believe that the behavioural results found in Experiment 1 were not due to differences in response modality.

We expected to observe IOR in both experiments, with participants responding faster to uncued than cued targets, although the size of the effect could be reduced and delayed due to the complexity of the task, in comparison to studies in which participants were only required to locate the target. Neutral cues that provide no spatial information were included to serve as a

control condition. Furthermore, in the manual response experiment (with EEG), we expected to find P1 attenuation for the cued relative to the uncued condition, because there is repeated peripheral stimulation and this condition should generate an input-based inhibitory cueing effect.

4.2 Experiment 1

This experiment followed a within-subjects design with three Cueing conditions: cued, uncued, and neutral cues.

4.2.1 Method.

***Participants*.** Nineteen right-handed undergraduate students (10 females), age ranged 18-38 (M = 21.4, SD = 4.6) from the University of Nottingham Malaysia participated in the study. Participants were all right-handed to exclude any potential confounds arising from hemispheric lateralisation of ERPs. All reported normal or corrected-to-normal vision and no neurological or psychological conditions. The experiment was approved by the Science and Engineering Research Ethics Committee.

Stimuli and apparatus. After measuring the circumference of participants' heads using a measuring tape to determine the size of the EEG cap to be used, the appropriate cap was soaked in an electrolyte solution before being positioned on the participants' head. The electrolyte solution is a saline solution made up of potassium chloride and baby shampoo that are dissolved in purified water. The sponges on the EEG cap that connect the electrodes to the scalp soak up this saline solution that acts as an electrical conductor.

Participants were then seated in an electrically shielded EEG booth in front of a 19-inch monitor. Stimuli were presented in white on a black background using E-Prime software running

on a Windows XP computer. 128-channel EGI HydroCel Geodesic Sensor Nets were used to record continuous EEG data at a 500 Hz sampling rate using NetStation software (Version 4.3; Electrical Geodesics, Inc., Eugene, OR).

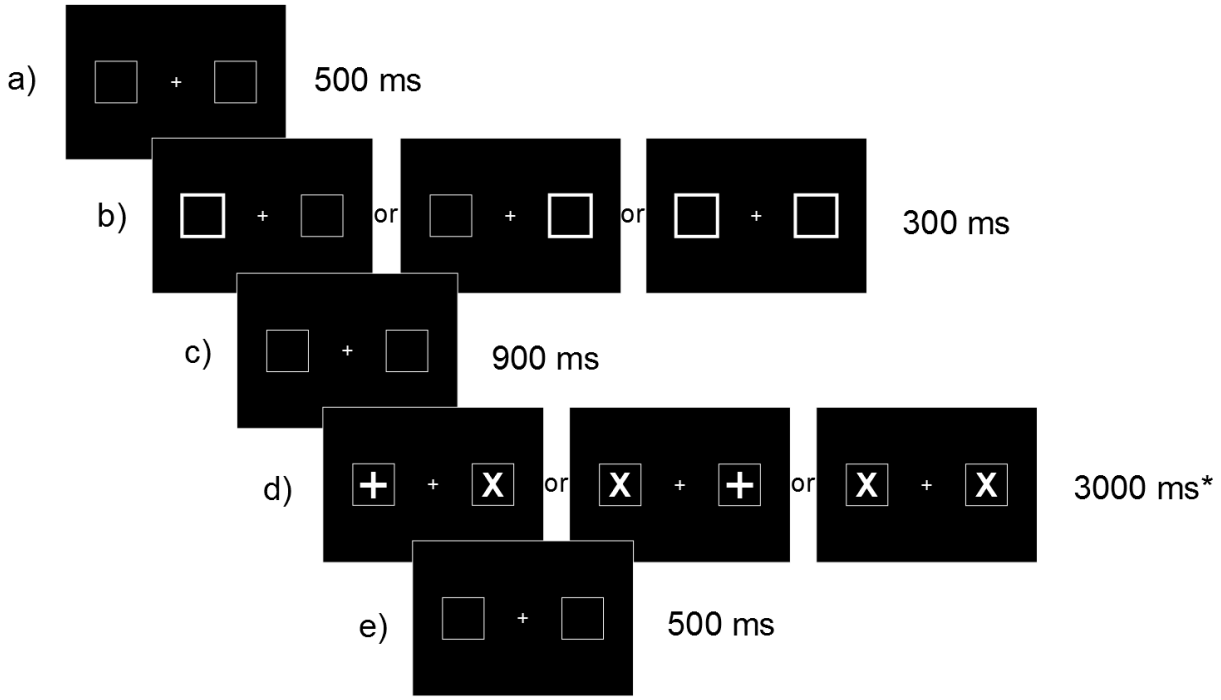

Figure 4.1. Illustration of the experimental design. **a)** Each trial began with a 500 ms fixation period followed by **b)** a left or right cue (highlighted box) or both boxes highlighted (neutral condition) for 300 ms. **c)** A 900 ms inter-stimulus interval (CTOA of 1,200 ms) then preceded **d)** the target, which could be a plus-target or a cross-target (half of the participants were told the plus was a target and half were told the cross was a target) that remained on screen for 3,000 ms or until a response was made (or in the case of catch trials, no targets appeared on screen for 1,000 ms). Participants were instructed to localise the appropriate target as quickly and accurately as possible with either manual (Experiment 1) or saccadic (Experiment 2) responses. **e)** Each trial ended with a 500 ms fixation screen.

Design and procedure. Participants were asked to stay fixated on a central fixation point throughout the experiment, with half of the participants instructed to make a response to a plus-

target (+) and the other half told to respond to a cross-target (x). Each trial began with a 500 ms central fixation flanked by two white empty boxes, one on each side (see Figure 4.1 for an illustration of the design). An irrelevant cue, which could be either one of the two boxes highlighted (or both), was then presented for 300 ms. Following the cue, there was a 900 ms fixation period before the target appeared (for a total CTOA of 1,200 ms). When the target appeared, participants were instructed to press the left button on the response box as fast as they could if the target appeared on the left and vice versa. If the participant was in the plus-target condition, the target appeared as a plus-sign in one box whereas the other box contained a cross. Likewise, if the participant was in the cross-target condition, the target appeared as a cross in one box whereas the other box contained a plus-sign. The target stayed on the screen for 3,000 ms or until the participant made a response, whichever came first. Participants were informed that the location of the cue was completely random and did not in any way predict the location of the target. A further 16.67% of the trials were catch trials, such that if the participant was in the plus-target condition, the catch trials presented two crosses as targets for 1,000 ms, and vice versa. Participants were not supposed to respond on the catch trials (no target appeared). Each trial ended with a 500 ms fixation period before the start of the next trial.

All trials were presented in a randomised order in four blocks of 180 trials per block, making up a total of 720 trials. Trials were referred to as cued trials when the target appeared at a cued location (e.g., left cue-left target or right cue-right target), whereas trials were uncued when targets appeared at a location opposite the cues (e.g., left cue-right target or right cue-left target). Neutral trials were cued at both the left and right locations regardless of where the target was, which allows us to gain insight into any covert attention effects that could be present. We also included catch trials with no targets (hence no response was required) to discourage participants

from selectively paying attention to only one side of the display. There were 200 trials in each of the cued, uncued, and neutral conditions, evenly divided between left and right, with an additional 120 non-target catch trials.

4.2.2 Results and discussion.

Behavioural performance. Participants scored at least 97.5% (mean accuracy was 99.13%) in the experiment. After excluding incorrect trials (0.87%), anticipatory responses (MRT < 2.5 MAD; 1.01%) and long outliers (MRT > 2.5 MAD; 7.61%), statistical analyses were performed on the remaining 90.51% of all trials. Means of correct MRTs for each condition are presented in Figure 4.2.

A repeated-measures analysis of variance (ANOVA) on the MRTs with three Cueing conditions (neutral vs. cued vs. uncued) revealed a main effect of Cueing [$F(2, 36) = 3.79$, $MSE = 47.09$, $p = .032$, $\eta^2 = .17$], whereby a difference between Cueing conditions was observed. A planned comparison, two-tailed paired-samples t-test revealed that cued ($M = 449.35$, $SD = 90.05$) trials were significantly slower than uncued ($M = 444.07$, $SD = 86.35$) trials [5.28 ms; $t(18) = 2.59$, $p = .019$, Cohen's $d = 0.59$], suggesting that there was an inhibitory cueing effect. Similarly, the MRT difference between uncued ($M = 444.07$, $SD = 86.35$) and neutral ($M = 449.41$, $SD = 85.44$) conditions was significant [5.34 ms; $t(18) = 2.34$, $p = .031$, Cohen's $d = 0.54$], which showed that the uncued condition was indeed different from the control condition. However, there was no significant difference between cued ($M = 449.35$, $SD = 90.05$) and neutral ($M = 449.41$, $SD = 85.44$) trials [$t(18) = -0.03$, $p = .980$, Cohen's $d = 0.01$] conditions.

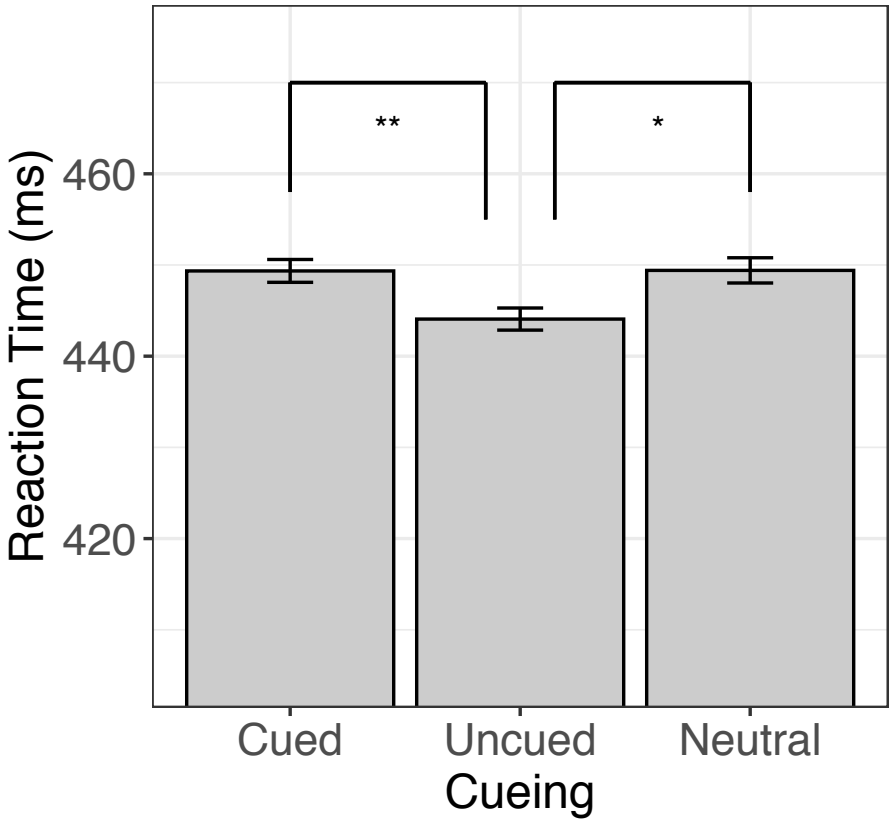

Figure 4.2. Mean MRTs (in ms) to Cued, Uncued, and Neutral targets. Asterisks indicate significant differences between cueing conditions (*$p < .05$, **$p < .01$). Error bars represent normalised standard errors according to Cousineau (2005).

Electrophysiological analyses.

Pre-processing. All electrodes were on-line referenced to the Cz electrode, with impedances maintained below 50 kΩ. Placement of the EEG nets were oriented such that the Cz electrode lied on the vertex of each participant's skull. A highpass filter of 1 Hz and lowpass filter of 30 Hz was performed on raw continuous EEG data using EGI NetStation Waveform Tools. Filtered data was then segmented into 1,600 ms epochs, time-locked to target onset with 100 ms pre-stimulus and 1,500 ms post-stimulus to include participant responses to the target in the epoched data. Segmented data was exported for subsequent pre-processing in EEGLAB

(Delorme & Makeig, 2004), a Matlab® toolbox, where bad electrodes were visually inspected and zeroed upon identification. A 100 ms baseline correction was applied prior to artefact rejection, in which excessively noisy segments (amplitude deflections of +/- 75 microvolts) were removed from the -100 to 400 ms time window. Trials with incorrect behavioural responses were also excluded from further analysis. Finally, ipsilateral and contralateral waveforms were averaged at electrode sites from the left parieto-occipital (PO7) and right parieto-occipital (PO8) scalp areas (EGI channels 65 and 90 respectively), selected based on the basis of relevant effects observed in previous studies (e.g., Prime & Jolicœur, 2009a; Prime & Ward, 2006; Satel, Hilchey et al., 2013; Van der Stigchel et al., 2006). An approximate correspondence between the International 10-20 system electrode positions with sensors on the 128-channel geodesic configuration were used to determine the aforementioned two channels to allow for easy comparison with other studies (Luu & Ferree, 2005).

ERP analyses. Visual inspection of the ipsilateral ERP waveforms revealed a modulation of the ERPs corresponding to cued, uncued, and neutral conditions over parieto-occipital regions (PO7/PO8) as a function of trial condition (see Figure 4.3). The earliest component (P1) had an average onset latency of about 80 ms and a peak latency around 120 ms. We found reduced P1 amplitude (μV) for the cued (M = 0.42, SD = 0.86) and neutral (M = 0.19, SD = 0.89) conditions relative to the uncued (M = 0.39, SD = 0.72) condition, although such differences were not statistically significant when subjected to an ANOVA with Cueing as the within-subjects variable [$F(2, 36) = 0.39$, $MSE = 0.80$, $p = .678$, $\eta^2 = 0.02$]. Planned comparisons (two-tailed) also revealed no significant differences between cued and uncued conditions [$t(18) = 0.12$, $p = .452$, Cohen's $d = 0.03$], cued and neutral conditions [$t(18) = 0.73$, $p = .252$, Cohen's $d = 0.17$], or uncued and neutral conditions [$t(18) = 0.68$, $p = .253$, Cohen's $d = 0.16$].

Because this experiment called for manual responses, ERPs that were obtained can only reflect input-based IOR and not output-based IOR. To also consider output-based IOR in a distractor paradigm, we conducted a second experiment that replicated the design of the first experiment but required saccadic responses instead.

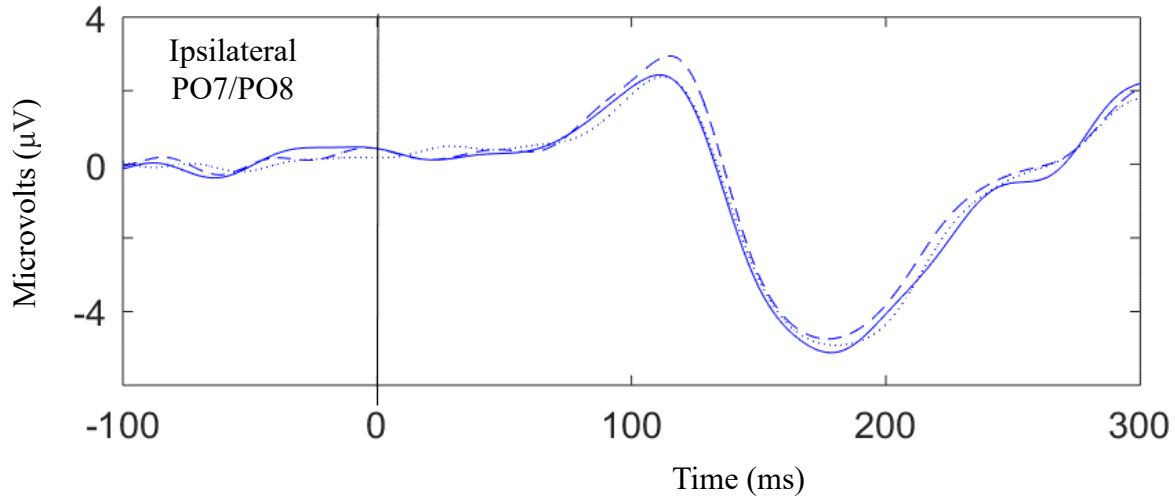

Figure 4.3. Grand average ERPs elicited at posterior electrode sites PO7/PO8 in response to cued (solid line), uncued (dashed line), and neutral (dotted line) targets. Waveforms are collapsed across left and right hemifield target stimuli and only scalp sites ipsilateral to the side of stimulation are plotted above.

4.3 Experiment 2

This experiment followed a within-subjects design with three Cueing conditions: cued, uncued, and neutral cues.

4.3.1 Method.

Participants. Twenty-five students from the University of Nottingham Malaysia participated in the study. Data from one participant who failed to complete the experiment due to eye-tracker technical issues and four participants with accuracy rates lower than 85% were omitted, leaving 20 participants (16 females, 17 right-handed) aged 18 to 34 (M = 22.20, SD = 3.79) that were used in further analyses. All reported normal or corrected-to-normal vision. The experiment was approved by the Science and Engineering Research Ethics Committee.

Stimuli and apparatus. Participants were seated in front of a 24-inch BenQ gaming monitor with their head positioned approximately 57 cm away from the screen. Stimuli were drawn with Matlab running on a Windows 7 computer that connects to an EyeLink 1000 Plus (SR Research, Ontario, Canada) eye-tracking system host computer. The desktop-mounted eye-tracker was used to monitor participants' eye movements and record their saccadic response times (SRTs) to targets at a sampling rate of 250 Hz.

All stimuli were presented white on black, with two peripheral boxes (visual angle at 4.5° x 4.5°) as placeholders 8.7° to the left and right of a 0.8° x 0.8° fixation cross that was displayed at the centre of the screen.

Design and procedure. Experiment 2 was identical to Experiment 1, but required saccade rather than manual response, with a reduced number of trials (288 instead of 720 trials). As there was no EEG recording nor ERP analyses involved in Experiment 2, there was no need for the increased number of trials.

Participants were asked to stay fixated on a central fixation point throughout the experiment, with half of the participants instructed to make a response to a plus-target (+) and the other half told to respond to a cross-target (x). Each trial began with a 500 ms central fixation flanked by two white empty boxes, one on each side (see Figure 4.1 for an illustration of the

design). An irrelevant cue, which could be either one of the two boxes highlighted (or both), was then presented for 300 ms. Following the cue, there was a 900 ms fixation period before the target appeared (for a total CTOA of 1,200 ms). When the target appeared, participants were instructed to look at the target as fast as they could. If the participant was in the plus-target condition, the target appeared as a plus-sign in one box whereas the other box contained a cross. Likewise, if the participant was in the cross-target condition, the target appeared as a cross in one box whereas the other box contained a plus-sign. The target stayed on the screen for 3,000 ms or until the participant made a response, whichever came first. Participants were informed that the location of the cue was completely random and did not in any way predict the location of the target. A further 16.67% of the trials were catch trials, such that if the participant was in the plus-target condition, the catch trials presented two crosses as targets for 1,000 ms, and vice versa. Participants were not supposed to respond on the catch trials (no target appeared). Each trial ended with a 500 ms fixation period before the start of the next trial. If participants ever made any incorrect eye movements (i.e., leaving fixation when they were not supposed to), then the trial was randomly recycled.

Trials are referred to as cued trials when the target appeared at a cued location (i.e., left cue-left target or right cue-right target), whereas trials are uncued when targets appeared at a location opposite of the cues (i.e., left cue-right target or right cue-left target). Neutral trials were cued at both locations regardless of where the target would appear. There were 80 trials in each of the cued, uncued, and neutral conditions, evenly divided between left and right, with an additional 48 non-target catch trials. All trials were presented in a randomised order in four blocks of 72 trials, making up a total of 288 trials.

4.3.2 Results and discussion.

Behavioural performance. All participants scored at least 87.50% (mean accuracy was 95.00%) in the experiment. After excluding incorrect trials (5.57 % of all trials), anticipatory responses (SRT < 2.5 MAD; 0.18%), and long outliers (SRT > 2.5 MAD; 5.18%), statistical analyses were performed on the remaining 89.07% of all trials. Means of correct SRTs for each condition are presented in Figure 4.4.

An ANOVA on the SRTs with the three Cueing conditions (neutral vs. cued vs. uncued) revealed a main effect of Cueing [$F(2, 38) = 3.31$, $MSE = 138.23$, $p = .047$, $\eta^2 = .15$]. Following that the reveal of the main effect, a two-tailed, planned comparison, paired-samples t-test revealed that cued ($M = 344.71$, $SD = 68.15$) trials were significantly slower than uncued trials ($M = 335.73$, $SD = 67.27$) trials [9 ms; $t(19) = 2.23$, $p = .038$, Cohen's $d = 0.50$]. The difference between cued and neutral trials ($M = 343.08$, $SD = 72.24$) were not significant [2 ms; $t(19) = 0.48$, $p = .634$, Cohen's $d = 0.121$], although we did find a marginally significant difference between uncued and neutral trials [7 ms; $t(19) = 1.97$, $p = .063$, Cohen's $d = 0.44$].

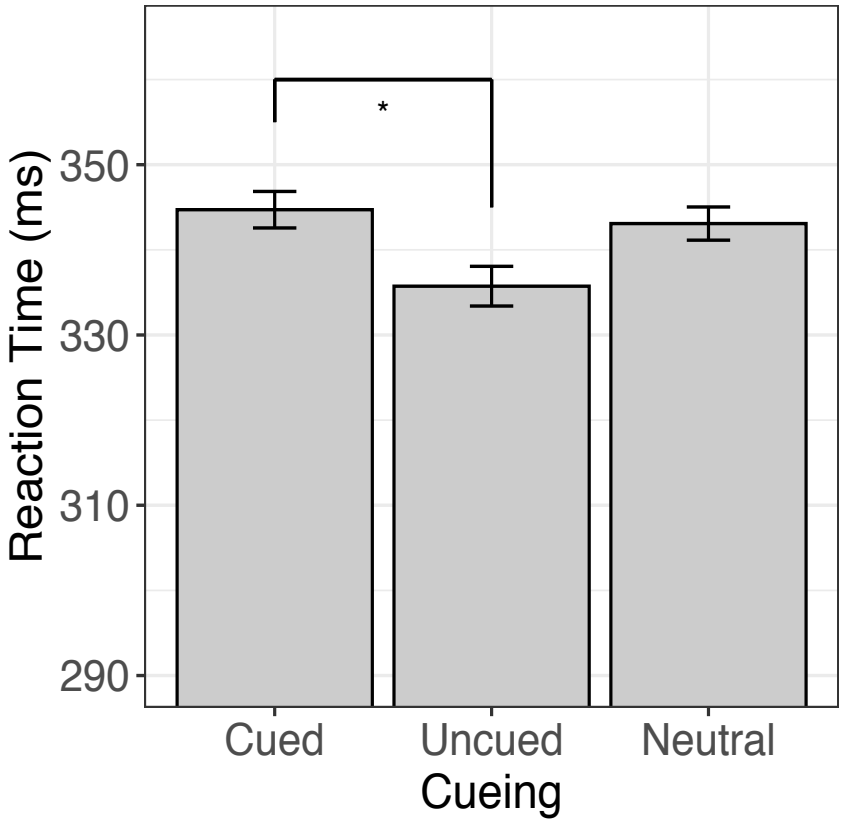

Figure 4.4. Mean SRTs (in ms) to cued, uncued, and neutral targets. Asterisks indicate significant differences between cueing conditions (*$p < .05$). Error bars represent normalised standard errors according to Cousineau (2005).

4.4 General Discussion

It was hypothesised that, despite the presence of distractors, behavioural IOR would be observed in both experiments, whereby the cued trials would have longer RTs relative to the uncued and neutral trials based on the findings of prior studies (e.g., Posner & Cohen, 1984; Prinzmetal, Taylor, Myers, & Nguyen-Espino, 2011). The results from the current study showed significantly longer RTs to the target for the cued trials relative to the uncued trials, with no significant difference between the cued and neutral trials. This finding suggests that IOR is not

just reflexive but encompasses a voluntary component as well and affects both input and output ends rather than just the output.

As introduced earlier, Rafal and colleagues (1989) previously demonstrated that IOR affects the output end but were sceptical as to whether IOR affects the input end due to the absence of IOR in the central arrow conditions that requires voluntary orienting of attention. However, the current study shows that IOR is present in a discrimination-localisation task with distractors that requires endogenous orienting of attention. Specifically, the presence of distractors mandates the respondent to visually search for, identify, and discriminate the target (Prinzmetal et al., 2011). One possible explanation for these inconsistent conclusions about the endogenous basis of IOR is that the central arrows used by Rafal et al. (1989) did not elicit all aspects of voluntary or endogenous orienting of attention and, therefore, their results could have represented the perceptual property of the central cue relative to that of peripheral cues rather than the different orienting of attention. On this basis, Hilchey, Dohmen, Crowder, and Klein (2016) argued that IOR affects both the input and output end of processing.

In this chapter, we have demonstrated that behavioural IOR is observed in the presence of distractors in a spatial orienting paradigm, regardless of response modality. However, behavioural IOR was much stronger when the oculomotor system was activated, as expected. When manual responses were used, there was no significant reduction of the P1 component that has been observed in previous EEG studies without distractors in such a paradigm. This is likely due to a reduced amount of input-based IOR owing to the presence of distractors when manual responses are used.

If the presence of distractors is the cause for reduced IOR, future research could investigate whether distractibility modulates the strength of IOR, perhaps by varying the number

of distractors around a target or by changing characteristics of the distractor. The strength of IOR could in turn be evaluated behaviourally, or electrophysiologically in terms of ERP components with reduced amplitudes, or delayed onset latency.

Because the present study only used peripheral cues and targets, one of the limitations of our experiments in this chapter is that we cannot tease apart the extent to which sensory inhibitory cueing effects at the input end interact with the output-based IOR. We therefore designed a series of experiments to explore the time course of IOR with both central and peripheral cues that we will describe in the following chapter. Subsequently, Chapter 6 continues along the same line of research to investigate the ERP modulations associated with cueing in a spatial orienting task when the oculomotor system is activated in a paradigm with distractors. Finally, a more in-depth discussion pertaining to the relevance of P1, Nd, and N2pc components in the context of IOR can be found in Chapter 6.

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Chapter 5 : Time Course of IOR with Distractors[4]

Having demonstrated the occurrence of IOR with distractors in Chapter 4, we next ran a time course study to determine the best CTOA that would allow us to isolate late output-based IOR, for use in an ERP study slated for Chapter 6. In the present chapter, the main goal of the first study was to establish how input-based and output-based IOR are affected over time by the interference from these distractors, with or without oculomotor activation and with endogenous (central) or exogenous (peripheral) cues. We therefore examined behavioural inhibition in four experiments where the target was always accompanied by a distractor. To dissociate output-based oculomotor IOR from input-based sensory IOR, we required participants to either remain fixated at a central point throughout the entire trial (Experiments 1 & 2) or to engage the oculomotor system and make eye movements in response to the cues (Experiments 3 & 4). We also manipulated the cue type (peripheral vs. central cues) to separate shifting of attention that is exogenous in nature (Experiments 1 & 3) from attention that is endogenous in nature (Experiments 2 & 4).

As far as we know, the present study is the first to compare the role of distractors under these different circumstances over a broad time range. Pratt (1995), for example, only used peripheral cues, and Lupiáñez et al. (2001) did not allow eye movements. Besides requiring participants to remain fixated or to make saccades to cues and using both peripheral and central cues, the present study made two other major changes in comparison to previous work. Similar

[4] A modified manuscript of this chapter and parts of the discussion chapter have been published in: Eng, V., Lim, A., Janssen, S. M. J., & Satel, J. (2018). Time course of inhibition of return in a spatial cueing paradigm with distractors. *Acta Psychologica, 183*, 51-57. doi:10.1016/j.actpsy.2017.12.011

to Lupiáñez et al.'s (2001, Exp. 2) discrimination task, the participants' task in the present study was to make a manual localisation key press when the target appeared (i.e., spatial discrimination). However, rather than using asterisks as distractors, our distractors were either an "x" or a "+", with either one representing the target. Finally, whereas studies have shown that IOR can last up to 3,000 ms (Samuel & Kat, 2003), until now, the role of distractors has only been examined in studies that used CTOAs up to 1,000 ms (Lupiáñez et al., 2001). We therefore extended the CTOA range (800, 1,600, and 2,400 ms), allowing us to examine whether later inhibitory or facilitatory effects in the temporal distribution of IOR differ when distractors are introduced in a spatial cueing paradigm under various conditions.

5.1 Study 1

We ran four behavioural experiments, where participants were asked to: i) ignore peripheral cues, ii) ignore central cues, iii) saccade to peripheral cues, or iv) saccade to central cues. Each experiment followed a within-subjects design with two Cueing conditions (cued and uncued) and three CTOAs (800, 1,600, and 2,400 ms).

5.1.1 Method.

Participants. There were 48 participants (31 females), age ranged from 17 to 33 (M = 20.10, SD = 2.20), who were split into four groups of 12. All reported normal or corrected-to-normal vision. Before starting the experiment, all participants provided informed consent. Participants received either course credit or financial compensation for their participation. The experiment was approved by the Science and Engineering Research Ethics Committee.

Stimuli and apparatus. Participants were seated in front of a 24-inch BenQ gaming monitor with their head positioned approximately 57 cm away from the screen. Stimuli were drawn with Matlab using the Psychophysics (Brainard, 1997; Kleiner et al., 2007) and Eyelink Toolbox (Cornelissen, Peters, & Palmer, 2002) extensions running on a Windows 7 computer that was connected to an EyeLink 1000 Plus (SR Research, Ontario, Canada) eye-tracking system host computer. The desktop-mounted eye-tracker was used to monitor participants' eye position during trials.

All stimuli were presented in white on a black background. At the beginning of every trial, three white placeholder boxes (each measuring 4.5° x 4.5° visual angle), separated centre to centre by 9.1°, were displayed along the horizontal meridian.

Design and procedure. Participants were asked to remain fixated on a central box throughout the experiment, except when instructed to saccade to cues and back to fixation. An illustration of the trial sequence is shown in Figure 5.1. Each trial began with a 500 ms fixation interval where participants were instructed to stay fixated at the centre of the central box. An irrelevant cue, that could be either a peripheral cue (visible amplification of placeholder, Exp. 1 and 3) or a central cue (directed arrow that indicates direction, Exp. 2 and 4) was then presented for 300 ms. Participants were instructed to either ignore the cues (Exp. 1 and 2), or saccade to the location directed by the cues and back to the original fixation before target onset (Exp. 3 and 4).

Following the cue, a randomly selected inter-stimulus interval of 500, 1,300, or 2,100 ms elapsed (corresponding with CTOAs of 800, 1,600, and 2,400 ms, respectively). When the target appeared, participants were instructed to press the 'z' key on the keyboard as quickly and accurately as they could if the target appeared on the left, or the '/' key for targets on the right. Half of the participants were instructed to make manual localisation responses to a plus-target

(+), whereas the other half was told to respond to a cross-target (x), counterbalanced across each of the four experiments. If the participant was in the plus-target condition, the target appeared as a plus-sign in one box whereas the other box contained a cross distractor, and vice versa for the cross-target condition. The target remained on the screen for 3,000 ms or until the participant made a response, whichever came first. Participants were informed that the location of the cue was completely random and did not in any way predict the location of the target. Each trial ended with a randomly selected inter-trial interval ranging between 1,000 and 1,500 ms before the start of the next trial. The interval timing was arbitrarily decided based on precedence from IOR studies in healthy participants (e.g., 500 ms in Pratt & McAuliffe, 2002; 1,000 ms in Bennett & Pratt, 2001; 1,250 ms in Butcher, Kalverboer, & Geuze, 1999; 1,500 ms in Bao & Pöppel, 2007; Bao, Zhou, & Fu, 2004). Where clinical population are concerned, inter-trial intervals were generally longer, for example, up to 4,000 ms in patients with Parkinson's disease (Poliakoff et al., 2003) and 1,000 ms in obsessive-compulsive disorder patients (Moritz & von Mühlenen, 2005).

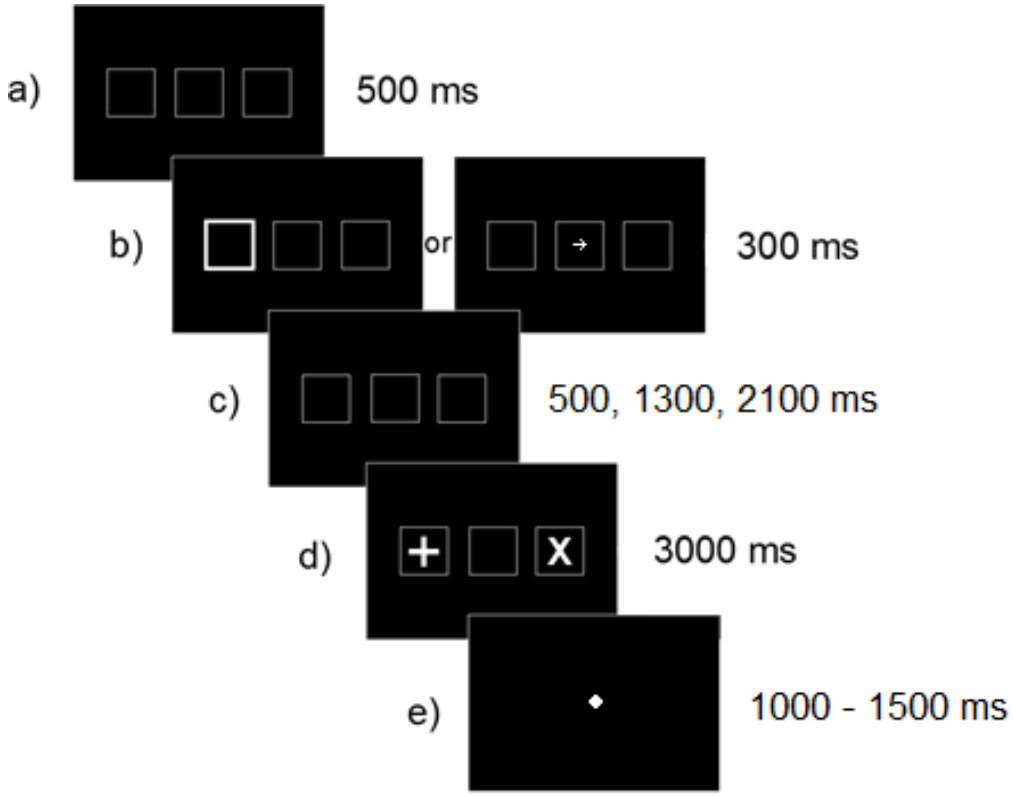

Figure 5.1. Illustration of the experimental design. **a)** Each trial began with a 500 ms fixation period followed by **b)** a left or right cue - either peripheral cues (visible amplification of placeholder, Experiments 1 and 3) or central cues (directed arrow, Experiments 2 and 4) were presented for 300 ms, and participants were asked to either ignore the cues (Experiments 1 and 2) or saccade to the cues and back to the original fixation before target onset (Experiments 3 and 4). **c)** An inter-stimulus interval was randomly selected from: 500, 1,300, and 2,100 ms (CTOAs of 800, 1,600, and 2,400 ms), then **d)** the target appeared along with a distractor for up to 3,000 ms or until a response. Participants were instructed to localise the appropriate target as quickly and accurately as possible with manual responses. **e)** Each trial ended with a fixation screen for a random duration between 1,000 and 1,500 ms.

Trials were abruptly terminated and recycled among the remaining trials at any point if: a) the participant's gaze position deviated by more than 3 degrees of visual angle from fixation when fixation was required, b) responses were made before the target appeared, c) participants

failed to respond to targets within 3,000 ms, or d) an invalid keypress was made. Visual feedback corresponding to the error made was presented on the screen, at which point participants could resume the experiment at their own pace.

Each participant took part in only one of the four experiments. In Experiments 1 and 3, participants were instructed to either ignore (Exp. 1) or saccade (Exp. 3) to peripheral cues. In Experiments 2 and 4, participants were instructed to either ignore (Exp. 2) or saccade (Exp. 4) to the location directed by central cues. Each experiment consisted of 240 trials. There were 120 trials in each of the cued and uncued conditions, evenly divided between left and right. The three CTOAs were also distributed evenly into 80 trials for each CTOA. All trials were presented in a randomised order in four blocks of 60 trials per block (30 cued and 30 uncued trials). Trials are referred to as cued trials when the target appeared at the cued location (i.e., left cue-left target or right cue-right target), whereas trials are uncued when the target appeared at the location opposite the cues (i.e., left cue-right target or right cue-left target).

5.1.2 Results.

Experiment 1: Ignore peripheral cues. In the first experiment, fixation was maintained during presentation of peripheral cues. All participants in this experiment scored at least 95.85% accuracy (mean accuracy was 98.93%). After excluding incorrect trials (1.11% of all trials), anticipatory responses (RTs < 2.5 Median Absolute Deviation (MAD); 0.24%) and long outliers (RT > 2.5 MAD; 5.49%), statistical analyses were performed on the remaining 93.16% of all trials. Cueing effects (cued - uncued) and RTs for each experiment are presented in Table 5.1 and Figure 5.2.

Table 5.1. Mean (and SD) of RTs and cueing effects (cued - uncued RTs) for each condition in Study 1.

		Peripheral cue			Central cue		
	CTOA (ms)	Cued	Uncued	Cueing effect	Cued	Uncued	Cueing effect
Ignore cues	800	515.07 (85.37)	508.58 (82.49)	6.49	465.27 (74.07)	473.72 (79.79)	-8.46
	1600	487.86 (74.68)	478.54 (71.80)	9.32†	445.64 (65.23)	444.89 (70.95)	0.74
	2400	472.88 (75.50)	464.56 (70.76)	8.32†	447.63 (70.10)	449.74 (74.21)	-2.11
Saccade to cues	800	539.51 (80.14)	511.84 (87.94)	27.66**	501.60 (82.43)	496.16 (83.94)	5.44
	1600	475.04 (60.97)	459.01 (61.87)	16.03**	457.30 (83.13)	458.53 (84.65)	-1.23
	2400	470.87 (65.06)	452.50 (64.64)	18.36*	463.08 (93.64)	448.44 (79.72)	14.64*

Note: †$p < .10$, *$p < .05$, **$p < .01$

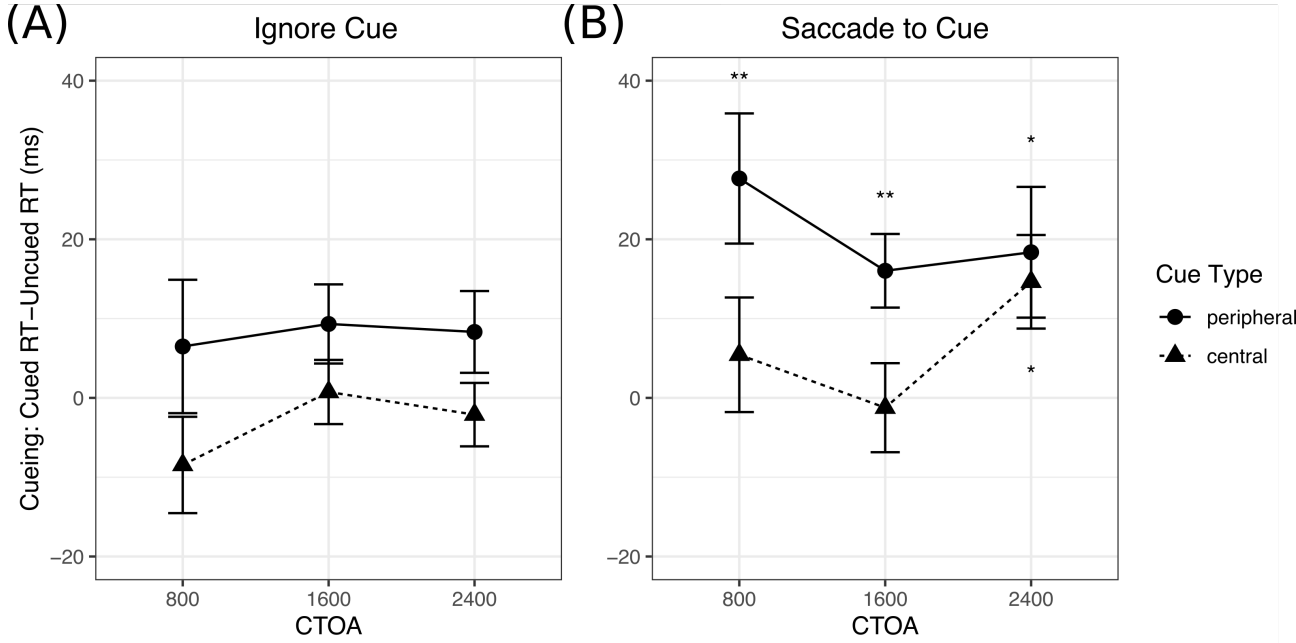

Figure 5.2. Cueing effects (cued - uncued RTs) obtained from the present experiments at various CTOAs for each condition. Solid lines represent trials where a peripheral cue was used; dashed lines represent trials where a central cue was used. (**A**) In Experiments 1 and 2, participants ignored the cues. (**B**) In Experiments 3 and 4, participants made saccades in response to cues. Asterisks indicate statistically significant differences between the cued and uncued conditions (*$p < .05$, **$p < .01$) and error bars are standard errors.

To examine whether the CTOA duration interacted with cueing effects, we performed a repeated-measures ANOVA on the RTs with Cueing (cued vs. uncued) and CTOA (800 vs. 1,600 vs. 2,400 ms) as within-subjects variables. Cueing was marginally significant [$F(1, 11) = 3.95$, $MSE = 294.43$, $p = .072$, $\eta^2 = .26$], because cued trials were overall slower than uncued trials. We also found a significant main effect of CTOA [$F(2, 22) = 24.30$, $MSE = 475.13$, $p < .001$, $\eta^2 = .69$], because mean RTs were overall faster at longer CTOAs. No significant interaction was observed between Cueing and CTOA [$F(2, 22) = 0.06$, $MSE = 219.44$, $p = .945$, $\eta^2 < .01$]. Particularly relevant to this study is the time course of cueing effects. We therefore performed planned comparisons in the form of one-tailed paired-samples t-tests that revealed no difference

between cued and uncued trials at the 800 ms CTOA [$t(11) = 0.77$, $p = .457$, $d = 0.59$, $BF_{10} = 0.37$]. However, with a 1,600 ms CTOA, mean RTs of cued trials were marginally slower than those of uncued trials [$t(11) = 1.87$, $p = .089$, $d = 0.54$, $BF_{10} = 1.08$], producing a 9 ms IOR effect. Finally, with a 2,400 ms CTOA, cued trials were also marginally slower than uncued trials, with an 8 ms IOR effect [$t(11) = 1.61$, $p = .068$, $d = 0.47$, $BF_{10} = 0.80$].

Experiment 2: Ignore central cues. In the second experiment, fixation was maintained during presentation of central cues. All participants in this experiment scored at least 94.78% accuracy (mean accuracy was 98.92%). After excluding incorrect trials (1.24% of all trials), anticipatory responses (RT < 2.5 MAD; 0.45%) and long outliers (RT > 2.5 MAD; 5.25%), statistical analyses were performed on the remaining 93.07% of trials.

We again performed a repeated-measures ANOVA on RTs with Cueing (cued vs. uncued) and CTOA (800 vs. 1,600 vs. 2,400 ms) as within-subjects variables. Cueing failed to reach significance [$F(1, 11) = 0.67$, $MSE = 289.62$, $p = .432$, $\eta^2 = .06$], although there was a significant main effect of CTOA [$F(2, 22) = 8.76$, $MSE = 470.32$, $p = .002$, $\eta^2 = .44$] indicating a difference in RTs between one or more of the CTOAs. There was no interaction between Cueing and CTOA [$F(2, 22) = 2.11$, $MSE = 62.99$, $p = .145$, $\eta^2 = .16$].

To examine cueing effects at the different CTOAs, planned comparisons in the form of one-tailed paired-samples t-tests were conducted. There was no significant difference between cued and uncued trials at 800 ms CTOA [$t(11) = -1.39$, $p = .191$, $d = 0.40$, $BF_{10} = 0.63$], nor at 1,600 ms [$t(11) = 0.18$, $p = .858$, $d = 0.05$, $BF_{10} = 0.29$] or 2,400 ms CTOA [$t(11) = -0.53$, $p = .608$, $d = 0.15$, $BF_{10} = 0.32$].

Experiment 3: Saccades in response to peripheral cues. In the third experiment, saccades were made to peripheral cues and back to central fixation before target onset. All

participants in this experiment scored at least 95.41% accuracy (mean accuracy was 98.61%). After excluding incorrect trials (1.42% of all trials), anticipatory responses (RT < 2.5 MAD; 0.28%) and long outliers (RT > 2.5 MAD; 5.24%), statistical analyses were performed on the remaining 93.06% of all trials.

We again performed a repeated-measures ANOVA on RTs with Cueing (cued vs. uncued) and CTOA (800 vs. 1,600 vs. 2,400 ms) as within-subjects variables. Cueing was significant [$F(1, 11) = 29.41$, $MSE = 261.87$, $p < .001$, $\eta^2 = .73$], because cued trials were overall slower than uncued trials. We also found a significant main effect of CTOA [$F(2, 22) = 10.35$, $MSE = 2923.08$, $p < .001$, $\eta^2 = .48$], because mean RTs were overall faster at longer CTOAs. There was no interaction between Cueing and CTOA [$F(2, 22) = 0.67$, $MSE = 339.70$, $p = .522$, $\eta^2 = .06$].

To examine the cueing effects at different CTOAs in more detail, planned comparisons in the form of one-tailed paired-samples t-tests were conducted. There was a significant difference between cued and uncued trials at the 800 ms CTOA [$t(11) = 3.37$, $p = .006$, $d = 0.97$, $BF_{10} = 8.69$], generating IOR effect of 28 ms, as well as for the 1,600 ms CTOA [IOR = 16 ms; $t(11) = 3.45$, $p = .005$, $d = 1.00$, $BF_{10} = 9.78$] and the 2,400 ms CTOA [IOR = 18 ms; $t(11) = 2.23$, $p = .048$, $d = 0.64$, $BF_{10} = 1.72$].

Experiment 4: Saccades in response to central cues. In the fourth experiment, saccades were made in response to central cues. All participants in this experiment scored at least 93.68% accuracy (mean accuracy was 98.53%). After excluding incorrect trials (1.60% of all trials), anticipatory responses (RT < 2.5 MAD; 0.14%) and long outliers (RT > 2.5 MAD; 4.58%), statistical analyses were performed on the remaining 93.68% of all trials.

We again performed a repeated-measures ANOVA on RTs with Cueing (cued vs. uncued) and CTOA (800 vs. 1,600 vs. 2,400 ms) as within-subjects variables. Cueing failed to reach

significance [$F(1, 11) = 2.81$, $MSE = 252.39$, $p = .122$, $\eta^2 = .20$], although there was a significant main effect of CTOA [$F(2, 22) = 22.04$, $MSE = 642.90$, $p < .001$, $\eta^2 = .67$], indicating a difference in RTs between one or more of the CTOAs. There was no interaction between Cueing and CTOA [$F(2, 22) = 1.66$, $MSE = 229.38$, $p = .213$, $\eta^2 = .13$].

To examine cueing effects in more detail, planned comparisons in the form of one-tailed paired-samples t-tests were also conducted. There was no significant difference between cued and uncued trials for the 800 ms CTOA [$t(11) = 0.75$, $p = .467$, $d = 0.22$, $BF_{10} = 0.37$], or the 1,600 ms CTOA [$t(11) = -0.22$, $p = .830$, $d = 0.06$, $BF_{10} = 0.29$]. However, there was a significant difference for the 2,400 ms CTOA [IOR = 15 ms; $t(11) = 2.48$, $p = .031$, $d = 0.72$, $BF_{10} = 2.43$].

5.1.3 Discussion.

In Study 1, we examined the effect of distractors on sensory inhibitory cueing effects and oculomotor IOR. We investigated the influence of distractors on input-based IOR in Experiments 1 and 2 by prohibiting eye movements to the cues, whereas we explicitly required eye movements in response to the cues in Experiments 3 and 4 to investigate the influence of distractors on output-based IOR. The four experiments did not include control conditions in which there were no distractors, but the present results can be compared to the results of studies from the literature that do not include such distractors in their experimental designs. This comparison allowed us to examine the influence of distractors on these two forms of behavioural inhibition. Because each experiment contained three CTOA conditions (800 vs. 1,600 vs. 2,400 ms), we could also examine whether the inclusion of distractors leads to a different time course of these cueing effects.

The results for Experiments 1 and 2, in which cues were ignored (i.e., suppressed oculomotor system), were consistent with the literature wherein peripheral cues elicit a general trend towards input-based inhibitory cueing effects but no effect is observed following central cues (Posner & Cohen, 1984; Taylor & Klein, 2000). However, although there was a marginally significant IOR effect at CTOAs of 1,600 ms and 2,400 ms with repeated peripheral stimulation, IOR was surprisingly not significant at the shorter CTOA of 800 ms (e.g., Lupiáñez et al., 2001; Lupiáñez et al., 2004). The inversed Bayes factor suggested that the support for IOR at 1,600 ms in the ignore peripheral cues condition was anecdotal, with no support for inhibition at 800 and 2,400 ms. There was no support for inhibition at any CTOA in the ignore central cues condition. This finding suggests that the distractor presence has led to a reduction in the magnitude of behavioural inhibition. To further investigate this issue, Study 2 re-examined this condition with the inclusion of a within-subjects control condition without distractors.

With saccades required in response to cues in Experiments 3 and 4 (i.e., activated oculomotor systems), we expected to observe equivalent IOR effects generated by both central and peripheral cues at all three CTOAs, as observed previously without distractors (e.g., Hilchey, Klein, & Satel, 2014; Taylor & Klein, 2000). As expected, peripheral cueing did in fact elicit significant IOR at all three CTOAs, with substantial support for inhibition at 800 ms and 1,600 ms and partial support for inhibition at 2,400 ms. However, this effect was not apparent for the shorter CTOAs (800 and 1,600 ms) with central cues – only at a CTOA of 2,400 ms did we observe IOR effects under both cueing conditions.

There are a number of potential explanations for this result. Given that observation of output-based IOR effects were delayed with endogenous stimuli (central cues) but not with exogenous stimuli (peripheral cues), it is likely that attentional capture at the time of the cue

contributes to the generation of IOR, because attentional capture by peripheral cues is conceivably stronger than central cues, leading to greater inhibition. Alternatively, the introduction of a distractor could be introducing a short-term facilitatory mechanism that interacts only with endogenous cueing (i.e., is IOR actually delayed, or is it suppressed early on). Another potential explanation is that the delay in IOR observation with central cues is related to a stimulus-response mapping bias similar to negative compatibility effect (NCE), because our targets were always peripheral (e.g., Hilchey, Satel, Ivanoff, & Klein, 2013). We discuss similarities between IOR and NCE in Chapter 7. Further experiments are encouraged to tease apart the implications of this result.

Additional support for the dissociation between input-based and output-based IOR can be seen in the varying time courses between peripheral cueing conditions with and without eye movements (Exp. 1 vs. 3). When distractors are present and eye movements are suppressed, behavioural inhibition is reduced in magnitude, if present at all – a marginally significant IOR was only observed at the CTOAs of 1,600 and 2,400 ms. This finding is in contrast with results observed without distractors, where inhibition is normally strong at much earlier time points and decays over time. On the other hand, with oculomotor activation (saccades in response to cues) inhibition was strongest at the earliest CTOA of 800 ms and then decreased in magnitude at longer CTOAs, as observed in the literature without distractors.

5.2 Study 2

One limitation of Study 1 was the lack of a control condition in our specific paradigm, which leaves open the possibility that our pattern of results was not due to the introduction of distractors. We thus sought to verify our findings by manipulating the presence of distractors in

Study 2 to ensure that distractors are the sole reason for the reduction/delay in the observation of an input-based IOR with peripheral cues and suppressed oculomotor systems. Should IOR "reappear" with the absence of distractors, we can be more confident that distractors do indeed contribute to the robustness of our finding.

5.2.1 Method.

Participants. Twenty-five students from the University of Nottingham Malaysia participated in the experiment. One participant was excluded from analysis because of a high error rate of 14.68% (the next highest rate was 7.94%), leaving 24 participants (18 females; age range: 18 to 25 years, $M = 20.5$, $SD = 1.86$). All reported normal or corrected-to-normal vision. Before starting the experiment, all participants provided informed consent. Participants received either course credit or financial compensation for their participation. The experiment was approved by the Science and Engineering Research Ethics Committee.

Design and procedure. In Study 2, we included distractor presence as a within-subjects variable, with the no-distractor condition serving as a control. We increased the total number of trials to 360, presented in four blocks of 90 trials. The distractor and no-distractor conditions were blocked (counterbalanced across participants), and each condition consisted of 180 trials in total, with half cued trials and half uncued trials and the three CTOAs equally divided. Otherwise, the procedure was identical to that of Experiment 1 in Study 1 (i.e., peripheral cues that must be ignored, CTOAs of 800, 1,600, and 2,400 ms, and manual responses).

5.2.2 Results.

Mean accuracy was 98.76% (99.68% accuracy when distractor was absent, 97.85% accuracy when distractor was present). After excluding incorrect trials (1.24% of all trials), anticipatory responses (RT < 2.5 MAD; 0.29%), and long outliers (RT > 2.5 MAD; 5.08%), statistical analyses were performed on the remaining 93.39% of all trials.

Table 5.2. Mean (and SD) of RTs and cueing effects (cued - uncued RTs) for each condition in Study 2.

	Distractor present			Distractor absent		
CTOA (ms)	Cued	Uncued	Cueing effect	Cued	Uncued	Cueing effect
800	488.65 (82.01)	482.09 (82.36)	6.56	446.90 (72.46)	427.71 (74.65)	19.19**
1600	471.65 (85.95)	456.83 (86.62)	14.82**	398.02 (67.81)	383.51 (66.52)	14.50*
2400	467.29 (82.08)	458.08 (82.15)	9.21	381.96 (66.15)	371.09 (60.68)	10.87*

Note: *$p < .05$, **$p < .01$

We performed a repeated-measures ANOVA on RTs with Distractor (absent vs. present), Cueing (cued vs. uncued), and CTOA (800 vs. 1,600 vs. 2,400 ms) as within-subjects variables (see Table 5.2). All three main effects of Distractor [$F(1, 23) = 47.10$, $MSE = 7326.93$, $p < .001$, $\eta^2 = .67$], Cueing [$F(1, 23) = 15.16$, $MSE = 745.42$, $p < .001$, $\eta^2 = .40$], and CTOA [$F(2, 46) = 65.96$, $MSE = 715.37$, $p < .001$, $\eta^2 = .74$] were significant as RTs were overall slower when distractors were present, RTs to cued trials were generally slower than RTs to uncued trials, and

RTs were faster at later CTOAs. There was also a significant CTOA and Distractor interaction [$F(2, 46) = 29.38$, $MSE = 307.53$, $p < .001$, $\eta^2 = .56$], but not between Cueing and CTOA [$F(2, 46) = 0.53$, $MSE = 246.01$, $p = .592$, $\eta^2 = .02$] or between Cueing and Distractor [$F(1, 23) = 1.28$, $MSE = 306.24$, $p = .270$, $\eta^2 = .05$]. The three-way Distractor × Cueing × CTOA interaction failed to reach significance as well [$F(2, 46) = 1.31$, $MSE = 222.35$, $p = .279$, $\eta^2 = .05$].

To examine cueing effects in more detail, planned comparisons in the form of one-tailed paired-samples t-tests were conducted. Where distractors were present, there was a significant delay in RT towards cued trials at 1,600 ms CTOA [$t(23) = 3.70$, $p = .001$, $d = 0.75$], producing a 15 ms ICE. This inhibitory effect was not significant at 800 ms [$t(23) = 1.17$, $p = .254$, $d = 0.24$] or 2,400 ms CTOAs [$t(23) = 1.61$, $p = .122$, $d = 0.33$]. When distractors were absent, the differences between cued and uncued trials were significant at all three CTOAs. We observed a 19 ms IOR at 800 ms [$t(23) = 3.22$, $p = .004$, $d = 0.66$], a 15 ms IOR at 1,600 ms [$t(23) = 2.58$, $p = .017$, $d = 0.53$], and a 11 ms IOR at 2,400 ms [$t(23) = 2.56$, $p = .018$, $d = 0.52$].

5.2.3 Discussion

In this follow-up study, we compared the effects of distractor presence in an ignore-peripheral paradigm to verify our conclusions with a within-subjects design. This comparison allowed us to directly examine the influence of distractors on the magnitude and latency of the sensory IOR. Because each experiment contained three CTOA conditions (800 vs. 1,600 vs. 2,400 ms), we could also examine whether the inclusion of distractors leads to a different time course of these cueing effects.

Results from Study 2 mirrored those of our first experiment in Study 1, with robust inhibition at all CTOAs when distractors were absent but significant inhibition only at the 1,600

ms CTOA (15 ms, $p = .001$) when distractors were present. These findings suggest that input-based IOR is delayed or reduced when a distractor is presented along with a target. This delay is likely due to the increased difficulty of the task (Lupiáñez et al., 1997; Lupiáñez et al., 2001) caused by competition from the distractor (Godijn & Theeuwes, 2002) and the nature of the discrimination-localisation task that requires not just discrimination but also a manual response to the location of the target.

5.3 General Discussion

In Study 1, we used overt and covert orienting tasks to measure the time course of IOR when distractors are introduced. Participants were presented with central and peripheral cues to which they either responded with a saccade or stayed fixated at the centre, followed by a manual response to peripheral targets at varying CTOAs. We found that input-based sensory inhibition is diminished when distractors are present. In Study 2, we confirmed that the time course of behavioural IOR remains similar in a blocked design with and without distractors. In this design, participants were presented with peripheral cues that had to be ignored, with and without distractors appearing at target onset. We found that the inclusion of distractors in a such a spatial cueing task diminished the magnitude and onset latency of behavioural inhibition when the oculomotor system is actively inhibited.

Our results indicate that at least two forms of inhibitory cueing arise when distractors are present in this cue-target paradigm, with oculomotor IOR starting early and slowly decaying and the non-motor IOR starting later but decaying quickly. Together, these observations support the notion that IOR is a relatively long lasting oculomotor novelty seeking mechanism (Posner et al., 1985) that is distinct from other neural mechanisms that lead to inhibitory cueing effects on

behaviour (Hilchey, Klein, & Satel, 2014) such as sensory adaptation (Satel et al., 2011) or habituation (Dukewich, 2009).

Further neurophysiological and neuroimaging studies could shed additional light on the mechanisms underlying the inhibitory effects demonstrated behaviourally in this study. For example, we surmise that in an event-related potential (ERP) study that implements this exact paradigm, repeated stimulation from peripheral cues and targets would manifest as a reduction in the magnitude of the early sensory P1 ERP component for cued targets compared to uncued targets, but that no P1 modulation would be observed with central cueing (e.g., Satel et al., 2014). Although a great deal of research has observed P1 modulations in spatial cueing tasks with repeated peripheral stimulation, such effects do not seem to be associated with oculomotor IOR and it is more likely that IOR is reflected in later modulation of attentional components like the Nd and N2pc (e.g., Satel et al., 2012, 2014; Satel, Hilchey et al., 2013). The N2pc has been implicated in selective visual attention (Eimer & Kiss, 2008; Woodman, Arita, & Luck, 2009; Woodman & Luck, 1999) and is thus highly promising as a neurophysiological index for oculomotor IOR. By presenting distractors along with targets in this design, the balanced sensory stimulation would allow us to more carefully examine N2pc modulations than previous research using only a single target (cf., McDonald et al., 2009). If N2pc modulation is a correlate of IOR, then at long CTOAs we would expect to observe such modulations for cued relative to uncued conditions, but only when there is oculomotor activation, thus reflecting output-based oculomotor IOR described in Posner et al. (1985). We examine the N2pc component in the next chapter.

Chapter 6 : The N2pc Component as an Index of Selective Attention in IOR

6.1 Introduction

In the previous two chapters, we examined IOR with distractors. Although we found behavioural evidence for input and output-based IOR in the presence of distractors, we found no support for P1 as a neurophysiological marker of IOR. In this chapter, we will examine the N2pc component as an index of selective attention in IOR. The N2pc (N2-posterior-contralateral) component is a negative going wave that appears around the 200-300 ms time window (or within the N2 time range), with a posterior scalp distribution that is contralateral to the attended location (Luck, Girelli, McDermott, & Ford, 1997; Luck & Hillyard, 1994a, 1994b; Woodman & Luck, 1999). Contralateral here refers to attention directed towards the left that is reflected at the right side (i.e., opposite side) of the brain and vice versa. We calculate the difference in voltages between ipsilateral (attention directed to the same side as the electrodes picking up the brain signals) and contralateral brain waves to obtain the N2pc component.

More recently, the N2pc component has been linked to the attentional selection of a target among distractors rather than the active suppression of distractor stimuli (Jolicœur, Sessa, Dell'Acqua, & Robitaille, 2006b; Mazza et al., 2009). Mazza et al. (2009) for example, varied the number of distractors (Exp. 1), distance between target and distractors (Exp. 2), and distractor homogeneity (Exp. 3), all of which should affect the difficulty in suppressing distractor stimuli. Participants responded with manual detection of whether the target of a different colour appear to the left or right of the fixation. However, there was no effect of distractor numerosity, distractor proximity, nor distractor heterogeneity on N2pc amplitudes, which suggests that N2pc is not solely a reflection of distractor suppression. Instead, the N2pc component may be a

summation of distractor-suppression and target-selection processing, both working in tandem during visual search (Hickey et al., 2009).

Studies examining N2pc in a visual search paradigm generally balance the sensory stimuli across visual hemifields (left and right half of the visual field separated vertically through the fovea) by presenting an equally salient distractor stimulus at the opposite location of the target to eliminate potential confounds that may arise due to differences in sensory processing (Hickey et al., 2009; Jolicœur et al., 2006b; Mazza et al., 2009). However, traditional spatial cue-target paradigms in IOR research only present a single target stimulus (but see Martín-Arévalo et al., 2014[5]).

This chapter is concerned with the P1, Nd, and N2pc components that have all, at one point or another, been implicated as a neurophysiological index of IOR, with an emphasis on the latter two components. Because P1 and N1 are particularly sensitive to sensory processes, differences in modulations between cued and uncued trials (Prime & Ward, 2004, 2006; Satel, Hilchey et al., 2013; Wascher & Tipper, 2004) are presumably caused by input-based IOR (or sensory adaptation at early CTOAs) rather than output-based oculomotor IOR.

Although there was a small P1 effect found to be associated with IOR in Chapter 4, we were not able to analyse the N2pc component due to unbalanced stimuli necessary for generating N2pc waveforms. To isolate the N2pc, one must subtract activity at the ipsilateral electrode sites from the contralateral electrode sites (e.g., PO7 from PO8 or PO8 from PO7). It is therefore

[5] This study used single target stimulus in extracting N2pc, with the assumption that the placeholder at the opposite location of the target serves as a "distractor" and provide equally balanced sensory stimulation at both visual hemifields. However, this practice is unusual and their findings of N2pc reduction in cued trials compared to uncued trials should be taken with a grain of salt.

crucial for stimuli to be balanced across the visual field to eliminate potential confounds that may arise from differences in sensory stimulation in lower-level visual processing.

The Nd component, a negative difference that occurs approximately 220-300 ms after stimulus onset, is derived by subtracting ERPs generated by unattended stimuli from the ERPs generated by stimuli that were attended to. It has been implicated as a cortical correlate of IOR in various studies (Hopfinger & Mangun, 2001; McDonald et al., 1999; Prime & Ward, 2004, 2006; Satel et al., 2014; Wascher & Tipper, 2004) because of two characteristics: (1) it occurs considerably later than sensory ERP components, such as P1 and N1, and (2) the difference in amplitude occurs between attended and unattended stimuli.

The N2pc component, on the other hand, has also been associated with the allocation of covert attention in visual space (Luck & Hillyard, 1994a, 1994b; Woodman & Luck, 1999, 2003). Characterised as a larger negative deflection at electrodes contralateral to an attended stimulus compared to an ipsilateral one, McDonald et al. (2009) observed attenuated N2pc when targets were cued compared to uncued targets. They suggested that the N2pc may reflect both target processing and distractor suppression (Hickey et al., 2009).

Given findings that suggest that the N2pc is a more reliable index of IOR (McDonald et al., 2009; Yang, Yao, Ding, Qi, & Lei, 2012), along with behavioural data from our time course experiments in Chapter 5, we conducted another EEG experiment to determine whether N2pc is a reliable neurophysiological index of output-based IOR. To test this hypothesis, we explored IOR using the same combination of stimuli and responses as described in the previous chapter for the saccade-to-peripheral cue experiment at a CTOA of 1,200 ms. The saccades engage the oculomotor system, and there is enough time for oculomotor IOR effects to emerge. Distractors,

appearing opposite target stimuli, allow us to measure the N2pc component, because visual stimulation is balanced across visual hemifields.

We predicted that there would be P1 cueing effects because of repeated stimulation at the same location for cued trials. We did, also, expect to see an enhancement of Nd (Satel et al., 2014). More pertinent to the goal of this study, we also predicted that we would find significant N2pc components where the difference between contralateral and ipsilateral waveforms is greater than zero, with attenuation on the cued trials due to modulation from inhibitory cueing effects.

6.2 Method

This experiment used a within-subject design.

6.2.1 Participants.

Thirty-eight students from the University of Nottingham Malaysia participated in the experiment for course credit or monetary compensation. We excluded the data of one participant from the analyses, because they completed less than 50% of all trials, whereas another participant was excluded because of relatively high error rate (> 10%). The remaining 36 participants (20 females) were aged between 19 and 32 years (M = 21.28, SD = 3.04). Two participants self-reported as being left-handed. All participants reported normal or corrected-to-normal vision with no neurological or psychiatric disorders. The experiment was approved by the Science and Engineering Research Ethics Committee.

6.2.2 Stimuli and apparatus.

The stimuli and apparatus used in this experiment were similar to those of the EEG experiments described in Chapter 4. We recorded EEG from participants in a dimly lit Faraday cage to minimise electromagnetic interference, using 32-channel geodesic sensor nets (rather than the 128-channel nets used in Chapter 4) with impedances kept below 50 kΩ at the beginning of the experiment (see Appendix, Figure 2 for channel layout). Data were sampled at 250 Hz using EGI amplifiers with NetStation software (Version 4.5.7; Electrical Geodesics, Inc., Eugene, OR) running on an Apple Macintosh, Mac Pro 5.1 computer (2.8 GHz Quad Core Intel Xeon, Mac OS 10.6.8 Snow Leopard) that was connected to the stimulus presentation computer.

All stimuli were presented in white on a black background, with two peripheral boxes (visual angle at 4.5° x 4.5°) as placeholders 8.7° to the left and right of a 0.8° x 0.8° fixation cross that was displayed at the centre of the screen. Participants were seated in front of a 24-inch BenQ gaming monitor with their head on a chin rest positioned approximately 57 cm away from the screen. Stimuli were drawn with MATLAB running on a Windows 7 computer connected to an EyeLink 1000 Plus (SR Research, Ontario, Canada) eye-tracking system host computer. The desktop-mounted eye-tracker was used to monitor participants' eye movements at a sampling rate of 250 Hz. The experiment was programmed and implemented in MATLAB using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and EyeLink Toolbox (Cornelissen et al., 2002) extensions.

6.2.3 Design and procedure.

After providing informed consent, participants were familiarised with the experimental procedure with 24 practice trials (which were excluded from the analyses). The main experiment

consisted of 4 blocks of 75 trials for a total of 300 trials per participant, with breaks between each block. Figure 6.1 describes the sequence of stimuli presented in each trial. A randomly selected inter-trial interval ranging between 1,000 and 1,500 ms elapsed before the start of each trial. In all other respects, the recording procedure was identical to experiments in Chapters 3 and 5.

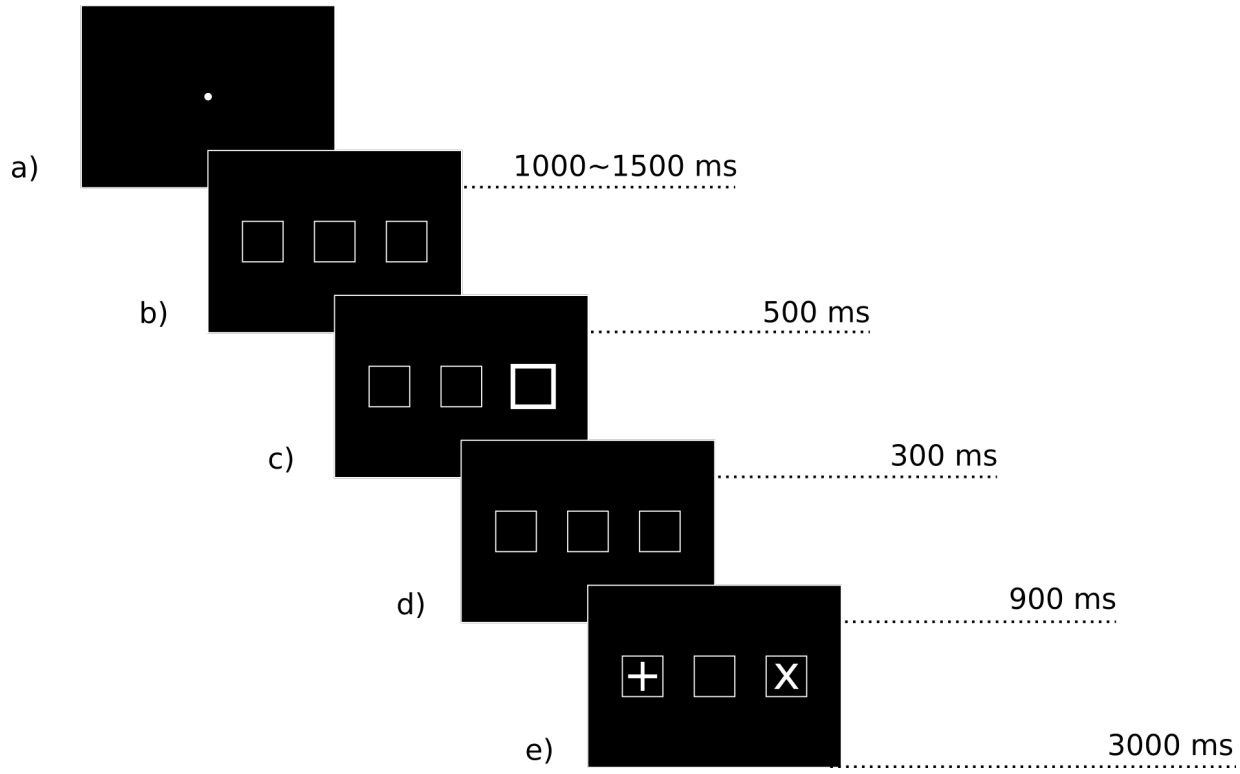

Figure 6.1. An illustration of the trial sequence used. Participants were instructed to make a saccadic response to cues followed by a manual response to targets.

6.2.4 EEG pre-processing.

EEG pre-processing procedures were identical to that of Chapter 3, with a few exceptions. In this experiment, ERPs were extracted from electrode sites O1/O2 (corresponding to EGI electrodes 9 and 10) instead of PO7/PO8, because we were reliant on available electrode

locations on the 32-channel EGI nets (see Figure 2 of the Appendix). During pre-processing, we discarded seven datasets that had O1/O2 electrodes identified as bad channels. Data from one other participant was excluded from further analyses because they completed less than half of the experiment leading to insufficient trials left after pre-processing, whereas two participants were removed due to technical difficulties. This procedure left 26 datasets that were subjected to statistical analyses of the ERP results.

Of the 26 datasets, participants made incorrect responses on 2.70% of all trials which were excluded from further analyses. We also filtered our data to exclude anticipatory responses (individual mean RT < 2.5 MAD; 2.66%) and slow responses (individual mean RT > 2.5 MAD; 9.47%). A further 2.36% of the trials that was identified as noisy by the algorithm was removed. Statistical analyses were performed on the remaining 82.81% of all ERP trials.

The N2pc components were formed by computing contralateral (average of targets in the left visual hemifield as recorded by electrodes over the right hemisphere and vice versa) minus ipsilateral (average of targets in the left visual hemifield as recorded by electrodes over the left hemisphere and vice versa) waveforms. A larger N2pc would thus appear as greater negative deflection due to greater negativity over the hemisphere contralateral to the target location.

6.3 Results

6.3.1 Behavioural performance.

Mean accuracy was 98.10% for this experiment. After excluding incorrect trials (2.07% of all trials), anticipatory responses (RT < 2.5 MAD; 0.15%) and long outliers (RT > 2.5 MAD; 4.87%), statistical analyses were performed on the remaining 92.91% of all trials. Paired-sample t-tests of the mean correct RT data revealed 18 ms of behavioural IOR where the means of cued

trials (M = 409.96, SD = 46.49) were significantly slower than the means of uncued trials [M = 391.80, SD = 42.08), $t(35) = 5.68$, $p < .001$, $d = 0.95$]. We can thus confidently state that behavioural IOR was generated in this cue-target paradigm despite the presence of a distractor.

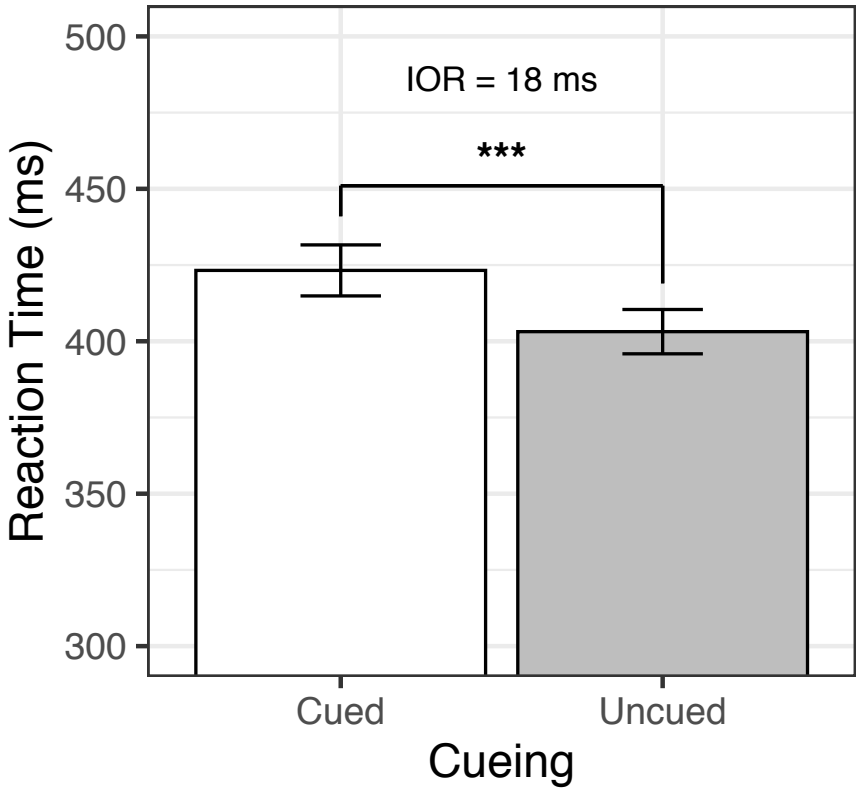

Figure 6.2. MRTs in response to targets. Asterisks (***$p < .001$) and standard error bars are shown, which indicate that mean RTs for cued targets were significantly slower than RTs for uncued targets.

6.3.2 ERP results.

Mean amplitude of P1 and Nd ERP components are presented in Table 6.1, whereas grand average waveforms are illustrated in Figure 6.3. Cueing effects were calculated by subtracting mean RTs and amplitudes to uncued targets from cued targets.

The mean amplitude of the P1 component was extracted from electrodes O1 and O2, with a 40 ms time window centred around the first highest peak in the ipsilateral and contralateral grand average waveforms. Two-tailed one-sample t-tests revealed no P1 cueing effects in both electrodes ipsilateral [$t(25) = 0.07$, $p = .946$, $d = 0.01$] and contralateral [$t(25) = -1.44$, $p = .162$, $d = 0.28$] to the target stimuli. Lack of differences in P1 amplitudes, which reflect early sensory activity in the extrastriate visual cortex, indicate that low-level sensory processing at the cue did not affect responses to repeated targets.

The Nd component was quantified as mean amplitude at O1/O2 between 220 and 300 ms post-target stimulus. Nd was reduced for cued trials versus uncued trials at contralateral electrode sites [$t(25) = -2.56$, $p = .017$, $d = 0.50$] but not ipsilateral electrode sites [$t(25) = -0.92$, $p = .365$, $d = 0.18$].

Table 6.1. Mean ERP amplitudes for cued and uncued targets.

		Cued	*Uncued*	*Cueing effect*
P1 (μV)	*Ipsi*	1.12 (2.13)	1.11 (2.00)	0.01
	Contra	1.00 (2.07)	1.27 (2.15)	-0.27
Nd (μV)	*Ipsi*	1.07 (2.56)	1.28 (2.93)	-0.22
	Contra	0.84 (2.47)	1.40 (2.85)	-0.56*

*$p < .05$.

Mean amplitude of event-related lateralisations (ERL) are presented in Table 6.2, whereas difference waveforms are illustrated in Figure 6.4 and Figure 6.5. In addition to the N2pc component, which we set out to investigate, we also found hemispheric asymmetry in the

post-target N1 time window, as well as a late lateralised component following the N2pc, that we infer to be a form of sustained posterior contralateral negativity (SPCN) in the Discussion.

Statistical comparisons between contralateral and ipsilateral waveforms in the N1 range, which we refer to as the N1pc, were performed around the mean peak of 108 ms (+/- 20 ms). At the 88~128 ms time window, one-sample t-test revealed a significant N1pc in cued trials [$t(25) = -2.47$, $p = .021$, $d = 0.48$] but uncued targets did not show hemispheric differences [$t(25) = 1.65$, $p = .111$, $d = 0.32$]. The N1pc component in cued trials was eliminated when targets were not cued, resulting in significant cueing differences [$t(25) = -2.92$, $p = .007$, $d = 0.57$].

For the N2pc component, we extracted mean amplitudes from a 40 ms time window centred around the largest difference between contralateral and ipsilateral waveforms (mean peak at 220 ms) for cued and uncued trials separately. A one-sample t-test revealed a significant N2pc in cued trials [$t(25) = -4.04$, $p < .001$, $d = 0.79$] but not in uncued trials [$t(25) = -1.15$, $p = .260$, $d = 0.23$]. We also compared the two types of trials and found a significant reduction in cued trials compared to uncued trials [$t(25) = -2.98$, $p = .006$, $d = 0.58$] within the 180~260 ms time window, as shown in Figure 6.5.

Finally, centred around the mean peak of 312 ms (+/- 40 ms, time window 272~352 ms), target-elicited contralateral positive deflections were significantly greater than ipsilateral deflections only when targets were uncued [$t(25) = 4.19$, $p < .001$, $d = 0.82$], whereas ERPs in this same time window recorded from the two hemispheres did not differ when targets were cued [$t(25) = -0.74$, $p = .464$, $d = 0.15$]. ERL amplitudes differed significantly between cued and uncued targets [$t(25) = -4.25$, $p < .001$, $d = 0.83$], with the presence of cues effectively eliminating hemispheric differences observed with uncued targets, indicating an SPCN that occurs in uncued trials only.

Table 6.2. Mean ERL (Contralateral-Ipsilateral) amplitudes for cued and uncued targets.

	Cued	*Uncued*	*Cueing effect*
N1pc (μV)	-0.19 (0.38)*	0.12 (0.38)	-0.31**
N2pc (μV)	-0.52 (0.66)***	-0.09 (0.40)	-0.43**
SPCN (μV)	-0.08 (0.54)	0.48 (0.58)***	-0.56***

*$p < .05$; **$p < .01$; ***$p < .001$.

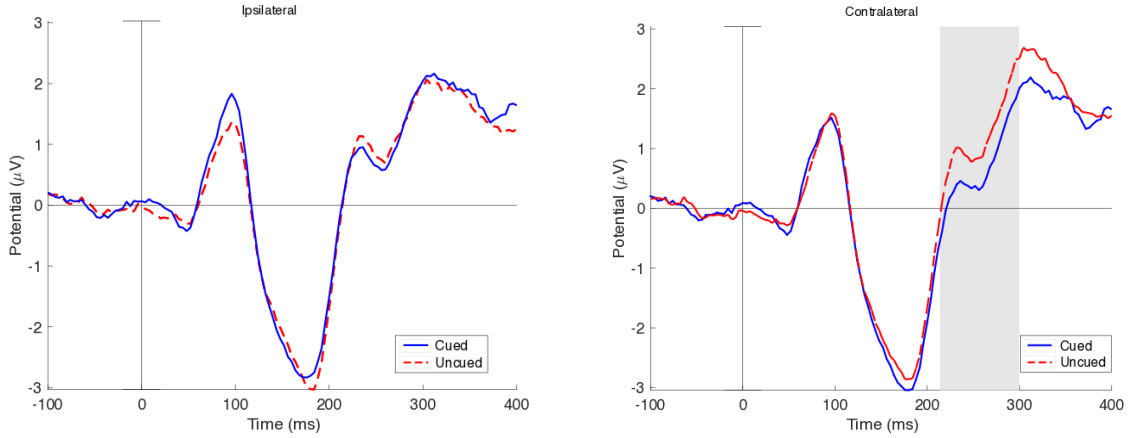

Figure 6.3. Grand average ERPs elicited at occipital electrode sites O1 and O2 for cued (blue solid lines) and uncued (red dashed lines) trials that were ipsilateral and contralateral to target location. Gray shadings in the contralateral panel denote the 220-300 ms time window where there is a significant difference between cued and uncued trials.

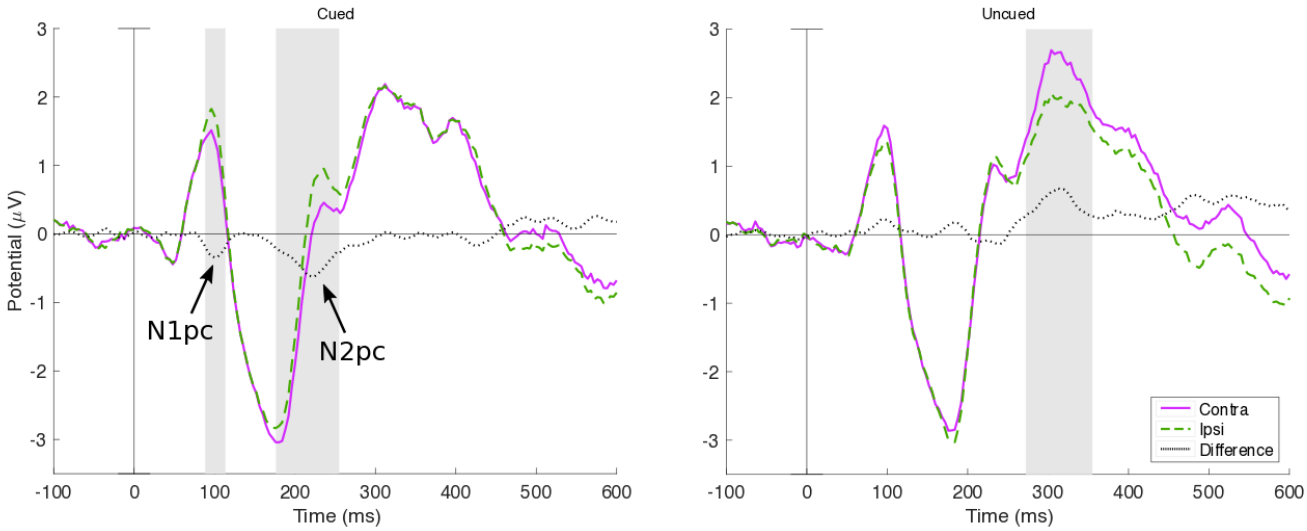

Figure 6.4. Contralateral (purple solid lines) minus ipsilateral (green dashed lines) difference waveforms for cued and uncued trials, time-locked to target onset at posterior electrode sites O1/O2. Gray shading denote the time window where hemispheric differences were significant, e.g., N2pc is observed at 180~260 ms in cued trials.

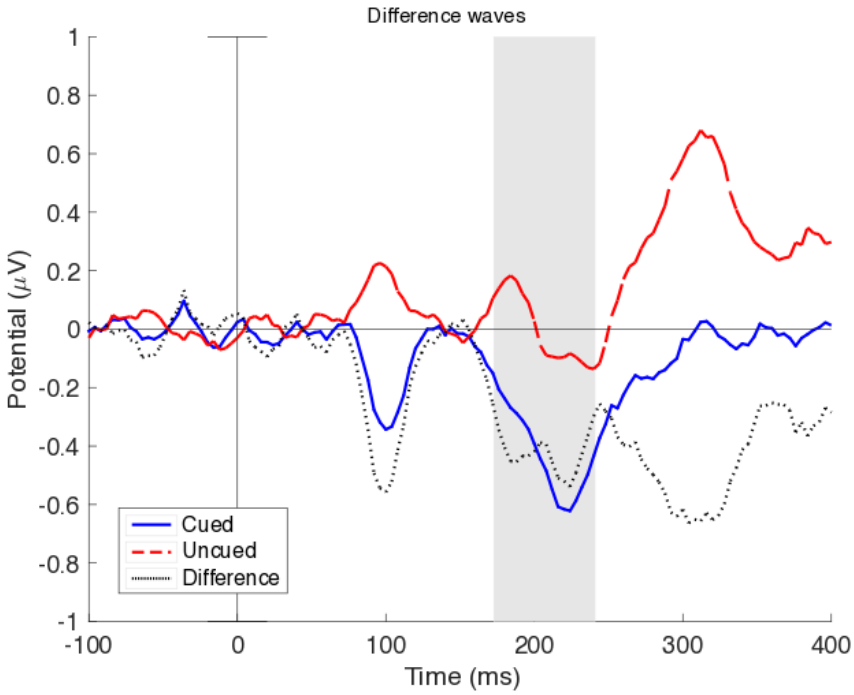

Figure 6.5. Grand average contralateral minus ipsilateral difference waveforms time-locked to target onset at posterior electrode sites O1/O2.

6.4 Discussion

The goal of the present study was to establish the N2pc component as a reliable index of output-based oculomotor IOR in a spatial cueing paradigm. Because ERPs are sensitive to low-level sensory differences, it is necessary for our stimuli to contribute equally to the averages for both cued and uncued conditions. The introduction of distractors allowed for such a visually balanced design that is crucial for the computation of N2pc. We also explicitly required eye movements to the cue to activate the oculomotor system, thereby eliciting output-based IOR.

Indeed, behavioural analysis showed a robust IOR effect of 18 ms, despite the presence of distractors that presumably reduced capture of attention at the target locations. This output-form of behavioural IOR echoes what we had previously reported in Chapters 4 and 5 (Eng et al., 2016; Eng, Lim, Janssen, & Satel, 2018; but see Pratt & Abrams, 1999 for counterevidence). The main finding from this chapter, however, is that the ERP analyses showed no P1 cueing effects, but significant differences in Nd and N2pc components. We discuss each component in the temporal order of their occurrence.

6.4.1 P1 component.

To reiterate, P1 is thought to correspond to early sensory-perceptual processing. In our paradigm, P1 amplitudes for cued trials should be reduced due to repeated stimulation at the same location (Satel et al., 2014). However, we found no cueing effects on P1 amplitudes. Our results are inconsistent with several studies that have found P1s for targets at the cued location to

be reduced in amplitude at late CTOAs (e.g., Prime & Ward, 2004, 2006; Satel, Hilchey et al., 2013; Wascher & Tipper, 2004).

To understand the relevance of the absence of the P1 cueing effect requires disentangling of the previously muddled mechanisms underlying behavioural IOR: sensory adaptation, input-based IOR, and output-based IOR. At early CTOAs (< 500 ms), sensory adaptation could be one of the contributing factors to behavioural inhibition (Lim et al., 2018). P1 effects found with early CTOAs could be indexing just sensory adaptation (Luck & Hillyard, 1994a). However, sensory adaptation is relatively short-lasting and therefore should not be affecting behavioural responses at long CTOAs (1,200 ms in our paradigm). The P1 effect found elsewhere at late CTOAs (e.g., McDonald et al., 2009; Yang et al., 2012) could therefore reflect input-based IOR, not oculomotor IOR, given that no eye movements were permissible in those studies. When eye movements were explicitly required, as was the case in one study requiring foveation to peripheral cues (Satel, Hilchey et al., 2013), P1 was still significantly reduced in the cued condition but this reduction did not correlate with RT cueing effects. We surmise that the absence of a P1 cueing effect is due to the presence of distractors that eliminated the P1 cueing effect. Although sensory adaptation is not a factor at this CTOA, input-based IOR still involves a sensory/attentional component.

Alternative explanations for our findings could be: (1) the lack of a cue-back leading to less efficient return of attention to the fixation, which is especially relevant because (2) the presence of a distractor creates competition with the target, thereby covert attention is further reduced. At the same time, it has been pointed out that the P1 effect does not necessarily need to be present when behavioural IOR is observed (Satel, Hilchey et al., 2013), so either the P1 effect is not sensitive enough to detect differences all the time, or the P1 component may be modulated

by cueing, but overlapping in time with another neural generator source that differs for cued and uncued targets. Multiple overlapping components are common in ERP research (Luck & Kappenman, 2011).

Outside of the IOR literature, Clark and Hillyard (1996) have shown that stimuli at attended locations elicit an enhanced P1 component at both ipsilateral and contralateral scalp sites compared to unattended locations (Clark & Hillyard, 1996; Hillyard, Vogel, & Luck, 1998). If attention was drawn to the target location and inhibited when cued, we should find a reduced P1 compared to uncued targets. However, because we presented a distractor alongside the target, attention to the target could be drawn away by the distractor, thereby eliminating differences between cued and uncued target-elicited P1. More research specifically looking at late CTOA input-based IOR will help clarify sensory and attentional modulation in the ERPs.

6.4.2 Nd component.

The Nd component in our paradigm occurred at 220~300 ms at electrode sites contralateral to the target stimuli location, with amplitudes to cued targets attenuated compared to uncued targets. Previously examined with spatially non-predictive peripheral cues and single targets, the Nd component is usually most pronounced at parietal-occipital sites PO7/PO8 or midline electrode Pz (Martín-Arévalo et al., 2014; Prime & Ward, 2004, 2006; Wascher & Tipper, 2004). Although the exact time window and electrode locations are different, our results are also consistent with Eimer (1994) who used distractor-target stimuli (manual response to "M" or "W" on either side of fixation) and found Nd differences to be maximal at midline electrodes (220~280 ms time window), as well as a relatively early Nd at 130~180 ms time window at ipsilateral electrodes.

We know that vision works by processing visual information contralaterally to the attended object (i.e., item perceived in the left visual field is processed in the right occipital cortex, whereas the right field is processed on the left). In other words, visual processing is lateralised with respect to the position of the attended object. However, the implications of a component that is generated exclusively in the ipsilateral hemisphere (e.g., the Nd in Eimer, 1996) versus one that is observable in the contralateral hemisphere (e.g., the Nd in this chapter) are unclear.

Of note, none of the studies discussed above actively monitored participants' eye movements. A few others have made use of horizontal electro-oculogram (HEOG) to keep track of and thereafter exclude trials with eye movements (Spencer et al., 2011; Van der Lubbe et al., 2005). Given the mounting evidence supporting the role of oculomotor activation in output-based IOR, as Hilchey, Klein, and Satel (2014) pointed out, studies that rely on participants' compliance to experimental instructions without monitoring eye movements often do not allow for clear dissociation of input-based vs. output-based IOR. Using an eye-tracking system, we were able to provide trial-by-trial feedback while making sure that there were no unintentional shifts of attention (only intentional foveated shifts of attention at S1) during data collection. Therefore, our results provide a more definitive interpretation for the Nd component playing a role in oculomotor IOR.

6.4.3 Lateralised components.

Having considered the early ERP components previously associated with IOR, we will next examine event-related lateralisations (ERLs) that emerged when ipsilateral waveforms were subtracted from contralateral ones. One well studied ERP hemispheric asymmetry is the

lateralised readiness potential (Coles, 1989; Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988). When making a manual response with one hand, cortical activation is greater over the motor cortex contralateral to the responding hand relative to the ipsilateral side. In visual attention, covert attention to a stimulus on one side of the visual field (e.g., the left visual field) can be observed in ERPs as a more negative potential at the contralateral side of the brain (over the right posterior area), and vice versa. The difference in amplitude between contralateral and ipsilateral electrodes around the N2 time window, a component known as the N2pc, has been studied in relation to IOR.

In our study, this potential electrophysiological marker, the N2pc, can be seen prominently in the cued condition beginning around 150 ms. Whether N2pc is a reflection of the detection and selection of task-relevant stimuli (Eimer, 1996), or the spatial filtering of irrelevant information (Luck & Hillyard, 1994b), our hypothesis was that N2pc should be attenuated for cued compared to uncued trials (McDonald et al., 2009; Pierce, McDonald, & Green, 2018). Recent findings suggest that what we used to think of as N2pc is actually made up of two subcomponents around the N2 time window (Hickey et al., 2009): a negativity contralateral to targets linked to the enhancement of targets, and a positivity contralateral to distractors (i.e., ipsilateral to targets) linked to the active inhibition of distractors. Should IOR, an inhibitory mechanism, work by reducing the enhancement of targets, the N2pc should appear smaller in the cued condition compared to the uncued condition, assuming that the inhibition of distractors would stay the same. Although we observed an N2pc in the cued condition, we did not find this difference to be "smaller" than the uncued condition.

Interestingly, uncued trials showed a small (but not statistically significant) N2pc of inverse polarity similar to the distractor positivity (P_D) observed in Hickey et al. (2009). Their

results suggested that P_D reflects an inhibitory mechanism that acts on the cortical representation of distractor stimuli. Like Sawaki and Luck (2010), who also found a P_D component to salient coloured distractors, our P_D component in the uncued condition shows up a little bit earlier than the N2pc. Somehow, in our uncued condition, distractors acted like they were more salient, despite being exactly the same as the distractors in our cued condition. It is unclear what could have influenced the direction of these results. We would have assumed that in the uncued condition (where RTs are faster), a distractor is easier to suppress, whereas the target is easier to detect. As much as it makes sense for P_D to occur, given that there is distractor suppression involved, it does not seem to make sense for P_D to be more prominent in the uncued condition than the cued condition, to the extent that it eliminates the negativity in N2pc.

6.4.4 Speculative components.

Besides the N2pc, we observed a negative-going deflection in the cued condition occurring before the N2pc and a corresponding positive deflection occurring before the P_D peaking around 100 ms. Although we first set out to investigate the N2pc component, other ERLs emerged unexpectedly. ERP hemispheric asymmetries in the form of a posterior, lateralised component around the N1 time window (peaking around 100 ms), which we shall refer to as the N1pc, has been linked to the activation of saccades, or shifts of attention to relevant stimuli (Akyürek & Schubö, 2011; Wascher & Beste, 2010).

In a study by Wauschkuhn et al. (1998) studying saccade preparation, negativity was shown to increase contralateral to saccade direction around 100 ms before saccade onset. However, this negativity does not account for the N1pc that we found in our cued condition, because saccades were made to the cue in our experiment, not to the target. With a relatively

long CTOA of 1,700 ms, we expect residual eye movement to the cue artefacts to be minimal. More importantly, modulations caused by saccade direction (if any) should be cancelled out in our paradigm, whether cued or uncued, because there is a 50-50 chance that the cue appears to the left or right side of the fixation.

Wascher, Hoffmann, Sänger, and Grosjean (2009), on the other hand, found N1pc under quite different circumstances, using a paradigm requiring no eye movements at all. Following a cue (filled circle in one of two placeholder boxes to the left and right of fixation), participants responded via manual detection to the target (central: target at fixation, or peripheral: thickening and changing of colour of both flanking placeholder borders). At a CTOA of 160 ms, ERLs at PO7/PO8 time-locked to cue onset revealed an early N1pc. When the target appeared, whether centrally located or peripheral to the fixation, a reversed N1pc emerged as a positive deflection with similar latency and topography to the typical N1pc, despite a visually balanced target array. Although not easily comparable, because their short CTOA (200 ms) lies within a time window where facilitation and sensory adaptation are likely to co-occur (which was not the focus of their study), it is nonetheless intriguing that lateralised cues followed by visually balanced target can elicit hemispheric asymmetry in the target-elicited ERP. The increased negativity that is contralateral to the relative position of the target, instead of the absolute position of the target, led Wascher et al. (2009) to postulate that peripheral cue onset led to a rapid remapping of the visual space from retinotopic to spatiotopic coordinates.

In a series of experiments closely following and extending upon Wascher et al. (2009), Casiraghi, Fortier-Gauthier, Sessa, Dell'Acqua, and Jolicœur (2013) argued that the remapping of visual space could be instead explained by the neural adaptation hypothesis. Their study demonstrated that N1pc is the result of greater adaptation in the form of temporary reduced

neuronal reactivity in the hemisphere contralateral to representation of the cue in cortical visual areas where a matching target was displayed. The direction of our N1pc is consistent with Casiraghi et al. (2013): a typical N1pc was observed in the cued condition (similar to the matching condition) only, when there was repetition of the stimulus at the target location. However, neuronal adaptation (i.e., sensory adaptation) cannot account for our pattern of results because again, at a CTOA of 1,700 ms, adaptation effects should be long gone (Lim et al., 2018), leaving output-based IOR as the only other viable interpretation for our observations.

Finally, electrophysiological results also revealed lateralised activity resembling a sustained posterior contralateral negativity (SPCN), most prominently with uncued trials beginning around 260 ms. The SPCN typically follows the N2pc component in a contralateral-ipsilateral difference wave where visual short-term working memory is involved (Brisson & Jolicœur, 2007, 2008; Jolicœur, Brisson, & Robitaille, 2008; Jolicœur, Sessa, Dell'Acqua, & Robitaille, 2006a, 2006b; Luria, Balaban, Awh, & Vogel, 2016; Schneider, Hoffmann, & Wascher, 2014), strikingly similar to the contralateral delay activity (CDA; McCollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004) and perhaps the same as the contralateral negative slow wave (CNSW; Klaver, Talsma, Wijers, Heinze, & Mulder, 1999). Measured at posterior scalp sites with negativity greater at electrodes contralateral to the visual hemifield where stimuli are located, SPCN is often present in tasks where lateralised target stimuli had to be maintained in visual short-term working memory. The component is further shown to be modulated by processing load, whereby increased SPCN amplitude reflected an increase in processing load (Jolicœur et al., 2008). Similarly, Schneider et al. (2014) found SPCN to be larger in amplitude when target discrimination was complicated by distractor.

Kiss, Van Velzen, and Eimer (2008) examined the SPCN with both predictive and non-predictive spatial cueing paradigms. Participants were to covertly attend to central cues, followed by an 800 ms CTOA prior to a search array onset, at which point manual responses were required in a discrimination task. Two of their findings are relevant to our experiment: one, their search target arrays were presented on screen for 200 ms, which required participants to hold in their working memory a representation of the search array to make a correct discrimination response. Therefore, it made sense that the SPCN would be present. However, given that our target array remained on the screen until a response was made, there was no need to hold target location in one's working memory, so there must be something else going on as well. Which brings us to Kiss et al.'s (2008) second observation: predictive cues elicit larger SPCN amplitude at the target, suggesting that informative spatial cues facilitate target processing by modulating the visual short-term working memory processes. Brisson and Jolicœur (2008) also used a predictive cueing paradigm (80% predictability), eliciting greater SPCN deflection for invalid trials compared to valid trials.

Although facilitation is reflected in bigger SPCN amplitudes, it is not clear how inhibition is reflected. Unlike the aforementioned studies, we used a spatially non-predictive cueing paradigm with a relatively long CTOA, where there should no longer be any behavioural facilitation towards cued targets. Instead, we expected (and demonstrated) behavioural inhibition. Because cues were non-informative (and participants were reminded of that prior to the start of the experiment), there was little reason for cueing to affect SPCN, because working memory load was presumably equivalent for cued and uncued trials during response to target. Where spatially non-informative peripheral cues are concerned, perhaps the lack of an SPCN with cued targets is indicative of oculomotor inhibition. Note that even invalid trials (Brisson &

Jolicœur, 2008; Kiss et al., 2008) showed an SPCN, albeit smaller than on valid trials. So even without facilitation, SPCN seems to occur. It is conceivable that SPCN differences could be eliminated with inhibition. In any case, the observed ERL differences between cued and uncued targets point towards underlying mechanisms that are closer to the output-end of IOR due to our design of the experiment involving oculomotor activation at late CTOAs.

Chapter 7 : General Discussion

7.1 Overview of Research Objectives

A question that remains unanswered in vision research is how our visual system keeps track of where attention has already been allocated so that it does not keep returning to the same location/object. This tendency to avoid returning to locations that have already been attended is called inhibition of return. In addition, when inhibition of return does occur, it is not clear what the underlying mechanisms are that present as slowed reaction time to cued locations, given sufficient delay between cues and targets. This slowed reaction, or behavioural cost, observed at long cue-target intervals (i.e., behavioural inhibition) were first ascribed to attentional mechanisms (Posner et al., 1985) that can be modulated at the perceptual (Handy et al., 1999) and cognitive-response level (Klein & Taylor, 1994). The idea is that a tag is applied at the cued location to discourage return of attention to said location, thereby encouraging the exploration of novel locations (Klein, 1988).

Research suggests that there are at least two tagging mechanisms: one that affects the input-end of the information processing cycle, before target selection, and one that acts upon the output-end of the visual system, at the oculomotor response level (Klein & Redden, 2018). Rather than discrete processes, here we make the assumption that cognitive processes encapsulate multiple stages of the information processing line, beginning with the decoding of sensory inputs, the processing of sensory information, and the transformation of such information into behavioural outputs. To examine input and output-based IOR, the research presented here explored late inhibitory cueing effects using two variants of the Posnerian cue-target paradigm. In the first variant, we manipulated task-set and stimulus-response compatibility

within saccadic and manual response modalities. In a compatible trial, the target and response locations are congruent (i.e., pro-saccades and pro-localisation responses), whereas target and response locations are incongruent for incompatible trials (i.e., anti-saccades and anti-localisation responses). Pro-saccades are generally considered to be reflexive, whereas anti-saccades involve volitional processes (Kristjánsson, 2007; Munoz & Everling, 2004). Klein and Hilchey (2011) proposed that the input-form of IOR is generated when anti-saccades to cues are used to generate the inhibitory effect, because reflexive eye movements to a salient stimulus were necessarily suppressed in order to perform an anti-saccade. Should that be the case, we wondered if we would we still see the same patterns when S-R compatibility is with targets instead of cues.

The second variant consisted of a series of experiments that utilised a single distractor alongside a single target. This paradigm takes us one step closer to visual search paradigms, which typically involve a search array with multiple distractors. We questioned whether the presence of a distractor eliminates IOR, and, if not, we wanted to know how the temporal dynamics of inhibition change with spatial repetition of the cue-target stimuli.

Finally, with both variants of the paradigm, we examined the underlying ERP components to investigate more directly whether the inhibitory effects act upon the input-end of visual processing, before response selection, or later, at the output-end that is oculomotor-related. Inconsistencies in ERP components identified as neurophysiological correlates to IOR (Martín-Arévalo et al., 2016) have motivated investigation using the above two variants of the Posnerian cueing paradigm. If inhibition has an effect on oculomotor processes, this effect should be reflected as differences in the N2pc component in a paradigm where there was oculomotor

activation (saccade to cues). Table 7.1 below outlines the list of key manipulations in each experimental chapter.

The approaches taken in previous studies have primarily focused on early inhibitory effects at short CTOAs (i.e., sensory adaptation) or late inhibitory effects without oculomotor inhibition that only represent input-based IOR. The experiments in this dissertation address specifically the distinction between late input and output-based IOR. We made sure that eye-tracking was incorporated in all behavioural and EEG experiments presented to prevent unintentional shifts of attention. The overall findings will be discussed in relation to literature on multiple inhibitory cueing effects contributing to IOR, with considerations for future research.

Table 7.1. Overview of key manipulations.

Chapter	*Exp*	*Task*	*Response*	*CTOA (ms)*
2		Compatible/incompatible	Ignore-saccade / Ignore-manual	1,500
3		Compatible/incompatible (w/ ERP)	Ignore-manual / Saccade-manual	1,500
4	1	Distractor (w/ ERP)	Ignore-manual	1,200
	2	Distractor	Ignore-saccade	
5	1 & 2	Distractor time-course	Ignore-manual	800/1,600/2,400
	3 & 4		Saccade-manual	
6		Distractor (w/ ERP)	Saccade-manual	1,700

7.2 Attentional Control Settings (Intermixed vs. Blocked Trials)

In Chapter 2, we examined the IOR effect with compatible and incompatible tasks when manual or saccadic responses were made to the target in both mixed and blocked trials. In all four experiments, a robust IOR effect was observed for compatible tasks regardless of response modality. It is less clear cut in the incompatible tasks. For incompatible tasks, IOR occurred for manual responses regardless of whether the task was mixed or blocked, but there was no IOR when saccadic responses were made. Instead, for anti-saccades, we found facilitation in the mixed-design experiment and no cueing effect in the blocked-design experiment.

We surmise that the element of uncertainty in mixed trials conceivably places greater demands on attentional resources as participants had to randomly switch back and forth between pro- and anti-saccades. On top of the already difficult task, there was an additional memory component involved as participants in the mixed-design experiments also had to remember that the green cue-back indicated that a compatible response was required, whereas the red cue-back indicated that an incompatible response was required. This switch cost could interfere with task set reconfiguration by interacting with the shifting of attention, whether it is inhibition of task-set related stimuli in the previous trial or the activation of the current task-set (see Monsell, 2003, for a review on task switching). For example, although cues are always irrelevant (i.e., cues have a 50-50 chance of predicting target location) in our experiments, requiring participants to constantly be on guard for which task-set to maintain (pro- or anti-) may have established an attentional control setting (ACS; Folk et al., 1992; Ivanoff & Klein, 2003) to be more vigilant throughout each trial, thereby encouraging attention to remain engaged at the cued location, leading to the elimination or delay of IOR.

We know that more difficult tasks can result in delayed onset of inhibition from the works of Lupiáñez and colleagues (Lupiáñez, Milán et al., 1997, 2001; Lupiáñez & Milliken, 1999). In a colour discrimination task where one responds depending on the colour of the target, Lupiáñez et al. (1997) showed that inhibition in a more difficult discrimination task begins at a later CTOA (around 700 ms) than does inhibition in simple detection tasks. Similarly, Lupiáñez et al. (2001) found that inhibition emerged at a 700 ms CTOA when discriminating between "X" and "O", which was further delayed until a 1,000 ms CTOA in a more challenging discrimination task between "M" and "N". By comparing regular and perceptually degraded targets that are more difficult to ascertain, Castel, Pratt, Chasteen, and Scialfa (2005) found that the onset of inhibition occurred later for harder detection tasks as well. Given the complexity of our task, inhibition could be extremely delayed when pro- and anti-saccade trials are intermixed (i.e., even later than 1,500 ms), but only moderately so for the blocked trials. Future research could determine the growth and decay of inhibition by exploring temporal dynamics of IOR at CTOAs greater than 1,500 ms.

7.3 S-R Activation-Inhibition (Compatibility)

Although the experiment described in Chapter 2 required compatible and incompatible responses where participants made pro- and anti-saccades to peripheral *targets*, Hilchey et al. (2016) required pro- and anti-saccades to peripheral *cues* to generate IOR instead. Their variant of this paradigm measured IOR with spatially congruent manual localisation responses to central arrow targets (also see Redden, Hilchey, & Klein, 2016, for responses to peripheral targets). Indeed, with oculomotor activation during pro-saccades, they found a robust IOR effect that was predominantly output based. Anti-saccades, however, generated an IOR effect that was closer to

the input form and could not be measured with manual responses to central targets. This finding is in accordance with Klein and Hilchey's (2011) hypothesis of an input-based form of IOR that develops upon oculomotor suppression. However, it does not explain the pattern of results presented here where an IOR effect was observed with incompatible responses when the oculomotor system was suppressed (in the manual incompatible condition) but not when it was activated (in the saccadic incompatible condition).

We also took into consideration that IOR in our paradigm could be mediated by the Simon effect (Simon & Rudell, 1967), a phenomenon whereby RTs are faster when stimulus and response location are spatially congruent. Specifically, at long CTOAs, the Simon effect is seen to be enhanced at the cued location (Ivanoff, Klein, & Lupiáñez, 2002), and interacts with IOR effects (Klein & Ivanoff, 2011). If anti-saccades generate the input form of IOR because of oculomotor suppression and pro-saccades generate the output form of IOR because of oculomotor activation, then it is unclear why there was neither input nor output IOR when incompatible saccade responses were required to the target, even if the Simon effect is taken into account.

The experiments in Chapter 2 all required fixation at the centre during presentation of the cues. In Chapter 3, we used saccades to cues to engage the oculomotor system, in search of neurophysiological evidence for output-based IOR. Although we found significant behavioural IOR with both manual and saccadic responses, ERP evidence was less compelling. The P1 effect we were expecting due to repeated peripheral stimulation was in the right direction (cued attenuated relative to uncued) but did not reach significance. Several researchers have suggested that modulations of the P1 ERP component reflect early sensory processes associated with IOR whereby neural activity is less positive for cued trials relative to uncued trials (Luck &

Kappenman, 2011). This suggestion has also been supported by single cell recording studies on monkeys when they were performing a spatial cueing task (Fecteau & Munoz, 2005).

However, recent studies have highlighted that P1 effects could be observed when behavioural IOR has not taken place or that P1 effects could be absent when behavioural IOR is present (see Satel, Hilchey et al., 2013, for a review). Their correlational analysis revealed that P1 modulations are only significantly correlated with behavioural IOR when eye movements were actively suppressed. In a following study, Satel et al. (2014) found that P1 effects were not observed during a central cuing task that did not involve repeated peripheral stimulation. Based on these results, it was suggested that P1 effects could be the result of repeated peripheral stimulation rather than reflecting the underlying neural activity of IOR (Hilchey, Klein, & Ivanoff, 2012). In contrast, the Nd (Negative difference) component has been suggested as a potential neurophysiological marker of true oculomotor IOR, because it was concurrently found in both peripheral and central cue conditions, when P1 effects were absent in the central cue condition (Satel et al., 2014). We found some evidence supporting the Nd component as a neurophysiological marker of output-based IOR, but only in the blocked-incompatible-contralateral condition.

7.4 Distractors in a Spatial Cueing Paradigm

In Chapter 4, we demonstrated that behavioural IOR can be observed in the presence of distractors in a spatial orienting paradigm, regardless of response modality. Although IOR is stronger when the oculomotor system is activated, this difference was not significant when only the first 288 trials were taken into account. When manual responses were used, there was no significant reduction of the P1 component that has been observed in previous EEG studies

without distractors (e.g., Chica & Lupiáñez, 2009; Prime & Ward, 2004, 2006). The absence of a P1 cueing effect is likely due to a reduced amount of IOR owing to the presence of distractors when manual responses are used.

We provided further support for the dissociation between input-based and output-based IOR in Chapter 5 by varying the time course in peripheral cueing conditions with and without eye movements (Exp. 1 vs. 3). Input-based IOR was not significant at the shortest CTOA of 800 ms but became significant at longer CTOAs of 1,600 and 2,400 ms, whereas output-based IOR was strongest at the CTOA of 800 ms and then decreased at longer CTOAs. These observations suggest differential time courses of the two forms of IOR – input-based IOR starts later but does not last very long whereas oculomotor IOR starts earlier and decays over time. These results correspond with the theoretical interpretation that input-based IOR is integrated along the input/sensory pathway when processing the target location, whereas oculomotor IOR is a long lasting, spatiotopically coded mechanism generated regardless of cue type that enhances novelty seeking (Hilchey, Klein, & Satel, 2014; Posner & Cohen, 1984).

7.5 Neurophysiological Correlates of IOR

In Chapter 6, we returned to ERP analyses of P1, Nd, and N2pc components, this time using a visually balanced paradigm that allowed for extraction of the N2pc component. We did not find evidence for P1 cueing effects, although there was a contralateral Nd. The introduction of distractors also complicated the interpretation of our results.

The N2pc (N2-posterior-contralateral) component has been found to be associated with attentional modulation of brain activity in the visual cortex contralateral to attended stimuli (e.g., Hopf et al., 2000) and shifts of attention (e.g., Hickey, McDonald, & Theeuwes, 2006). For

example, McDonald and colleagues (2009) found diminished amplitude of the N2pc when the target appeared at the same location as a previous target, whereas Yang et al. (2012) found delayed onset of N2pc in response to cued trials. These divergent findings suggest contradictory accounts for how attention is deployed in input-based IOR, because the experimental procedures in both studies required suppression of eye movements when responding to targets. Unlike McDonald et al. (2009) and Yang et al. (2012), however, we required explicit eye movements to the cue to activate the oculomotor system so that we could investigate ERPs elicited when output-based IOR was generated. We did not find evidence for either the biased or delayed-attention hypothesis. Instead, we believe inhibitory tagging at the cued location did not result in an obvious response bias due to distractors taking away attention from the target. Another possibility could be facilitatory effects elicited by the distractor masking potential inhibitory effects. Finally, although many IOR studies manipulate selective focal attention and eye movements independently, often with the peripheral cues and no eye movement combination, our experiment included foveation of cues and attention was directed to the same spatial location in the visual field. The introduction of more than one variable at a time complicated the interpretation of our results, and, in hindsight, a control study consisting of saccade-to-cue, no distractors would have been helpful for making comparisons.

Nevertheless, in examining the N2pc component, we stumbled upon other potentially informative components that have gone previously unnoticed: an N1pc and an SPCN component. Although our results are preliminary, the main takeaway from these lateralised components is that these relatively unexamined components may very well be candidates as indexes of output-based IOR. Echoing Hilimire and Corballis (2014), who reported an SPCN component in a

visual search array, future studies could directly manipulate the magnitude of IOR and compare that with SPCN amplitudes.

Because of the inverse problem in EEG source localisation, where theoretically an infinite number of neural sources can generate a given scalp distribution, it is difficult, if not impossible, to approximate from where in the brain an ERP component originates. After all, we use ERPs to take advantage of their excellent temporal resolution, not for their spatial resolution. However, there are some who have attempted to solve the inverse problem mathematically by applying certain constraints to the source (e.g., McDonald et al., 2009; or see Grech et al., 2008, for a review). Source localisation methods allow for investigations into the cortical basis of relevant ERP components that can provide corroborating evidence for lesion studies involving IOR. In a study comparing healthy controls and patients with midbrain lesions, Posner et al. (1985) first identified the superior colliculus (SC) as a necessary oculomotor component within the retinotectal pathway involved in the tagging of IOR at the cue location. Later studies suggested that, although inhibitory tagging may originate in the SC, the parietal cortex is responsible for remapping the salience map from retinotopic to spatiotopic coordinates (Danziger, Fendrich, & Rafal, 1997; van Koningsbruggen, Gabay, Sapir, Henik, & Rafal, 2010). On the dissociation between input-based vs. output-based IOR, Klein and Redden (2018) postulated that the neural mechanisms for input-based IOR could lie within the ventral visual pathways, unlike the output form of IOR that is modulated by the SC and operates along the dorsal visual pathways. Future research could benefit from magnetoencephalography studies (e.g., Ayabe et al., 2008) that combine high temporal resolution with greater spatial resolution than EEG, or the combined use of both MEG and EEG (Sharon, Hämäläinen, Tootell, Halgren, & Belliveau, 2007).

7.6 Negative Priming and the Negative Compatibility Effect

When considering various theories of IOR, it would be remiss to overlook research on negative priming (NP; Tipper, 1985). NP is borne out of priming literature, where *positive* priming effects refer to selective attention to a prime stimulus that facilitates processing of subsequent (semantically) similar probe stimuli (e.g., Carr, McCauley, Sperber, & Parmelee, 1982). The opposite of that, *negative* priming, describes impaired processing of subsequent probe stimuli (Tipper, 1985; for reviews, see D'Angelo, Thomson, Tipper, & Milliken, 2016, and Frings, Schneider, & Fox, 2015). Tipper, Brehaut, and Driver (1990) later modified the experimental design into a negative *spatial* priming paradigm where participants responded via manual localisation to a specific stimulus in the 'prime' array, followed by a subsequent response to the stimuli in 'probe' array. They found that RT was delayed if stimuli in the 'probe' array appeared in the same location as stimuli in the 'prime' array. This delayed RT bears a striking resemblance to results from target-target spatial cueing paradigms used in investigating IOR, where RTs to targets that appeared in a previously cued location were delayed (Tanaka & Shimojo, 1996). The relationship between spatial NP and IOR was further scrutinised by Milliken, Tipper, Houghton, and Lupiáñez (2000), who concluded that the processes that underlie spatial NP and IOR may very well be the same (also see Houghton & Tipper, 1984, for a computational perspective).

Meanwhile, the priming community also introduced the negative compatibility effect (NCE) described by Eimer and Schlaghecken (1998). Using endogenous 'primes' in the form of spatially non-informative central arrows (i.e., irrelevant central cues), followed by backward masking, responses to congruent targets that match the primed stimuli (i.e., cued targets) are

facilitated. Despite masking effects preventing the priming stimuli to be consciously perceived, therefore rendering primes non-informative, a positive compatibility effect (PCE) is elicited such that RTs are faster to congruent vs. incongruent targets. Curiously, but perhaps not surprising to cognitive scientists familiar with IOR, a delay between prime and target impairs responses towards congruent (cued) stimuli, the so-called NCE (see Sumner, 2007, for a review). NCEs appear to operate independently from the orienting of attention (Klapp & Hinkley, 2002; Schlaghecken & Eimer, 2000) but can nevertheless be modulated by attention (Sumner, Tsai, Yu, & Nachev, 2006). Discussed in relation to IOR, Hilchey et al. (2013) postulated that cueing effects generated by central arrows can instead be explained by the stimulus-response (S-R) activation-inhibition hypothesis. This hypothesis suggests that inhibitory cueing effects measured by responses to central arrow targets at relatively long CTOAs are qualitatively different from input-based IOR, despite often being lumped together with other inhibitory cueing effects, such as output-based IOR. Rather, S-R activation-inhibition tries to explain slowed response to cued central arrows as withholding of motor response during the cue disrupting manual response at the target. Hilchey et al. (2013) further linked S-R activation-inhibition with NCEs that, again, should be considered separately from IOR. Thus far, only Hilchey et al. (2013) has discussed both NCE and IOR in the same article. Future research could directly compare NCE and IOR to examine whether they are the same, or perhaps operate using the same underlying mechanism as IOR.

7.7 Limitations

As described in the Introduction chapter, we chose to only examine cueing effects at 50% predictability to eliminate expectations from non-informative cues as a contributing factor to

IOR. Endogenous signals can contribute to facilitation effects in IOR (see for example, Wright & Richard, 2000), in which facilitation increases with greater predictability. However, even though we controlled for spatial predictability, there is still temporal predictability that we cannot eliminate (Gabay & Henik, 2008). After presentation of the cue or cue-back, participants expect targets to appear. Gabay and Henik (2010) showed further evidence that temporal predictability modulates IOR in discrimination tasks. This is especially relevant given that our distractor paradigms in Chapters 4, 5, and 6 all require some form of discrimination in order to perform the task correctly.

Other than that, while it is generally recommended to conduct a-priori power analysis to determine the sample size of an experiment, we have not done so at the planning stage of our experiments. This is not a cause for concern given that effect sizes are always reported alongside p-values, which readers can use to stay informed when interpreting the results of our studies. In addition, in Chapter 5, we presented results from Bayesian analysis which can be used to complement classical null hypothesis significance testing.

Behavioural limitations aside, one of the challenges in any ERP experiment is to achieve sufficient signal-to-noise ratio, especially when the experimental design involves saccades. In fact, the vast majority of ERP studies of IOR can only measure modulations of covert attention (fixation at target during response) to avoid large ocular artefacts contaminating brain signals. So, although behavioural IOR has been thoroughly investigated using manual and saccadic responses, EEG correlates of IOR have thus far been studied exclusively with the manual response modality. Chapter 6 is our attempt to fill in the gap by examining ERP components in conjunction with oculomotor activation, but, still, saccades were to cues instead of targets.

I believe it would be invaluable to run an experiment where EEG is recorded simultaneously with high resolution eye-tracking (as we did in Chapters 3 and 6), but with saccades to targets in spatial cueing stimulus-response paradigms. A more sophisticated analytical method has been proposed by Plöchl, Ossandón, and König (2012), using synced eye movement data to train algorithms for precise identification of eye movement electrical signals that are unrelated to the task itself. Although we did use eye-tracker information to monitor and provide real time feedback for participants' eye movements, eye-tracker and EEG data were not co-registered. Co-registration opens up the possibility of analysing EEG data epoched to saccade onset (instead of stimulus onset), allowing for more efficient ocular artefact detection and correction, even extending IOR investigations to naturalistic conditions in free viewing paradigms (Nikolaev, Meghanathan, & van Leeuwen, 2016).

Ideally, investigations into ERP/ERL components should also take into account scalp topography and statistical differences in onset latency (if any), other than polarity and mean peak timing that we examined here. The literature on ERP pre-processing is vast and continually improved upon. Even though guidelines for best practices exist, there is no one-size-fits-all procedure, and each stage of the pre-processing pipeline can affect the outcome of the waveform. One could argue that the average reference used in this experiment is not ideal. With high density electrode nets (such as the 128-channel nets used in Chapter 3 EEG experiments), average referencing is a good option because it is less susceptible to scalp currents at any one electrode channel (Dien, 1998; but see Hagemann, Naumann, & Thayer, 2001). However, the 32-channel nets used in the present chapter have relatively low-density electrode coverage, which could cause distortions in ERP waveforms when using an average reference (Dien, 1998; Junghöfer, Elbert, Tucker, & Braun, 1999; Woodman, 2010), rendering data difficult to interpret due to

sampling limitations. Alternative reference points like the mastoid and Cz are not suitable candidates either because the electrodes of interest (O1/O2) are too close (any effects would be minimised as they are closer to the reference electrode). Our EEG system does not allow for ear-lobe or nose references.

Although we make references to latency differences in Chapters 3 and 6, these observations should be treated with caution. Multiple approaches have been developed to investigate onset latency differences statistically (Miller, Patterson, & Ulrich, 1998; Mordkoff & Gianaros, 2000; Schwarzenau, Falkenstein, Hoormann, & Hohnsbein, 1998), but these were not utilised here. Analysing both mean amplitude *and* latency differences comes at a cost, because Type I error rate (i.e., false positives) increases with the number of tests conducted. We have already examined P1, Nd, and N2pc amplitudes using a considerable number of statistical tests. The reader should treat N1pc and SPCN ERL components found in Chapter 6 as mainly explorative.

In addition to the lack of statistical evidence for latency differences, we also did not show whether our ERP results were correlated to the behavioural results like some previous studies have (Satel, Hilchey et al., 2013; Satel et al., 2014). Thus, we cannot reliably show that the ERP components were associated with behavioural IOR, other than they both arose at the same time. We cannot rule out a third variable affecting both behavioural and ERP results that we are not aware of. Future research could also distinguish the ERP of participants who show a large IOR effects from the ERP of participants who show no, or small, IOR effects.

7.8 Outstanding Questions and Future Directions

We have laid out several interpretations of our present findings – IOR effects were produced in all tasks except for incompatible responses with saccades, perhaps because of differential mechanisms underlying the generation of IOR in this condition. However, these behavioural results are but a reflection of cortical and subcortical regions of the visual system. We recognise that to provide a comprehensive account of the cause and effect of IOR, there needs to be corroborating evidence from neurophysiological studies. Hence, we introduced distractors to a traditional cue-target paradigm in search of neurophysiological correlates in an ERP study. Without engaging the oculomotor system, however, our findings could not be extended to output-based IOR. We therefore investigated ERP modulations associated with cueing in a spatial orienting paradigm when the oculomotor system was activated in a paradigm with distractors.

Although there has been some behavioural research on IOR in visual search tasks (Klein & MacInnes, 1999; Müller & von Mühlenen, 2000), less is known regarding IOR and ERP components that can be reliably demonstrated in a visual search paradigm, specifically one where a "search" is brought about by increasing the number of placeholder boxes (e.g., Tian, Chica, Xu, & Yao, 2011). For example, in a within-subject study, instead of just two placeholder boxes to the left and right of the fixation, having eight boxes arranged in a circle around the fixation would increase the difficulty in finding a target, thereby requiring the execution of a search to perform the task correctly. We could then have one placeholder brightened, acting as the cue, followed by a delay before a target on the same or opposite location comes onto the screen. It is important that our findings be extended in a visual search paradigm that has arguably

greater ecological validity than that of a spatial cueing paradigm, as real-world situations hardly ever involve attention only being allocated to one of two locations.

Building upon that, real-world scenes are also more complex and dynamic, requiring IOR not only at tagged locations, but also on tagged objects (Tipper, Driver, & Weaver, 1991). Research in object-centred IOR is in its infancy (see, for example, Redden, Hilchey, & Klein, 2018) and is ripe for future investigation. Using a moving box paradigm where the cue placeholders are animated to look like they have moved to a new location during target selection, we could dissociate between traditionally location-tagged IOR and object-based IOR (Abrams & Dobkin, 1994, Experiment 3 & Experiment 4; Tipper et al., 1991). Especially, combining behavioural methods with multiple neuroimaging tools would allow us to have a clearer view of how multiple processes combine to affect behaviour.

7.9 Conclusions

Although it is relatively easy to establish that participants respond slower to cued than to uncued target stimuli, discerning whether this difference in RTs is due to faster (or inhibited) processing at the attentional (Posner et al., 1985), perceptual (Handy et al., 1999), or response level (Klein & Taylor, 1994) has been far more challenging. The term IOR was previously used too liberally to describe any inhibitory cueing effects, when there are actually multiple mechanisms at play. The experiments described in this dissertation have significant implications in adding to the growing literature that differentiates Posner and Cohen's (1984) input-based IOR with Posner et al.'s (1985) output-based IOR (Klein & Redden, 2018). We found that by imposing constraints on critical elements, such as the CTOA and the activation of the oculomotor system, we were able to elicit either one of the two forms of IOR.

The contribution of this dissertation is two-fold. First, we integrated the existing cue-target spatial paradigm with anti-saccade tasks, showing differential effects of input vs. output-based IOR. Second, we empirically tested output-based IOR with distractors, showing evidence for response level effects caused by attentional modulation. Our findings allow for a better psychophysical and electrophysiological understanding of the temporal dynamics of output-based IOR, to be considered separate from input-based IOR.

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Appendix

Channel Layouts

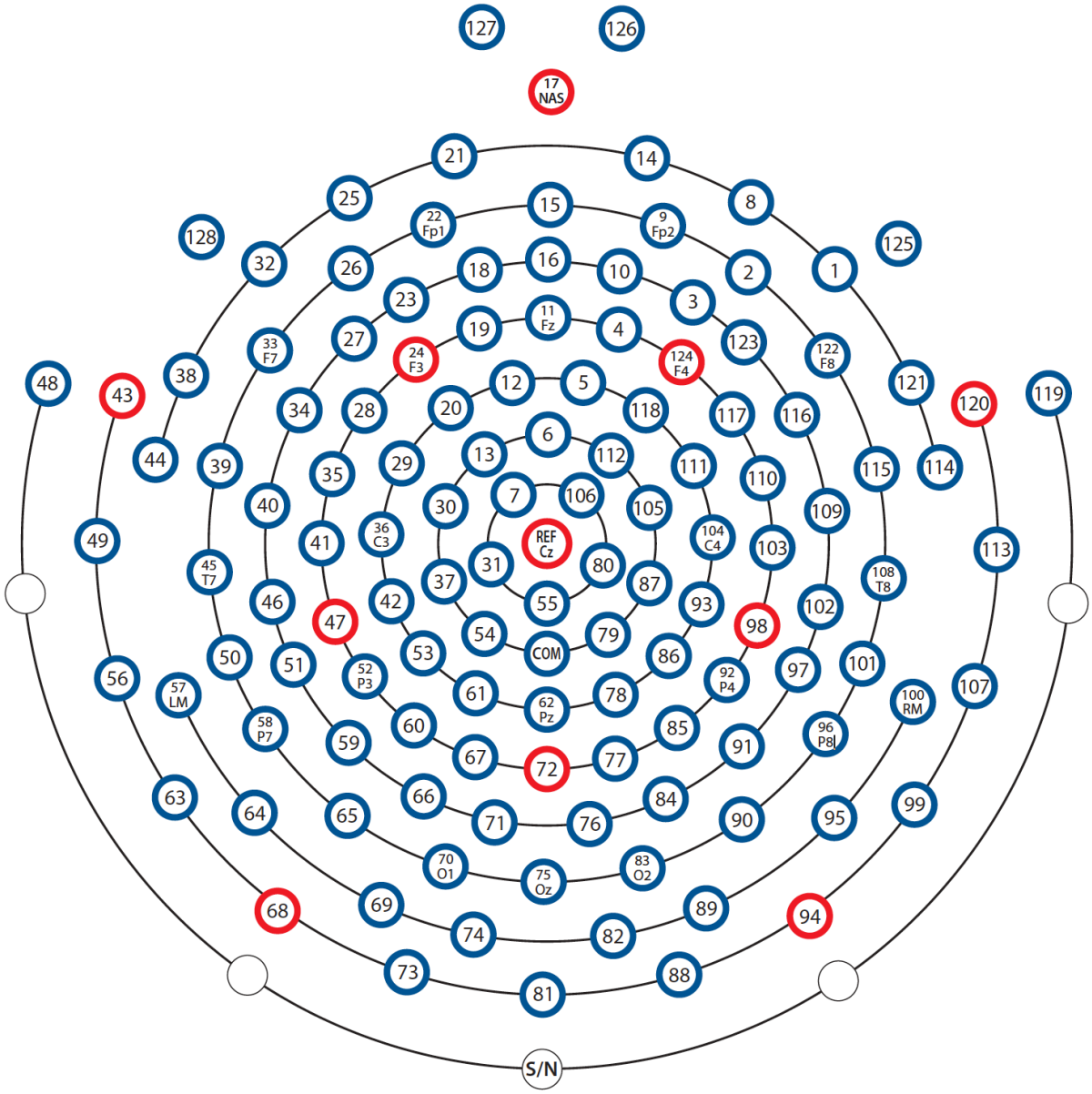

Figure 1. Channel montage of a 128-channel EGI HydroCel Geodesic Sensor Net (Electrical Geodesics, Inc., Eugene, OR).

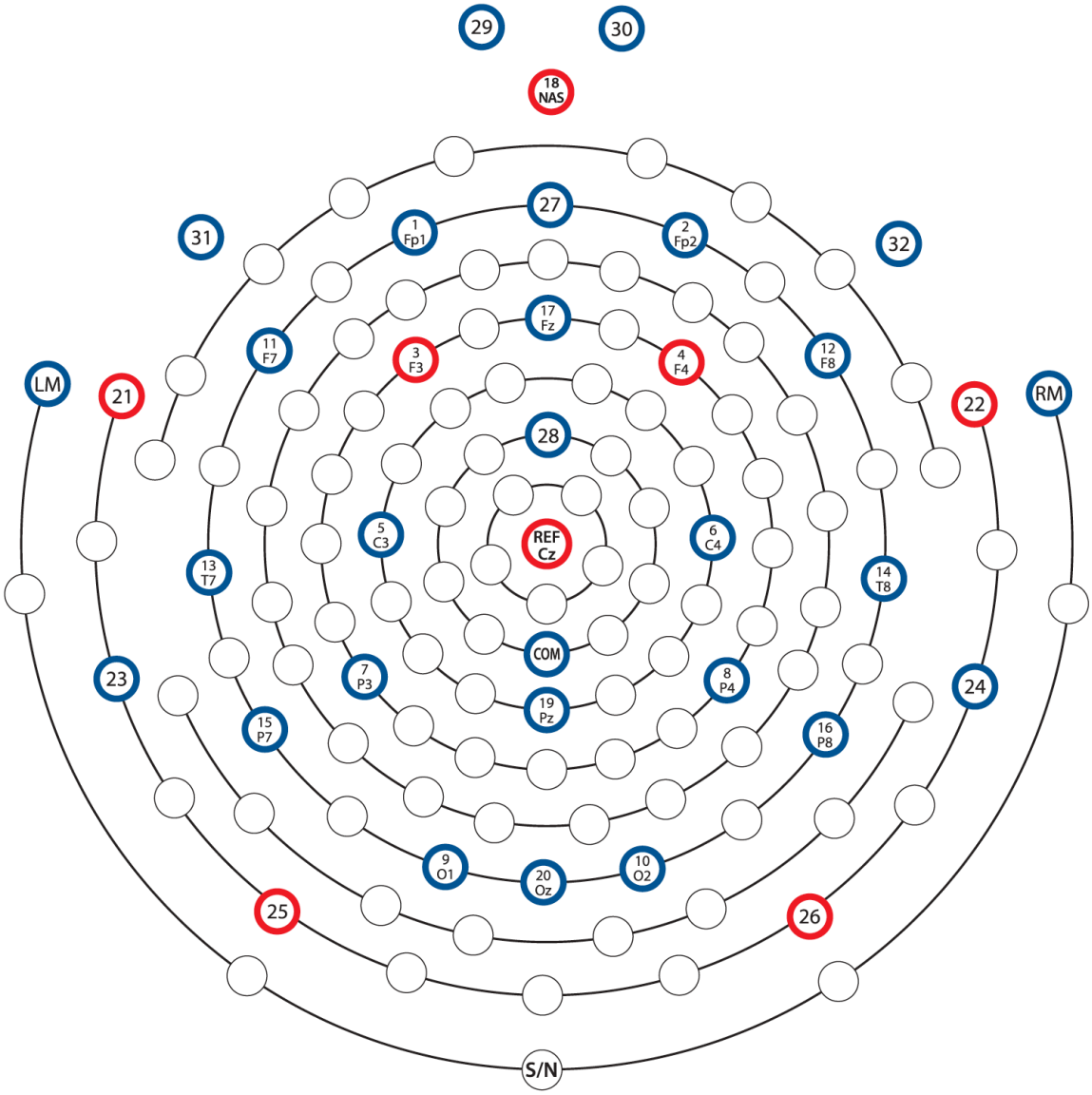

Figure 2. Channel montage of a 32-channel EGI HydroCel Geodesic Sensor Net (Electrical Geodesics, Inc., Eugene, OR).