WHAT'S YOUR NEXT MOVE? MULTIPLE SPATIALLY DEFINED RESPONSE BIASES AFFECT CONSECUTIVE EYE AND ARM MOVEMENTS

by

Chris Cowper-Smith

Submitted in partial fulfilment of the requirements
for the degree of Doctor of Philosophy

at

Dalhousie University
Halifax, Nova Scotia
June 2018

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Inhibition of return (IOR) is an orienting phenomenon thought to promote efficient visual search by biasing attention, eye movements, or both, toward novel locations. When IOR is present, reaction times (RTs) are slowest at previously cued locations and monotonically decrease as the spatial offset between cue and target increases from 0° to 180°. Although the monotonic pattern of IOR is well established, based on a prior study of directionally selective neural adaptation effects, we had reason to believe that a non-monotonic pattern of RTs could be revealed when consecutive eye or arm movements were required from a common starting point in the centre-out IOR task. Specifically, if adaptation effects were present, we predicted that responses offset by 90° would be faster than responses offset by either 0° or 180°. In five studies, we therefore examined the pattern of RTs for consecutive eye or arm movements offset by 0°, 90°, or 180°. Consecutive responses were required from a common starting point and were prompted using either central arrowhead or peripheral onset stimuli. Study 1 used four possible target locations and reveals evidence of adaptation and IOR with central and peripheral signals respectively. In Studies 2 and 3, we attempt to eliminate adaptation effects by allowing participants to fully prepare their response in advance of a response execution signal. Unexpectedly, IOR was observed, suggesting that adaptation effects may have delayed 180° but not 0° responses in Study 1. Studies 4 and 5 replicated Study 1 but optimized the chances of observing IOR by presenting two rather than four target locations while retaining our ability to measure RTs at 0° and 90° or 0° and 180° offsets on different trials. The results of Studies 4 and 5 demonstrate evidence suggesting that IOR and adaptation effects can delay 0° and 180° responses respectively. Together, the results of the present thesis highlight the importance of (1) signal type (2) set size and (3) motor programming in determining the nature of the response bias(es) observed in the widely used centre-out task.

LIST OF ABBREVIATIONS AND SYMBOLS USED

ANOVA	Analysis of variance
BOLD	Blood-oxygen-level dependent
E1	Experiment 1
E2	Experiment 2
E3	Experiment 3
E4	Experiment 4
FEF	Frontal eye fields
fMRI	Functional magnetic resonance imaging
Hz	Hertz
ICE	Inhibitory cueing effect
IOR	Inhibition of return
MSE	Mean square error
n	Sample size
$\eta^2{}_p$	Partial eta squared
p	p-value for significance testing
PD	Preferred direction
px	Pixel
PMC	Premotor cortex
S1	Signal 1
S2	Signal 2
SC	Superior colliculus
SD	Standard deviation
RT	Reaction time
SEF	Supplementary eye fields
SC	Superior colliculus
SOA	Stimulus onset asynchrony
UL	Up-left
UR	Up-right
DL	Down-left
DR	Down-right
$\mathbf{x}$	Sample mean
α	Alpha
°	Degrees

ACKNOWLEDGEMENTS

First, I wish to thank my supervisors, Drs. David Westwood and Gail Eskes. You have both taught me so much. David, thank you for your incredible mentorship, for always providing the perfect balance of feedback and encouragement, for letting me win the occasional squash game, and for helping me set “Reviewer #2” straight when they clearly didn’t understand our work! Gail, thank you for challenging me to be my best, for opening my eyes to clinical research, and for giving me a nudge whenever I needed it.

I am fortunate to have Drs. Raymond Klein and Nathan Crowder as PhD committee members. Ray and Nathan, thank-you for helping me navigate the nuanced world of IOR and for your guidance as I progressed through my degree.

To my family, words cannot express the gratitude I have for your support and encouragement over the years. Special thanks are owed to Lisandra for her daily support and in particular for all the extra things she did to make my life easier while I was simultaneously working to finish my thesis and run a start-up company. I couldn’t have done it without you.

CHAPTER 1: INTRODUCTION

The completion of most motor tasks rarely involves the execution of a single isolated movement. Rather, in everyday tasks ranging from reaching for one's coffee cup to searching for a friend in a crowd, we engage in *sequences* of spatially directed movements [1–3]. For example, when reaching to grasp an object, it is common to first extend the arm before opening the hand to form an appropriate grip [4]. After successfully grasping, the arm may then flex and rotate at the shoulder and elbow before returning the object to the individual's mouth, or alternatively, it's desired location. This type of goal-oriented behavior requires that a variety of distinct functionally related movements be carefully planned and coordinated in both time and space [4,5]. Similarly, during visual search, it is normal to execute several distinct saccadic eye movements in sequence, to ultimately identify and fixate an object of interest [2,6]. Here, the coordination of successive eye movements is necessary to promote efficient and expedient visual search away from previously inspected locations and toward novel uninspected locations [2,6–8].

While the temporal and spatial coordination of consecutive, functionally related movements is often necessary for the completion of goal-oriented behaviours [5], it is less clear if and how consecutive movements are coordinated when they are not planned as part of a functional action sequence [9]. However, because behaviour unfolds over time, the need to execute consecutive movements planned independently is common (e.g., pushing a button on the elevator, then reaching to your pocket for your phone). Moreover, there are many ways in which the execution of a movement might affect future movements, independent from any shared functional relationship. For example, using proprioceptive or kinesthetic information about the position of a limb, the brain and spinal cord may bias movements away from a joint's terminal range of motion and toward more neutral/central postures in order to prevent injury [10,11]. Here, the execution of a first movement extending a limb close to its terminal range of motion may create a preference for movements back to a more neutral vs. extended posture. Alternatively, the brain may bias movements toward neutral or central postures in order to optimize the control and coordination of future movements [12]. Interactions between consecutive movements might also emerge simply because the generation of movement is reliant on finitely available neural processing resources that might be subject to habituation or neural adaptation effects [13–17]. For example, if the execution of a spatially directed movement temporarily suppresses, adapts, or otherwise fatigues underlying neural processing resources [13,14], one might expect to observe a delay in the initiation of subsequent movements made in the same direction [cf. 15–17].

Based on an interest in the possible coordination of consecutive but independently planned movements, the present dissertation explores whether the direction of an executed eye or arm movement can create spatiotemporal biases for subsequent movements made with the same effector system. If such bias exists, it could manifest in one or several aspects of the subsequent movement, for example, to slow reaction time (RT) or movement time, or to alter movement direction, trajectory, endpoint, acceleration, or velocity [18–20]. However, given (1) the exploratory nature of the present work; (2) the well-established use of RTs in mental chronometry for studying perceptual, attentional, and motor processing efficiency [21–23]; and, (3) the relative insensitivity of RTs to practice based effects in simple stimulus-response movement tasks [24], RTs were adopted as the dependent variable of interest herein.

The present body of work was specifically focused on whether the direction of a discrete first movement could systematically result in different RTs for a second movement made in either the same or a different direction. Such a finding would suggest the presence of a basic motor processing bias generated by a prior movement and favoring the initiation of certain spatially directed movements over others. This area of study is of interest to better characterize the basic principles of motor control in the human motor system. A better understanding of how consecutive movements are spatially and temporally coordinated by the motor system may have significant implications, for example, in improving brain machine interfaces and the control of neuroprosthetics [e.g., 60,97], exoskeletons [e.g., 67], or within neuro-rehabilitation science more broadly [e.g., 13].

1.1 Encoding of Movement Direction

One reason to believe RT biases could be generated by the execution of a prior spatially directed movement lies in the basic neurophysiology of the motor control system. The accurate control of upper limb movements requires a specification of the intended movement direction during motor programming. Underpinning the directional control of movement is the presence of neural populations that exhibit directional preference in their firing rates found in pre-motor cortex (PMC) [29,30], primary motor cortex [31,32], and cerebellum [33]. These directionally selective neural populations have been well characterized in microelectrode studies of non-human primates and (1) are most active during the RT phase (i.e., after stimulus onset and before movement onset); and, (2) have efferent connections that ultimately control motor outputs [34–37]. More recently, neuroimaging studies have confirmed functionally homologous direction encoding properties also exist in several areas of human sensorimotor cortex [13,14,37,38].

Direction-encoding neurons exhibit broad tuning profiles where the highest frequency of neural firing occurs when movements are planned in their preferred direction (PD) and progressively lower firing rates occur as movements are made at increasing angular offsets from their PD [12,32,33,40–44]. The most common tuning profile of direction-encoding neurons is unimodal with maximum firing rates at a 0° offset from the cell's PD, half-maximal firing rates between a 30° and 90° offset from the PD, and minimal firing rates 180° opposite [44]. These broadly tuned but directionally selective neurons are found in a distributed manner throughout the motor cortex and cerebellum and the PDs of different cells are distributed across the 3-dimensional continuum of all possible movement directions [12,29,34,43,45].

Given the breadth of tuning profiles in direction-encoding cells, changes in the activity of a particular neuron cannot predict or specify the direction of an upcoming movement [31]; however, the net activity of the directionally tuned population can [43,46]. Mathematically, the net activity of directionally selective neural populations can be calculated by assigning vectors to individual cells, where the direction of the vector is defined by the PD and the magnitude of the vector is proportional to the firing rate of the cell prior to and during a particular movement. When the individual cell vectors are summed, the resulting population vector accurately predicts the direction of the upcoming movement [12,34,36,43].

How might direction encoding influence the spatiotemporal relationship between consecutive movements? In an fMRI study Cowper-Smith et al. [13] used a variant of the centre-out task (Figure 1.1) requiring joystick responses to reveal evidence of directionally selective adaptation (i.e., reduction) of the BOLD response in several areas of human sensorimotor cortex when consecutive movements were repeated in the same direction [13]. During this task, after a target was indicated, participants executed a spatially congruent joystick response then relaxed their wrist which caused the joystick to return to centre. This type of joystick response is different than that normally required in the centre-out task, where after reaching to an indicated target, the participant must reach (and not simply relax their arm) in order to return to the central starting position. In short, these types of joystick responses only require the specification of a movement toward the indicated target, and not the specification of a return-to-centre movement[1]. As predicted by Cowper-Smith et al. [13] adaptation as

---

[1] The use of a joystick rather than reaching-localization response was chosen in order to (1) examine the breadth of directional tuning free from possible adaptation effects resulting from the return-to-centre movement; and, (2) reduce fMRI signal motion artifacts [113]. When using a joystick, the ulnar-lunate side of the wrist is placed at the base of the joystick. To indicate a particular direction, the top but not bottom of the joystick handle is deflected a short distance. After deflecting the top of the joystick and relaxing the hand, the hand returns to the central starting location where the ulnar-lunate side of the wrist and

measured by the fMRI BOLD response only occurred for consecutive responses offset by 0° (i.e. when movements were made in the same direction), while a spatial offset of 90° or 180° between repeated movements did not reveal adaptation.

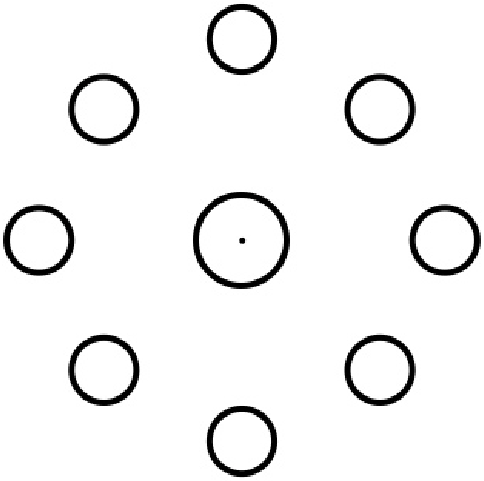


Figure 1.1. Example stimulus configuration of the centre-out task commonly used to study both preferred direction coding and neural adaptation effects [13,31,32,36,39,47]. *Consecutive movements are made from a common central starting location to localize equidistant targets that are distributed evenly along the circumference of a circle. Adjacent targets are distributed at equal angular offsets from the central location, allowing even sampling of the directional continuum within a particular movement plane. During the task, after localizing an indicated target (e.g., by moving toward, pointing at, or touching the target), the limb is returned to the central starting (or "home") location before localizing the next indicated target. All target locations have an equal probability of being indicated and are randomly presented, thus making it impossible to predict the direction of a movement until it is signaled. A similar centre-out task has been widely used in reaction time studies focused on sensory, attentional, and oculomotor behavior* [2,6,48,49]*, as described further below.*

---

joystick are neutrally anchored. Under these circumstances, after responding to the target stimulus, a directionally opposite motor signal is not required to return the wrist to centre. By contrast, when reaching-localization responses are required in the centre-out task, the entire hand and limb is moved in the direction of the target, then back to centre; under these circumstances, directionally opposed motor signals are required [c.f. 39].

In the context of the traditional centre-out response task used to study direction encoding (Figure 1.1), when localization responses are made to touch a first target (Movement 1), then return to centre (Movement 2), and finally to a second target (Movement 3), the aforementioned fMRI results [13] predict that neural adaptation will occur when the second target is at a 0° *or* 180° spatial offset from the first target. This is because both the 0° or 180° offset conditions require that Movement 3 is a repetition of a recently completed movement direction: either a repetition of the movement to the first target (movement 1), or a repetition of the opposite, return-to-centre movement (movement 2). By contrast, adaptation will be minimal for 90° offsets, when Movement 3 is in a different direction from both Movement 1 and 2. As a result, if adaptation within direction encoding neurons can affect manual localization RTs, 90° responses should be faster than 0° and 180° responses (0°>90°<180°) in the centre-out task.

If our predictions regarding the neural adaptation mechanism underlying the spatial relationship between consecutive reaching movements are correct, then a similar pattern of performance should be observed in the oculomotor system, where the distributed encoding of movement direction has also been demonstrated [50–53]. Like the reaching control system, the direction of saccadic eye movements are controlled by populations of directionally tuned neurons found throughout the oculomotor system, including within frontal and supplementary eye fields [26,50], posterior parietal cortex [54], cerebellum [55], and superior colliculus [51,52]. Also similar to the reaching control system, directionally tuned cells in the oculomotor system generally have broad tuning profiles with maximum firing rates at a 0° offset from the cell's PD, half-maximal firing rates between a 30° and 90° offset from the cell's PD, and minimal firing rates 180° opposite [50,51,56]. Given the similarity in how movement direction is encoded between the reaching and oculomotor control systems, we suspected that if adaptation occurs during the centre-out task, it should be present regardless of whether consecutive saccadic or reaching-localization responses are required.

Assuming that adaptation effects are associated with decreased neural firing rates [16], then within the context of the centre-out task, we predicted that RTs would be slowest in conditions where adaptation is expected (0° and 180° offsets) relative to those conditions where adaptation is not expected (90° offsets). Herein, the aforementioned prediction is referred to as the "Adaptation Hypothesis" (RTs will follow the pattern: 0°>90°<180°). Consistent with prior research, the Adaptation Hypothesis assumes that (1) directionally selective adaptation in motor cortex reflects deceased neural firing rates [16] and (2) that decreased neural firing rates in motor cortex are associated with delayed reaction times [57,58].

While the centre-out task has been used in various forms to study direction encoding in primate and human sensorimotor cortex [12,13,24,31,39,42,44], a similar task has also been used in studies focused on the sensory, attentional, and motor processing behaviors associated with orienting and inhibition of return (IOR; see below) [2,6,49,59,60]. These IOR studies suggest several other ways in which RTs may be affected or spatially distributed when consecutive responses are required to visual stimuli in the centre-out task. Therefore, before establishing the precise task parameters under which to study possible adaptation-based RT effects, it is important to review the ways in which sensory, attentional, and oculomotor processing might affect RTs in the centre-out task.

1.2 Orienting and Inhibition of Return

Orienting refers to a set of mechanisms resulting in the preferential sensory or attentional processing of certain input stimuli relative to others [61]. In basic cued orienting tasks, spatial attention is attracted to a location using a peripheral or central cue, and then a simple detection or saccadic localization response is made to a target that can appear in either the same or a different location as the cue [7,62,63]. In traditional studies of IOR, 2 target locations are typically arranged on either side of a central fixation point, similar to the configuration shown in Figure 1.2[2]. For relatively brief stimulus onset asynchronies (SOAs; i.e., the time between the onsets of the cue and target is 200 ms or less), the general pattern observed in such tasks is a benefit in response speed or accuracy for targets presented at the location where attention was previously drawn by the cue as compared to the opposite, uncued location. This benefit is consistent with the general notion that attention facilitates sensory and motor processing. However, for longer SOAs (i.e., 300 ms or greater in young adults; [64]), the pattern reverses and performance tends to be poorer for stimuli at the previously attended location compared to the uncued location; summarizing the bias against

---

[2] In other studies of IOR, a variable number of cue and target locations are arranged at equal distances around a central fixation point, similar to the configuration shown in Figure 1.1.

orienting to previously attended locations, this paradoxical performance deficit was coined “inhibition of return” (IOR) by Posner, Rafal, Choate, and Vaughn [60].

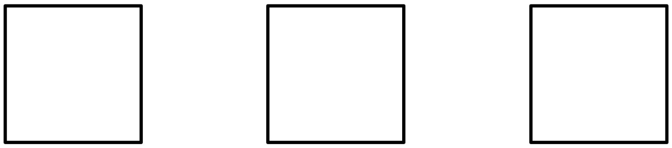


Figure 1.2. Typical stimulus configuration for the centre-out task commonly used to study orienting and inhibition of return (IOR). In the basic paradigm, attention, an eye movement, or both are attracted form the central square to one of the adjacent flanking squares by a first signal (S1). After S1, subjects are instructed to return their attention (and eyes, if they were moved) to the central square. A second signal (S2) is then presented, again indicating one of the flanking squares and participants are instructed to respond by pressing a spatially congruent button or moving their eyes to the signaled location. The reaction time (RT) for S2 is examined as a function of the angular offset between S1 and S2 directions, i.e., 0° (same previously signaled target) or 180° (different target). When IOR is present, 0° responses are slower than 180° responses.

Since the original discovery of IOR, the phenomenon has been widely studied in an attempt to uncover both the mechanism(s) of IOR as well as its potential function(s). Emerging from this literature, and in particular, from studies examining RTs across a wider range of spatial offsets (e.g., using a stimulus array such as that shown in Figure 1.1; also discussed further below in section 1.5), is the commonly held view that IOR functions as a visual search or foraging facilitator [2,6,7,65–67], biasing attention and/or future eye movements away from previously inspected locations [but see 68–70]. The putative mechanisms underlying IOR are nuanced and varied [71–76], however, the results reported in the literature generally indicate that two forms of IOR operate under different task circumstances: one that affects early (sensory/attentional) input processes, and another that affects late stage (oculomotor) output processes

[59,65,71,72,77–86]. As discussed further below, because the sensory/attentional form of IOR delays the processing of sensory *input* stimuli, when present, sensory/attentional IOR should delay any response type (e.g., saccadic or manual). By contrast, because the oculomotor form of IOR is thought to delay specifically saccadic outputs, when present, the oculomotor form of IOR should be revealed by saccadic but not manual responses [65,87, but see 59].

1.3 Sensory and Oculomotor IOR

Many different task parameters have been used to elicit and measure the oculomotor and sensory/attentional forms of IOR respectively. Perhaps the most commonly manipulated variables are: (1) response type (manual button press or saccadic localization) and (2) signal type (central arrow or peripheral onset).

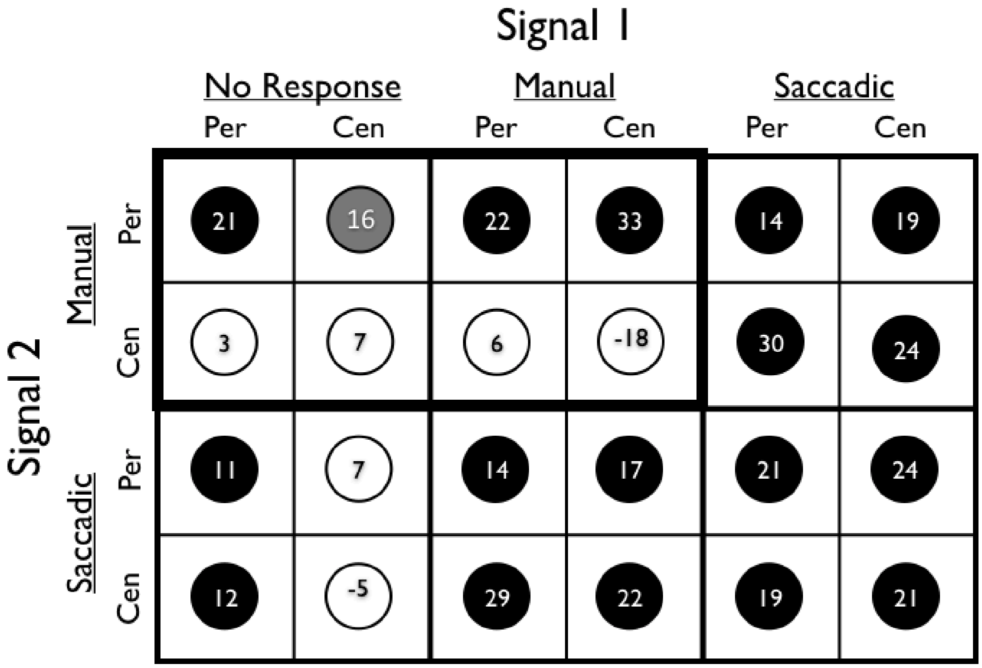
To explore the importance of response and signal types in IOR, in their seminal paper, Taylor and Klein [59] tested for IOR in 24 different stimulus-response conditions (Figure 1.3). These conditions were derived from (1) all possible paired combinations of peripheral onset and central arrowhead signals and (2) three responses types (no response, an overt saccadic localization response, or a manual button press response). In each trial, participants were required to make one of the three response types to a first signal (S1), and either a saccadic or button press response to a second signal (S2).

In considering the results of all 24 conditions, Taylor and Klein [59] put forward their “Oculomotor Hypothesis”, that two possible forms of IOR are dissociated based on the state (active or inactive) of the oculomotor system. The first form of IOR occurred because of inhibited sensory or attentional processing of a peripherally signaled location (regardless of whether a central or peripheral S1 was used), which was inferred from the fact that when no eye movements were made (to S1, S2, or both; i.e., all conditions contained within the bold line in Figure 1.3), IOR was revealed only with peripheral, but not central, S2 stimuli. In short, this form of IOR appeared to reduce the efficiency of sensory or attentional processing specifically in the spatial location of peripheral S2 stimuli. The second form of IOR was revealed in almost all circumstances when a saccadic or manual motor response was required to S2, independent of signal type (peripheral or central). Taylor and Klein [59] concluded that this second form of IOR was dependent on the activation of the saccadic eye movement system and was observed *provided* an oculomotor response was made to *either* S1, S2, or both[3]. Moreover, the oculomotor form of IOR was thought to occur independently from inhibited sensory processes, because IOR in these conditions "did not depend on the nature of the S2 stimulus, but instead, depended on having to produce a response in the same direction as signaled by S1" (Taylor and Klein, [59], p. 1652)[4].

---

[3] Subsequently, Klein and Hilchey [114] refined the oculomotor hypothesis to state that the oculomotor machinery involved in specifically the generation of *reflexive* eye movements must be active to observe oculomotor IOR, an idea which was later empirically supported by Hilchey et al. [80]. Other theories have suggested that the execution of a saccade to S1 may be necessary to generate the oculomotor form of IOR [65]. Consistent with this prior work, the present thesis assumed the oculomotor form of IOR would be generated by the execution of a saccadic localization response to S1 [59,65,78,87,88].

[4] If sensory/attentional and oculomotor IOR operate to serially slow (1) the processing of peripheral stimuli and (2) saccadic eye movements respectively, then according to additive factors logic [23], the magnitude of IOR (magnitude = 0°-180° RTs) should be larger when saccadic responses are required to peripheral versus central stimuli [59,65,72,87,90]. Consistent with this line of thinking, following a peripheral cue requiring no response, Abrams and Dobkin [90] observed a larger magnitude of IOR for saccades to peripheral versus central stimuli; however, Taylor and Klein [59] failed to replicate this observation. As a result, Taylor and Klein [59] concluded that when saccades are made, only the oculomotor form of IOR operates independent of signal type. Further research from Klein's group [65,87]



		Signal 1					
		No Response		Manual		Saccadic	
		Per	Cen	Per	Cen	Per	Cen
Signal 2 Manual	Per	21	16	22	33	14	19
	Cen	3	7	6	-18	30	24
Signal 2 Saccadic	Per	11	7	14	17	21	24
	Cen	12	-5	29	22	19	21

Figure 1.3. The 24 stimulus – response combinations examined by Taylor and Klein [59]*. Signal 1 (central or peripheral) could require no response, a manual button press, or a saccadic localization response. Signal 2 (central or peripheral) would require a manual button press or saccadic localization response. Filled in circles represent the stimulus-response combinations that revealed significant IOR*[5]*; unfilled circles represent conditions where IOR was not statistically significant. The bold line enclosing stimulus-response combinations that required no saccade to either S1 or S2 show conditions where IOR is considered sensory/attentional in nature (i.e., where IOR inhibited the processing of peripherally localized S2 stimuli). Inhibition of return observed in conditions outside of this bold line are considered motoric in nature and according to Taylor and Klein* [59]*, are dependent upon the activation of the oculomotor system to respond to either S1 or S2. Numbers within each circle represent the magnitude of IOR (0°-180° reaction times) observed in each condition.*

---

later demonstrated additive effects of sensory/attentional and oculomotor IOR in the target-target task when consecutive saccades are required to peripheral but not central stimuli. Correspondingly, the present thesis assumed that both sensory/attentional and oculomotor IOR may be present when peripheral (but not central) stimuli are used to prompt consecutive saccadic responses [65,87].

[5] The grey circle represents a stimulus-response combination in which delayed RTs were later shown to be an artefact of Taylor and Klein's [59] study design which created a subthreshold response association between keypress responses and arrowhead stimuli. Without such an association, IOR is not expected to be generated by a central arrow requiring no response (see Hilchey et al. [115])

Since the publication of Taylor and Klein's (2000) study, several studies have converged on the idea that the two forms of IOR can be dissociated in part through the use of central versus peripheral signals [e.g. 59,65,77,84,87–90]. In summary, when consecutive peripheral stimuli are used, IOR can inhibit information received from a particular location in space (i.e., sensory/attentional processing) *or* an associated saccadic response (i.e., oculomotor processing); as a result, any observed IOR may be the result of combined sensory/attentional and oculomotor-based effects. If central stimuli are used however, any inhibition attached to a peripheral location could not disrupt the processing of the imperative stimulus, but oculomotor response-based inhibition is possible. Correspondingly, studies attempting to "isolate" the oculomotor form of IOR have used centrally presented stimuli to evoke directional responses, such as making a saccade to a target indicated by an arrow presented at fixation [29,91,92,103,107]. Finally, although a number of studies have revealed IOR using various manual responses (e.g., button presses and reaching localization responses [18,19,92–96]), these studies unanimously relied upon the use of peripheral signals, and therefore may have revealed sensory/attentional rather than the motor form of IOR. Furthermore, with few exceptions [73,81; addressed later], the consensus found in the IOR literature is that the motor form of IOR is tightly linked with and likely not found outside of the oculomotor system [2,6,19,59,64,65,81,85,97–99].

1.4 The Spatial Distribution of IOR

Whereas the term IOR has been loosely used [76] to describe both sensory/attentional and oculomotor phenomena affecting participant responses, beyond the observation of slowed responses for previously signaled locations, the degree of similarity between the two forms of IOR remains unclear, in particular with respect to the pattern of RTs expected across unsignaled locations. However, an analysis of the pattern of RTs across more than one unsignaled location (e.g., using a stimulus arrangement similar to that shown in Figure 1.1) may be important in understanding the possible mechanisms underlying IOR and how it ultimately shapes behavior. Moreover, studying the pattern of RTs across more than 2 possible target locations is important to test for the presence of other possible sensorimotor processing biases, e.g., the possible adaptation-based effects of interest herein.

The spatial distribution of sensory/attentional IOR (i.e., when peripheral cues and targets are used, cf. 10-13) is now well characterized, and is associated with a clear monotonic relationship between response latency and the angular spatial offset between the first and second stimuli [2,6,63,75,100–105]. Specifically, the latency of a response to the second stimulus is greatest when it shares the same location as the first stimulus (i.e., a 0° offset), and decreases as the spatial offset between stimuli increases to 90°; thereafter, latencies may further decease or stabilize as the spatial offset increases to 180° (no reversal in the function can occur to satisfy the definition of monotonic). In other words, when sensory/attentional IOR is likely present, RTs across target locations typically follows the following pattern: 0° > 90° >/=180° [2,6,63,75,100–104]. This monotonic pattern of RTs has been replicated using peripheral target stimuli across a wide range of possible target offsets (e.g., [2,100]) and in a large number of studies [2,6,63,75,100–105]. Surprisingly, the spatial topography of the putative oculomotor IOR phenomenon, i.e., that expected when only central signals are used, has not been described with the same precision. In fact, previous studies of oculomotor IOR have explored only 0° and 180° offsets (e.g., as shown in Figure 1.2), finding that, like sensory/attentional IOR, response latencies are greater for 0° versus 180° conditions (e.g., [59,74,85,88]). Presumably, however, if the sensory/attentional and oculomotor phenomena are variations of the same basic process or mechanism (i.e., IOR), and if both forms of IOR serve a similar functional purpose such as the facilitation of visual search or foraging behavior [2,6,63,65], then their spatial distributions ought to be similar across a broader range of angular offsets between the first and second stimulus.

Emerging from the IOR literature, a simple 2x2 matrix can be constructed outlining the stimulus-response combinations traditionally used to reveal the sensory and oculomotor forms of IOR [59,65,78,87,88]. Several important observations should be made regarding this matrix. First, as indicated on the left side of the matrix, the hallmark pattern of IOR is well established and is consistently expected when either manual or saccadic responses are made to peripheral targets [2,6,63,75,100–104]. Second, as shown in the upper right cell of Table 1, previous research suggests the oculomotor form of IOR will occur when saccades are required in response to central arrowhead stimuli [29,91,92,103,107]. Notably, however, as discussed above, the spatial distribution of oculomotor IOR elucidated by central signals has not been previously established across more than 2 possible target locations (i.e., 0° and 180° offsets), leaving open the possibility that a pattern of RTs consistent with that predicted by neural adaptation effects may be observed (0°>90°<180°). Finally, as shown in the lower right cell of Table 1, IOR is not expected for manual detection or localization responses when consecutive central signals are used, provided the oculomotor system is inactive [59,88]. This observation is important, because it provides a stimulus-response condition where possible adaptation-based effects can be studied independent of well-established and expected IOR-based effects.

		Signal Type	
		Peripheral	Central
Oculomotor System	Active	Sensory/Oculomotor Well established spatial topography of sensory/attentional IOR where RTs consistently follow the pattern: 0° > 90° >/=180°	Oculomotor Spatial topography of oculomotor IOR unknown; neural adaptation effects predict RTs will follow: 0° > 90° < 180°.
	Inactive	Sensory Well established spatial topography of sensory/attentional IOR where RTs consistently follow the pattern: 0° > 90° >/=180°	-- Neural adaptation effects predict RTs will follow: 0° > 90° < 180°.

Table 1: The form of IOR (sensory or oculomotor) predicted by the IOR literature when the oculomotor system is active or inactive and either peripheral or central arrowhead stimuli are used for both S1 and S2. Note that the state of the oculomotor system would be considered active only if an eye movement was made in the direction of S1 or S2 as the preparation of saccadic responses in the absence of saccadic movement execution does not reveal IOR [106]. *Note that Table 1 assumes that when the oculomotor system is inactive, manual responses are instead required. Based on the above review of the IOR literature, IOR should not occur when central signals are used and manual responses are used.*

1.5 Competing Predictions: Oculomotor IOR or Adaptation?

The original goal of the present dissertation was to explore whether behavioural correlates of neural adaptation could be revealed through an examination of RTs when consecutive eye or arm movements were required in the centre-out task. Of interest was comparing the pattern of RTs across more than 2 target locations when central versus peripheral stimuli instructed target responses for the first time. The second and related goal of the dissertation was to test opposing predictions regarding the spatial distribution of RTs for consecutive movements while assuming different underlying mechanisms might affect RTs: neural adaptation or IOR.

To address these goals, throughout the dissertation, the pattern of RTs for consecutive saccades and manual-localization responses was examined across 4 possible target locations using both peripheral and central stimuli. If IOR was present, we expected to observe the well-established monotonic pattern of RTs (0°>90° >/=180°). By contrast, if adaptation-based effects were present, as discussed earlier, we expected to observe fastest RTs for 90° offsets and relatively slower RTs for 0° and 180° offsets (0° > 90° < 180°; the Adaptation Hypothesis).

It is important to note that the centre-out task with four possible target locations was used in order to (1) control movement starting point; and (2) directly test whether evidence of both IOR and neural adaptation can be revealed within the widely used centre-out paradigm. The first point is important given that RTs can vary as a function of movement starting point, for example, depending on the eccentricity of the eye or arm relative to a central fixation point or midline [19,107]. The second point is important because observing evidence of an adaptation-based motor response bias would both challenge the idea, proposed by Taylor and Klein [59], that a single form of IOR can account for the pattern of RTs observed in the in the centre-out task (e.g., when eye movements are required) and further, demonstrate the importance of examining RTs across more than two target locations offset by 0° and 180° in the centre-out task, as is common in the IOR literature[6].

1.6 Outline of the Present Thesis

In Study 1 (Chapter 2) [108], the traditional centre-out paradigm was used to measure RTs for consecutive eye and arm movements as a function of their angular offset from the direction of a prior movement made with the same effector. Participants were presented with either consecutive peripheral or central arrowhead signals. When peripheral signals were used, we expected to replicate the hallmark pattern of sensory/attentional IOR (0° > 90° >/= 180°). However, when central signals were used, we expected to "isolate" possible motor based effects from sensory/attentional IOR [59,65,87,88] which inhibits the processing of peripheral target locations. If our Adaptation Hypothesis was correct, we anticipated a pattern of slowed RTs for conditions where adaptation was present (0°>90°<180°) when central signals were

---

[6] While the centre-out task was deemed most appropriate for the purpose of the present thesis, it does come with some limitations. Most notably, the centre-out task requires that between S1 and S2 responses, a return-to-centre movement is required. As a result, three movements are made on each trial, and a return-to-centre movement always intervenes S1 and S2. While returning to centre is important to control movement starting point, other paradigms, including free visual search [2,6] the 'random walk' paradigm [107,116] may be useful for examining the pattern of RTs without the return to centre movement. As discussed later, the use of these more ecologically valid paradigms may be warranted to explore additional questions related to the present thesis.

used. On the other hand, if IOR was present, we expected to observe the hallmark monotonic pattern of RTs (0°>90°>/=180°). The pattern of RTs observed with central targets (0°>90°<180°) was consistent with the Adaptation Hypothesis, while as expected, the pattern of RTs observed with peripheral targets replicated the well-established spatial topography of IOR (0°>90°>/=180°).

Given that adaptation-based effects would by definition delay motor preparation processes (e.g., in PMC) [34–37], we were interested in whether we could eliminate the adaptation effect by allowing participants sufficient time to fully program their response, thus overcoming any possible adaptation effects. Such a finding would be consistent with an adaptation-based explanation of Study 1 and help to narrow down the possible range of neural mechanisms explaining the non-monotonic pattern of RTs observed. In Studies 2 and 3 (Chapters 3 and 4 respectively) [109,110] we therefore designed a paradigm allowing participants to fully prepare their saccadic or manual localization response in advance of being signaled to execute the movement. Consequently, any observed RT bias must be the result of motor execution processes rather than earlier sensory, attentional, or motor planning (e.g., adaptation) based processes. To our surprise, although the pattern of RTs supporting our original Adaptation Hypothesis was at least partially eliminated, we observed the hallmark pattern of IOR (0° > 90° >/= 180°) [109,110]. This result suggested that an IOR-like pattern of RTs can emerge as a late-stage motor *execution* bias when possible motor programming biases (such as those potentially caused by neural adaptation) are overcome.

While the results of Studies 2 and 3 were intriguing, the unique study design might have introduced an artifactual form of response inhibition due to the requirement to actively inhibit the execution of a prepared movement prior to the imperative stimulus. In Study 4 (Chapter 5), we therefore repeated the experimental paradigm used in Study 1 while using only 2 rather than 4 target locations [111] and focusing on arm movements. On separate trials, the target locations varied between 90° or 180° offsets, both of which were possible in Studies 1-3. This design was intended to maximize our chances of observing IOR (not seen in Chapter 2 with central signals), which is most commonly studied using 2 target locations. Observing IOR in Study 4 would (1) suggest that two different spatial topographies of motor response bias are possible under different task circumstances (i.e., dependent on the set size of possible target locations); (2) alleviate concerns that the results of Studies 2 and 3 were due to an artifact of our study design (i.e. by demonstrating IOR can occur with central stimuli in our target-target paradigm, without the use of a preparation signal); and, (3) reveal a motor form of IOR affecting reaching movements to central stimuli for the first time. Interestingly, independent of signal type, a unique pattern of RTs was observed (0°>90°<180°; 0°>180°) where 0° responses were slowest (consistent with IOR), 180° responses were intermediate, and 90° responses were fastest (consistent with motor adaptation effects).

In the final study of the present thesis (Study 5; Chapter 6), we repeated Study 4 while requiring saccadic rather than manual localization responses. When peripheral stimuli were used, we predicted and observed the well-established pattern of oculomotor IOR (0°>90°>/=180°). By contrast, and consistent with the presence of combined IOR and adaptation-based effects, when central signals were used, we replicated the pattern of RTs observed in Study 4 (0°>90°<180°; 0°>180°) with eye rather than arm movements. The results demonstrate multiple response biases can affect consecutive saccades in the center-out task and together with Studies 1 and 4, highlight the importance of examining RTs across more than two target locations in the target-target IOR paradigm.

Many of the methods and ideas that led to the specific experiments contained in the present thesis came from the wealth of IOR literature. It therefore seemed prudent to frame the individual studies in the context of IOR for increased impact within the field. However, in returning to the original motivation for exploring possible adaptation-based effects, within the General Introduction and General Discussion of the present thesis, some ideas and concepts have been refined to be more neutral with respect to IOR as a unifying theory or construct.

Whether any of the RT biases observed in the present thesis reflect neural adaptation or IOR requires further investigation and in some cases may ultimately be a question of theory (e.g., related to the putative adaptive significance of IOR [2,6,7]) or construct (e.g., related to the defining circumstances under which IOR was originally discovered [80,112])[7]. Nonetheless, the results of the present thesis collectively suggest

---

[7] For consistency in writing and terminology, when 0° RTs are slower than 90° or 180° RTs, in the present thesis, the effect is generally labelled IOR. This approach is consistent with the typical "convention" in the field where IOR is used to loosely refer to the observation of slowest RTs for responses to previously signalled compared to unsignaled locations. Furthermore, when a preference for 90° RTs is observed, the

that (1) spatially defined RT biases can emerge from the simple execution of a prior movement made with the same effector; (2) that these RT biases can occur outside of the oculomotor system; and (3) that IOR-like motor biases can emerge from late-stage motor execution processes.

---

effect is usually referred to as adaptation. The contribution of the present thesis to the literature is not related to the labels used to describe the response biases observed, but rather, is derived from the systematic investigation of RTs across four target locations in the target-target task when signal type, set-size, and stage of information processing variables are manipulated [cf. 66].

1.7 References

[1] J. Laczko, M.L. Latash, Progress in motor control: theories and translations, Springer International Publishing, 2016.

[2] J.W. MacInnes, R.M. Klein, Inhibition of return biases orienting during the search of complex scenes, Sci. World J. 3 (2003) 75–86.

[3] A.D. Milner, M.A. Goodale, The visual brain in action, 2nd ed., Oxford University Press, New York, NY, US, 2006.

[4] J.M. Karl, I.Q. Whishaw, Different evolutionary origins for the reach and the grasp: an explanation for dual visuomotor channels in primate parietofrontal cortex, 4 (2013) 1–13.

[5] N. Hogan, E. Bizzi, F. Mussa-Ivaldi, T. Flash, Controlling multijoint motor behaviour, Exerc. Sport Sci. Rev. 15 (1987) 153–190.

[6] R.M. Klein, W.J. MacInnes, Inhibition of return is a foraging facilitator in visual search, Psychol. Sci. 10 (1999) 346–352.

[7] Z. Wang, R.M. Klein, Searching for inhibition of return in visual search: a review, Vision Res. 50 (2010) 220–8.

[8] R.M. Klein, Inhibitory tagging system facilitates visual search, Nature. 334 (1988) 430–431.

[9] J. Diedrichsen, R. Shadmehr, R.B. Ivry, The coordination of movement: optimal feedback control and beyond, Trends Cogn. Sci. 14 (2010) 31–39.

[10] F. Clarac, D. Cattaert, D. Le Ray, Central control components of a ‘ simple ’ stretch reflex, (2000) 199–208.

[11] M.J.L. Perenboom, M. Van De Ruit, J.H. De Groot, A.C. Schouten, C.G.M. Meskers, Evidence for sustained cortical involvement in peripheral stretch reflex during the full long latency reflex period, Neurosci. Lett. 584 (2015) 214–218.

[12] T. Naselaris, H. Merchant, B. Amirikian, A.P. Georgopoulos, Large-scale organization of preferred directions in the motor cortex. I. Motor cortical hyperacuity for forward reaching, J Neurophysiol. 96 (2006) 3231–3236.

[13] C.D. Cowper-Smith, E.Y.Y. Lau, C.A. Helmick, G.A. Eskes, D.A. Westwood, Neural coding of movement direction in the healthy human brain, PLoS One. 5 (2010) e13330.

[14] M. Eisenberg, L. Shmuelof, E. Vaadia, E. Zohary, Functional organization of human motor cortex: directional selectivity for movement, Life Sci. 30 (2010) 8897–8905.

[15] K. Grill-Spector, R. Henson, A. Martin, Repetition and the brain: neural models of stimulus-specific effects, Trends Cogn Sci. 10 (2006) 14–23.

[16] K. Grill-Spector, R. Malach, fMR-adaptation: a tool for studying the functional properties of human cortical neurons, Acta Psychol. 107 (2001) 293–321.

[17] B. Krekelberg, G.M. Boynton, R.J. van Wezel, Adaptation: from single cells to BOLD signals, Trends Neurosci. 29 (2006) 250–256.

[18] H.F. Neyedli, T.N. Welsh, The processes of facilitation and inhibition in a cue-target paradigm: insight from movement trajectory deviations, Acta Psychol. (Amst). 139 (2012) 159–65.

[19] L. Tremblay, T.N. Welsh, D. Elliott, Between-trial inhibition and facilitation in goal-directed aiming: manual and spatial asymmetries, Exp. Brain Res. (2005) 79–88.

[20] T.N. Welsh, D. Elliott, Effects of Response Priming and Inhibition on Movement Planning and Execution, J. Mot. Behav. 36 (2004) 200–211.

[21] M.I. Posner, Chronometric explorations of mind, Hillsdale (N.J.) : Erlbaum, 1978.

[22] M.I. Posner, Timing the brain: Mental chronometry as a tool in neuroscience, PLoS Biol. 3 (2005) 0204–0206.

[23] S. Sternberg, The discovery of processing stages: extensions of donders' method, Acta Psychol. (Amst). 30 (1969) 276–315.

[24] A.P. Georgopoulos, J.F. Kalaska, J.T. Massey, Spatial trajectories and reaction times of aimed movements: effects of practice, uncertainty, and change in target location, J. Neurophysiol. 46 (1981) 725–743.

[25] A. Tankus, Y. Yeshurun, T. Flash, I. Fried, Encoding of speed and direction of movement in the human supplementary motor area, J. Neurosurg. 110 (2009) 1304–1316.

[26] J. Lee, H. Choi, S. Lee, B.H. Cho, K.H. Ahn, I.Y. Kim, K.M. Lee, D.P. Jang, Decoding saccadic directions using epidural ECoG in non-human primates, J. Korean Med. Sci. 32 (2017) 1243–1250.

[27] J. Morimoto, M. Kawato, Creating the brain and interacting with the brain: an integrated approach to understanding the brain, J. R. Soc. Interface. 12 (2015) 20141250–20141250.

[28] M.C. Cirstea, A.B. Mitnitski, A.G. Feldman, M.F. Levin, Interjoint coordination dynamics during reaching in stroke, Exp. Brain Res. 151 (2003) 289–300.

[29] R. Caminiti, P.B. Johnson, A. Urbano, Making arm movements within different parts of space: dynamic aspects in the primate motor cortex, J Neurosci. 10 (1990) 2039–2058.

[30] S. Kakei, D.S. Hoffman, P.L. Strick, Direction of action is represented in the ventral premotor cortex, Nat. Neurosci. 4 (2001) 1020–5.

[31] A.P. Georgopoulos, J.F. Kalaska, R. Caminiti, J.T. Massey, On the Relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex, J. Neurosci. 11 (1982) 1527–1537.

[32] S. Kakei, D.S. Hoffman, P.L. Strick, Muscle and movement representations in the primary motor cortex, Science (80-.). 285 (1999) 2136–2139.

[33] P.A. Fortier, J.F. Kalaska, A.M. Smith, Cerebellar neuronal activity related to whole-arm reaching movements in the monkey, J Neurophysiol. 62 (1989) 198–211.

[34] A.P. Georgopoulos, H. Merchant, T. Naselaris, B. Amirikian, Mapping of the preferred direction in the motor cortex, Proc. Natl. Acad. Sci. USA. 104 (2007) 11068–11072.

[35] A.P. Georgopoulos, R.E. Kettner, A.B. Schwartz, Primate motor cortex and free arm movements to visual targets in three-dimensional space. II. Coding of the direction of movement by a neuronal population, J Neurosci. 8 (1988) 2928–2937.

[36] A.. Georgopoulos, Neural integration of movement: role of motor cortex in reaching, FASEB J. 2 (1988) 2849–2857.

[37] B.M. Koeppen, B.A. Stanton, Berne and Levy physiology e-book, Elsevier Health Sciences, 2017.

[38] M. Davare, A. Zénon, M. Desmurget, E. Olivier, Dissociable contribution of the parietal and frontal cortex to coding movement direction and amplitude, Front. Hum. Neurosci. 9 (2015) 1–12.

[39] S. Fabbri, A. Caramazza, A. Lingnau, Tuning curves for movement direction in the human visuomotor system, J. Neurosci. 30 (2010) 13488–13498.

[40] B. Amirikian, A.P. Georgopoulos, Modular organization of directionally tuned cells in the motor cortex: is there a short-range order?, Proc. Natl. Acad. Sci. USA. 100 (2003) 12474–12479.

[41] A.P. Georgopoulos, J.F. Kalaska, R. Caminiti, J.T. Massey, On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex, J Neurosci. 2 (1982) 1527–1537.

[42] R. Caminiti, P.B. Johnson, C. Galli, S. Ferraina, Y. Burnod, Making arm movements within different parts of space: the premotor and motor cortical representation of a coordinate system for reaching to visual targets, J Neurosci. 11 (1991) 1182–1197.

[43] A.P. Georgopoulos, A.B. Schwartz, R.E. Kettner, Neuronal population coding of movement direction, Science (80-.). 233 (1986) 1416–1419.

[44] B. Amirikian, A.. Georgopulos, Directional tuning profiles of motor cortical cells, Neurosci. Res. 36 (2000) 73–79.

[45] A.B. Schwartz, R.E. Kettner, A.P. Georgopoulos, Primate motor cortex and free arm movements to visual targets in three-dimensional space. I. Relations between single cell discharge and direction of movement, J Neurosci. 8 (1988) 2913–2927.

[46] A.P. Georgopoulos, On reaching, Annu Rev Neurosci. 9 (1986) 147–170.

[47] P.A. Fortier, A.M. Smith, J.F. Kalaska, Comparison of cerebellar and motor cortex activity during reaching: directional tuning and response variability, J Neurophysiol. 69 (1993) 1136–1149.

[48] A.B. Sereno, C.B. Jeter, V. Pariyadath, K.A. Briand, Dissociating sensory and motor components of inhibition of return, Sci. World J. 6 (2006) 862–887.

[49] J.J. Snyder, A. Kingstone, Inhibition of return at multiple locations in visual search: when you see it and when you don't, Q. J. Exp. Psychol. 54 (2001) 1221–1237.

[50] C.J. Bruce, M.E. Goldberg, Primate frontal eye fields. I. Single neurons discharging before saccades, J. Neurophysiol. 53 (1985) 603–635.

[51] G.D. Horwitz, W.T. Newsome, Target selection for saccadic eye movements: direction-selective visual responses in the superior colliculus, J. Neurophysiol. 86 (2001) 2527–2542.

[52] D.A. Robinson, Eye movements evoked by collicular stimulation in the alert monkey, Vis. Res. 12 (1972) 1795–1808.

[53] P.H. Schiller, M. Stryker, Single-unit recording and stimulation in superior colliculus of the alert rhesus monkey, J. Neurophysiol. 35 (1972) 915–924.

[54] R. Quian Quiroga, Movement intention is better predicted than attention in the posterior parietal cortex, J. Neurosci. 26 (2006) 3615–3620.

[55] D.J. Herzfeld, Y. Kojima, R. Soetedjo, R. Shadmehr, Encoding of action by the Purkinje cells of the cerebellum, Nature. 15 (2015) 439–442.

[56] S. Squatrito, M.G. Maioli, Encoding of smooth pursuit direction and eye position by neurons of area MSTd of macaque monkey, J. Neurosci. 17 (1997) 3847–3860.

[57] A. Afshar, G. Santhanam, B.M. Yu, S.I. Ryu, M. Sahani, K. V Shenoy, Single-trial neural correlates of arm movement preparation, Neuron. 71 (2011) 555–64.

[58] M.M. Churchland, G. Santhanam, K. V Shenoy, Preparatory activity in premotor and motor cortex reflects the speed of the upcoming reach, J. Neurophysiol. 96 (2006) 3130–46.

[59] T.L. Taylor, R.M. Klein, Visual and motor effects in inhibition of return, J. Exp. Psychol. Hum. Percept. Perform. 26 (2000) 1639–1656.

[60] J. Posner, M I, Rafal, R D, Choate, L S, Vaughan, Inhibition of Return: Neural Basis and Function, Cogn. Neuropsychol. (1985) 211–228.

[61] E.N. Sokolov, Higher nervous functions: the orienting reflex, Annu. Rev. Physiol. 25 (1963) 545–580.

[62] P.A. McCormick, R. Klein, The spatial distribution of attention during covert visual orienting, Acta Psychol. (Amst). 75 (1990) 225–242.

[63] R.M. Klein, Inhibition of return, Trends Cogn. Sci. 4 (2000) 138–147.

[64] M. Posner, Y. Cohen, Components of visual orienting, in: H. Bouma, D.G. Bouwhuis (Eds.), Atten. Perform. X, Amsterdam: North Holland, 1984: pp. 531–556.

[65] Z. Wang, J. Satel, R.M. Klein, Sensory and motor mechanisms of oculomotor inhibition of return, Exp. Brain Res. 218 (2012) 441–53.

[66] S.P. Tipper, B. Weaver, L.M. Jerreat, A.L. Burak, Object-based and environment-based inhibition of return of visual attention, J. Exp. Psychol. Hum. Percept. Perform. 20 (1994) 478–499.

[67] S.P. Tipper, B. Weaver, F.L. Watson, Inhibition of return to successively cued spatial locations: commentary on Pratt and Abrams (1995), J. Exp. Psychol. Hum. Percept. Perform. 22 (1996) 1289–1293.

[68] T.J. Smith, J.M. Henderson, Looking back at waldo: oculomotor inhibition of return does not prevent return fixations, J. Vis. 11 (2011) 3–3.

[69] T.J. Smith, J.M. Henderson, Facilitation of return during scene viewing, Vis. Cogn. 17 (2009) 1083–1108.

[70] W.J. MacInnes, A.R. Hunt, M.D. Hilchey, R.M. Klein, Driving forces in free visual search: An ethology, Attention, Perception, Psychophys. 76 (2014) 280–295.

[71] K.R. Dukewich, Reconceptualizing inhibition of return as habituation of the orienting response., Psychon. Bull. Rev. 16 (2009) 238–51.

[72] M.D. Hilchey, R.M. Klein, J. Ivanoff, Perceptual and motor inhibition of return: components or flavors?, Atten. Percept. Psychophys. 74 (2012) 1416–29.

[73] T.L. Taylor, R.M. Klein, On the causes and effects of inhibition of return, Psychon. Bull. Rev. 5 (1998) 625–643.

[74] R.D. Rafal, P.A. Calabresi, C.W. Brennan, T.K. Sciolto, Saccade preparation inhibits reorienting to recently attended locations, J Exp Psychol Hum Percept Perform. 15 (1989) 673–685.

[75] J.J. Snyder, A. Kingstone, W.C. Schmidt, Attentional momentum does not underlie the inhibition of return effect, J. Exp. Psychol. Hum. Percept. Perform. 27 (2001) 1420–1432.

[76] G. Berlucchi, Inhibition of return: A phenomenon in search of a mechanism and a better name., Cogn. Neuropsychol. 23 (2006) 1065–74.

[77] E. Martín-arévalo, A. Kingstone, J. Lupiáñez, Is “Inhibition of Return” due to the inhibition of the return of attention?, Q. J. Exp. Psychol. 66 (2013) 347–359.

[78] J. Satel, M.D. Hilchey, Z. Wang, C.S. Reiss, R.M. Klein, In search of a reliable electrophysiological marker of oculomotor inhibition of return, Psychophysiology. 51 (2014) 1037–1045.

[79] A. Bourgeois, A.B. Chica, R. Migliaccio, M.T. de Schotten, P. Bartolomeo, Cortical control of inhibition of return: Evidence from patients with inferior parietal damage and visual neglect, Neuropsychologia. 50 (2012) 800–809.

[80] M.D. Hilchey, R.M. Klein, J. Satel, Returning to “inhibition of return” by dissociating long-term oculomotor IOR from short-term sensory adaptation and other nonoculomotor “inhibitory” cueing effects, J. Exp. Psychol. Hum. Percept. Perform. 40 (2014) 1603–1616.

[81] A.B. Chica, T.L. Taylor, J. Lupiáñez, R.M. Klein, Two mechanisms underlying inhibition of return, Exp. Brain Res. 201 (2010) 25–35.

[82] R.S. Abrams, R.A., Dobkin, Inhibition of return: effects of attentional cueing on eye movement latencies, J. Exp. Psychol. Hum. Percept. Perform. 20 (1994) 467–477.

[83] M.C. Dorris, T.L. Taylor, R.M. Klein, D.P. Munoz, Influence of previous visual stimulus or saccade on saccadic reaction times in monkey, J Neurophysiol. 81 (1999) 2429–2436.

[84] J.H. Fecteau, D.P. Munoz, Correlates of capture of attention and inhibition of return across stages of visual processing, J. Cogn. Neurosci. 17 (2005) 1714–1727.

[85] A.R. Hunt, A. Kingstone, Inhibition of return: dissociating attentional and oculomotor components, J. Exp. Psychol. Hum. Percept. Perform. 29 (2003) 1068–1074.

[86] J. Lupianez, Inhibition of return, in: H. Nobre, J.T. Coull (Eds.), Atten. Time, 2010: pp. 17–34.

[87] J. Satel, Z. Wang, Investigating a two causes theory of inhibition of return, Exp. Brain Res. 223 (2012) 469–478.

[88] M.H. Fischer, J. Pratt, S.F. Neggers, Inhibition of return and manual pointing movements, Percept. Psychophys. 65 (2003) 379–387.

[89] R. Rafal, R. Egly, D. Rhodes, Effects of inhibition of return on voluntary and visually guided saccades, Can J Exp Psychol. 48 (1994) 284–300.

[90] R.A. Abrams, R.S. Dobkin, Inhibition of return: effects of attentional cuing on eye movement latencies, J. Exp. Psychol. Hum. Percept. Perform. 20 (1994) 467–477.

[91] M.D. Hilchey, D. Dohmen, N. Crowder, R.M. Klein, When is inhibition of return input- or output-based? It depends on how you look at it, Can. J. Exp. Psychol. 70 (2016) 325–334.

[92] K.A. Briand, A.L. Larrison, A.B. Sereno, Inhibition of return in manual and saccadic response systems, Percept Psychophys. 62 (2000) 1512–1524.

[93] L. Howard, J. Lupiáñez, S. Tipper, Inhibition of return in a selective reaching task: an investigation of reference frames, J. Gen. Psychol. 126 (1999) 421–42.

[94] S. Khatoon, K. a Briand, A.B. Sereno, The role of response in spatial attention: direct versus indirect stimulus-response mappings, Vision Res. 42 (2002) 2693–708.

[95] J. Pratt, B. Neggers, Inhibition of return in single and dual tasks: Examining saccadic, keypress, and pointing responses, Percept. Psychophys. 70 (2008) 257–265.

[96] A.B. Sereno, C.B. Jeter, V. Pariyadath, K.. Briand, Dissociating sensory and motor components of inhibition of return, Sci. World J. 6 (2006) 862–887.

[97] A. Kingstone, J. Pratt, Inhibition of return is composed of attentional and oculomotor processes, Percept Psychophys. 61 (1999) 1046–1054.

[98] J. Ristic, A. Wright, A. Kingstone, The number line effect reflects top-down control, Psychon. Bull. Rev. 13 (2006) 862–868.

[99] L.A. Howard, J. Lupianez, S.P. Tipper, Inhibition of return in a selective reaching task: an investigation of reference frames, J. Gen. Psychol. 126 (1999) 421–442.

[100] P.J. Bennett, J. Pratt, The spatial distribution of inhibition of return, Psychol Sci. 12 (2001) 76–80.

[101] E.A. Maylor, R. Hockey, Inhibitory component of externally controlled covert orienting in visual space, J. Exp. Psychol. Hum. Percept. Perform. 11 (1985) 777–787.

[102] J. Pratt, R.A. Abrams, Inhibition of return to successively cued spatial locations, J Exp Psychol Hum Percept Perform. 21 (1995) 1343–1353.

[103] J. Pratt, J., Adam, J.J., McAuliffe, The spatial relationship between cues and targets mediates inhibition of return, J. Exp. Psychol. 52 (1998) 213–216.

[104] J. Pratt, T.M. Spalek, F. Bradshaw, The time to detect targets at inhibited and noninhibited locations: Preliminary evidence for attentional momentum, J. Exp. Psychol. Hum. Percept. Perform. 25 (1999) 730–746.

[105] B. Wang, C. Yan, R.M. Klein, Z. Wang, Inhibition of return revisited: Localized inhibition on top of a pervasive bias, Psychon. Bull. Rev. (2017) 1–7.

[106] A.B. Chica, R.M. Klein, R.D. Rafal, J.B. Hopfinger, Endogenous saccade preparation does not produce inhibition of return: failure to replicate Rafal, Calabresi, Brennan, & Sciolto (1989)., J. Exp. Psychol. Hum. Percept. Perform. 36 (2010) 1193–206.

[107] A.J. Anderson, H. Yadav, R.H.S.S. Carpenter, Directional prediction by the saccadic system, Curr. Biol. 18 (2008) 614–618.

[108] C.D. Cowper-Smith, J. Harris, G.A. Eskes, D.A. Westwood, Spatial interactions between successive eye and arm movements: signal type matters, PLoS One. 8 (2013) e58850.

[109] C.D. Cowper-Smith, G.A. Eskes, D.A. Westwood, Motor inhibition of return can affect prepared reaching movements, Neurosci. Lett. 541 (2013) 83–86.

[110] C.D. Cowper-Smith, G.A. Eskes, D.A. Westwood, Saccadic inhibition of return can arise from late-stage execution processes, Neurosci. Lett. 531 (2012) 120–4.

[111] C.D. Cowper-Smith, D.A. Westwood, Motor IOR revealed for reaching, Atten. Percept. Psychophys. 75 (2013) 1914–22.

[112] G. Berlucchi, Inhibition of return: A phenomenon in search of a mechanism and a better name, Cogn. Neuropsychol. 23 (2006) 1065–1074.

[113] I. Havsteen, A. Ohlhues, K.H. Madsen, J.D. Nybing, H. Christensen, A. Christensen, Are movement artifacts in magnetic resonance imaging a real problem? - A narrative review, Front. Neurol. 8 (2017) 1–8.

[114] R.M. Klein, M.D. Hilchey, Oculomotor inhibition of return, in: S. Liversedge, I. Gilchrist, S. Everline (Eds.), Oxford Handb. Eye Movements, Oxford University Press, London, UK, 2011: pp. 471–492.

[115] M.D. Hilchey, J. Satel, J. Ivanoff, R.M. Klein, On the nature of the delayed “inhibitory” cueing effects generated by uninformative arrows at fixation, Psychon. Bull. Rev. (2013).

[116] S.A.H. Jones, C.D. Cowper-Smith, D.A. Westwood, Directional interactions between current and prior saccades, Front. Hum. Neurosci. 8 (2014) 1–10.

CHAPTER 2: SPATIAL INTERACTIONS BETWEEN SUCCESSIVE EYE AND ARM MOVEMENTS: SIGNAL TYPE MATTERS

C.D. Cowper-Smith, J. Harris, G.A. Eskes, D.A Westwood, Spatial interactions between successive eye and arm movements: signal type matters, PLoS One 8 (2013) e58850.

2.1 Abstract

Spatial interactions between consecutive movements are often attributed to inhibition of return (IOR), a phenomenon in which responses to previously signaled locations are slower than responses to unsignaled locations. In two experiments using peripheral target signals offset by 0°, 90°, or 180°, we show that consecutive saccadic (Experiment 1) and reaching (Experiment 3) responses exhibit a monotonic pattern of reaction times consistent with the currently established spatial distribution of IOR. In contrast, in two experiments with central target signals (i.e., arrowheads pointing at target locations), we find a non-monotonic pattern of reaction times for saccades (Experiment 2) and reaching movements (Experiment 4). The difference in the patterns of results observed demonstrates different behavioural effects that depend on signal type. The pattern of results observed for central stimuli are consistent with a model in which neural adaptation is occurring within motor networks encoding movement direction in a distributed manner.

2.2 Introduction

In everyday tasks such as reading, driving, or eating, we engage in sequences of spatially directed movements. Whereas each movement might have an independent goal, the planning and execution of consecutive movements made with the same effector is likely to rely on overlapping spatial representations. As such, it is of interest to explore the spatial interactions that occur between movements made close together in time.

Such interactions have been explored extensively for orienting responses, in which participants respond to a target stimulus after a preceding cue stimulus. As initially described by Posner and Cohen [25], for cue-target onset asynchronies of approximately 300 ms (or more), responses are slower to targets appearing at cued versus uncued locations – a phenomenon later given the name 'inhibition of return,' (IOR) to reflect the selective bias against responding to previously signaled locations [26].

Many different task parameters have been adopted in order to study IOR, however two commonly manipulated variables are: (1) response type (e.g. manual or saccadic) and (2) signal type (e.g. peripheral onset or central arrowhead) [20, 25, 26, 30, 31, 39, 41]. Although the presence or absence of IOR has been studied across all possible combinations of these response and signal types [39][8], the spatial distribution of IOR, i.e. the pattern of RTs observed for targets that are presented at, intermediate to, or opposite the cued location, remains incompletely characterized for different signal types. In particular, although the spatial distribution of IOR is well established when peripheral stimuli are used [as described below; 3, 18, 19, 21, 23, 27-29, 36], the same cannot be said when central arrowhead stimuli are used. This is because previous studies using central signals have relied on the use of two target locations, typically aligned to the left and right of fixation [e.g. 15, 30, 39]. While these conditions enable

---

[8] It is important to note that Taylor and Klein used a choice-location discrimination task for their manual responses (i.e. where participants responded to different target locations with different spatially congruent buttons). The presence or absence of IOR has not been fully studied for other types of manual responses (e.g. simple detection or reaching-localization).

one to determine the presence and magnitude of an RT difference between the cued and uncued target locations, they do not enable a comprehensive analysis of the spatial properties of the putative IOR phenomenon. Therefore, previous work that has inferred the presence of IOR while using central signals and only two possible target locations, may have missed important data points regarding the spatial properties of the (putatively observed) IOR phenomenon. In particular, it remains unclear whether IOR experiments using central signals reveal similarly distributed behavioural effects to that observed with peripheral signals.

Some lines of evidence provide reason to believe that different forms of IOR can be observed depending on the type of signal used to prompt responses. For example, some scholars have argued that peripheral and central stimuli can be used to reveal the sensory/attentional and motor forms of IOR respectively [e.g. 15, 20, 30, 31, 33, 38, 39, 41; see 41 for a well-articulated description]. Specifically, when consecutive peripheral stimuli are used, IOR might inhibit either (1) information received from a particular location in space (i.e., sensory/attentional processing) or (2) the production of any required response (i.e., motor processing). In contrast, when central stimuli are used, any inhibition attached to a peripheral location cannot disrupt the processing of the imperative stimulus, but response-based inhibition is possible. Correspondingly, IOR observed with central stimuli might be considered to affect motor-based processes [15, 20, 30, 31, 33, 38, 39, 41]. Notably however, other scholars have shown that late-stage attentional processes can be tied to the generation of motor responses [e.g. a movement of attention that immediately precedes the execution of an eye or arm movement; 11, 35]; it is therefore possible that motor, late-stage attentional, or some combination of these processes are affected by IOR when central signals are used to prompt motor responses[9].

If different sensory/attentional and response-based forms of IOR can in fact be dissociated by signal type (at least in part), then given that the sensory/attentional and motor response systems represent space differently [depending on the stage of processing affected; cf. 4, 14, 25, 40, 41], it is possible that different spatial distributions of IOR will be observed depending on signal type. The spatial distribution of IOR observed with peripheral stimuli is associated with a clear monotonic relationship between response latency and the angular spatial offset between the first and second stimuli [3, 18, 19, 21, 23, 27-29, 36]: the latency of a response to the second stimulus is greatest when it shares the same location as the first stimulus (i.e., a 0° offset), and decreases as the spatial offset between stimuli increases to 180°. This monotonic pattern of IOR has been established by examining RTs across many different angular offsets ranging between 0° and 180°, although many studies have adopted 0°, 90° and 180° offsets. As discussed earlier, the spatial distribution of RTs observed when central signals are used remains un-established. On one hand, if IOR is similar when peripheral and central stimuli are used [e.g. as suggested by previous research using only two

---

[9] If late-stage attentional processes that are tied to the execution of a movement are inhibited when central stimuli are used, they are nonetheless likely to be different from the sensory/attentional processes that are inhibited when peripheral stimuli are used. For example, when simple detection responses are required in cue-target tasks, IOR is only observed when peripheral, but not central target stimuli are used; this observation indicates that the presentation of the arrow alone is insufficient to reveal IOR, and moreover, that peripheral target stimuli can be used to reveal a spatially localized deficit in sensory/attentional processing.

target locations; 39] then one would expect to observe similar spatial distributions of RTs independent of signal type. On the other hand, if sensory/attentional and motor forms of IOR can be dissociated, at least in part by signal type, then it is possible that different spatial distributions will be observed when motor responses are instructed by central versus peripheral stimuli.

Using variations of the traditional centre-out consecutive target paradigm (where participants respond to the first signal and then return to centre before responding to the second signal [e.g., 39]), we examined the pattern of RTs observed in four experiments when participants were required to make consecutive eye (E1 and E2) or arm (E3 and E4) movements to either peripheral (E1 and E3) or central (E2 and E4) stimuli (because consecutive responses are required, this task is referred to as a target-target paradigm)[10]. We predicted that if signal type plays an important role in shaping the pattern of RTs observed, then the pattern of RTs observed should vary as a function of signal type but be relatively independent of the effector system used to respond. For the experiments involving peripheral stimuli, based on prior work [3, 18, 19, 21, 23, 27-29, 36], we predicted a monotonic spatial relationship between RT and target-target spatial offset (0° > 90° >/= 180°; see the introduction to E1 for more details) for saccades (E1) and reaching movements (E3) alike. If the spatial topography of IOR (as traditionally defined) is insensitive to signal type, then one would expect to observe a similar monotonic spatial distribution of RTs across all offset conditions when central

---

[10] This type of target-target paradigm was previously used [39] to reveal IOR in all of the stimulus-response combinations adopted presently (except when manual responses were required to consecutive arrowhead stimuli), across two target locations aligned to the left and right of fixation.

arrowhead signals (rather than peripheral onsets) were used to prompt responses. To anticipate the results, different spatial patterns of RTs were observed when peripheral and central signals were used to prompt consecutive responses respectively. These results are interpreted and discussed in the context of the possible mechanisms and functions underlying the observed RT patterns.

2.1 Experiment One: Peripheral Target - Eye

In E1 we aimed to extend the monotonic spatial pattern of IOR [cf. 3, 18, 19, 21, 23, 27-29, 36], observed in previous cue-target studies to a target-target task that required participants to make two consecutive saccades to peripheral target stimuli. Previous cue-target studies revealed a monotonic pattern of RTs ($0^\circ > 90^\circ \geq 180^\circ$), where (1) RTs are greatest at the cued location, (2) RTs drop off sharply as the cue-target offset increases from 0° to 90°, and (3) RTs do not increase, but will either remain stable or continue to decrease slightly (both patterns fit the monotonic definition) from 90° to 180°. Consistent with previous work examining the spatial distribution of IOR [e.g., 20, 29, 36, 40], we used four target locations (up, down, left and right of fixation) that allowed us to vary the degree of directional offset between the first and second stimuli from 0° (i.e., same direction) to 180° (opposite direction), in 90° increments. Confirmation of the monotonic IOR pattern in this paradigm was important, in order to subsequently compare the topography of RTs when central rather than peripheral signals were used in E2.

2.1.1 Method

All experimental procedures were approved by the local research ethics board in the Department of Psychology and Neuroscience at Dalhousie University, and participants in all studies provided written informed consent.

Participants. Nineteen (11 female, 8 male) undergraduate students participated in E1. All participants were recruited through the Department of Psychology subject pool at Dalhousie University. Participants were right handed, had normal or corrected-to-normal vision and reported no history of visual, motor, or neurological abnormalities.

Apparatus and Stimuli. Stimuli were displayed using Experiment Builder v1.3 software (EyeLink II; SR Research, Mississauga, Ontario, Canada). Eye position was monitored with an EyeLink™II (SR Research, Osgoode, ON) eye-tracking system (sampling rate = 500 Hz; spatial precision <0.01; spatial accuracy <0.8 root mean square error). Calibration of the EyeLink II was carried out in the same horizontal viewing plane that was used to display the target stimuli. Participants were seated at a viewing distance of approximately 58 centimeters from the screen.

Stimuli consisted of a fixation circle 3.15° in diameter that was surrounded by 4 equidistant peripheral placeholders (circles that were 2.5° in diameter; *Figure 2.1*). Placeholders were spaced 4.6 degrees away from fixation (measured from the centre of fixation to the centre of the placeholder) and were separated by 90° from each other (i.e., up, right, down, left). The outlines of the central fixation circle and peripheral placeholders were presented with a 4px weight on a 30-inch Elo touch screen LCD monitor (11.7 ms response time; Elo TouchSystems, Menlo Park, California, USA).

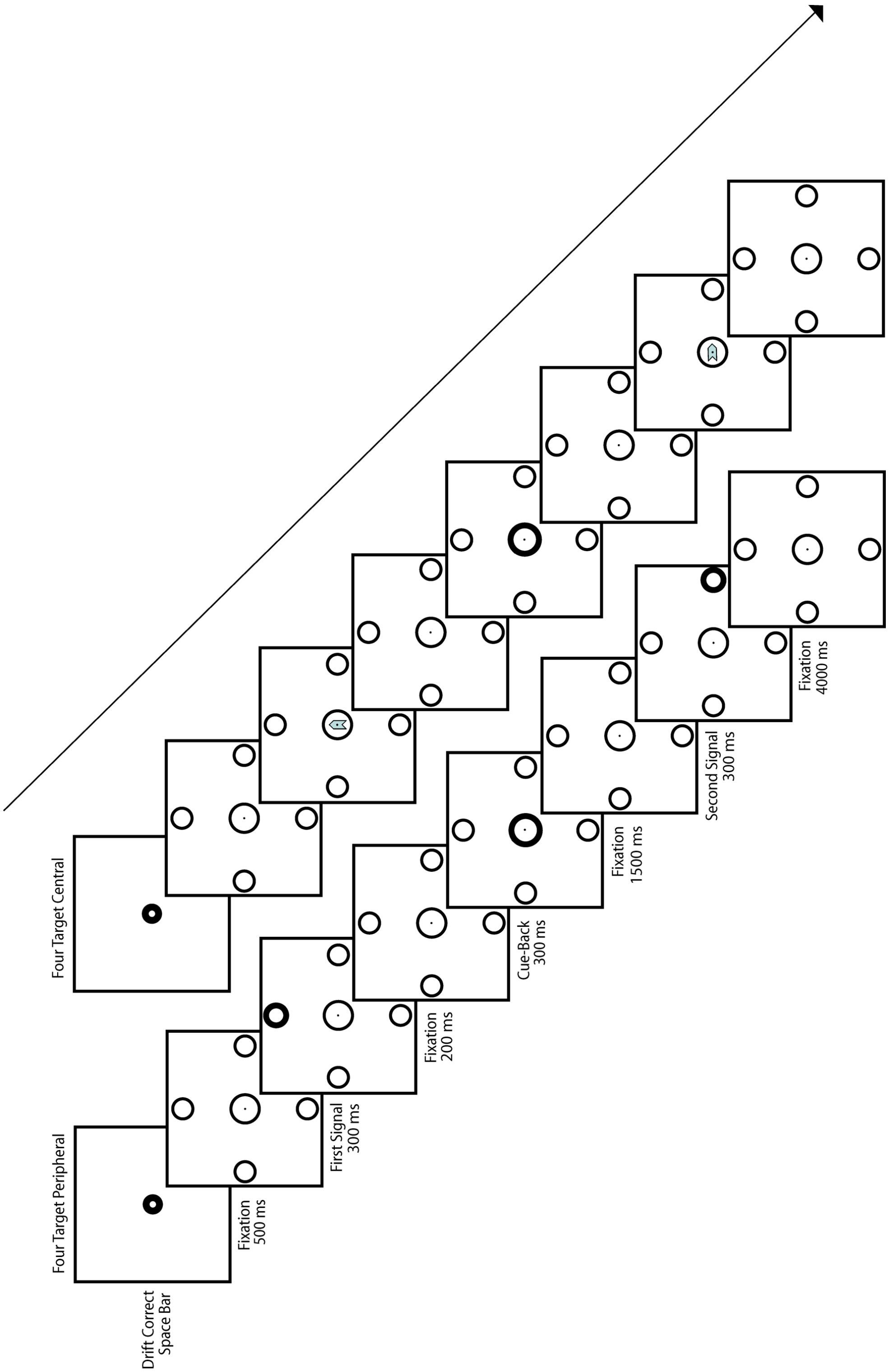
Procedure. The EyeLink®II system was calibrated using a 9-point routine. Participants practiced trials selected randomly from the main experiment until the successful completion of 8 consecutive trials. Participants were required to complete these trials without any error feedback, as described below. Trials consisted of two consecutive signals (S1 and S2) where the border of a peripheral placeholder temporarily changed from a 4px line-weight to an 8px line-weight. Participants were instructed to saccade to the target with the bolded outline. S1 and S2 indicated each of the four possible target locations with equal probability (0.25), creating a total of 16 equally possible S1/S2 pairings. These pairings therefore signaled consecutive saccadic responses that were offset from each other by 0°, -90°, +90°, or 180. After practice was completed, each S1/S2 pairing was presented 12 times for a total of 192 trials which were divided into two runs of 96 trials separated by a short break. S1/S2 pairings were randomized on a trial-by-trial basis.

The timing of stimuli within a single trial for E1 is shown in *Figure 2.1*. Participants were instructed to make a saccade toward and fixate the signaled targets as quickly and accurately as possible, and to return their eyes to centre upon display of the cue-back as well as after completing their S2 response. If participants did not respond within 1.5 seconds to S1 or S2, if they did not return their eyes to centre between S1 and S2, or if they failed to maintain fixation during the fixation stimulus (immediately prior to S1 or S2), an error message was displayed, the trial was aborted, and was not recycled. Data from aborted trials were excluded from all subsequent analyses. Less than 5% of trials were aborted due to a slow response, a failure to return their eyes to centre between S1 and S2, or a failure to maintain fixation. The key dependent measure for all experiments reported herein is the reaction time (RT) for the response to the *second* target in the sequence (i.e., S2 RT).

Data Analysis. The description of data analyses here applies to all four experiments in the present paper. Trials with S2 RTs less than 100 ms (anticipation) or greater than 1000 ms (miss) were flagged during data processing and excluded from all analyses. Consistent with previous work [39], data were also flagged and excluded if the S1 response was greater than 500 ms. Trials in which participants moved their eyes to the wrong S2 target were flagged as directional errors. Directional error trials were eliminated from the main RT analysis but were tallied and analyzed to determine the possibility of speed-accuracy tradeoffs. The frequency of anticipation, miss, and directional errors out of the total trials (N = 192) accounted for less than 5% of trials.

Because we were interested in demonstrating that the typical monotonic pattern of RTs observed previously in cue-target IOR studies (0° > 90° >/= 180° [3, 18, 19, 21, 23, 27-29, 36]) also occurs in a target-target paradigm, mean RTs for S2 saccades were analyzed using a repeated-measures ANOVA ($\alpha = 0.05$) with the sole factor of offset (i.e., the angular offset between S1 and S2: 0°, 90° or 180°). Note that +90° and -90° conditions were collapsed into a single 90° condition for the purpose of these analyses. Mauchly's test was used to test the assumption of sphericity ($\alpha = 0.05$); if sphericity was violated, the Greenhouse-Geisser correction was applied and adjusted degrees of freedom are reported. All offset conditions were compared using planned pairwise comparisons ($\alpha = 0.01$), in order to determine if a monotonically declining pattern of RTs was observed. Directional errors within each offset condition (0°, 90°, or 180°) were analyzed to detect possible speed-accuracy trade-offs, in order to determine if a reduction in movement accuracy accompanied reduced reaction times. The frequency of directional errors in each offset condition was first used to calculate a percent error rate for each offset condition; a repeated measures ANOVA with the sole factor of offset was then conducted on these values.

Figure 2.1. Sequence of Stimuli. Example stimuli and sequence timing from a single trial when peripheral (E1 and E3) and central (E2 and E4) signals were used to prompt responses. Each trial began with a drift correction procedure that required the participant to press the space bar with their left hand while fixating within the fixation circle. The fixation array was then displayed for 500 ms after which the first signal (S1) was displayed for 300 ms. Following the offset of S1, fixation was displayed for 200 ms followed by a cue-back stimulus (change of the fixation circle outline from 4px to 8px weight) for 300 ms. The fixation array (with all circles in 4px weight) was again displayed for 1500 ms, providing ample time for participants to return their eye/arm to centre prior to the onset of the second signal (S2). The S2 stimulus was added for 300 ms, followed again by an inter-trial interval of 4 seconds during which the fixation array was displayed. Participants were instructed to maintain fixation throughout the trial. During each trial, participants were asked to make an eye or arm movement to touch the centre of the signaled targets as quickly and accurately as possible, and to return to centre upon display of the cue-back, as well as after completing their S2 response. The overall fixation array was present throughout each trial, thereby providing a stable stimulus background while S1, S2, and the cue back were overlain as described above.


Four Target Peripheral
Drift Correct
Space Bar
Fixation
500 ms
First Signal
300 ms
Fixation
200 ms
Cue-Back
300 ms
Fixation
1500 ms
Second Signal
300 ms
Fixation
4000 ms
Four Target Central

2.1.2 Results

Errors. Error rates were calculated independently within each offset condition. Directional errors were minimal and accounted for 0.27% (range = 0-1.6%, SD = 0.4%), 0.78% (range = 0-2.1%, SD = 0.9%), and 0.33% (range = 0-1.5%, SD = 0.5%) of the total trials in the 0°, 90°, and 180° conditions respectively. Because error rates were less than 1% in each offset condition, they were not analyzed further.

Saccadic Reaction Time to S2. Saccadic S2 RTs are shown in Figure 2.2 ("Peripheral - Eye"). A main effect of offset was observed, $F(2,36) = 15.56$, $p < 0.001$. Pairwise comparisons revealed slower RTs in the 0° relative to 90°, $F(1,18) = 17.87$, $p < 0.001$, and the 0° relative to 180°, $F(1,18) = 17.88$, $p < 0.001$ offset conditions. Reaction times were not significantly different for the 90° and 180° offsets, $F(1,18) = 0.43$, $p = 0.52$.

Many previous IOR studies contained only two possible target locations to the left and right of fixation [e.g. 15, 30, 39]. To compare our results to these studies, we analyzed separately those trials where the S1-S2 responses were restricted to the horizontal (left or right), and vertical (up or down) axis. We further compared amongst each of the possible 90° offset combinations (up/right = upper right [UR], right/down = lower right [LR], down/left = lower left [LL], left/up = upper left [UL]) to determine if the overall faster S2 RTs for the 90° offset condition were attributable to specific target combinations.

Zero-degree offset responses were significantly slower than 180° offset responses within both the horizontal, $F(1,18) = 7.42$, $p < 0.05$ and vertical $F(1,18) =$

12.09, $p < 0.005$ axes. No differences in the magnitude of IOR (where magnitude of IOR = RTs for “same” S1 and S2 trials minus RTs for “different” S1 and S2 trials) were observed between any of the possible 90° offset combinations (UL, UR, LR, LL), $F(3,18) = 0.55$, $p = 0.65$, indicating that the overall faster RTs for the 90° offset condition were not driven by any specific 90° S1/S2 combination(s).

2.1.3 Discussion

As predicted, the results of E1 extend the monotonic pattern of IOR ($0^\circ > 90^\circ >/= 180^\circ$) observed in previous cue-target studies using peripheral stimuli to a target-target task. The results from E1 were used as a baseline against which to compare the data from E2 in which central stimuli were adopted.

2.2 Experiment 2: Central Target – Eye

Experiment 2 mirrored E1 except the peripheral signals (S1 and S2) were replaced by central signals. Similar to E1, peripheral placeholders were continuously present in E2, ensuring that participants made responses that were metrically identical to those in E1, i.e. with a similar movement direction and amplitude. If the same spatial distribution of RTs is observed between E1 and E2, then it would be reasonable to conclude that IOR is similarly implemented independent of signal type. If markedly different patterns of RTs are observed between E1 and E2, it would suggest an important role of signal type.

2.2.1 Method

Participants. Twenty (15 female, 5 male) undergraduate students participated in E2. All participants were recruited through the Department of Psychology subject pool at Dalhousie University. All participants were right handed, had normal or corrected-to-normal vision and reported no history of visual, motor, or neurological abnormalities.

Apparatus and Stimuli. The stimulus configuration and sequence were identical to those used in E1 except rather than using peripheral signals (i.e., bolded placeholders), eye movements were signaled to continuously present peripheral placeholders using arrowheads displayed at fixation (*Figure 2.1*). Arrows were 1.5 visual degrees in length and 0.5 degrees in width.

Procedure and Data Analyses. The procedure was identical to E1 except that eye-movement signals in each trial consisted of arrowhead stimuli presented at central fixation rather than peripheral stimuli. The protocol for RT and error data analyses were equivalent between E1 and E2. The frequency of anticipation, miss, and directional errors (all removed from subsequent analyses) accounted for less than 5% of trials.

2.2.2 Results

Errors. Directional errors accounted for 0.76% (range = 0-3.6%, SD = 1.0%), 1.3% (range = 0-5.7%, SD = 1.8%), and 0.89% (range = 0-2.6%, SD = 1.2%) of the total trials in the 0°, 90°, and 180° conditions respectively. No significant difference was observed in the directional error rates between offset conditions, $F(2,38) = 2.68$, $p = 0.08$.

Saccadic Reaction Time to S2. Saccadic RTs are shown in Figure 2.2 ("Central - Eye"). A main effect of offset was observed, $F(2,38) = 10.6$, $p < 0.001$. Pairwise comparisons revealed slower RTs for 0° relative to 90° offset conditions, F(1,19) = 50.1, $p < 0.001$ and for 180° relative to 90° offsets, F(1,19) = 8.8, $p < 0.01$. Reaction times were not significantly different for 0° and 180° offsets, F(1,19) = 1.2, $p = 0.28$. In order to compare the spatial distribution of IOR observed in E2 to that observed in E1, we conducted a 2x3 mixed ANOVA with factors of signal type (peripheral [E1] or central [E2]) and offset (0°, 90°, and 180°). Significant main effects of signal type F(1,18) = 31.3, $p < 0.001$, and offset, F(2,36) = 17.9, $p < 0.001$, were observed. Moreover, a significant interaction between signal type and offset was observed F(2,36) = 7.9, $p < 0.001$, indicating a difference in overall spatial topographies observed between experiments.

The lack of difference between RTs for 0° and 180° offsets is inconsistent with Taylor and Klein's [39] study which showed significantly slower RTs for 0° versus 180° offsets when consecutive eye movements were required. However, as discussed earlier, those authors employed a task with only two targets, on the left and right of fixation. Similar to E1, we therefore analyzed the 0° and 180° offset conditions for the horizontal and vertical axes separately. We further compared each of the 90° offset combinations (UL, UR, LR, LL) to determine if the overall faster S2 RTs observed could be accounted for by any particular 90° S1/S2 combination(s).

Consistent with Taylor and Klein [39], within the horizontal axis, RTs were greater in the 0° compared to 180° offset condition, F(1,19) = 6.68. $p = 0.018$. Within the vertical axis however, RTs were not significantly different for 0° and 180° conditions, F(1, 19) = 1.4, $p = 0.25$. No differences in the magnitude of IOR (magnitude = same S1/S2 location RTs – different S1/S2 location RTs) were observed between any of the possible

90° offset combinations (UL, UR, LR, LL), F(1,19) = 1.7, p = 0.18, indicating that the overall faster RTs for the 90° offset condition were not driven by a specific combination of first and second saccade directions.

2.2.3 Discussion

The results of E2 demonstrate a distinct topography of RTs to that observed in E1, and indeed in all previous IOR research [3, 18, 19, 21, 23, 27-29, 36]. Unlike the monotonic pattern observed in E1 ($0^\circ > 90^\circ = 180^\circ$), in E2 we observed a non-monotonic pattern of RTs where 90° offsets were faster than both 0° and 180° offsets. This empirical observation is important, because IOR is commonly defined by its spatial topography [3, 18, 19, 21, 23, 27-29, 36]; as such, the present result is inconsistent with the currently established spatial definition of IOR.

Interestingly, when we grouped the data from E2 into 0° and 180° offset trials that were aligned with the horizontal and vertical axes, we found a significant difference between 0° and 180° offsets for the horizontal but not vertical axis. In contrast with the majority of previous research that has examined IOR across only two target locations aligned to the left and right of fixation, the results of E2 therefore highlight the importance of analyzing RT effects across multiple spatial locations aligned in different axes[11].

---

[11] In the present experiments, we used a stimulus array consisting of targets aligned with the cardinal axes around a central fixation point, as is typical of many other studies. One consideration arising from this stimulus array relates to the possibility that targets on the horizontal meridian might be represented on opposite sides of the nervous system, whereas targets aligned with the vertical meridian might be represented bilaterally. Following this logic, 90° offset conditions would always involve a transition in control from a unilateral to bilateral representation, or vice versa. It is conceivable that this transition

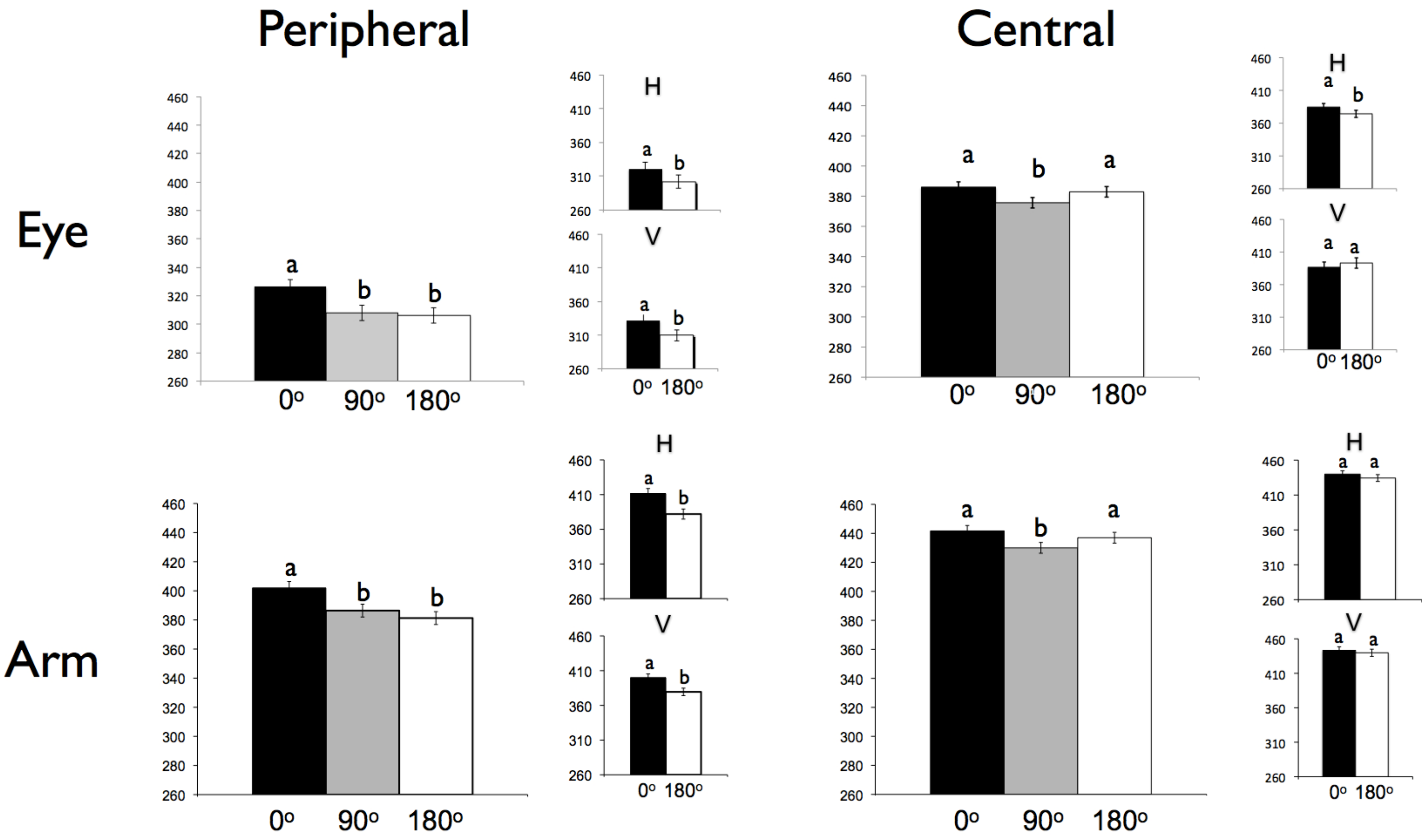
One concern emerging from E2 is that the cue-back stimulus (which is aligned 180° opposite S1) somehow generated IOR for S2 responses also offset by 180° [e.g. through consecutive stimulation of the retinotopic location encoding both the cue-back and the 180° target location; cf. 41]. We think this is unlikely for three reasons. First, the cue-back stimulus, which was present in both E1 and E2, did not produce IOR at 180° offsets in E1. Second, a previous unpublished study conducted in our lab was identical to E2, except that 8 target locations were possible, and no cue-back stimulus was used. In that experiment, the same non-monotonic pattern of RTs was observed, despite the fact that no cue-back stimulus was used. Third, as will be seen, in E4 participants made consecutive arm movements to central stimuli while keeping their eyes at fixation; as a result, the retinotopic position of the cue-back stimulus would not overlap with targets offset by 180°. However, both E2 and E4 reveal a similar non-monotonic pattern of results.

---

might account for the decreased latency of movements in the 90° offset conditions as compared to 0° and 180° conditions. This explanation is unlikely for several reasons. First and foremost, this line of reasoning would apply equally well to the tasks in E1 and E2, but these experiments yield different results with respect to the comparison of 0°, 90°, and 180° offset conditions. Nevertheless, in order to rule out concerns about the use of targets aligned with the horizontal and vertical meridia, we selectively analyzed target locations between those used in the present study (i.e., upper left, upper right, lower left and lower right), taken from a previous unpublished data set from our laboratory. The data arise from an experiment employing similar methods to E2 (i.e., consecutive saccades to peripheral placeholders were signalled by central arrows), but that used 8 target locations surrounding fixation, and that did not involve a cue-back stimulus. In order to address concerns about the different lateralization of targets on the horizontal and vertical meridian, comparisons were made for 0° and 90° offset RTs for targets within only the left hemifield (i.e., comparing RTs to the upper-left vs. lower-left target) or right hemifield (i.e., upper-right vs. lower-right). The same comparison was made when targets were located in different hemifields (i.e., upper-left vs. upper-right, and lower-left vs. lower-right). The difference in RTs between 0° and 90° offset conditions was very similar, regardless of whether the S1 and S2 targets were located in the same hemifield (magnitude of IOR = 10.1 ms) or different hemifields (magnitude of IOR = 10.8 ms), F(1,19) = 0.27, p=.87.

The next two experiments were conducted in order to extend the results of E1 and E2 to a different effector system. If signal type plays an important role in shaping the pattern of RTs observed, then the pattern of RTs observed should vary as a function of signal type but be relatively independent of the effector system used to respond.

Figure 2.2. Reaction Times. Mean saccadic reaction times to the second signal (S2) for Experiments 1-4 are presented on the Y axis with RTs for each offset condition (0°, 90°, and 180°) presented as separate bars. Experiment 1 (Peripheral – Eye) is shown in the upper left; Experiment 2 (Central - Eye) is shown in the upper right; Experiment 3 (Peripheral - Arm) is show in the lower left; Experiment 4 (Central - Arm) is shown in the lower right. Conditions labelled with different letters (a, b, or c) are significantly different from each other. Error bars show within-subjects 95% confidence intervals, as described by Masson [22] using the Offset x Subject MSE term. H stands for horizontal axis; V stands for vertical axis.


Peripheral
Central
Eye
Arm
460
440
420
400
380
360
340
320
300
280
260
410
360
310
H
V
a
b
0o
90o
180o

2.3 Experiment 3: Peripheral Target-Arm

In E3, we required consecutive reaching movements to peripheral stimuli. If the use of peripheral stimuli is associated with the monotonic pattern of IOR, then a similar topography of RTs should be observed for E3 as compared to E1 (0° > 90° >/= 180°).

2.3.1 Methods

Participants. Sixteen (12 female, 4 male) undergraduate students participated in E2. All participants were recruited through the Department of Psychology subject pool at Dalhousie University. All participants were right handed, had normal or corrected-to-normal vision and reported no history of visual, motor, or neurological abnormalities.

Apparatus, Stimuli, Procedure and Data Analysis. The apparatus, stimuli, procedure and data analyses were equivalent between E1 and E3 except that consecutive arm movements were required instead of eye movements. Participants began each trial by placing their right index finger at central fixation; responses to S1, the cue-back, and S2 were the same as in E1 and E2 except that participants were required to localize each target (and the fixation circle for the cue-back movements) by moving their arm to touch each marked location with their finger. Throughout each trial, participants were required keep their eyes at fixation. Reaction times were collected on the same 30-inch Elo touch screen LCD monitor (Elo TouchSystems, Menlo Park, California, USA) used in E1 and E2, and were defined by the moment participants lifted their finger from central fixation (relative to stimulus onset). If participants failed to keep their eyes at fixation, an error message was displayed, the trial was aborted, and not recycled. Similar to E1 and E2, if participants did not respond within 1.5 seconds to

S1 or S2, if they did not return their finger to centre between S1 and S2, or if they failed to keep their finger at centre during the fixation intervals (immediately prior to S1 or S2), an error message was displayed, the trial was aborted, and was not recycled. Data from aborted trials were excluded from all subsequent analyses. Less than 5% of trials were aborted due to a slow response, a failure to return their finger to centre between S1 and S2, or a failure to keep the eyes at fixation. The frequency of anticipation, miss, and directional errors (all removed from subsequent analyses) accounted for less than 5% of trials.

2.3.2 Results

Errors. Directional errors accounted for 0.54%, 0.54%, and 0.71% of the total trials in the 0°, 90°, and 180° conditions respectively. Because error rates were less than 1% in each offset condition, they were not analyzed further.

Reaction Time to S2. Reaching RTs are shown in Figure 2.2 ("Peripheral – Arm"). A main effect of offset was observed, $F(2,30) = 25.24$, $p < 0.001$. Pairwise comparisons revealed slower RTs for 0° relative to 90°, $F(1,15) = 58.14$, $p < 0.001$ and 180°, $F(1,15) = 30.07$, $p < 0.001$. Reaction times were marginally slower for 90° compared to 180° offsets, $F(1,15) = 4.34$, $p = 0.055$.

Zero-degree offset responses were significantly slower than 180° responses within both the horizontal, $F(1,15) = 18.84$, $p < 0.001$ and vertical $F(1,15) = 28.75$, $p < 0.001$ axes. No differences in the magnitude of IOR (where the magnitude of IOR = "same" S1/S2 RTs minus "different" S1/S2 RTs) were observed between any of the possible 90° offset combinations (UL, UR, LR, LL), $F(3,45) = 0.38$, $p = 0.76$, indicating that the overall faster RTs for the 90° offset condition were not driven by any specific 90° S1/S2 combination(s).

2.3.3 Discussion

The results of E3 confirm that when consecutive arm movements are required to peripheral signals, the spatial topography of IOR is similar to the pattern of IOR observed in previous IOR tasks using peripheral stimuli [3, 18, 19, 21, 23, 27-29, 36]. Taken together, the results of E1 and E3 reveal for the first time that the monotonic pattern of RTs can be expected when a *target-target* task is used to prompt either consecutive eye or arm movements.

2.4 Experiment 4: Central Target - Arm

In E4, we required consecutive reaching movements to peripheral placeholders as signaled by central stimuli. If the pattern of RTs observed in E2 (0° = 180° > 90°) is related to the use of central stimuli, independent of the effector system used to respond, then a similar pattern of RTs should be observed in E4.

2.4.1 Method

Participants. Twenty (13 female, 7 male) undergraduate students participated in E4. All participants were recruited through the Department of Psychology subject pool at Dalhousie University. Participants were right handed, had normal or corrected-to-normal vision and reported no history of visual, motor, or neurological abnormalities.

Apparatus, Stimuli, Procedure and Data Analysis. The apparatus, stimuli, procedure and data analyses were equivalent between E3 and E4 except that rather than using peripheral signals, arm movements were signaled using the same arrowheads used in E2 (*Figure 2.1*). The frequency of anticipation, miss, and directional errors (all removed from subsequent analyses) accounted for less than 5% of trials.

2.4.2 Results

Errors. Directional errors accounted for 0.42%, 0.24%, and 0.35% of the total trials in the 0°, 90°, and 180° conditions respectively. Because error rates were less than 1% in each offset condition, they were not analyzed further.

Reaction Time to S2. Reaching RTs are shown in Figure 2.2 ("Central – Arm"). A main effect of offset was observed, F(2,36) = 9.38, $p < 0.001$. Pairwise comparisons revealed slower RTs for 0° relative to 90°, F(1,18) = 16.03, $p < 0.001$ and 180° relative to 90°, $F(1,18) = 10.17$, $p < 0.005$. RTs were not significantly different for 0° and 180° offsets, F(1,18) = 2.53, $p = 0.13$. In order to compare the spatial distribution of IOR observed in E4 to that observed in E3, we conducted a 2x3 mixed ANOVA with factors of signal type (peripheral or central) and offset (0°, 90°, and 180°). Significant main effects of signal type F(1,15) = 11.4, $p < 0.051$, and offset, F(2,30) = 15.9, $p < 0.001$, were observed. Moreover, a significant interaction between signal type and offset was observed F(2,30) = 6.7, $p < 0.005$, indicating a difference in overall spatial topographies observed between experiments.

Within both the horizontal, F(1,18) = 2.44, $p = 0.14$, and vertical, F(1, 18) = .86, $p = 0.37$, axis, RTs did not differ for the 0° and 180° offset conditions. No differences in the magnitude of S2 RTs (magnitude = same RT – different RT) were observed between any of the possible 90° offset combinations (UL, UR, LR, LL; $F(3,60) = 0.57$, $p = 0.63$), indicating that the overall faster RTs for the 90° offset condition were not driven by a specific combination of first and second movement directions.

2.4.3 Discussion

Like E2, significantly faster RTs were observed in the 90° offset condition relative to both the 0° and 180° offset conditions. Taken together, the results of E2 and E4 reveal that the non-monotonic pattern of RTs observed occurs independent of the effector system used to respond. Moreover, the non-monotonic pattern of RTs appears to depend on the use of central signals.

Previous work using central stimuli to examine manual responses to target locations aligned to the left and right of fixation have failed to observe IOR [e.g. 15, 39]. Consistent with those observations, we failed to observe a RT difference between the 0° and 180° offset conditions (in either the horizontal or vertical axis). Notably, E4 demonstrates that a response bias does in fact exist for consecutive manual localization responses made to central stimuli; however, previous studies appear to have missed this observation due to their use of only two target locations offset by 180°.

2.5 General Discussion

Here we compared the pattern of RTs observed as a function of the angular offset between two consecutive eye or arm movement responses that were required to *either* peripheral or central signals. If IOR is present, the latency to initiate a saccade or reaching movement should be delayed by an amount of time that is related to its angular offset from a preceding movement [3, 18, 19, 21, 23, 27-29, 36]. In particular, based on the current spatial definition of IOR, RTs should decrease monotonically as the angular offset between the first and second stimuli increases from 0° to 180° (0° > 90° >/= 180°).

When peripheral stimuli were used to prompt either saccadic (E1) or reaching responses (E3), we replicated the monotonic pattern of RTs commonly observed in the IOR literature. In contrast, when we used central stimuli, we found a non-monotonic spatial topography of RTs for both saccades (E2) and reaching movements (E4), where responses were fastest for movements offset by 90° compared to either 0° or 180°.

Defining IOR. The characteristics, possible mechanisms and functions, and indeed, the very definition of IOR is commonly debated with reference to the spatial distribution of RTs observed [3, 18, 19, 21, 23, 27-29, 36]. Notably however, this debate has occurred primarily in the context of experiments that used peripheral rather than central stimuli. The results of our experiments highlight the importance of examining the spatial topography of RTs and provide an important reference point for future theories and studies of IOR. Indeed, the present results may be useful in attempts to clarify the definition of IOR, a phenomenon that is loosely ascribed to reaction time differences observed by scholars [12]. In this regard, an important question will regard whether or not the non-monotonic topography observed presently can be classified as IOR. On one hand, the non-monotonic topography violates existing characterizations of IOR as a behavioural phenomenon that selectively biases responses away from *previously signaled* locations, for example to facilitate visual search [e.g. 18, 19, 21]. On the other hand, it might be possible to argue that different forms of IOR can have different spatial distributions, (e.g. depending on signal type or other experimental manipulations), while being reconciled in other critical ways (e.g., if the different spatial distributions of RTs are implemented functionally, to prevent repetitive behaviours at different levels of sensorimotor processing). We anticipate that future research will be informative in this debate.

Possible Mechanisms. What mechanisms might underlie the different spatial topographies of RTs observed? As mentioned in the general introduction, some scholars have suggested that IOR might affect response-based processes, (and in particular, motor-based processes), when central rather than peripheral signals are used [15, 20, 30, 31, 33, 38, 39, 41]. The logic behind such claims rests on two interrelated observations. First, IOR is present when peripheral but *not* central targets follow a *peripheral* cue, and simple detection responses are required. This observation suggests that peripheral cues can generate a spatially restricted sensory processing deficit; notably, there is compelling neurophysiological evidence in support of this kind of IOR mechanism [4, 14]. Qualifying the first observation, IOR is present when *either* a peripheral or central target is used (regardless of cue type), *provided* a motor response is required to the target[12]. Taken together, these two observations converge on the idea that primarily response-based processes are be affected by IOR (where present), when central signals are used.

---

[12] IOR appears to be present regardless of signal type, provided a motor response is made to the target, and regardless of whether or not a response is made to the cue, with one exception. When a central cue is used, IOR is observed for central and peripheral targets provided a motor response (either manual or saccadic) is made to *both* the cue and target [39].

If response-based processes (whether motor or late-stage attentional) are indeed isolated through the use of central stimuli, the range of possible mechanisms underlying the non-monotonic pattern of RTs in E2 and E4 is presumably limited to the neural mechanisms controlling the programming or execution of a response. Below we speculate a mechanism that can predict the pattern of results observed in E2 and E4.

In an fMRI study of arm movements instructed by central stimuli, we found evidence of directionally selective adaptation (i.e., reduction) of the BOLD response in several areas of human sensorimotor cortex, when consecutive movements were repeated in the same direction. Notably, adaptation only occurred for consecutive responses offset by 0° (i.e. when movements were made in the same direction), while a spatial offset of 90° or 180° between repeated movements did not reveal adaptation [9][13]. In the context of the centre-out IOR task adopted presently, our fMRI results predict that neural adaptation will occur in the 0° and 180° spatial offset conditions, because both conditions require the repetition of a recently completed movement – either a repetition of the movement to the first target, or a repetition of the opposite, return-to-centre movement. Given the relatively narrow tuning function for adaptation in most neurons (i.e., where movements offset by 90° show little to no adaptation [9, 13]), our fMRI results predict that neural adaptation will be minimal for 90° offset

---

[13] It is well established that neurons in motor cortex show maximal firing rates for a particular ‘preferred’ direction [2, 5-7, 9, 13, 16, 17, 24, 32, 34] and a median tuning width (defined by the angular offset from the preferred direction that elicits half-maximal firing rates) of between 30° and 90°. The results of our fMRI study were predicted based on the simple idea that repeated movements offset by 0° degrees will engage the same subpopulation of neurons in motor cortex leading to neural ‘fatigue’ or adaptation. In contrast, adaptation should be less pronounced (or absent) for movements offset by 90° degrees or more, because different subpopulations of neurons are engaged for each movement.

conditions because the second target response is 90° away from both the first target movement and the return-to-centre movement. Assuming that adaptation effects revealed by fMRI are associated with decreased neural firing rates and therefore processing efficiency (e.g., where it takes longer to reach response threshold), one would predict an increased response latency for conditions associated with the presence of adaptation [24]. Indeed, the pattern of RTs observed in E2 and E4 are consistent with the neural adaptation mechanism described.

The Relationship Between Adaptation and Reaction Times. The neural adaptation model proposed is attractive because it can parsimoniously explain the spatial topography of RTs observed in E2 and E4[14]. Like any inference regarding the neurophysiological underpinnings of a behavioural phenomenon, the adaptation model relies on certain assumptions. The assumption that neurons encoding movement direction adapt following the execution of a single movement is well supported by fMRI research examining the control of movement direction in human motor cortex [9,13]. This research has revealed the presence of directionally selective adaptation effects after the execution of a single movement. Indeed, the predominant tuning width of directional selectivity appears to be less than 90° [2, 9,13]; therefore, adaptation effects likely only occur within neurons whose preferred directions are within 90° or less of the produced movement. As a consequence, S2 movements offset by 90° or more should

---

[14] Given the similar direction-encoding properties of neurons associated with the control of reaching movements [26, 27, 31-33] and eye movements [34-39], one would expect similar adaptation effects in both effector systems.

engage neurons that were not adapted by the S1 or return-to-centre movement. Key to the adaptation explanation of E2 and E4 is the additional assumption that a reduction of firing rates causes a delay in the time taken to reach response threshold and corresponding RTs. This idea is supported by research revealing that movement RTs can be predicted from neural firing rates [1,8].

Adaptation and Inhibition of Return for Consecutive Motor Responses. If adaptation effects are observed in participant RTs for consecutive movement responses, why are different spatial topographies of RTs observed when peripheral versus central stimuli are used, despite the fact that the movements required (to localize a peripheral placeholder) are the same in both cases? At least two options can explain this difference. First, it is possible that similar motor adaptation effects occur for both central and peripheral signals; however, in the case of peripheral stimuli, sensory/attentional effects (i.e., associated with detecting and processing spatial information about the target's location) may also be present [4, 14]. Indeed, as demonstrated by Wang et al. [41], the use of peripheral stimuli in a target-target task (i.e. where participants respond to both the first and second signal, as in the present study) is likely to engage *both* sensory and motor-based effects that operate on different stages of processing. It is therefore likely that the spatial topography of RTs observed is determined by some combination of sensory/attentional and motor-based effects when responses are made to peripheral stimuli. A second possibility is that responses to central and peripheral stimuli involve different populations of sensorimotor neurons and therefore result in independent adaptation effects. This is possible if adaptation occurs at earlier rather than later stages of sensorimotor processing, as the later stages of motor output are likely shared by responses regardless of the eliciting stimulus. Future studies that pair central-peripheral and peripheral-central targets might help to shed light on these possibilities.

Spatial Attention and Motor Based Effects. As discussed, previous research has argued that motor-based effects in IOR may be isolated through the use of central rather than peripheral signals. This idea is well supported; however, it is important to note that certain alternatives to this explanation may exist. In particular, if one assumes a tight link between the deployment of spatial attention and the planning or execution of an eye or arm movement, e.g., where spatial attention is deployed to the target of the movement immediately prior to execution, then it is possible that a late-stage attentional effect is involved in the response biases observed, *any* time a movement is planned [11, 35]. Given the use of a target-target task in the present study (where responses were required to both S1 and S2), it is therefore possible that the response biases observed are somehow associated with this late-stage attentional process. Notably however, because the deployment of late-stage attention is likely similar independent of signal type (and rather, dependent on the planning or execution of movement), if such an explanation is possible, it is not immediately clear how it could account for the different spatial topographies observed between E1/E3 and E2/E4.

Reaction Times in the Vertical and Horizontal Axes. An interesting result emerging from our study is a difference in the comparison of 0° and 180° RTs observed in the horizontal axis, when eye versus arm movements were elicited by central stimuli (in E2 and E4 respectively). For eye movements, 180° offset responses were faster than 0° responses in the horizontal axis; this did not occur in the vertical axis (180° was similar to 0°), and it did not occur for arm movements in the horizontal axis (180° was similar to 0°). We suspect that the presence of a 180° RT advantage for consecutive eye movements in the horizontal axis might arise from learned behaviours such as scanning the horizon or reading [37]. If this is the case, then given that the arm is not necessarily specialized for movements in the horizontal axis, one would expect similar RT effects for consecutive arm movements in both the vertical and horizontal axis (as seen in E4). These observations highlight the importance of examining RTs across target locations aligned in different movement axes.

Motor IOR in the Reaching System. The presence of motor IOR in the reaching control system remains controversial, and some authors have concluded that motor IOR is restricted to the oculomotor system (e.g., Fischer et al.[15]). In Fischer et al.'s study [15], only 0° and 180° target offsets were considered and reaction times for reaching movements were reported to be similar, which is also true for the 0° and 180° offsets in the present investigation. Of course, in the present investigation, 90° offsets were also included and RTs in this condition were found to be faster in comparison to both 0° and 180° offsets. Therefore, it is possible that Fischer et al. might also have observed some evidence of a spatially-tuned pattern of RTs in their experiment had additional spatial offsets been included. However, given that the pattern of RTs observed in the central-target conditions of our study do not resemble the current monotonic spatial definition of IOR, consistent with Fischer et al. [15], our study provides reason to question the idea that motor IOR can affect reaching responses to central stimuli.

2.6 Conclusion and Future Directions.

To our knowledge, the present study is the first to provide behavioural evidence of a non-monotonic pattern of RTs within a target-target IOR paradigm using central stimuli. An important question for future studies will be to determine whether the 90° RT advantage has any adaptive value, or if it is merely an epiphenomenon of neural adaptation (or perhaps some other mechanism involved in the control of movement). In any case, the fact that 90° offsets exhibit a performance advantage (characterized by faster RTs) when central stimuli are used, suggests that future studies of IOR should include more than the traditional 0° (same) and 180° (different) spatial offset conditions. Given that the monotonic pattern of RTs [3, 18, 19, 21, 23, 27-29, 36] has only been revealed in a select range of experimental conditions that might produce IOR [39], it would be useful for future research to establish the topography of RTs under these different experimental conditions. Indeed, an examination of the spatial distribution of RTs under these different task circumstances may be informative with respect to the ongoing debate surrounding the mechanism and function of IOR and other potentially related response biases. Finally, it is important for ongoing research to establish the different task circumstances that reveal different topographies of RTs. For example, it might be the case that the pattern of results observed is inherently related to the use of a centre-out paradigm; future research interested in the mechanisms underlying orienting behaviour should use variants of the present paradigm to further address this and related questions.

2.7 References

[1] A. Afshar, G. Santhanam, B.M. Yu, S.I. Ryu, M. Sahani, K. V Shenoy, Single-trial neural correlates of arm movement preparation, Neuron. 71 (2011) 555–64.

[2] B. Amirikian, A.P. Georgopoulos, Directional tuning profiles of motor cortical cells, Neurosci Res. 36 (2000) 73–79.

[3] P.J. Bennett, J. Pratt, The spatial distribution of inhibition of return, Psychol Sci. 12 (2001) 76–80.

[4] G. Berlucchi, Inhibition of return: A phenomenon in search of a mechanism and a better name, Cogn. Neuropsychol. 23 (2006) 1065–74.

[5] C.J. Bruce, M.E. Goldberg, Primate frontal eye fields. I. Single neurons discharging before saccades, J. Neurophysiol. 53 (1985) 603–635.

[6] C.J. Bruce, M.E. Goldberg, M.C. Bushnell, G.B. Stanton, Primate frontal eye fields. II. Physiological and anatomical correlates of electrically evoked eye movements, J. Neurophysiol. 54 (1985) 714–734.

[7] R. Caminiti, P.B. Johnson, C. Galli, S. Ferraina, Y. Burnod, Making arm movements within different parts of space: the premotor and motor cortical representation of a coordinate system for reaching to visual targets, J Neurosci. 11 (1991) 1182–1197.

[8] M.M. Churchland, G. Santhanam, K. V Shenoy, Preparatory activity in premotor and motor cortex reflects the speed of the upcoming reach, J. Neurophysiol. 96 (2006) 3130–46.

[9] C.D. Cowper-Smith, E.Y.Y. Lau, C. a Helmick, G.A. Eskes, D.A. Westwood, Neural coding of movement direction in the healthy human brain, PLoS One. 5 (2010) e13330.

[10] T.B. Crapse, M.A. Sommer, Frontal eye field neurons with spatial representations predicted by their subcortical input, J. Neurosci. 29 (2009) 5308–5318.

[11] H. Deubel, W.X. Schneider, Saccade target selection and object recognition: evidence for a common attentional mechanism, Vision Res. 36 (1996) 1827–37.

[12] M.C. Dorris, R.M. Klein, S. Everling, D.P. Munoz, Contribution of the primate superior colliculus to inhibition of return, J. Cogn. Neurosci. 14 (2002) 1256–63.

[13] M. Eisenberg, L. Shmuelof, E. Vaadia, E. Zohary, Functional Organization of Human Motor Cortex : Directional Selectivity for Movement, Life Sci. 30 (2010) 8897–8905.

[14] J.H. Fecteau, D.P. Munoz, Correlates of Capture of Attention and Inhibition of Return across Stages of Visual Processing, (2005) 1714–1727.

[15] M.H. Fischer, J. Pratt, S.F. Neggers, Inhibition of return and manual pointing movements, Percept. Psychophys. 65 (2003) 379–387.

[16] A.P. Georgopoulos, A.B. Schwartz, R.E. Kettner, Neuronal population coding of movement direction, Science. 233 (1986) 1416–1419.

[17] G.D. Horwitz, W.T. Newsome, Target selection for saccadic eye movements: direction-selective visual responses in the superior colliculus, J. Neurophysiol. 86 (2001) 2527–2542.

[18] R.M. Klein, Inhibition of return, Trends Cogn. Sci. 4 (2000) 138–147.

[19] R.M. Klein, W.J. MacInnes, Inhibition of return is a foraging facilitator in visual search, Psychol. Sci. 10 (1999) 346–352.

[20] L. Machado, R.D. Rafal, Inhibition of return generated by voluntary saccades is independent of attentional momentum, Q. J. Exp. Psychol. A, Hum. Exp. Psychol. 57 (2004) 789–796.

[21] J.W. MacInnes, R.M. Klein, Inhibition of return biases orienting during the search of complex scenes, Sci. World J. 3 (2003) 75–86.

[22] M.E. Masson, Using confidence intervals for graphically based data interpretation, Can. J Exp. Psychol. 57 (2003) 203–220.

[23] E.A. Maylor, R. Hockey, Inhibitory component of externally controlled covert orienting in visual space, J. Exp. Psychol. Hum. Percept. Perform. 11 (1985) 777–787.

[24] T. Naselaris, H. Merchant, B. Amirikian, A.P. Georgopoulos, Large-scale organization of preferred directions in the motor cortex. I. Motor cortical hyperacuity for forward reaching, J Neurophysiol. 96 (2006) 3231–3236.

[25] M.I. Posner, Y. Cohen, Components of visual orienting, in: H. Bouma & D.G. Bouwhuis (Eds.) Attention and performance X, Amsterdam: North-Holland, 1984, pp. 243-258.

[26] J. Posner, M I, Rafal, R D, Choate, L S, Vaughan, Inhibition of Return: Neural Basis and Function, Cogn. Neuropsychol. (1985) 211–228.

[27] J. Pratt, R.A. Abrams, Inhibition of return to successively cued spatial locations, J. Exp. Psychol. Hum. Percept. Perform. 21 (1995) 1343–1353.

[28] J. Pratt, J., Adam, J.J., McAuliffe, The Spatial Relationship between Cues and Targets Mediates Inhibition of Return, J. Exp. Psychol. 52 (1998) 213–216.

[29] J. Pratt, T.M. Spalek, F. Bradshaw, The time to detect targets at inhibited and noninhibited locations: Preliminary evidence for attentional momentum, J. Exp. Psychol. Hum. Percept. Perform. 25 (1999) 730–746.

[30] R.D. Rafal, P.A. Calabresi, C.W. Brennan, T.K. Sciolto, Saccade preparation inhibits reorienting to recently attended locations, J. Exp. Psychol. Hum. Percept. Perform. 15 (1989) 673–685.

[31] R. Rafal, R. Egly, D. Rhodes, Effects of inhibition of return on voluntary and visually guided saccades, Can. J. Exp. Psychol. 48 (1994) 284–300.

[32] D.A. Robinson, Eye movements evoked by collicular stimulation in the alert monkey, Vision Res. 12 (1972) 1795–1808.

[33] J. Satel, Z. Wang, Investigating a two causes theory of inhibition of return, Exp. Brain Res. 223 (2012) 469–478.

[34] P.H. Schiller, M. Stryker, Single-unit recording and stimulation in superior colliculus of the alert rhesus monkey, J. Neurophysiol. 35 (1972) 915–924.

[35] W.. Schneider, VAM: A neuro-cognitive model for visual attention control of segmentation, object recognition, and space-based motor action, Vis. Cogn. 2 (1995) 331–376.

[36] J.J. Snyder, A. Kingstone, W.C. Schmidt, Attentional momentum does not underlie the inhibition of return effect, J. Exp. Psychol. Hum. Percept. Perform. 27 (2001) 1420–1432.

[37] T.M. Spalek, S. Hammad, The left-to-right bias in inhibition of return is due to the direction of reading, Psychol. Sci. 16 (2005) 15–18.

[38] T.L. Taylor, R.M. Klein, On the causes and effects of inhibition of return, Psychon. Bull. Rev. 5 (1998) 625–643.

[39] T.L. Taylor, R.M. Klein, Visual and motor effects in inhibition of return, J. Exp. Psychol. Hum. Percept. Perform. 26 (2000) 1639–1656.

[40] S.P. Tipper, B. Weaver, F.L. Watson, Inhibition of return to successively cued spatial locations: commentary on Pratt and Abrams (1995), J. Exp. Psychol. Hum. Percept. Perform. 22 (1996) 1289–1293.

[41] Z. Wang, J. Satel, R.M. Klein, Sensory and motor mechanisms of oculomotor inhibition of return, Exp. Brain Res. 218 (2012) 441–53.

CHAPTER 3: SACCADIC INHIBITION OF RETURN CAN ARISE FROM LATE-STAGE EXECUTION PROCESSES

C.D. Cowper-Smith, G.A. Eskes, D.A. Westwood, Saccadic inhibition of return can arise from late-stage execution processes, Neuroscience Letters 531 (2012) 120–4.

3.1 Abstract

Inhibition of return (IOR) is thought to improve the efficiency of visual search behaviour by biasing attention, eye movements, or both, toward novel stimuli. Previous research suggests that IOR might arise from early sensory, attentional or motor programming processes. In the present study, we were interested in determining if IOR could instead arise from processes operating at or during response execution, independent from effects on earlier processes. Participants made consecutive saccades (from a common starting location) to central arrowhead stimuli. We removed the possible contribution of early sensory/attentional and motor preparation effects in IOR by allowing participants to fully prepare their responses in advance of an execution signal. When responses were prepared in advance, we continued to observe IOR. Our data therefore provide clear evidence that saccadic IOR can result from an execution bias that may arise from inhibitory effects on motor output neurons, or alternatively from late attentional engagement processes.

3.2 Introduction

Visual search is an adaptive function commonly engaged in everyday life. Searching a complex environment typically requires a sequence of eye movements to fixate and selectively attend to individual stimuli. However, in order for visual search to be most efficient, a mechanism that biases eye movements *away* from previously inspected stimuli, and *toward* novelty is helpful.

Inhibition of return (IOR) is a phenomenon thought to underlie efficient search behaviour [11, 12] by biasing attention, eye movements, or both away from previously inspected locations. Experimentally, IOR is commonly observed as increased reaction times (RTs) for responses made to a target stimulus presented in the same location as a preceding cue, compared to uncued locations, once attention is removed from the cued location (typically after approximately 300 ms from the cue onset) [15, 16].

The mechanism underlying IOR remains poorly understood; however, previous research suggests that IOR could operate by attenuating [cf. 8, 23], and thereby slowing, neural processes that range between the level of early sensory/attentional [e.g. 19, 27] and late motor programming processes [e.g. 20, 27]. The stage of information processing affected by IOR is sensitive to task conditions; when participants are prevented from making eye movements (while making simple button press responses), IOR is likely to arise from sensory/attentional-based processes. However, when eye movements are required, IOR is likely to arise from motor-based processes ranging from saccadic response programming to initiation or execution (hence, this form of IOR is referred to as “saccadic IOR” herein) [10, 28]. Critically however, the possibility that saccadic IOR can occur as the result of processes operating at or during response *execution* has not been tested.

If saccadic IOR operates by slowing motor programming processes, then delayed RTs must be attributed to a delay in processes that occur *before* the initiation of response execution. In contrast, if IOR is implemented as an execution bias (i.e. that directly slows orienting responses), then the delay in RTs must be attributed to a delay in either response programming or execution processes. In standard IOR tasks, it is impossible to determine the stage of information processing affected by IOR through an assessment of behaviour, because participants are simply instructed to respond 'as quickly and accurately' as possible to the onset of the target stimulus. Given that sensory/attentional, motor programming, and response execution processes are completed serially before RT can be measured, a delay in RTs could arise from delays in any of these processes; it is therefore unclear which processing stage(s) are delayed when IOR is present.

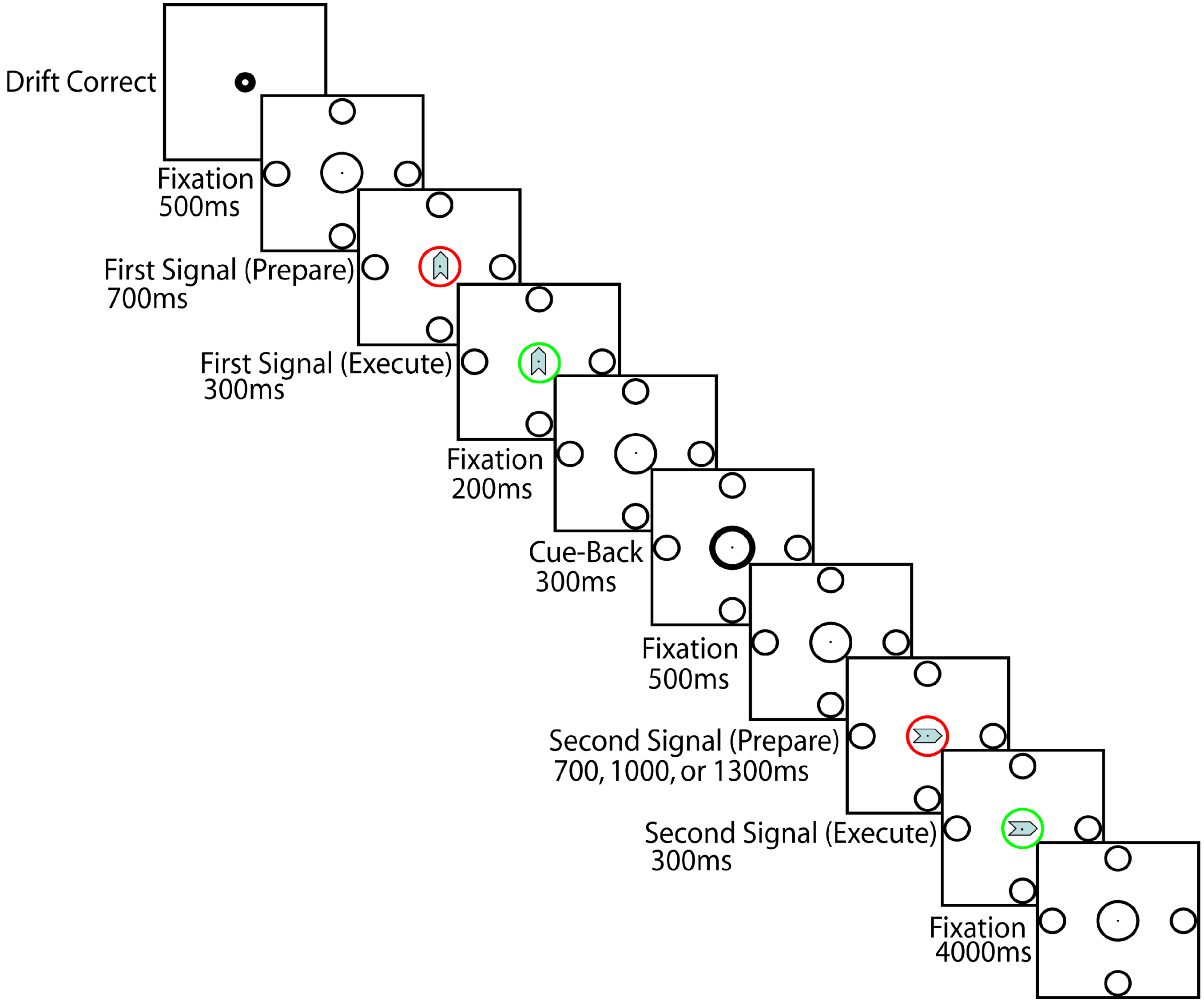
In the present study we developed a paradigm to directly test whether IOR can arise from processes operating at or during response execution. In order to assess the presence of IOR, we required participants to make consecutive saccades (originating from a central fixation point) to targets specified by directional arrows presented at fixation [cf. the target-target paradigm used by Taylor and Klein, 28]; because eye movements were required, the saccadic form of IOR should be activated [28]. Given that IOR is a spatially defined effect, we measured RTs for the second saccade as a function of the angular offset between consecutive saccades. Consistent with previous research [2, 12, 17, 18, 26], if IOR was present, we expected RTs to be slowest for consecutive saccades that were offset by 0°, and fastest 180° opposite. Unlike previous studies using the target-target paradigm [e.g. 28], participants were informed of the required responses well in advance of the signal to initiate their response. We accomplished this by presenting a 100% predictive arrow at fixation that was surrounded by a red circle for between 700-1300 ms, when participants were instructed to prepare a saccadic response in the direction indicated. After this preparation time, the circle surrounding the arrow turned green, providing a signal for participants to execute their prepared response as quickly and accurately as possible. Given that participants can detect, prepare, and execute a saccadic response to a central arrowhead within approximately 400 ms, even when IOR is active [5, 28], it is fair to assume that 700 ms is sufficient to fully prepare an appropriate response in our task. Given that participants can completely prepare the required response and merely have to wait for a signal to initiate their response, all processes up to and including response programming are likely to be bypassed immediately before response production, leaving only initiation or execution processes to be affected by any IOR that might be operating. In other words, if IOR is observed in the present task, it cannot arise from slowed of sensory/attentional or motor preparation processes, because these processes should be completed prior to the initiation signal; rather, if IOR is observed, it has to arise from processes operating *at* response initiation, or *during* response execution.

3.3 Materials and Methods

Fifteen undergraduate students (9 female, 6 male) were recruited at Dalhousie University. Participants were right handed, had normal vision and reported no history of visual, motor, or neurological abnormalities.

Eye position was monitored with an EyeLink™II (SR Research, Osgoode, ON) eye-tracking system. The stimulus sequence and task are described in Figure 3.1. With the exception of 44 catch trials, two central arrowhead signals (S1 and S2) were presented on each trial that pointed toward one of the four possible target locations with equal probability (0.25). These pairings signaled consecutive saccadic responses offset from each other by 0° (i.e., previously cued location), 90°, or 180°. Each S1/S2 pairing was presented 12 times and all pairings were randomized on a trial-by-trial basis. The central fixation circle was 3.15° (diameter) while the 4 peripheral placeholders were 2.5° in diameter. Placeholders were spaced 4.6° from fixation.

Figure 3.1. Example stimuli and sequence timing from a single trial. Participants were instructed to prepare a saccade in the direction indicated (for each prepare signal) and to execute the response as quickly and accurately as possible when the fixation circle turned from red to green.


Drift Correct
Fixation
500ms
First Signal (Prepare)
700ms
First Signal (Execute)
300ms
Fixation
200ms
Cue-Back
300ms
Fixation
500ms
Second Signal (Prepare)
700, 1000, or 1300ms
Second Signal (Execute)
300ms
Fixation
4000ms

Each trial began with an EyeLink drift correction procedure that required the participant to press the space bar with their left hand while fixating within the fixation circle that was always present throughout the trial. After 500 ms, S1 (an arrow pointing at one of the four peripheral placeholders) was presented while the fixation circle simultaneously turned red for 700 ms, then green for 300 ms (i.e. a total of 1000 ms). Following the offset of S1, the fixation circle turned black (for 200 ms), and a cue-back stimulus (change of the fixation circle outline from 4 px to 8 px weight) was then displayed for 300 ms. After another 500 ms (during which fixation was displayed in black at 4 px weight), S2 was presented (i.e., another arrow was displayed, pointing at one of the four peripheral placeholders) and the fixation circle changed to red for 700-1300 ms (depending on the stimulus onset asynchrony [SOA]), then green for 300 ms, followed by S2 disappearance. As a consequence of the variable presentation time of the red S2 signal (700, 1000, or 1300 ms), three different SOA times were possible: 2000, 2300, or 2600 ms. The inter-trial interval was 4 seconds. For both S1 and S2, participants were instructed to prepare their eye movement while the fixation circle was red, and to execute the corresponding saccadic response when the fixation circle turned green. Consequently, in our task, in order to initiate a pre-programmed motor response, participants were merely required to detect a colour change at fixation. Participants were informed that the preparation signal (i.e., when fixation was red) was 100% informative. Participants were instructed to make a saccade toward and fixate the signaled targets as quickly and accurately as possible (following onset of the green circle), and to return their eyes to centre upon display of the cue-back as well as after completing their S2 response. On catch trials, the S1 signal was displayed within a red fixation circle for 1300 ms that did not change to green; after 1300 ms, the inter-trial interval commenced.

If participants did not respond within 1.5 seconds to the green circle surrounding each signal, if they did not return their eyes to centre between S1 and S2, or if they failed to maintain fixation during the fixation stimulus or when fixation circle was red (e.g. immediately prior to S1 or S2, and on catch trials), an error message was displayed, the trial was aborted and was randomly inserted (recycled) later in the experiment. Data from aborted trials were excluded from all data analysis. A total of 4.1% of trials were recycled due to a slow response, a failure to return their eyes to centre between S1 and S2, or a failure to maintain fixation.

3.4 Data Analysis

Trials with S2 RTs less than 100 ms (anticipation) or greater than 1000 ms (miss) were flagged during data processing and excluded from analyses. Mean RTs for correct S2 saccades were analyzed using a repeated-measures ANOVA ($\alpha = 0.05$) with the factors offset (i.e., the angular offset between S1 and S2: 0°, 90° or 180°) and SOA (i.e., 2000, 2300, or 2600 ms). Offset conditions were further compared using planned pairwise comparisons ($\alpha = 0.01$).

3.5 Results

Errors. An average of 0.3% of trials were classified as anticipations (RT < 100 ms following onset of the green circle surrounding S2), and 0.4% as misses (RT > 1000 ms following S2 onset). Participants did not make any wrong direction errors (i.e., did not look at unsignaled locations).

Saccadic Reaction Times. Saccadic RTs are shown in Figure 3.2. Main effects of offset $F(2,28) = 11.48$, $p < 0.001$, $\eta^2_p = 0.45$ and SOA $F(2,28) = 3.86$, $p < 0.05$, $\eta^2_p = 0.21$ were observed. No interaction between offset and SOA was observed, $F(4,56) = 1.74$, $p = 0.16$, $\eta^2_p = 0.11$. Demonstrating characteristic IOR, pairwise comparisons revealed slower RTs for the 0° relative to 90°, $F(1,14) = 13.18$, $p < 0.005$, $\eta^2_p= 0.5$ and 180°, $F(1,14) = 12.5$, $p<.005$, $\eta^2_p = 0.47$ conditions; 90° and 180° RTs were equivalent, $F(1,14) = 0.36$, $p = 0.56$, $\eta^2_p = 0.03$. Pairwise comparisons conducted on the different levels of SOA revealed significantly faster overall RTs for the 2300 ms SOA ($\mathbf{x} = 270.5$ ms) compared to both the 2000 ms ($\mathbf{x} = 280.8$ ms), $F(1,14) = 5.42$, $p < 0.05$, $\eta^2_p = 0.28$, and 2600 ms ($\mathbf{x} = 281.1$ ms), $F(1,14) = 10.09$, $p < 0.01$, $\eta^2_p = 0.41$ SOA. Equivalent overall RTs were observed for the 2000 and 2600 ms SOAs, $F(1,14) = 0.002$, $p = 0.96$, $\eta^2_p = 0$.

In order to determine if participants prepared their responses prior to the initiation cue as instructed, saccadic RTs were compared to a previous version of this study ($n = 19$) using identical methods, but without pre-cueing of the required S1 and S2 responses [5]. In other words, participants were not given the 700-1300 ms preparation signal, and the initial onset of the directional arrow was the signal to initiate the saccade. Under these task circumstances, participants were required to detect and interpret the direction of a central arrow, then select, initiate, and execute an appropriate motor response; in contrast, in the present study, participants were only required to detect a colour change (at fixation) in order to release a pre-programmed motor response. In the present study, RTs could only therefore consist of (1) the time required detect the go signal plus (2) the time required to initiate a response. Saccadic RTs were an average of 105.2 ms faster in the present experiment F(1,14) = 64.95 $p < 0.001$, $\eta^2_p = 0.83$.

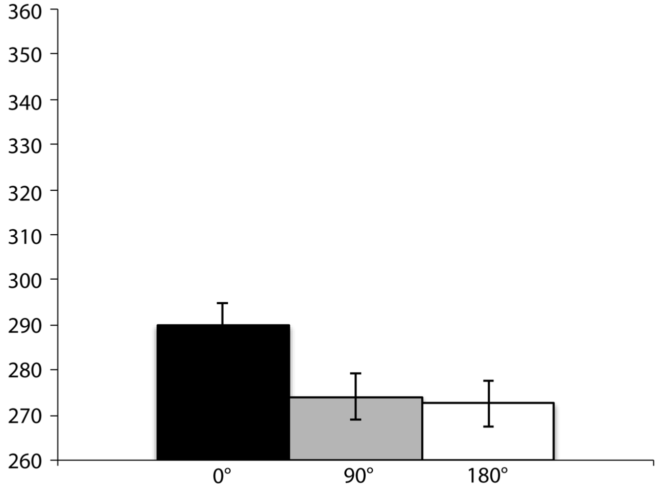


Figure 3.2. Saccadic reaction times to the second signal (S2) for each offset condition (0°, 90°, and 180°). Within-subjects 95% confidence intervals were generated as described by Masson [13] using the Offset x Subject MSE term.

3.6 Discussion

If IOR occurs at the level of early sensory/attentional or motor programming processes, then by allowing participants to prepare their responses prior to execution, IOR should have been eliminated in our study. Surprisingly however, we observed the defining pattern of IOR, where responses were slowest at the previously cued 0° location relative to 90° and 180° offsets [2].

The present data provide the first clear evidence that IOR can arise from processes operating at or during response execution. We note that Hooge and Frens [10] previously reported IOR (or as they called it, “inhibition of saccade return”) in a task requiring participants to execute known sequences of saccades. However, as suggested by Hooge and Frens [10], their study left open the possibility that IOR arose from motor programming effects occurring between each individual saccade in the movement sequences utilized. In contrast, our study ruled out motor programming effects by ensuring that motor programming was complete prior to the execution of each individual saccade.

What processes might be affected by IOR during response execution? Two main possibilities exist. First, it is possible that IOR operates to affect motor execution processes. If IOR is indeed implemented as a *motor* execution bias, there are very few neural substrates where IOR could be implemented. Given the established role of the SC in the programming of saccades [14], it appears that for IOR to be implemented as a motor execution bias, it would have to arise from effects on neural activity that is downstream, or efferent, from the SC. For example, it is possible that IOR emerged from inhibitory activity within output neurons of the reticular formation, the abducens nuclei, or the oculomotor nuclei, which are innervated by the SC and which relay pre-programmed commands to the extraocular muscles [14]. These motor output neurons might be inhibited via projections from a centralized IOR mechanism [7], or alternatively, inhibition might originate from interactions between these output neurons. Further narrowing the possible substrates for IOR to operate as a motor execution bias, it appears unlikely that IOR could be implemented at the muscle level, e.g. as muscle fatigue, given the exceptionally high fatigue resistance of the extraocular muscles [9].

A second possibility is that IOR is implemented to affect attentional processes that are engaged *specifically* at the time of response execution. This idea is plausible if one assumes attentional processes are tightly coupled to oculomotor activity such that the allocation of attention can immediately precede and define the goal of a saccadic eye movement [cf. 6, 24]. A delay in the allocation of this late-stage attention would therefore be able to slow an otherwise programmed saccadic response. If late-stage attentional processes can account for the observed IOR, then the range of possible neural substrates underlying the observed inhibition is much larger, e.g., and may occur within posterior parietal cortex, prefrontal cortex, or within subcortical regions such as the SC [24].

While the present data cannot disentangle the two possibilities described above, we note the nature of the coupling between spatial attention and saccadic programming remains controversial, and several lines of evidence suggest that oculomotor programming both *precedes* and *defines* the spatial deployment of attention [1, 21, 25]. If this is the case, it appears unlikely that a shift of attention occurring at response initiation could account for the IOR observed, because attentional allocation would be pre-determined via motor programming. Regardless of the mechanism underlying IOR in our study, we note that our study is the first to reveal that IOR may operate on processes occurring at or during response *execution* rather than *preparation*. This observation is thus consistent with the notion of “saccadic IOR” but offers a significant departure from the theoretical framework applied in the design and interpretation of previous IOR studies.

Our analysis of SOA revealed overall fastest RTs for 2300 ms SOAs compared to both 2000 and 2600 ms SOAs. Given that the SOA was determined by the variable presentation time assigned to the S2 preparation signal (700, 1000, or 1300 ms), this result suggests some limited variability in overall RTs as a function of the preparation time allotted to participants. The absence of an interaction between SOA and offset direction shows that equivalent IOR was revealed regardless of preparation time, demonstrating that responses were well within the inhibitory stage of IOR; this observation provides further support that responses were made within a relatively stable range of SOA values that each tap into the IOR processes observed.

Consistent with the putative function of IOR, the execution bias observed presently may contribute to the facilitation of efficient visual search [11, 16], at least when saccadic responses are generated from a common starting point. We suspect however, that during natural search behaviour, IOR may arise from effects on more than one stage of information processing [cf. 3], and that collectively, different varieties of IOR are likely to contribute to the functional operation of the gaze control system. In other words, while we reveal IOR at or during response execution, our study does not rule out the possibility that other forms of IOR can operate under different task circumstances. Future research should therefore examine the contribution of execution biases, in addition to earlier sensory/attentional and motor preparation effects, in search behaviour. Given the adaptive value of IOR in search, it may be interesting to determine if a late-stage execution bias is similarly observed in other species that exhibit IOR like behaviour during search [e.g. 4]. Finally, the present paradigm may be useful not only for ongoing studies of IOR, but also as a tool for studying the coupling between attention and motor execution processes.

3.7 References

[1] A.V. Belopolsky, J Theeuwes, When are attention and saccade preparation dissociated? Psychol. Sci. 20 (2009) 1340-1347

[2] P.J. Bennet and J. Pratt, The spatial distribution of inhibition of return, Psychol. Sci. 12 (2001) 76-80.

[3] G. Berlucchi, Inhibition of Return: A phenomenon in search of a mechanism and a better name, Cogn. Neuropsych. 23 (2006) 1065-74

[4] R.G. Cook, J.S. Katz, A.P. Blaisdell, Temporal properties of visual search in pigeon target localization, J. Exp. Psych.: Animimal Behavior Processes (2012) Epub.

[5] C.D. Cowper-Smith, J. Harris, G.A. Eskes, D.A Westwood, Spatial interactions between successive eye and arm movements: signal type matters, PLoS One 8 (2013) e58850.

[6] H. Deubel, W.X. Schneider, Saccade target selection and object recognition: evidence of a common attentional mechanism, Vis. Res. 36 (1996) 1827-1837.

[7] M.C. Dorris, R.M. Klein, S. Everling, D.P. Munoz, Contribution of the primate superior colliculus to inhibition of return, J. Cogn. Neuro. 5 (1994) 1256-1263.

[8] K.R. Dukewich, Reconceptualizing inhibition of return as habituation of the orienting response, Psych. Bull. Rev. 16 (2009) 238-251.

[9] A.F. Fuchs, M.D. Binder, Fatigue resistance of human extraocular muscles. J. Neurophys. 49 (1983) 28-34.

[10] I.T. Hooge, M.A. Frens, Inhibition of saccade return (ISR): spatio-temporal properties of saccade programming, Vis. Res. 40 (2000) 3415-3426.

[11] R.M. Klein, W.J. MacInnes, Inhibition of return is a foraging facilitator in visual search, Psychol. Sci. 10 (1999) 346-352.

[12] J.W. MacInnes, R.M. Klein, Inhibition of return biases orienting during the search of complex scenes, ScientificWorldJournal. 3 (2003) 75-86.

[13] M.E. Masson, G.R. Loftus, Using confidence intervals for graphically based data interpretation, Can. J. Exp. Psych. 57 (2003), 203-220.

[14] D.P. Munoz, M.S. Dorris, M. Paré, S. Everling, On your mark, get set: brainstem circuitry underlying saccadic initiation, Can. J. Phys. Pharm. 78 (2000), 934-944.

[15] M.I. Posner, Y. Cohen, Components of visual orienting, in: H. Bouma and D.G. Bouwhuis (Eds.) Attention and performance X, Amsterdam: North-Holland, 1984, pp. 243-258.

[16] M.I. Posner, R.D. Rafal, L.S. Choate, J. Vaughan, Inhibition of return: neural basis and function, Cogn. Neuropsych. 2 (1985) 211-228.

[17] J. Pratt, J.J. Adam, J. McAuliffe, The spatial relationship between cues and targets mediates inhibition of return, Can. J Exp. Psych/Rev. Can. Psych. Exp. 52 (1998), 213-216.

[18] J. Pratt, T.M. Spalek, F. Bradshaw, The time to detect targets at inhibited and noninhibited locations: Preliminary evidence for attentional momentum, J. Exp. Psych.: Hum. Percep. Perf. 25 (1999), 730-746.

[19] D.J. Prime, L.M. Ward, Cortical expressions of inhibition of return, Brain Res. 1072 (2006) 161-174.

[20] R.D. Rafal, P.A. Calabresi, C.W. Brennan, T.K. Sciolto, Saccade preparation inhibits reorienting to recently attended locations, J. Exp. Psych.: Hum. Percep. Perf. 15 (1989), 673-685.

[21] G. Rizzolatti, L Riggio, I Dascola, C Umilta, Reorienting of attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention, Neuropsych. 25 (1987), 31-40.

[22] T. Ro, J. Pratt, R.D. Rafal, Inhibition of return in saccadic eye movements, Exp. Brain Res. 130 (2000), 264-268.

[23] J. Satel, Z. Wang, T.P. Trappenberg, R.M. Klein, Modeling inhibition of return as short term depression of early sensory input to the superior colliculus, Vis. Res. 51 (2011), 987-996

[24] W.X. Schneider, VAM: A neuro-cognitive model for visual attention control of segmentation, object recognition, and space-based motor action, Vis. Cogn. 2 (1995), 331-375.

[25] D.T. Smith, T. Schenk, The premotor theory of attention: time to move on? Neuropsychol. 50 (2012), 1104-1114.

[26] J.J. Snyder, A. Kingstone, W.C. Schmidt, Attentional momentum does not underlie the inhibition of return effect, J. Exp. Psych.: Hum. Percep. Perf. 27 (2001), 1420-1432.

[27] P. Sumner, P. Nachev, N. Vora, M. Husain, C. Kennard, Distinct cortical and collicular mechanisms of inhibition of return revealed with S cone stimuli, Curr. Bio. 14 (2004) 2259-2263.

[28] T.L. Taylor, R.M. Klein, Visual and motor effects in inhibition of return, J. Exp. Psych.: Hum. Percep. Perf. 26 (2000) 1639-1656.

CHAPTER 4: MOTOR INHIBITION OF RETURN CAN AFFECT PREPARED REACHING MOVEMENTS

C.D. Cowper-Smith, G.A. Eskes, D.A Westwood, Motor inhibition of return can affect prepared reaching movements, Neuroscience Letters 541 (2013) 83–86.

4.1 Abstract

Inhibition of return (IOR) is a widely studied phenomenon that is thought to affect attention, eye movements, or reaching movements, in order to promote orienting responses toward novel stimuli. Previous research in our laboratory demonstrated that the motor form of *saccadic* IOR can arise from late-stage response execution processes. In the present study, we were interested in whether the same is true of *reaching* responses. If IOR can emerge from processes operating at or around the time of response execution, then IOR should be observed even when participants have fully prepared their responses in advance of the movement initiation signal. Similar to the saccadic system, our results reveal that IOR can be implemented as a late-stage execution bias in the reaching control system.

4.2 Introduction

Inhibition of return (IOR) refers to a delay in responding to visual targets appearing in a location previously occupied by a cue or another target and is typically observed when the time between the onset of the two stimulus events is greater than approximately 300 ms. Early accounts of the phenomenon ascribed IOR to the presence of an inhibitory mechanism that discourages the return of eye movements, spatial attention, or both to recently attended locations, perhaps to increase the efficiency of visual search behavior [8,10,21].

Further research indicated that a motor form of IOR can be observed [4,7,13,14,19,21], for example, when consecutive responses are signaled by central stimuli, an observation that cannot easily be explained by sensory or attentional mechanisms [6,18,19,21]. Using central stimuli, the motor form of IOR has been reported for saccadic eye movements [e.g., 14, 19, 20] and more recently, reaching movements (See Study 4 below; [3]). While evidence for IOR is usually based on reaction time (RT), this measure alone cannot reveal the stage at which IOR arises in the stimulus-response sequence.

In a recent experiment with saccadic eye movements [4], we demonstrated that the motor form of IOR can arise from processes operating at or around the time of response execution; even when participants could prepare a saccadic movement in advance, the execution of that response was delayed when it was preceded by a saccade in the same direction compared to a saccade in the opposite direction. Although the motor form of IOR can arise from late-stage execution processes within the saccadic control system, it remains unclear whether IOR can be similarly implemented at this late stage within the reaching control system. This question is important for gaining a clearer understanding of the mechanism(s) underlying IOR. For example, if IOR operates as a late-stage execution bias only within the oculomotor system, it would suggest the presence of a relatively specialized or unique mechanism designed to influence eye movements; alternatively, if IOR can operate as a late-stage execution bias in multiple effector systems, it would suggest the presence of a more generalized mechanism. In the present investigation, we therefore examined whether motor IOR can be observed in late-stage response execution processes when reaching rather than saccadic responses are required. If IOR was present, we expected to observe the defining pattern of IOR, where responses are slowest in a previously signaled location (0° offset), but relatively faster when offset by 90° or 180° [2]. Such an observation would show, for the first time, that motor IOR can arise at or during late-stage execution processes within the reaching control system. Our experimental paradigm replicated that of Cowper-Smith et al. [4], with the only exception that reaching rather than saccadic responses were required.

4.3 Methods

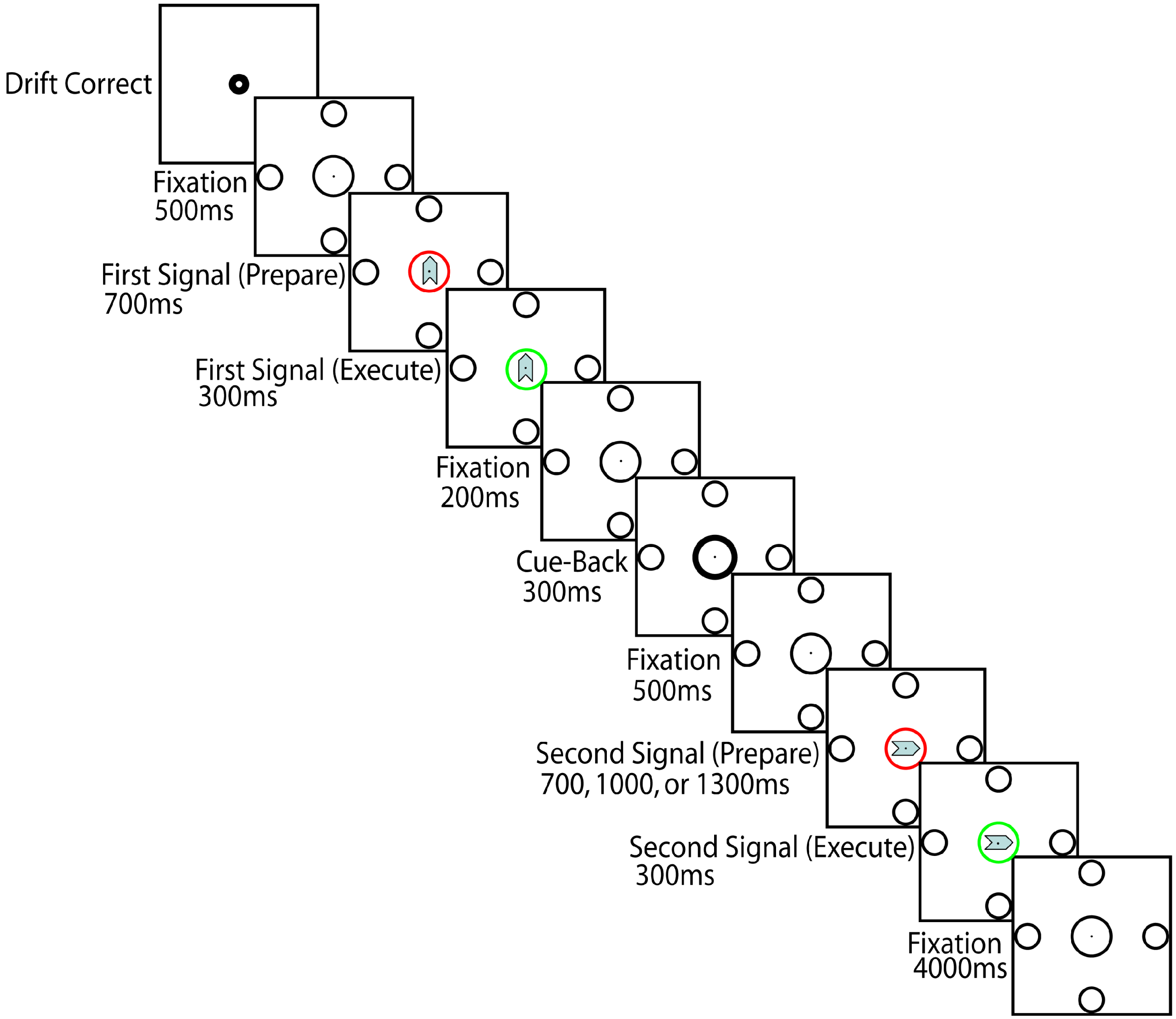
Seventeen undergraduate students (13 female, 4 male) were recruited at Dalhousie University. Participants were right handed, had normal vision and reported no history of visual, motor, or neurological abnormalities.

The methods for the experimental paradigm were presented by Cowper-Smith et al. [4]. The present study replicated these methods exactly, except that consecutive reaching responses, rather than saccadic responses, were required. The sequence of stimuli and task are presented in Figure 4.1.

With the exception of 44 catch trials, two central arrowhead signals (S1 and S2) were presented on each trial that pointed toward one of the four possible target locations with equal probability (0.25). These pairings signaled consecutive reaching responses offset from each other by 0°, 90°, or 180° . Each S1/S2 pairing was presented 12 times and all pairings were randomized on a trial-by-trial basis. For both S1 and S2, participants were instructed to prepare their reaching movement while the fixation circle was red, and to execute the corresponding reaching response when the fixation circle turned green. At response execution, participants were instructed to reach and touch the signaled targets as quickly and accurately as possible, and to return their finger to centre upon display of the cue-back as well as after completing their S2 response. Participants were informed that the preparation signal (i.e., when fixation was red) was 100% informative. On catch trials, the S1 signal was displayed within a red fixation circle for 1300 ms that did not change to green; after 1300 ms, the inter-trial interval commenced. Stimuli were presented, and reaching responses were recorded using a 30-inch Elo touch screen LCD monitor (Elo TouchSystems, Menlo Park, California, USA). Reaction times were defined by the moment participants lifted their finger off the screen relative to the onset of the execution signal, and the accuracy of reaching movement endpoints was monitored to ensure participants responses landed (i.e., touched) within the boundary of the indicated target location.

An error message was displayed, the trial was aborted and was randomly inserted (recycled) later in the experiment if participants: (1) moved their eyes outside of central fixation; (2) did not respond within 1.5 seconds to the green execution signal (with a reaching response); (3) did not return their finger to centre between S1 and S2; (4) failed to keep their index finger within the boundary of the centrally marked fixation location before the green execution signal was presented, (i.e., prior to S1 or S2, and on catch trials) or (5) failed to point and touch within the boundary of the indicated target. Data from aborted trials were excluded from all data analysis.

Figure 4.1. Example stimuli and sequence timing from a single trial. Each trial began with an EyeLink drift correction procedure that required the participant to press the space bar with their left hand while maintaining fixation within the fixation circle that was always present throughout the trial. After completing the drift correction, participants were instructed to place the index finger of their right hand within the central fixation circle. After 500 ms, S1 (an arrow pointing at one of the four peripheral placeholders) was presented while the fixation circle was red (preparation signal) for 700 ms, then green (execution signal) for 300 ms. Following the offset of S1, the fixation circle turned black (for 200 ms), and a cue-back stimulus (change of the fixation circle outline from 4px to 8px weight), reminding participants to return their finger to centre, was then displayed for 300 ms. After another 500 ms (during which fixation was displayed in black at 4px weight), S2 was presented (i.e., another arrow was displayed, pointing at one of the four peripheral placeholders) within the fixation circle that was first red (preparation signal) for 700–1300 ms (depending on the stimulus onset asynchrony [SOA]), then green (execution signal) for 300 ms, followed by S2 disappearance. As a consequence of the variable presentation time of the red S2 signal (700, 1000, or 1300 ms), three different SOA times were possible: 2000, 2300, or 2600 ms. The intertrial interval was 4 seconds. For both S1 and S2, participants were instructed to prepare their reaching movement while the fixation circle was red, and to execute the corresponding reaching response when the fixation circle turned green. Between trials, participants were instructed to rest their right arm on the desk.


Drift Correct
Fixation
500ms
First Signal (Prepare)
700ms
First Signal (Execute)
300ms
Fixation
200ms
Cue-Back
300ms
Fixation
500ms
Second Signal (Prepare)
700, 1000, or 1300ms
Second Signal (Execute)
300ms
Fixation
4000ms

4.4 Data Analysis

Trials with S2 RTs less than 100 ms (anticipation) or greater than 1000 ms (miss) were flagged during data processing and excluded from analyses. The frequency of aborted trials, anticipation, miss, and directional errors accounted for less than 5% of trials. Mean RTs for correct S2 reaches were analyzed using a repeated-measures ANOVA ($\alpha = 0.05$) with factors of offset (i.e., the angular offset between S1 and S2: 0°, 90° or 180°) and SOA (i.e., 2000, 2300, or 2600 ms). Offset conditions were further compared using planned pairwise comparisons ($\alpha = 0.01$).

4.5 Results

Errors. Only one participant made one wrong direction error (i.e., reached to an unsignaled location).

Reaction Times. Reaching RTs are shown in Figure 4.2. Main effects of offset, F(2,32) = 26.2, $p < 0.001$, $\eta^2_p = 0.62$ and SOA were observed, F(1.2,19.2) = 5.7, $p < 0.05$. No interaction between offset and SOA was observed, F(2.4,39.5) = 2.09, $p = 0.13$. Revealing characteristic IOR, pairwise comparisons revealed slower RTs for the 0° relative to 90°, F(1,16) = 29.7, $p < 0.001$, $\eta^2_p = 0.65$ and 180° , F(1,16) = 35.5, $p < 0.001$, $\eta^2_p = 0.69$ conditions; 90° and 180° RTs were equivalent, F(1,16) = 1.4, $p = 0.26$, $\eta^2_p = 0.08$. Pairwise comparisons conducted on the different levels of SOA revealed significantly faster over all RTs for the 2300 ms SOA ($\mathbf{x} = 368.3$ ms) compared to both the 2000 ms ($x = 383.2$ ms), F(1,16) = 10.2, $p < 0.01$, $\eta^2_p = 0.38$, and 2600 ms ($\mathbf{x} = 383.4$ ms), F(1,16) = 21.4, $p < 0.001$, $\eta^2_p = 0.57$, SOA. Equivalent overall RTs were observed for the 2000 and 2600 ms SOAs, F(1,16) = 0.001, $p = 0.97$, $\eta^2_p = 0$. The differences observed in

RTs as a function of SOA is consistent with that observed by Cowper-Smith et al. [4]. Given that SOA was defined by the variable preparation time before the S2 execution signal, this result reflects variability in overall RTs as a function of the preparation time allotted to participants. Critically, that no interaction was observed between SOA and offset demonstrates that equivalent IOR was observed independent of preparation time.

In order to determine if participants prepared their responses prior to the initiation cue as instructed, reaching RTs were compared to a previous version of this study (*n* = 19) using identical methods, but without pre-cueing of the required S1 and S2 responses [5]. In our previous study, participants were not given the 700-1300 ms preparation signal, and the initial onset of the directional arrow was the signal to initiate a reaching response. Under these task circumstances, RTs were made up of the time to detect and interpret the direction of a central arrow, then select, initiate, and execute an appropriate reaching response; in contrast, in the present study, RTs were made up of the time to detect a color change (at fixation) plus the time required to execute a pre-selected motor response. In other words, because a motor response was pre-programmed, the time to select a motor response should not be included in the observed RTs. Consistent with pre-programming of motor responses, reaching RTs were an average of 70 ms faster in the present experiment $F(1,15) = 49.7$ $p < 0.001$, $\eta^2_p = 0.77$.

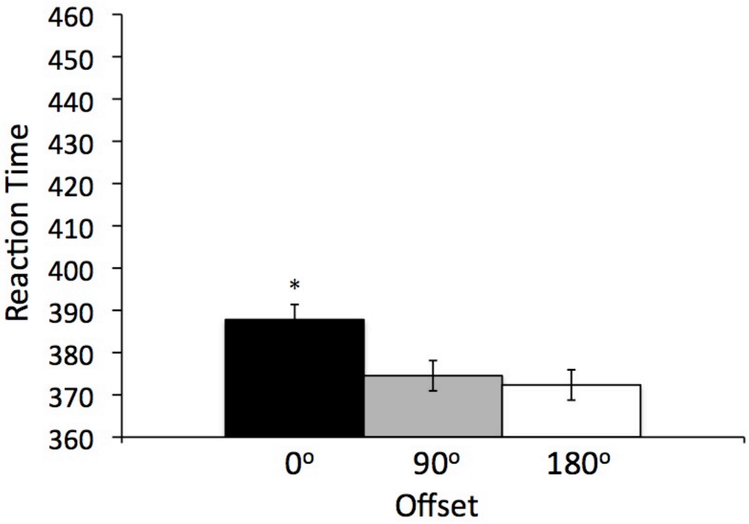


Figure 4.2. Manual reaction times for responses to the second signal (S2) in each offset condition (0°, 90°, and 180°). Within-subjects 95% confidence intervals were generated as described by Masson [11] using the Offset × Subject MSE term.

4.6 Discussion

Following the logic outlined by Cowper-Smith et al. [4], the motor form of IOR could in principle arise from processes occurring relatively early (prior to execution) or late (at or around the time of execution) in the transformation of a central stimulus into an action. Allowing participants to prepare a response prior to the signal to respond should eliminate IOR if it is due to relatively early processes; thus, like our previous study of saccadic eye movements, the results of the present study support the conclusion that motor IOR for reaching movements can be implemented by processes operating at or around the time of response execution.

What neural substrates might produce IOR during response execution in the present study? The exact timing and neural locus defining the onset of motor *execution* (i.e., when a motor program has been fully specified by motor *programming*) is a question that is open to debate. One view is that motor execution processes commence once a motor program is fully specified and sent as an impulse signal to the spinal cord. From this perspective, our results suggest that IOR could arise from inhibitory activity operating within, or efferent from corticospinal projection neurons that innervate both interneurons and motoneurons throughout the spinal cord [9]. These motor output neurons could be inhibited via projections from a centralized IOR mechanism, or alternatively, from interactions between these output neurons.[15] While we refrain from making any strong conclusions regarding the precise neural locus of IOR in the present study, it is clear that the IOR observed presently arises at or during response execution rather than response programming.[16] This conclusion is based on the evidence (described earlier) that motor responses were in fact pre-programmed in the present study; assuming this is the case, it follows that only response execution processes can be affected by IOR. Notably however, the response execution processes affected by IOR in the present study could include both purely motor or alternatively, late-stage attentional processes that might be inherently linked to the execution of a motor program. The possible mechanisms underlying the observed IOR are described further below.

---

[15] It is further unlikely that IOR emerged from muscle fatigue effects; given that prior to the S2 response, a movement was made to both the S1 location, and 180◦ opposite (in order to return to centre), if fatigue effects were present, one would expect them to affect both 0◦ and 180◦ response directions.

[16] Although a movement can be prepared in advance of an execution signal, this preparation must be maintained up until response execution [e.g. 1]. In light of the evidence presented that motor preparation is indeed complete prior to execution in the present study (i.e., overall faster RTs when participants are given a preparation signal compared to similar task conditions without a preparation signal), it is unlikely that the maintenance of preparatory activity can account for the IOR observed.

Taking the results of the present study together with our prior observation of a similar late-stage execution bias for saccadic eye movements is informative regarding the possible mechanisms underlying the putative motor form of IOR observed. In particular, the observation of a similar effect in both the oculomotor and reaching system suggests three possibilities: first, there might be distinct, but similarly operating mechanisms within each motor system. Second, a common (or central) mechanism might be implemented to similarly affect the behavioural output of both systems [cf. 16]. A third alternative is that if attentional processes are engaged immediately prior to response execution – regardless of which motor system is activated [cf. premotor theory of attention, 15, 17] – then IOR could arise from a delay in the deployment of this late-stage attentional process.

Regardless of the mechanism posited, the observation that IOR-like phenomena can emerge from late-stage execution processes raises questions surrounding the functional and adaptive significance of this type of IOR. For example, it is commonly argued that the IOR phenomenon exists to influence future actions, in order to reduce the likelihood of repetitive actions [8,10,12,13,21]. However, a mechanism operating at the level of response execution alone could not achieve this purpose because it would merely delay the implementation of a chosen action and not discourage it from being selected in the first place [cf. 20]. Consequently, rather than serving the function of discouraging repetitive actions in the future, we argue that the form of IOR observed in the present study might simply be an epiphenomenon, e.g., arising as a by-product of the processes engaged in the execution of a prior movement. If, however, under real-world circumstances, the observed execution bias operates simultaneously with other mechanisms, it is possible that a delay in execution RTs may be somehow useful for influencing action, e.g., by allowing a competing response to occur.

While the present study reveals that a pattern of RTs resembling IOR can arise at or during manual response execution, it does not rule out the possibility that other forms of IOR operate under different task circumstances. It will be interesting for future research to explore whether the motor form of IOR can arise during motor preparation rather than execution. Further examining questions like these will be useful for gaining a better understanding of how movement sequences are coordinated across different levels of response processing.

4.7 Acknowledgements

This research was funded by NSHRF. Author salaries were supported by CIHR (CCS and DAW), the Dalhousie Faculty of Medicine (GE), and NSERC (DAW).

4.8 References

[1] A. Bastian, G. Schöner, A. Riehle, Preshaping and continuous evolution of motor cortical representations during movement preparation, Eur. J. Neurosci. 18 (2003) 2047–2058.

[2] P.J. Bennet, J. Pratt, The spatial distribution of inhibition of return, Psychol. Sci. 12 (2001) 76–80.

[3] C.D. Cowper-Smith, D.A. Westwood, Motor IOR revealed for reaching, Att. Percept. Psychophys. 75 (2013) 1914–22.

[4] C.D. Cowper-Smith, G.A. Eskes, D.A. Westwood, Saccadic inhibition of return can arise from late-stage execution processes, Neurosci. Lett. 531 (2012) 120–124.

[5] C.D. Cowper-Smith, J. Harris, G.A. Eskes, D.A Westwood, Spatial interactions between successive eye and arm movements: signal type matters, PLoS One 8 (2013) e58850.

[6] M.H. Fischer, J. Pratt, S.F. Neggers, Inhibition of return and manual pointing movements, Percept. Psychophys. 65 (2003) 379–387.

[7] A.R. Hunt, A. Kingstone, Inhibition of return: dissociating attentional and oculomotor components, J. Exp. Psychol. Hum. Percept. Perform. 29 (2003) 1068–1074.

[8] R.M. Klein, W.J. MacInnes, Inhibition of return is a foraging facilitator in visual search, Psychol. Sci. 10 (1999) 346–352.

[9] R.N. Lemon, P.A. Kirkwood, M.A. Maier, K. Nakajima, P. Nathan, Direct and indirect pathways for corticospinal control of upper limb motorneurons in the primate, Prog. Brain Res. 143 (2004) 263–279.

[10] J.W. MacInnes, R.M.Klein, Inhibition of return biases orienting during the search of complex scenes, ScientificWorldJournal 3 (2003) 75–86.

[11] M.E. Masson, G.R. Loftus, Using confidence intervals for graphically based data interpretation, Can. J. Exp. Psychol. 57 (2003) 203–220.

[12] M.I. Posner, Y. Cohen, Components of visual orienting, in: H. Bouma, D.G. Bouwhuis (Eds.), Attention and performance X, North-Holland, Amsterdam, 1984, pp. 243–258.

[13] M.I. Posner, R.D. Rafal, L.S. Choate, J. Vaughan, Inhibition of return: neural basis and function, Cogn. Neuropsychol. 2 (1985) 211–228.

[14] R.D. Rafal, P.A. Calabresi, C.W. Brennan, T.K. Sciolto, Saccade preparation inhibits reorienting to recently attended locations, J. Exp. Psychol. Hum. Percept. Perform. 15 (1989) 673–685.

[15] G. Rizzolatti, L. Riggio, I. Dascola, C. Umilta, Reorienting of attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention, Neuropsychologia 25 (1987) 31–40.

[16] J.-H. Song, R.D. Rafal, R.M. McPeek, Deficits in reach target selection during inactivation of the midbrain superior colliculus, PNAS 108 (51) (2011) E1433–E1440.

[17] D.T. Smith, T. Schenk, The premotor theory of attention: time to move on? Neuropsychologia 50 (2012) 1104–1114.

[18] T.L. Taylor, R.M. Klein, On the causes and effects of inhibition of return, Psychon. Bull. Rev. 5 (1998) 625–643.

[19] T.L. Taylor, R.M. Klein, Visual and motor effects in inhibition of return, J. Exp. Psychol. Hum. Percept. Perform. 26 (2000) 1639–1656.

[20] Z. Wang, R.M. Klein, Searching for inhibition of return in visual search: a review, Vision Res. 50 (2010) 220–228.

[21] Z. Wang, J. Satel, R.M. Klein, Sensory and motor mechanisms of oculomotor inhibition of return, Exp. Brain Res. 218 (2012) 441–453.

CHAPTER 5: MOTOR INHIBITION OF RETURN REVEALED FOR REACHING

C.D. Cowper-Smith, D.A. Westwood, Motor IOR revealed for reaching, Attention Perception and Psychophysics 75 (2013) 1914–22.

5.1 Abstract

Inhibition of return (IOR) is a spatial phenomenon that is thought to promote visual search functions by biasing attention and eye movements toward novel locations. Considerable research suggests distinct sensory and motor flavors of IOR, but it is not clear whether the motor type can affect responses other than eye movements. Most studies claiming to reveal motor IOR in the reaching control system have been confounded by their use of peripheral signals, which can invoke sensory rather than motor-based inhibitory effects. Other studies have used central signals to focus on motor, rather than sensory, effects in arm movements but have failed to observe IOR and have concluded that the motor form of IOR is restricted to the oculomotor system. Here, we show the first clear evidence that motor IOR can be observed for reaching movements when participants respond to consecutive central stimuli. This observation suggests that motor IOR serves a more general function than the facilitation of visual search, perhaps reducing the likelihood of engaging in repetitive behavior.

5.2 Introduction

Responses to visual targets are faster when preceded by a visual cue in the same location, provided that the two stimulus events are separated by approximately 150 ms or less. For longer cue-target asynchronies however, this relationship reverses, such that responses are slower for previously cued locations [30]. The reversal in reaction times (RTs) at longer cue–target intervals, coined inhibition of return (IOR) by Posner, Rafal, Choate, and Vaughan [31], is generally thought to reflect a mechanism that promotes efficient foraging and visual search behavior by preventing attention and eye movements from returning to previously inspected locations [22,40,41].

At least two forms of IOR can be observed, depending on task conditions: one that slows the detection of spatially localized sensory inputs and another that slows the generation of motor outputs to target stimuli [1,7,11,13,15,17,20,24,27,39,44]. Although IOR is commonly studied in relation to oculomotor responses (i.e., saccades), the phenomenon has also been explored using various other manual responses, such as keypresses and reaching movements. Indeed, many studies have reported IOR for reaching movements [4,19,21,29,32,37,42,45,46]. Importantly, however, all of these studies used peripheral targets to assess the presence of IOR.

When peripheral stimuli are used, IOR can be associated specifically with the detection of sensory information originating from the inhibited location [12,15,16,30,36,39,43]. To the extent that a particular response depends upon the detection of a peripheral stimulus, it would not be surprising to detect a sensory form of IOR in that response, regardless of the specific effector used. As a consequence of using peripheral targets to study IOR for reaching movements, it is therefore unclear whether previous studies have demonstrated a specifically motor form of IOR (i.e., a specific bias against preparing reaching movements to a target location) or, instead, a more general sensory form of IOR (i.e., affecting detection and/or processing of a target stimulus). This is an important theoretical distinction, because the demonstration of a specifically motor form of IOR for arm movements would cast doubt on the widely held view that the primary function of the IOR phenomenon is to facilitate visual search, since the arms are not normally required for such searching.

A small set of studies has focused on IOR for manual responses to targets signaled by central arrows [9,16,39], thereby avoiding concerns that IOR results from a spatially localized sensory processing deficit—that is, where the processing of sensory information is selectively delayed at or near the peripheral target location [12,15,16,16,30,36,38,39,44][17,18]. Recognizing that central arrows can be used to probe for the presence of motor IOR, Fischer et al. [16] attempted to measure IOR for various types of manual responses instructed by either peripheral or central arrowhead targets. In both target conditions, participants were instructed to ignore an uninformative peripheral cue, which could occur in one of two locations, and then respond with one of four types of manual responses (simple or choice keypress responses and simple or choice reaching movements). Under similar cue–target conditions involving saccades rather than manual responses, Taylor and Klein [39] had previously demonstrated IOR for both central arrow and peripheral targets, arguing that peripheral cues could

---

[17] Although the presentation of a central arrowhead stimulus is capable of inducing what appear to be automatic shifts of attention [23,26,34], it is clear that IOR is generated independently of any such shift of attention per se [3,6,25,27,30].

[18] If central arrowhead stimuli reveal IOR associated with a deficit in the speed of sensory or attentional processing, it should be reliably observed in studies requiring button press responses to detect the onset of central arrowhead target stimuli. However, in both cue-target and target-target studies using consecutive arrowhead stimuli, IOR is not observed with button press responses [39]. In contrast, when peripheral stimuli are used, IOR is reliably observed for button press responses (e.g., [2,30,39]). These observations unequivocally demonstrate that unlike peripheral onsets, central arrowhead stimuli are insufficient for revealing the sensory form of IOR.

generate a motor form of IOR in the oculomotor system that could subsequently be revealed using either peripheral or central arrowhead targets.

Whereas Fischer et al. [16] observed IOR for all types of manual responses to peripheral targets, they found no evidence of IOR for central arrowhead targets for any type of manual response. The authors therefore concluded that the presence of IOR for manual responses in general—and for reaching movements in particular—is attributable to sensory rather than motor effects. By extension, all previous studies using reaching movements and peripheral targets could be demonstrating sensory, rather than motor, effects [4,19,21,29,32,37,39,42,45,46]. On the strength of their failure to observe IOR for manual responses to central arrowhead targets, Fischer et al. reached the strong conclusion that "motor-based IOR is restricted to the oculomotor system" (see Satel and Wang [36], for a similar conclusion).

An alternative explanation for the lack of IOR observed by Fischer et al. [16] is that peripheral cues are insufficient to generate a motor form of IOR in the reaching control system, unlike the case for the oculomotor control system (e.g., [39]). It has been argued that peripheral cues automatically engage saccade preparation in the oculomotor system even if no movement is executed (cf. [33,39]). However, it is not clear that reaching movements are prepared in response to peripheral cues if there is no intention to execute a movement (for related arguments, see [10,21]). If the generation of a motor form of IOR requires activation in the relevant motor networks (cf. [18]), the mere presentation of peripheral cues might be insufficient to generate motor IOR in the reaching control system.

To generate—and reveal—motor IOR in the manual control system, it might be necessary to use a target–target paradigm in which manual responses are made to consecutive stimuli, in contrast to the more typical cue–target paradigm in which a response is made to only the second stimulus. Two studies we are aware of have examined whether motor IOR can occur for consecutive upper limb movements using target–target paradigms. In 2 of their 24 experimental conditions, Taylor and Klein [39] required participants to make lateralized keypress responses to two consecutive peripheral or central arrowhead stimuli and found IOR for peripheral targets but facilitation for central arrowhead targets. Consistent with the conclusions of Fischer et al. [16], these results suggest the presence of sensory, but not motor, IOR for manual responses.

In contrast to the facilitation observed by Taylor and Klein [39], Cowper-Smith et al. [9] recently demonstrated IOR in a target–target task requiring reaching responses to consecutive arrowhead stimuli. In an effort to separate early- and late-stage motor processes, however, Cowper-Smith et al. [9] presented the central arrowheads (with 100 % validity) 700–1,300 ms before the imperative signal to respond, thereby providing participants the opportunity to prepare their responses before executing them. This is quite unlike traditional IOR paradigms in which participants are required to respond to the central arrowhead stimulus immediately upon its presentation. Providing advance information about an upcoming response [9] might create a unique form of response inhibition due to the requirement to actively inhibit the execution of a prepared movement for some period of time prior to the imperative stimulus. Thus, it is unclear whether the results obtained by Cowper-Smith et al. [9] would be found in a more traditional target–target paradigm in which participants make reaching movements immediately upon the presentation of central arrowhead targets.

In the present study, we adopted a target–target IOR paradigm similar to that used by Taylor and Klein [39], but participants were required to reach and touch the indicated targets, rather than press spatially congruent keys. In Experiment 1 (E1), we used peripheral targets for the first and second stimuli; as was noted earlier, however, the use of peripheral stimuli can reveal IOR associated with the detection of visual information [16,39] or the preparation of a reaching response. In Experiment 2 (E2), we therefore used centrally presented arrowheads for both the first and second stimuli to eliminate the possibility of sensory IOR. The results of our experiments confirm that IOR can arise from motor-based processes in the reaching control system.

5.3 Experiment 1: Peripheral Targets

5.3.1 Method

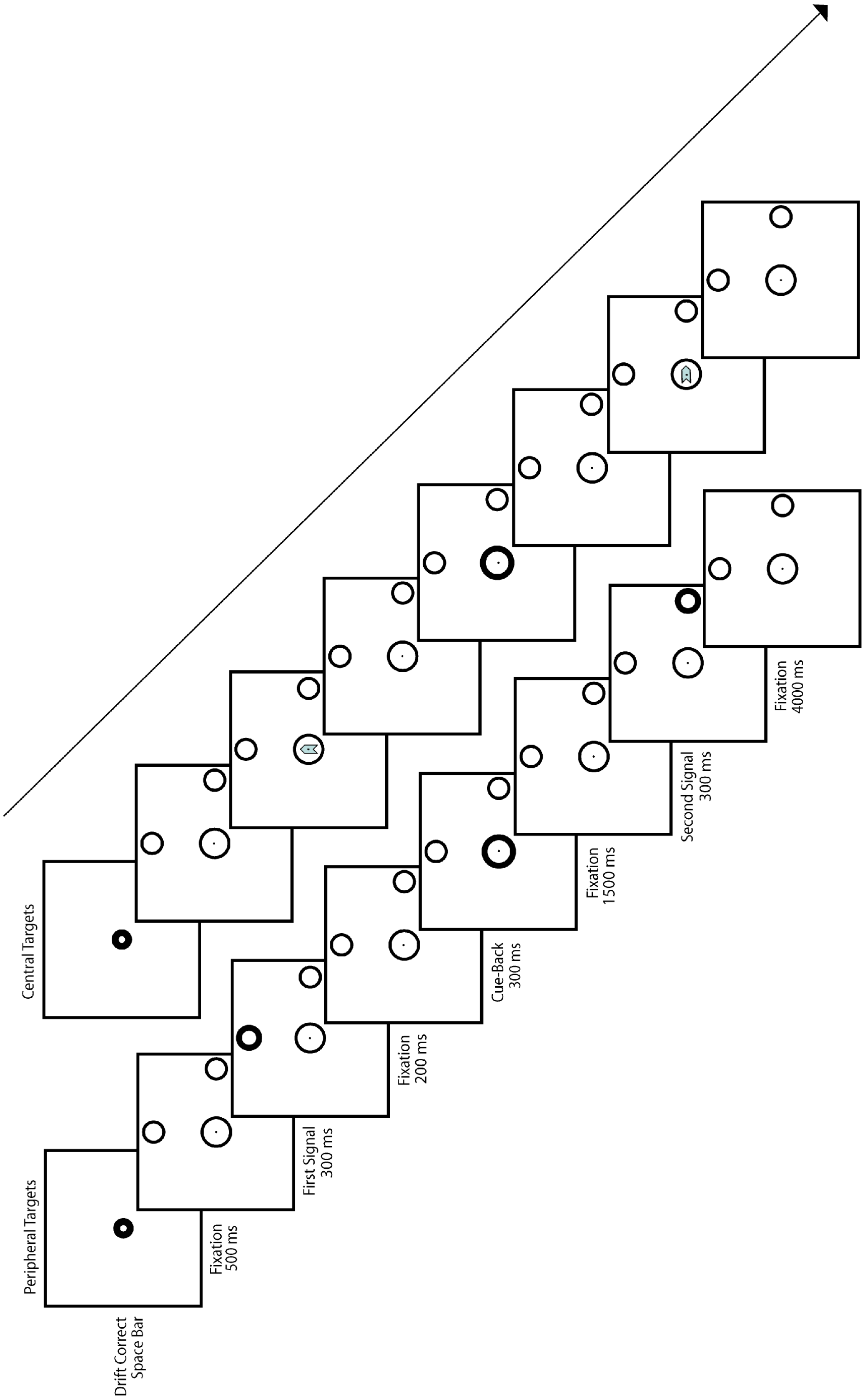
Participants. There were 21 participants (16 female, 5 male; mean age = 23.0) in E1. Participants were right-handed, had normal or corrected-to-normal vision, and reported no history of visual, motor, or neurological abnormalities.

Apparatus and Stimuli. Stimuli were displayed using Experiment Builder v1.3 software (SR Research, Osgoode, ON). Eye position was monitored (to ensure participants did not move their eyes during the trials) with an EyeLink II (SR Research, Osgoode, ON) eye-tracking system (sampling rate = 500 Hz; spatial precision < 0.01°;

spatial accuracy < 0.8° RMS error). Calibration of the EyeLink II was carried out in the same horizontal viewing plane that was used to display the target stimuli. Participants were seated at a viewing distance of approximately 58 cm from the screen.

Stimuli, depicted in Figure 5.1, consisted of a fixation circle 3.75 visual degrees in diameter that was surrounded by two peripheral placeholders (circles that were 2.5 visual degrees in diameter). Placeholders were spaced 6.0 visual degrees away from fixation (measured from the centre of fixation to the centre of the placeholder) and, on separate trials, were separated by angular offsets of either 90° or 180° (relative to central fixation); in other words, on each trial, placeholders were presented that occupied two of four possible positions: above, right of, below, or left of fixation. For two of the display configurations (horizontal and vertical), this created 0° and 180° offsets, while in the remaining four configurations (up–left [UL], up–right [UR], down–left [DL], and down–right [DR]), this created 0° and 90° offsets. These different configurations were randomly presented throughout the experiment, but the configuration was stable within any given trial. The arrangement of stimuli allowed participants to place their limb in a constant position at the start of each trial, where their index finger touched the central fixation point, while their forearm was aligned at a 45° angle, extending from the fixation point to the lower right corner of the screen. Because no stimuli were presented at a 45° offset, no target location was obscured by the participant's hand or arm. The outlines of the central fixation circle and peripheral placeholders were presented with a 4px weight on a 30-in. Elo touch screen monitor (Elo TouchSystems, Menlo Park, CA).

Figure 5.1. Example stimuli and sequence timing from a single trial in Experiments 1 and 2. Each trial began with a drift correction procedure that required the participants to press the space bar with their left hand while fixating within the fixation circle. The fixation array was then displayed for 500 ms, after which S1 was displayed for 300 ms. Following the offset of S1, fixation was displayed for 200 ms followed by a cue-back stimulus (change of the fixation circle outline from 4px to 8px weight) for 300 ms. The fixation array (with all circles in 4px weight) was again displayed for 1,500 ms, providing ample time for participants to return their arm to centre prior to the onset of S2. The S2 stimulus was added for 300 ms, followed again by an intertrial interval of 4 s during which the fixation array was displayed. Participants were instructed to maintain fixation throughout the trial. During each trial, participants were asked to make an arm movement to touch the centre of the signaled targets as quickly and accurately as possible and to return their arm to centre upon display of the cue-back, as well as after completing their S2 response. Reaction times were defined as the difference in time between the onset of the target stimulus and the time when the finger was lifted from the screen


Peripheral Targets
Drift Correct
Space Bar
Fixation
500 ms
First Signal
300 ms
Fixation
200 ms
Cue-Back
300 ms
Fixation
1500 ms
Second Signal
300 ms
Fixation
4000 ms
Central Targets

Procedure. On each trial, one of six different arrays (horizontal, vertical, UL, UR, DL, and DR) was presented. Each array was presented with equal probability (p = 0.167) in random order. During each trial, two consecutive signals (S1 and S2) were presented, where the border of a peripheral placeholder temporarily changed from a 4px line-weight to an 8px line-weight. Depending on the stimulus configuration, this permitted different angular offsets between S1 and S2 (0° was possible in all configurations, 90° was possible in the UL, UR, DL, and DR configurations, and 180° was possible in the horizontal and vertical configurations); the angular offset between consecutive movements was the independent variable of interest. Participants were instructed to make an arm movement (without an accompanying eye movement) to touch the target with the boldened outline. On any given trial, S1 and S2 could appear at either placeholder with equal probability (0.5), creating four possible response combinations within each of the six stimulus arrays. Participants practiced trials selected randomly from the main experiment until the successful completion of 8 consecutive trials. Participants were required to complete these trials without any error feedback, as described below. During the main experiment (following practice), each display configuration was shown 40 times, for a total of 240 trials; participants were given a short break after completing 120 trials.

The timing of stimuli within a single trial for E1 is shown in Figure 5.1 (see the left-hand sequence). If participants did not initiate a response within 1.5 seconds to S1 or S2, if they did not return their arm to centre between S1 and S2, or if they failed to maintain fixation, an error message was displayed, and the trial was aborted and was not recycled. Data from aborted trials were excluded from all subsequent analyses. Manual RTs were used as the dependent variable, as in previous IOR research, and were defined as the difference between the onset of the target stimulus and the time when the participants lifted their finger off of the screen.

Data Analysis. The description of data analyses here applies to both experiments in the present article. Trials with S2 RTs less than 100 ms (anticipation) or greater than 1,000 ms (miss) were flagged during data processing and excluded from all analyses. Consistent with previous work [39] data were also flagged and excluded if the S1 response was greater than 500 ms. Trials in which participants moved their arm to the wrong S2 target were flagged as directional errors. Directional error trials were eliminated from the main RT analysis but were tallied and analyzed to determine the possibility of speed–accuracy trade-offs. The frequency of aborted trials, anticipation, miss, and directional errors accounted for fewer than 5% of trials.

Mean RTs for S2 responses were analyzed using a repeated measures ANOVA ($\alpha = 0.05$) with the sole factor of offset (i.e., the angular offset between S1 and S2: 0°, 90°, or 180°). The frequency of directional error trials within each offset condition (0°, 90°, or 180°) was analyzed using a separate repeated measures ANOVA, again with the sole factor of offset. Mauchly's test was used to test the assumption of sphericity ($\alpha = 0.05$); if sphericity was violated, the Greenhouse–Geisser correction was applied, and adjusted degrees of freedom are reported. All offset conditions were compared using planned pairwise comparisons ($\alpha = 0.01$). Because our experimental design allowed us to assess IOR across different stimulus configurations, we analyzed 0° and 180° responses that were made when stimuli were stimulus configurations aligned in the vertical and horizontal axes separately. We further analyzed 0° and 90° responses within each of the possible 90° offset configurations (UL, UR, DL, DR).

5.3.2 Results

Errors. Error rates were calculated independently within each offset condition. Directional errors were minimal and accounted for 0.19%, 0.25%, and 0.12% of the total trials in the 0°, 90°, and 180° conditions, respectively. No significant difference was observed in the wrong-direction error rates between offset conditions, $F(2,40) = 1.21$, $p = 0.31$.

Reaction Time to S2. Manual RTs for 0°, 90°, and 180° offset conditions are shown in Figure 5.2. A main effect of offset was observed, $F(2,40) = 43.42$, $p < 0.001$. Pairwise comparisons revealed longer RTs for 0°, relative to 90°, $F(1,20) = 57.78$, $p < 0.001$, and 180°, $F(1, 20) = 40.21$, $p < 0.001$. RTs were significantly shorter for 90°, as compared with 180°, offsets, $F(1,20) = 12.1$, $p < 0.005$.

Zero-degree responses were significantly slower than 180° responses within both the horizontal, $F(1,20) = 31.53$, $p < .001$, and vertical, $F(1, 20) = 10.32$, $p < 0.005$, axes. Zero-degree responses were significantly slower than 90° responses within all 90° offset quadrants [UL, $F(1,20) = 28.7$, $p < 0.001$; UR, $F(1, 20) = 26.8$, $p < .001$; DL, $F(1, 20) = 31.8$, $p < 0.001$; and DR, $F(1,20) = 38.7$, $p < 0.001$].

5.3.3 Discussion

Consistent with previous research using peripheral signals [2,39] the results of E1 reveal an RT advantage for both 90° and 180°, relative to 0°, responses. As was expected, this result confirms that IOR can be extended to a target–target task requiring consecutive reaching responses (rather than button press responses; [39]), where participants point toward and touch the indicated target locations. Due to the use of peripheral stimuli in E1, the IOR observed in reaching movements could be due to inhibition operating at the level of sensory or motor processing. In E2, we therefore used central arrowhead stimuli to focus selectively on motor processing to determine whether a uniquely motor form of IOR can be observed for reaching movements [16,36,38,39,44].

5.4 Experiment 2: Central Targets

In E2, we extended the results of E1 by replacing the peripheral signals with central arrowhead signals. As was discussed in the general introduction, because responses to central arrowhead stimuli do not require participants to detect a visual stimulus in a potentially inhibited peripheral location, IOR observed with central arrowhead signals is considered the result of motor, rather than sensory-based, effects [16,36,38,39,44].

5.4.1 Method

Participants. There were 29 participants (19 female, 10 male; mean age = 22.4) in E2. The same exclusion criteria were used as in E1.

Apparatus Procedure and Data Analyses. The apparatus was identical to that used in E1. The procedure was identical to that in E1, except that arm movement signals on each trial consisted of two consecutive arrowhead stimuli presented at fixation, rather than two consecutive peripheral stimuli. The arrowhead stimuli were 3×1.5 visual degrees in size, which ensured that the ends of the arrow were large enough to be viewed, below the participant's finger at fixation. The sequence of stimuli and their respective timing are shown in Figure 5.1 (see right-hand sequence). The protocol for RT and error data analyses was equivalent between E1 and E2. Fewer than 5 % of trials were aborted due to a slow response, a failure to return the arm to centre between S1 and S2, or a failure to maintain fixation.

5.4.2 Results

Errors. Directional errors accounted for 0.98%, 0.5%, and 0.25% of the total trials in the 0°, 90°, and 180° conditions, respectively. A significant difference was observed in the wrong-direction error rates between offset conditions, F(2,58) = 7.1, $p < 0.005$. Pairwise comparisons revealed significantly more wrong-direction errors for 0°, relative to 180°, F(1, 28) = 15.34, $p < .001$, and the effect approached significance for 0°, relative to 90°, F(1, 28) = 3.8, $p = 0.06$. No difference was observed for the error rates between 90° and 180°, F(1, 28) = 2.9, $p = 0.1$, although the effect was marginal.

Reaction Times. Manual RTs for 0°, 90°, and 180° offset conditions are shown in Figure 5.2. A main effect of offset was observed, F(2,56) = 30.34, $p < 0.001$. Pairwise comparisons revealed longer RTs for 0°, relative to 90°, F(1,28) = 49.18, $p < 0.001$, and 180°, F(1,28) = 10.36, $p < 0.001$.

Zero-degree responses were significantly slower than 180° responses within both the horizontal, $F(1, 28) = 7.28$, $p < 0.01$, and vertical, $F(1, 28) = 9.06$, $p < 0.01$, axes. Zero-degree responses were significantly slower than 90° responses within all 90° offset quadrants [UL, $F(1, 28) = 38.0$, $p < 0.001$; UR, $F(1, 28) = 39.6$, $p < 0.001$; DL, $F(1, 28) = 23.4$, $p < 0.001$; DR, $F(1, 28) = 34.8$, $p < 0.0001$].

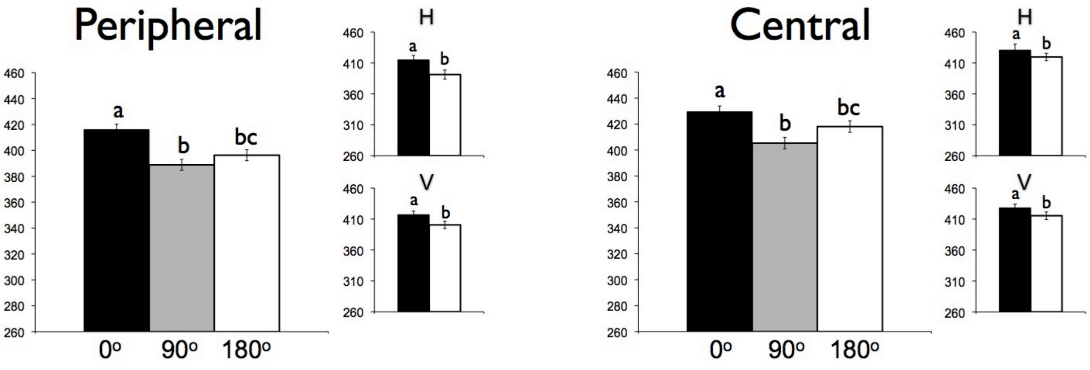


Figure 5.2. Manual reaction times to the second signal (S2) for Experiments 1 and 2 are presented on the Y axis with RTs for each offset condition (0°, 90°, and 180°) presented as separate bars. Experiment 1 is shown on the left; Experiment 2 is shown on the right. Conditions labelled with different letters (a, b, or c) are significantly different from each other. H stands for horizontal axis; V stands for vertical axis.

5.4.3 Discussion

We previously demonstrated a motor form of IOR for reaching movements in a target–target task using central arrowhead stimuli [9]; however, in that study, participants were provided with advance information about the direction of the required movements, which may have created a unique inhibitory effect due to the requirement to refrain from responding until an imperative stimulus was presented. In E2, using a traditional target–target reaching task in which participants responded at the onset of the central arrowhead stimuli, we observed clear evidence of motor IOR: Reaching RTs were longest for 0°, as compared with both 90° and 180°. Similar to E1, and consistent with our prior observations with both eye and arm movements [9], 90° RTs were shorter than both 0° and 180° RTs. These findings demonstrate that, unlike lateralized keypress manual responses [39], motor IOR can be observed in the reaching control system when responses are made to both the first and second target stimuli. These results therefore challenge the notion that the motor form of IOR is restricted to the oculomotor system [20,33,39,44].

If motor IOR can be revealed for reaching movements, why have previous studies that used superficially similar methods [e.g., 16,39] failed to detect it? As we proposed earlier, the lack of IOR observed by Fischer et al. [16] in their peripheral-cue/central-arrowhead-target experiments (conditions that have the potential to reveal motor IOR if it exists) could be accounted for if their use of a peripheral cue was insufficient to generate IOR within the upper limb motor system, perhaps because such stimuli do not automatically engage the preparation of reaching plans. Assuming that the generation of motor IOR relies on the prior engagement of a relevant motor program toward the cued location, one would not expect to observe IOR for arm movement responses to S2, unless a prior arm movement program was generated toward the S1 location. In other words, our results suggest that motor IOR affecting arm movement responses depends on the use of tasks that ensure the generation—and perhaps, execution—of arm movement programs to both the first and second target stimuli.

Taylor and Klein [39] required participants to press spatially congruent keys to indicate the targets indicated by consecutive central arrowhead stimuli, yet the results did not reveal IOR but, rather, facilitation: Keypress responses were, in fact, faster when preceded by the same keypress response, as compared with a different response. In Taylor and Klein's [39] study, participants used one finger for each response key and did not reach to the key from a common starting position. Moreover, the keys were on a keyboard that was spatially separated from the visual display. In short, the manual responses in the study were fundamentally different from actual reaching movements in which a single limb is used to reach from a starting location to touch the real location of a visual target. In other words, the results of the present study suggest that motor IOR in the upper limb control system depends on the use of a localization response that is directed toward the indicated location. This idea is not surprising, given that the analogous form of motor IOR for saccadic responses is typically revealed using saccadic localization responses directed toward the target location [20,30,32,39]. Indeed, a common interpretation of motor IOR within the oculomotor system is that motor IOR inhibits saccadic responses directed toward a location that was previously specified by an oculomotor program [22,28,39].

Notably, in E2, participants made significantly more wrong-direction errors when signaled to make an S2 response that was offset by 0° from S1. The increased number of wrong-direction errors for 0° S2s suggests that on some trials, participants preferentially responded toward the different (rather than same) target location when it was offset by 180°. Taken together with the delayed RTs for 0° responses, this pattern of errors is consistent with an IOR mechanism that decreases the efficiency of information processing [cf. 47] during the generation of motor programs toward the 0° location.

It is worth noting a potential bias in the 90° results reported in E1 and E2, arising from the unbalanced distribution of stimuli within the visual field. Specifically, in the 90° conditions, the placeholder stimuli create a net increase in visual stimulation within the visual quadrant in which the two possible reaching movements will occur. This alone could facilitate the programming of movements in the 90° conditions, particularly if one assumes that the preparatory state of the manual control system can be affected by the alignment of static visual stimuli (e.g., via some visuomotor transformation). However, this possibility seems unlikely, because we recently demonstrated shorter RTs for eye and arm movements offset by 90° in a target-target task when central, but not peripheral, stimuli were used and when the arrangement of stimuli was balanced across the visual field (by using four target locations arranged around fixation on all trials; [9]). Taken together, these results suggest that the shorter 90° RTs are a feature of motor-based inhibitory effects in target–target tasks.

5.5 General Discussion

By removing sensory effects associated with the use of peripheral stimuli in previous experiments [e.g., 4,19,21,29,32,37,42,45,46], as well as the preparatory interval given to participants by Cowper-Smith et al. [9], the results of our study allow us to confidently conclude that motor IOR can be implemented within the reaching control system and dismiss a popular view that motor IOR is restricted to the oculomotor system. This observation is important because it undermines two major pillars of existing IOR theories. First, observing motor IOR in the reaching system demonstrates that the mechanisms of IOR are not limited to sensory or oculomotor processes (a commonly held assumption; e.g., [5, 16,20,43,44]. Second, motor IOR in the reaching system is inconsistent with the presumed function of IOR as a visual search facilitator.

Specifically, while motor IOR might facilitate visual search when implemented within the oculomotor system, our result suggests that it might serve a more general function across a variety of motor systems that have little to do with search behavior. One possibility is that motor IOR exists to help prevent the motor system from falling into a cycle of repetition that might often be counterproductive for goal-directed action (e.g., if such repetition deterred the programming or execution of different movements). Another possibility, discussed below, is that motor IOR is merely an epiphenomenon arising from neural adaptation within motor control networks that encode movement direction in a distributed manner. While both possibilities can account for the presence of motor IOR in multiple motor systems, they are not incompatible with the idea that preventing the repetition of movements to old locations would support efficient searching behavior in the context of oculomotor systems [22,40,41].

It is noteworthy that RTs were shortest for responses offset by 90°, relative to both 0° and 180°, because such a pattern is consistent with the presence of neural adaptation within motor networks encoding direction in a distributed manner. Briefly, direction encoding units exhibit tuning profiles that are characterized by maximum neural firing rates in a preferred direction that decline to half-maximal rates for movements offset by approximately 90° [8]. Following the execution of an arm movement, neurons encoding the corresponding movement direction can become adapted or fatigued – that is, where their peak firing rates are temporarily reduced for subsequent movements in the same direction [cf. 8,14]. Assuming that a reduction in peak firing rates leads to a delay in the time taken to reach response threshold, movements that are made in the same direction as a previous movement (0°) will be slower than those made in the opposite direction (180°), with a graded influence for intermediate spatial offsets. Applying these principles to our task requirements allows relatively simple predictions to be made regarding the pattern of RTs expected. Before executing a response to S2, participants made two movements: one to the indicated S1 location and one 180° opposite in order to return to centre. Each movement will create maximal adaptation within neurons with preferred directions in the 0° and 180° directions and relatively less adaptation within neurons preferring directions in the 90° directions. Consequently, RTs should be shortest for S2 movements offset by 90° from the S1 movement.

If adaptation effects are present for both the 0° and 180° offset conditions, why are RTs nonetheless slower in the 0°, as compared with the 180°, condition? Notably, in E2, we observed evidence of an increased number of wrong direction errors in the 0°, as compared with 90° and 180°, offset condition. As was discussed earlier, this observation is consistent with an IOR mechanism that decreases the efficiency of information processing [47]; such a mechanism could be designed to promote reaching movements away from the previously signaled S1 location (i.e., toward the only unsignaled S2 location, whether offset by 90° or 180°). If adaptation effects and IOR are present concurrently, one would predict longer RTs for the 0° condition, as compared with both the 90° and 180° offset conditions (due to IOR), but, overall, the shortest 90° RTs (due to neural adaptation effects).

Whereas the type of IOR observed for cue-target tasks with peripheral stimuli is usually considered the result of sensory processes [16.38,39,44], our use of a (peripheral) target–target paradigm in E1 raises the possibility that sensory and motor-based effects are both possible. The spatial topography of sensory IOR has been described as monotonic in nature for cue-target offsets ranging between 0° and 180° [2], so the observation of non-monotonic IOR in our E1 (which was similar to the topography observed in E2) might suggest some motor-based contribution to the observed IOR.

5.5.1 Conclusion

The results of our study demonstrate that IOR affecting participant RTs can arise from motor-based effects outside of the oculomotor system. This observation suggests that motor IOR, while potentially useful in visual search behavior, likely arises from a general mechanism that can affect multiple motor systems.

5.6 Acknowledgements

This research was funded by NSHRF. Authors were supported by CIHR (C.D.C.-S. and D.A.W.), the Dalhousie Faculty of Medicine (G.E.), and NSERC (D.A.W.).

5.7 References

[1] R.S. Abrams, R.A., Dobkin, Inhibition of Return: Effects of Attentional Cueing on Eye Movement Latencies, J. Exp. Psychol. Hum. Percept. Perform. 20 (1994) 467–477.

[2] P.J. Bennett, J. Pratt, The spatial distribution of inhibition of return, Psychol. Sci. 12 (2001) 76–80.

[3] A. Berger, A. Henik, R. Rafal, Competition between endogenous and exogenous orienting of visual attention, J. Exp. Psychol. Gen. 134 (2005) 207–221.

[4] K.A. Briand, A.L. Larrison, A.B. Sereno, Inhibition of return in manual and saccadic response systems, Percept. Psychophys. 62 (2000) 1512–1524.

[5] A.B. Chica, R.M. Klein, R.D. Rafal, J.B. Hopfinger, Endogenous saccade preparation does not produce inhibition of return: failure to replicate Rafal, Calabresi, Brennan, and Sciolto (1989), J. Exp. Psychol. Hum. Percept. Perform. 36 (2010) 1193–206.

[6] A.B. Chica, J. Lupiáñez, P. Bartolomeo, Dissociating inhibition of return from endogenous orienting of spatial attention: Evidence from detection and discrimination tasks, Cogn. Neuropsychol. 23 (2006) 1015–34.

[7] A.B. Chica, T.L. Taylor, J. Lupiáñez, R.M. Klein, Two mechanisms underlying inhibition of return, Exp. Brain Res. 201 (2010) 25–35.

[8] C.D. Cowper-Smith, E.Y.Y. Lau, C. a Helmick, G.A. Eskes, D.A. Westwood, Neural coding of movement direction in the healthy human brain, PLoS One. 5 (2010) e13330.

[9] C.D. Cowper-Smith, G.A. Eskes, D.A. Westwood, Motor inhibition of return can affect prepared reaching movements, Neurosci. Lett. 541 (2013) 83–86.

[10] M. Desmurget, D. Pélisson, Y. Rossetti, C. Prablanc, From eye to hand: planning goal-directed movements, Neurosci. Biobehav. Rev. 22 (1998) 761–88.

[11] M.C. Dorris, T.L. Taylor, R.M. Klein, D.P. Munoz, Influence of previous visual stimulus or saccade on saccadic reaction times in monkey, J Neurophysiol. 81 (1999) 2429–2436.

[12] M.C. Dorris, R.M. Klein, S. Everling, D.P. Munoz, Contribution of the primate superior colliculus to inhibition of return., J. Cogn. Neurosci. 14 (2002) 1256–63.

[13] K.R. Dukewich, Reconceptualizing inhibition of return as habituation of the orienting response., Psychon. Bull. Rev. 16 (2009) 238–51.

[14] M. Eisenberg, L. Shmuelof, E. Vaadia, E. Zohary, Functional organization of human motor cortex: directional selectivity for movement, Life Sci. 30 (2010) 8897–8905.

[15] J.H. Fecteau, D.P. Munoz, Correlates of Capture of Attention and Inhibition of Return across Stages of Visual Processing, J. Cogn. Neurosci. 17 (2005) 1714–1727.

[16] M.H. Fischer, J. Pratt, S.F. Neggers, Inhibition of return and manual pointing movements, Percept. Psychophys. 65 (2003) 379–387.

[17] M.D. Hilchey, R.M. Klein, J. Ivanoff, Perceptual and motor inhibition of return: components or flavors? Atten. Percept. Psychophys. 74 (2012) 1416–29.

[18] M.D. Hilchey, J. Satel, J. Ivanoff, R.M. Klein, On the nature of the delayed "inhibitory" cueing effects generated by uninformative arrows at fixation, Psychon. Bull. Rev. (2013).

[19] S. Howard, LA, Lupiáñez, J, Tipper, Inhibition of Return in a Selective Reaching Task: An Investigation of Reference Frames, J. Gen. Psychol. 126 (1999) 421–442.

[20] A.R. Hunt, A. Kingstone, Inhibition of return: dissociating attentional and oculomotor components, J. Exp. Psychol. Hum. Percept. Perform. 29 (2003) 1068–1074.

[21] S. Khatoon, K. a Briand, A.B. Sereno, The role of response in spatial attention: direct versus indirect stimulus-response mappings, Vision Res. 42 (2002) 2693–708.

[22] R.M. Klein, W.J. MacInnes, Inhibition of return is a foraging facilitator in visual search, Psychol. Sci. 10 (1999) 346–352.

[23] G. Kuhn, A. Kingstone Look away! Eyes and arrows engage oculomotor responses automatically, 71 (2009) 314–327.

[24] J. Lupiáñez, Inhibition of return., in: H. Nobre, J.T. Coull (Eds.), Atten. Time, 2010: pp. 17–34.

[25] J. Lupiáñez, C. Decaix, E. Siéroff, S. Chokron, B. Milliken, P. Bartolomeo, Independent effects of endogenous and exogenous spatial cueing: inhibition of return at endogenously attended target locations., Exp. Brain Res. 159 (2004) 447–57.

[26] A. Marotta, J. Lupiáñez, M. Casagrande, Investigating hemispheric lateralization of reflexive attention to gaze and arrow cues, Brain Cogn. 80 (2012) 361–6.

[27] E. Martín-arévalo, A. Kingstone, J. Lupiáñez, Is "Inhibition of Return" due to the inhibition of the return of attention?, Q. J. Exp. Psychol. 66 (2013) 347–359.

[28] J.W. MacInnes, R.M. Klein, Inhibition of return biases orienting during the search of complex scenes, ScientificWorldJournal. 3 (2003) 75–86.

[29] H.F. Neyedli, T.N. Welsh, The processes of facilitation and inhibition in a cue-target paradigm: insight from movement trajectory deviations, Acta Psychol. (Amst). 139 (2012) 159–65.

[30] M.I. Posner, Y. Cohen, Components of visual orienting, in: H. Bouma & D.G. Bouwhuis (Eds.) Attention and performance X, Amsterdam: North-Holland, 1984, pp. 243-258.

[31] J. Posner, M I, Rafal, R D, Choate, L S, Vaughan, Inhibition of Return: Neural Basis and Function, Cogn. Neuropsychol. (1985) 211–228.

[32] J. Pratt, B. Neggers, Inhibition of return in single and dual tasks: Examining saccadic, keypress, and pointing responses, Percept. Psychophys. 70 (2008) 257–265.

[33] R.D. Rafal, P.A. Calabresi, C.W. Brennan, T.K. Sciolto, Saccade preparation inhibits reorienting to recently attended locations, J. Exp. Psychol. Hum. Percept. Perform. 15 (1989) 673–685.

[34] J. Ristic, A. Kingstone, Attention to arrows: pointing to a new direction, Q. J. Exp. Psychol. (Hove). 59 (2006) 1921–1930.

[35] J. Ristic, A. Wright, A. Kingstone, Attentional control and reflexive orienting to gaze and arrow cues, Psychon. Bull. Rev. 14 (2007) 964–969.

[36] J. Satel, Z. Wang, Investigating a two causes theory of inhibition of return, Exp. Brain Res. 223 (2012) 469–478.

[37] A.B. Sereno, C.B. Jeter, V. Pariyadath, K.. Briand, Dissociating sensory and motor components of inhibition of return, ScientificWorldJournal. 6 (2006) 862–887.

[38] T.L. Taylor, R.M. Klein, On the causes and effects of inhibition of return, Psychon. Bull. Rev. 5 (1998) 625–643.

[39] T.L. Taylor, R.M. Klein, Visual and motor effects in inhibition of return, J. Exp. Psychol. Hum. Percept, Perform. 26 (2000) 1639–1656.

[40] S.P. Tipper, B. Weaver, L.M. Jerreat, A.L. Burak, Object-based and environment-based inhibition of return of visual attention, J. Exp. Psychol. Hum. Percept. Perform. 20 (1994) 478–499.

[41] S.P. Tipper, B. Weaver, F.L. Watson, Inhibition of return to successively cued spatial locations: commentary on Pratt and Abrams (1995), J. Exp. Psychol. Hum. Percept. Perform. 22 (1996) 1289–1293.

[42] L. Tremblay, T.N. Welsh, D. Elliott, Between-trial inhibition and facilitation in goal-directed aiming: manual and spatial asymmetries, Exp. Brain Res. (2005).

[43] Z. Wang, R.M. Klein, Searching for inhibition of return in visual search: a review, Vision Res. 50 (2010) 220–8.

[44] Z. Wang, J. Satel, R.M. Klein, Sensory and motor mechanisms of oculomotor inhibition of return, Exp. Brain Res. 218 (2012) 441–53.

[45] T.N. Welsh, D. Elliot, Effects of response priming and inhibition on movement planning and execution, J. Mot. Behav. 36 (2004) 200–11.

[46] T.N. Welsh, J. Pratt, Inhibition of return in cue-target and target-target tasks, Exp. Brain Res. 174 (2006) 167–75.

[47] Y. Zhao, D. Heinke, J. Ivanoff, R.M. Klein, G.W. Humphreys, Two components in IOR: evidence for response bias and perceptual processing delays using the SAT methodology, Atten. Percept. Psychophys. 73 (2011) 2143–59.

CHAPTER 6: CONSECUTIVE EYE MOVEMENTS ARE AFFECTED BY INHIBITION OF RETURN AND MOTOR ADAPTATION EFFECTS

C.D. Cowper-Smith, D.A. Westwood, Consecutive eye movements are affected by inhibition of return and motor adaptation effects. Manuscript in preparation for publication.

6.1 Abstract

Inhibition of return (IOR) refers to a response bias where RTs are slower for previously signaled compared to unsignaled locations. The phenomenon is routinely demonstrated through an analysis of reaction times across two target locations aligned in the horizontal axis. In two experiments requiring consecutive saccadic responses offset by 0°, 90°, or 180° to peripheral (E1) and central (E2) stimuli, we show different patterns of RTs as a function the angular offset between movements. In E1, we demonstrate the well-established pattern of RTs associated with IOR. In E2, we demonstrate a unique pattern of RTs that is predicted by a combination of IOR and neural adaptation effects in direction encoding neurons found throughout the oculomotor system. The results demonstrate the importance of examining RTs across more than two target locations in the IOR paradigm (in particular when central signals are used) and suggests previous work may have missed key data points regarding the nature of reported response biases.

6.2 Introduction

During visual search, it is normal to execute several saccadic eye movements in sequence to ultimately identify and fixate an object of interest [1,2]. To promote efficiency, visual search function is thought to rely (in part) on inhibitory tags that discourage eye movements to previously inspected locations [1–4]. This inhibitory tagging system is best known as inhibition of return (IOR).

Inhibition of return has been extensively characterized in the cue-target task [5–15]. In the basic IOR task, three placeholder stimuli are aligned equidistant on the horizontal axis. Participants are instructed to maintain fixation within the central placeholder while a non-predictive cue is presented that either points at or appears within one of the flanking placeholders. Shortly thereafter, a target stimulus is presented and a saccadic localization or spatially congruent button press is required in response to the indicated target. In the target-target variant of the task, responses are required to both signals on each trial. Regardless of which task is used, when reaction times (RTs) are slower at previously signaled compared to unsignaled locations, investigators tend to loosely label the effect as IOR (for different views on the appropriate use of the term, see [16–18]).

Depending on the nature of the signals used, when saccadic responses are required, two forms of IOR can emerge: one that slows the detection of spatially localized sensory information and another that slows the generation of oculomotor responses [6,13,14,16,19–21]. When consecutive peripheral stimuli are used, IOR can slow both the detection of sensory information occurring at the inhibited peripheral location or the generation of the required saccadic response [16,22]. Notably, when consecutive saccadic responses are required to peripheral stimuli, both forms of IOR appear to additively slow responses [16,19][19]; however, when central stimuli are used, only the motor form of IOR associated with the inhibition of consecutive responses is revealed [6,14,16,19–21].

---

[19] The magnitude of IOR observed in the target-target task with peripheral stimuli is approximately double that observed in the cue-target task. Moreover, the magnitude observed with peripheral stimuli is approximately double that observed with central stimuli in the target-target task [16,19]. These observations suggest that the sensory/attentional and motor forms of IOR are additive and both affect consecutive saccadic responses made to peripheral stimuli.

While most studies of IOR have relied on the use of two target locations aligned on either side of central fixation (i.e., at a 180° angular offset) [6,12–14,16,19,20,23–25], others have examined reaction times across a broader range of spatial offsets, finding that RTs are slowest at the previously signaled location and monotonically decrease as the spatial offset between cue and target increases from 0° to 180° (0°>90°>/=180°) [1–3,5,7–9,11,16,26–28]. Importantly however, with only one exception (discussed below), studies looking at the spatial distribution of IOR have relied upon the use of peripheral and not central target stimuli. As a result, the monotonic pattern of RTs thought to be characteristic of IOR has only been established when sensory/attentional effects are likely.

To our knowledge, only one study has looked at the spatial distribution of RTs when consecutive eye movements are required to central rather than peripheral stimuli [29]. Using the target-target variant of the IOR task and four target locations offset in 90° increments, Cowper-Smith et al. [29], demonstrated distinct patterns of RTs as a function of signal type (central or peripheral), for both consecutive eye and arm movements. Consistent with previous studies, when peripheral signals were used, the hallmark pattern of IOR was observed (RTs follow the pattern: 0°>90°>/=180°) [1–3,5,7–9,11,16,26–28]. However, when central signals were used, a "U" shaped pattern of RTs was observed where 0° and 180° responses did not differ, while 90° responses were comparatively faster (0°>90<180°, 0°=180°) [29].

Cowper-Smith et al. [29], speculated that the "U" shaped pattern of RTs observed with central signals may be consistent with directionally selective adaptation effects in populations of neurons encoding movement direction [30–42]. Like the reaching control system, the direction of saccadic eye movements are controlled by populations of directionally tuned neurons found throughout the oculomotor system. Neurons encoding saccade direction are found within the superior colliculus (SC) [40,42], supplementary eye fields (SEF), and frontal eye fields (FEF) [38–42] each of which are critically involved in the generation of saccadic eye movements [43]. Similar direction-encoding neurons are observed in regions of the parietal [31–33] and prefrontal [30] cortex, within regions heavily interconnected with the SC, SEF, and FEF. The tuning profiles of direction-encoding units within the saccadic eye movement system exhibit maximal firing rates in their preferred direction (PD), decline to half-maximal rates for movements offset by 30° to 90° from the PD, and exhibit minimum firing rates 180° opposite [40–42,44][20]. As a consequence of a single eye movement, current evidence suggests that neurons encoding the associated movement direction may become adapted or fatigued (i.e. exhibit reduced peak firing rates for subsequent movements in the same direction; [45,46]). If this is the case, then assuming a reduction in firing rates can delay the time taken to reach response threshold [47,48], subsequent movements in the same direction may be delayed as a consequence of neural adaptation.

In target-target IOR tasks such as that used presently [cf. 14,16,19,29], participants are required to make consecutive saccadic responses, starting from a

---

[20] Populations of direction encoding neurons with similar tuning profiles are found in the neural substrates controlling both reaching and eye movements.

central location and moving to a peripherally marked location, in response to both a first and second signal (S1 and S2 respectively). In order to make both responses from a common starting location, following the response to S1, participants are required to return their eyes to centre. Therefore, *prior* to the execution of the S2 response, participants make two eye movements: one to the indicated S1 location and one 180° opposite (in order to return their eyes to centre). If both of these movement directions are affected by neural adaptation when S2 is presented, then RTs for S2s offset by either 0° or 180° should be delayed. However, because of the shape of the tuning functions in direction encoding units, firing rates are diminished by half at a 90° offset from the PD; consequently, a relatively distinct population of neurons is responsible for movements made at a 90° offset from the first movement. Correspondingly, neural adaptation would minimally affect S2 movements offset by 90°.

Based on the neurophysiological properties of direction-encoding neurons outlined above, and assuming adaptation effects can result in a delay to reach response threshold [47,48], it is possible to make relatively simple predictions regarding the topography of RTs expected for consecutive eye or arm movements made with various spatial offsets: S2 saccadic responses that are offset by 90° from the S1 response should exhibit faster RTs compared to responses that are offset by 0° or 180°. As such, Cowper-Smith et al. [29] suggested that adaptation effects may underpin the “U” shaped pattern of RTs (0°>90°<180°; 0°=180°) they observed when central signals prompted consecutive saccadic or manual localization responses[21].

That Cowper-Smith et al. [29], observed no difference between 0° and 180° RTs when central signals were used was inconsistent with prior work demonstrating IOR for saccadic responses in the target-target task when two targets (presented on either side of fixation) were possible on each trial [14,16,19]. However, when RTs were analyzed within the horizontal and vertical axis separately, Cowper-Smith et al. [29], found evidence of IOR in the horizontal (thus replicating prior 2-target studies; [14,16,19]) but not vertical axis for eye movements. By contrast, no evidence of IOR was observed in either axis for manual localization responses. This result might suggest that an oculomotor form of IOR operates only within the horizontal but not vertical axis when consecutive saccadic responses are required to central stimuli, e.g., to aid in reading or scanning the horizontal meridian [29]. Most importantly, for eye movements, it is possible that the simple failure to observe IOR in the vertical axis explains the "U" shaped pattern of results observed by Cowper-Smith et al. [49], rather than the proposed adaptation-based effects.

In a follow up study of consecutive *reaching* movements, Cowper-Smith and Westwood [49] revealed IOR in both the horizontal and vertical axis when two [49] rather than four [29] target locations were possible on each trial. Moreover, when only

---

[21] This explanation would apply to tasks in which the eye movements are instructed by central signals and which therefore eliminate a contribution from sensory/attentional IOR. As discussed earlier, previous studies reveal that when peripheral stimuli are used, IOR exhibits a different pattern of RTs (0°>90°>/=180°) from that predicted by motor adaptation (0°>90°<180°).

two targets were used on each trial, a unique pattern of RTs was observed (0°>90°<180°, 0°>180°) suggesting the presence of *both* IOR (overall slowest 0° RTs) and adaptation-based effects (overall fastest 90° RTs). These results demonstrate that set size (i.e., the number of possible targets on each trial) can change the pattern of RTs observed for consecutive reaching movements in the target-target task. As such, similar to the pattern of results observed for consecutive reaching movements [29,49], it is possible that a combination of IOR and adaptation-based effects can be observed with saccadic eye movements when two but not four targets are used, provided 90° as well as 0° and 180° spatial offsets are examined. If this is the case, it would highlight the importance of examining a broader range of spatial offsets than the 0° and 180° offsets commonly used to study oculomotor IOR in the centre-out task [14,16,19].

The present study was designed to investigate whether evidence of both IOR and adaptation can be observed for consecutive eye movements in the commonly used target-target task. In order to optimize the chances of observing oculomotor IOR, which is usually studied with two rather than four target locations [cf. 49], and consistent with the traditional IOR paradigm, only two rather than four target locations were presented on each trial. However, unlike the traditional IOR paradigm, on separate trials the two target locations could be offset by 180° in either the horizontal or vertical axis, or alternatively, the two target locations could be offset by 90° in any of four possible quadrants. These stimulus configurations replicated those used by Cowper-Smith and Westwood [49] and allowed us to simultaneously test for IOR (which should result in overall slowest 0° responses), and adaptation (which should result in overall fastest 90°

responses). Finally, in order to directly compare the pattern of results when two rather than four target locations were used on each trial, the methods were otherwise identical to those used by Cowper-Smith et al. [29].

If both IOR and adaptation-based effects can affect consecutive oculomotor responses to central stimuli when set size is reduced from four to two, a 'blended' pattern of RTs should be observed (0°>90°<180°; 0°>180°), where 0° responses will be slower than both 90° and 180° responses (owing to IOR based effects), while 90° responses will be overall fastest (owing to adaptation-based effects). This pattern of results (0°>90°<180°; 0°>180°) would be clearly distinct from the typical pattern of IOR observed with peripheral signals (0°>90°>/=180°) and from that previously observed in the target-target task with four target locations (0°>90°<180°; 0°=180°). Finally, the introduction of IOR for saccadic responses to central stimuli should slow 0° responses and therefore increase the magnitude of the RT difference between 0°-90° and 0°-180°. However, given that there is no reason to suspect the magnitude of adaptation effects should change as a function of set size, there should be no change in the magnitude of the 90°-180° RT difference when two versus four targets are used on each trial. The results of the present study, together with a direct comparison to the results of Cowper-Smith et al. [29] support these predictions and therefore suggest that multiple response biases (IOR and adaptation) can affect consecutive eye movements made to central stimuli in the target-target task.

6.3 Experiment 1: Peripheral 2 Target – Eye

In E1, peripheral targets were used and consistent with a wealth of prior studies, we expected to observe the well-established pattern of RTs (0°>90°>/=180°) associated with sensory/attentional IOR. Furthermore, because IOR was observed for saccadic responses to peripheral (but not central) stimuli by Cowper-Smith et al. [29], and consistent with work demonstrating that the magnitude of IOR is insensitive to set size when peripheral signals are used [26], unlike E2, we did not predict an increased magnitude of IOR in E1 when set size was two rather than four [29].

6.3.1 Method

Participants. Seventeen undergraduate students (11 Female, 6 male; mean age = 20.5) were recruited through the Department of Psychology subject pool at Dalhousie University. Participants were right-handed, had normal or corrected-to-normal vision, and reported no history of visual, motor, or neurological abnormalities.

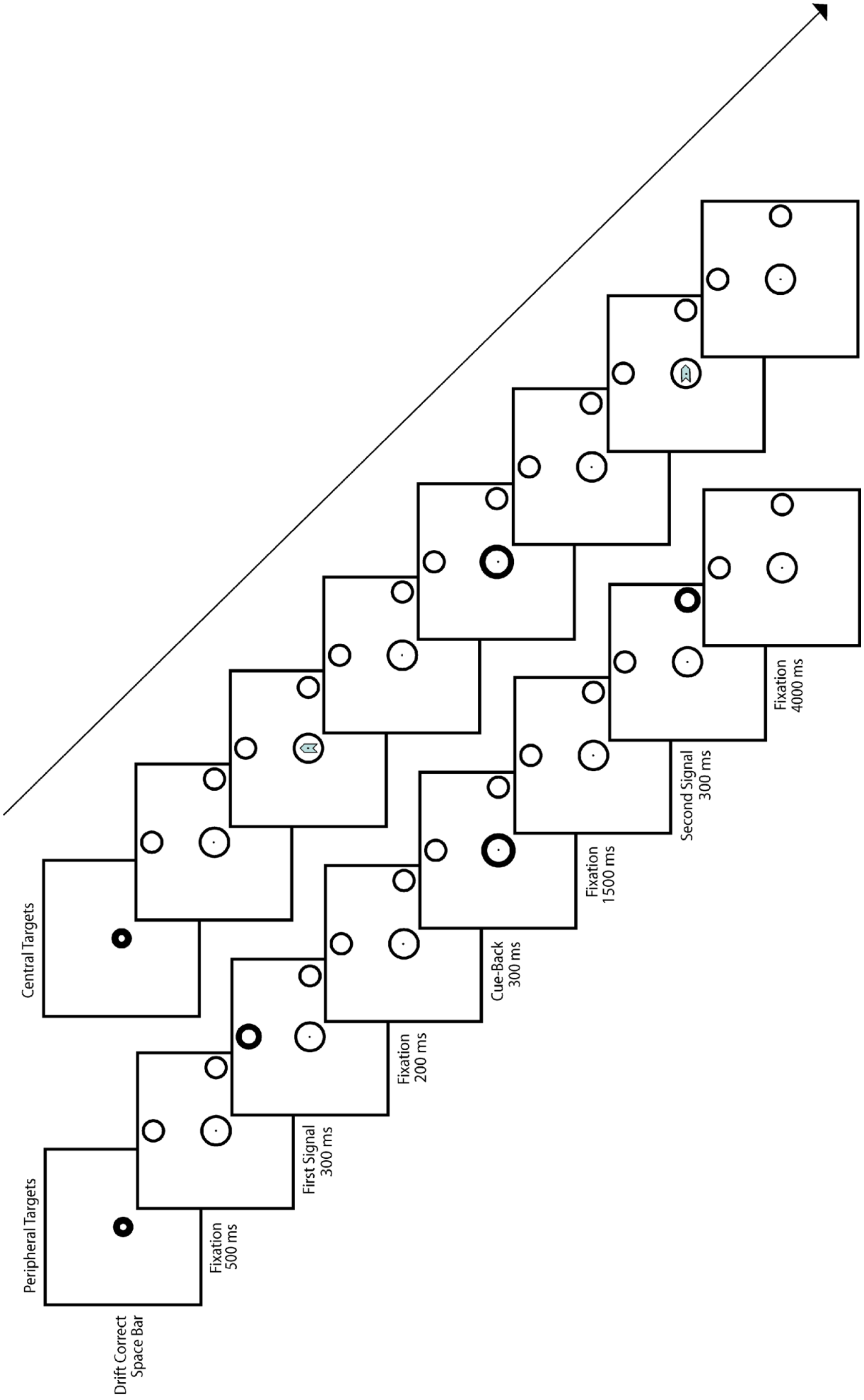
Apparatus and Stimuli. The apparatus was identical to that used by both Cowper-Smith and Westwood [49] as well as Cowper-Smith et al. [29]. In order to have all possible pairings of two targets in the up, down, left and right locations, six two-place holder arrays were constructed. Only one of these arrays was shown on each trial. For two of the display configurations (horizontal and vertical), this created 0° and 180° offsets, while in the remaining 4 configurations (UL, UR, DL, DR), this created 0° and 90° offsets.

Procedure. The procedure was identical to that used by Cowper-Smith and Westwood [49]. Each array was presented with equal probability ($p = 0.167$) in random order. On any given trial, S1 and S2 could point to either placeholder with equal probability (0.5), creating 4 possible response combinations within each of the 6 stimulus arrays. Each display configuration was shown 20 times for a total of 120 trials.

Data Analyses. The protocol for RT and error data analyses was the same as that used by Cowper-Smith and Westwood [49] as well as Cowper-Smith et al. [49]. Trials with S2 RTs less than 100 ms (anticipation) or greater than 1,000 ms (miss) were flagged during data processing and excluded from all analyses. Consistent with previous work [39] data were also flagged and excluded if the S1 response was greater than 500 ms. Trials in which participants moved their eyes to the wrong S2 target were flagged as directional errors. Directional error trials were eliminated from the main RT analysis but were tallied and analyzed to determine the possibility of speed–accuracy trade-offs. The frequency of aborted trials, anticipation, miss, and directional errors accounted for fewer than 5% of trials.

Mean RTs for S2 responses were analyzed using a repeated measures ANOVA ($\alpha = 0.05$) with the sole factor of offset (i.e., the angular offset between S1 and S2: 0°, 90°, or 180°). The frequency of directional error trials within each offset condition (0°, 90°, or 180°) was analyzed using a separate repeated measures ANOVA, again with the sole factor of offset. Mauchly's test was used to test the assumption of sphericity ($\alpha = 0.05$); if sphericity was violated, the Greenhouse–Geisser correction was applied, and adjusted degrees of freedom are reported. All offset conditions were compared using planned pairwise comparisons ($\alpha = 0.01$). In order to explore whether IOR occurred within both the vertical and horizontal axis, we separately analyzed 0° and 180° responses when stimulus configurations were aligned in the vertical and horizontal. We further analyzed 0° and 90° responses within each of the possible 90° offset configurations (UL, UR, DL, DR). Finally, in order to compare the magnitude or RT differences across previously signaled versus unsignaled locations as a function of set size, we conducted a 2x3 mixed ANOVA with factors of set size (two or four) and offset-magnitude (where the magnitude of RT differences was calculated separately as 0°- 90°, 0° - 180°, and 90°-180°). For the purpose of this analysis, four-target data was obtained from Experiment 1 of Cowper-Smith et al. [29] (peripheral target-eye movement condition).

Figure 6.1. Example stimuli and sequence timing from a single trial in Experiments 1 and 2. Each trial began with a drift correction procedure that required the participants to press the space bar with their left hand while fixating within the fixation circle. The fixation array was then displayed for 500 ms, after which S1 was displayed for 300 ms. Following the offset of S1, fixation was displayed for 200 ms followed by a cue-back stimulus (change of the fixation circle outline from 4px to 8px weight) for 300 ms. The fixation array (with all circles in 4px weight) was again displayed for 1,500 ms, providing ample time for participants to return their arm to centre prior to the onset of S2. The S2 stimulus was added for 300 ms, followed again by an intertrial interval of 4 s during which the fixation array was displayed. Participants were instructed to maintain fixation throughout the trial. During each trial, participants were asked to make an arm movement to touch the centre of the signaled targets as quickly and accurately as possible and to return their arm to centre upon display of the cue-back, as well as after completing their S2 response. Reaction times were defined as the difference in time between the onset of the target stimulus and the time when the finger was lifted from the screen


Peripheral Targets
Central Targets
Drift Correct
Space Bar
Fixation
500 ms
First Signal
300 ms
Fixation
200 ms
Cue-Back
300 ms
Fixation
1500 ms
Second Signal
300 ms
Fixation
4000 ms

6.3.2 Results

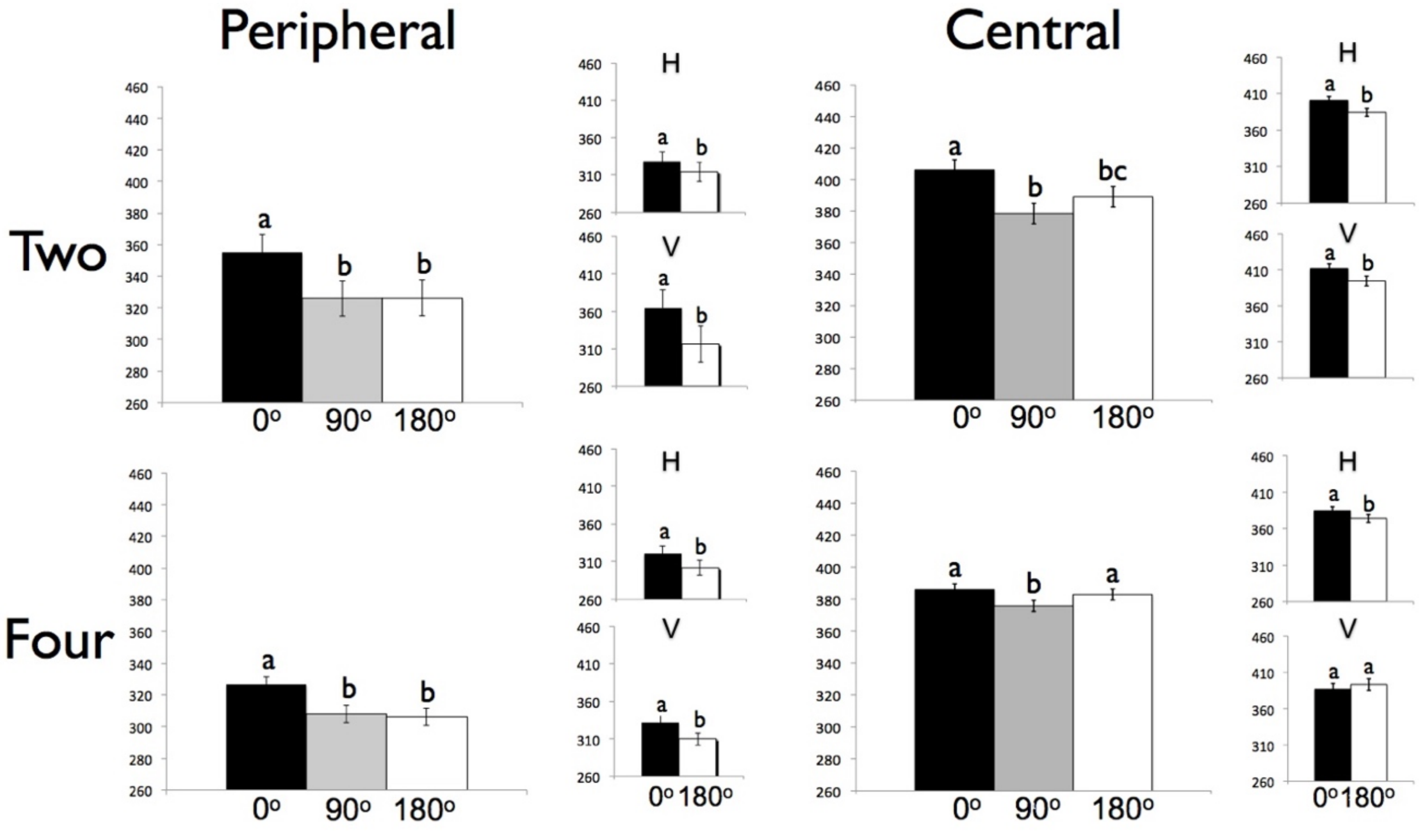
Errors. An average of 2.3% (range = 0-6.6%, SD = 2.2%) of trials of were classified as anticipations (RT < 100ms following S2 onset), and 2.5% (range = 0-5.8%, SD = 1.6%) as misses (RT > 1000ms following S2 onset); these trials were removed from subsequent analyses. Participants made directional errors to S2 on an average of 2.01% (range = 0-3.3%, SD = 1.0%) of the total trials; of these trials, 1.00% (range = 0-2.1%, SD = 0.7%), 0.76% (range = 0-2.1%, SD = 0.7%), and 0.25% (range = 0-1.3%, SD = 0.4%) were made in the 0°, 90° and 180° conditions respectively. Because error rates were 1% or less in each offset condition, they were not analyzed further.

Saccadic Reaction Time to S2. Reaction times for 0°, 90°, and 180° offset conditions are shown in Figure 6.2 ("Two Target-Peripheral"). A main effect of offset was observed, F(2,32) = 8.46, $p < 0.001$. Pairwise comparisons revealed slower RTs for 0° relative to 90°, F(1,16) = 17.95, $p < 0.001$ and 180° F(1,16) = 13.89, $p < 0.005$ responses. Slower 0° compared to 180° responses were observed in both the horizontal F(1,16) = 8.38, $p < 0.05$ and vertical axes F(1,16) = 7.47, $p < 0.05$. Reaction times were not significantly different between 90° and 180° offsets, F(1,16) = 0.001, $p = 0.97$. No differences in the magnitude of S2 RTs were observed between any of the possible 90° offset combinations (UL, UR, LR, LL), F(1,21) = 0.46, $p = 0.71$, indicating that the overall faster RTs for the 90° offset condition were not driven by responses within one of the four 90° arrays.

In E1, there were 6 different stimulus configurations that were equally likely on any given trial: two 180° configurations and four 90° configurations. Given these configurations, it is possible that the 180° configurations could involve a requirement for broader attentional processing that 90° configurations thereby altering participant RTs [50]. If 0° RTs were systematically altered between the 180° and 90° configurations, it is possible that the overall pattern topography of IOR observed is biased in favour of one of these configuration types. To assess this possibility, we therefore compared the average 0° RTs between the 180° and 90° configurations in E1; no difference was observed between 0° RTs in either configuration, $F(1,16) = 1.45$, $p = 0.25$.

In order to examine possible differences in the magnitude of RT effects observed between Cowper-Smith et al. [29] (peripheral target-eye movement condition) and E1, we conducted a 2x3 mixed ANOVA with factors of set size (two or four) and offset-magnitude (calculated as the difference between 0°-90°, 0°-180°, and 90°-180° RTs). A main effect of offset-magnitude, $F(2,32) = 11.85$, $p < 0.001$ was observed; however, as expected, no main effect of set size, $F(1,16) = 1.16$, $p = 0.30$ and no interaction between set size and offset-magnitude was observed, $F(2,32) = 0.57$, $p = 0.57$.

Figure 6.2. Saccadic reaction times for responses to the second signal (S2) in each offset condition (0°, 90°, and 180°). Results for E1 and E2 are presented in the top row ("Two" target experiments). For convenience, results from Cowper-Smith et al. [29] *are reproduced in the bottom row ("Four" target experiments). Within-subjects 95% confidence intervals were generated as described by Masson [11] using the Offset × Subject MSE term.*


Peripheral
Central
Two
Four
H
V
460
440
420
400
380
360
340
320
300
280
260
410
310
a
b
bc
0°
90°
180°
0° 180°

6.3.3 Discussion

As expected, the results of E1 replicate the well-established pattern of sensory/attentional IOR (0°>90°>/=180°) and by comparison to the results of Cowper-Smith et al. [29] demonstrate that the magnitude IOR effects in the target-target task are insensitive to set size when peripheral signals are used [cf. 18]. These data provide an important baseline against which to compare the pattern of results expected in E2.

6.4 Experiment 2: Central 2 Target – Eye

Experiment 2 replicated E1 but used central signals in order to eliminate the presence sensory/attentional IOR that is associated with the use of peripheral stimuli [1,2,5–11]. Under these task circumstances, when four rather than two targets were presented on each trial, Cowper-Smith et al. [29] reported IOR in the horizontal but not vertical axis. However, previous work in our lab focused on reaching movements suggested that by changing set size from four [29] to two [49], IOR may be emerge within *both* the horizontal and vertical axes. This observation suggested that unlike the cue-target task [26], IOR effects may be increased in the target-target task when two rather than four target locations are presented on each trial.

In E2, we therefore predicted a blended pattern of IOR and adaptation-based effects (0°>90°<180°; 0°>180°) where IOR would slow 0° relative to 90° and 180° RTs, while adaptation effects would slow 180° relative to 90° RTs. More specifically, if IOR effects are introduced to the pattern of RTs predicted by neural adaptation (0°>90°<180°; 0°=180°) when set size is changed from four to two, the difference in RTs between 0-180° and 0°-90° should increase due inhibition of the 0° target location. By contrast, because adaptation effects are considered a by-product of movement direction encoding which should be insensitive to the number of target locations, the magnitude of the RT difference between 90°-180° should be equivalent across different set sizes.

6.4.1 Method

Participants. Twenty-two (18 female, 4 male; mean age = 19.8) undergraduate students were recruited through the Department of Psychology subject pool at Dalhousie University. The same exclusion criteria were used as in E1.

Apparatus and Stimuli. The apparatus was identical to that used in E1. As in E1, all six possible two-target arrays were created from the 4-target array used by Cowper-Smith et al. [29]: one vertical, one horizontal, and four 90° arrays (UR, LR, LL, UL).

Procedure and Data Analyses. The procedure was identical to E1 except that central rather than peripheral movement signals were used. The protocol for RT and error data analyses were equivalent between E1 and E2. Less than 5% of trials were aborted due to a slow response, a failure to return their eyes to centre between S1 and S2, or a failure to maintain fixation.

6.4.2 Results

Errors. An average of 2.1% (range = 0-7.5%, SD = 1.9%) of trials were classified as anticipations (RT < 100ms following S2 onset), and 0.6% (range = 0-2.1%, SD = 0.8%) as misses (RT > 1000ms following S2 onset); these trials were removed from subsequent analyses. Participants made directional errors to S2 on an average of 5.6% (range = 0-

12.9%, SD = 2.8%) of the total trials; of these trials, 4.98% (range = 0-7.1%, SD = 2.2%), 0.42% (range = 0-3.8%, SD = 0.8%), and 0.19% (range = 0-2.1%, SD = 0.5%) were made in the 0°, 90°, and 180° conditions respectively. A significant difference was observed in the directional error rates between offset conditions, $F(2,42) = 211.83$, $p < 0.001$. Pairwise comparisons revealed significantly more directional errors for 0° compared to 180°, $F(1,21) = 242.82$, $p < 0.001$ and 0° compared to 90°, $F(1,16) = 208.31$, $p < 0.001$. No difference was observed between 90° and 180°, although the effect verged on significance $F(1,16) = 4.1$, $p = 0.056$.

Saccadic Reaction Times. Reaction times for 0°, 90°, and 180° offset conditions are shown in Figure 6.2 ("Two Target-Central"). As in Cowper-Smith et al. [29] (central-eye condition), RTs for the 0° offset trials were greater than 90° offset trials, $F(1,21) = 71.6$, $p < 0.001$. However, unlike Cowper-Smith et al. [29] (central-eye condition), RTs were greater for 0° compared to 180° offsets, $F(1,21) = 31.86$, $p < 0.001$. Furthermore, 0° RTs were slower than 180° RTs in *both* the horizontal, $F\ (1,21) = 17.7$, $p < 0.001$ and vertical, $F\ (1,21) = 12.8$, $p < 0.002$ axes. As expected, 180° offsets were slower than 90° offsets $F(1,21) = 14.5$, $p < 0.001$.

Confirming similar RT effects independent of stimulus configuration, no difference was observed between the average 0° RTs taken from the 180° and 90° configurations, $F(1,21) = 0.03$, $p = 0.87$. Furthermore, no differences in the magnitude of S2 RTs were observed between any of the possible 90° offset combinations (UL, UR, LR, LL), $F(1,21) = 2.54$, $p = 0.065$, indicating that the overall faster RTs for the 90° offset condition were not driven by a specific combination of first and second saccade directions.

In order to compare the magnitudes of RT differences between Cowper-Smith et al. [29] (central target-eye movement condition) and E2, we conducted a 2x3 mixed ANOVA with factors of set size (two or four) and offset-magnitude (0°-90°, 0°-180°, and 90°-180°). A significant main effect of offset-magnitude, $F(2,32) = 40.82$, $p < 0.001$ but not set size, $F(1,19) = 16.73$, $p < 0.001$ was observed. A significant interaction between set size and offset-magnitude was observed, $F(2,36) = 5.65$, $p = 0.015$. As predicted, pairwise comparisons revealed that the magnitude of the 0°-90° ($F(1,19) =16.94$, $p < 0.001$) and 0°-180° ($F(1,19) =8.92$, $p < 0.01$) differences were significantly larger when two rather than four targets were presented on each trial. Finally, the magnitude of the 90°-180° difference did not change as a function of set size, $F(1,19) = 0.297$, $p = 0.59$.

6.4.3 Discussion

Consistent with our prediction and the introduction or magnification of IOR effects when set size is changed from four to two, the results of E2 revealed: (1) a significant IOR effect in both the horizontal and vertical axes and (2) an increased magnitude of the RT difference between 0°-90° and 0°-180° as set size was decreased from four to two. Furthermore, and consistent with the expectation that adaptation-based effects should remain constant regardless of whether four [29] or two targets were used on each trial, the magnitude of the 90°-180° difference did not change as a function of set size. Together, these changes results in a ‘blended’ pattern of RTs

(0°>90°<180°; 0°>180°) that can be explained by a combination of IOR and adaptation effects.

Notably, the presence of IOR when set size is changed from four to two might be the consequence of altered participant strategies; participants made significantly more directional errors for 0° relative to 90° and 180° offset conditions in E2. By contrast, no difference in directional error rates was observed between offset conditions when four targets were presented on each trial [29], and error rates were overall less than 1% in each offset condition in E1 (which therefore did not justify an analysis of possible differences [cf. 26]). This finding suggests that, in E2, participants employed a response strategy for S2s where they preferentially generated motor programs toward the only different (90° or 180° offset) rather than same (0°) target location indicated by S1.

6.5 General Discussion

The purpose of the present study was examine whether multiple response biases (IOR and adaptation) can influence RTs when consecutive saccades are executed in the target-target task. When peripheral stimuli were used, we observed the well-established pattern of monotonically declining RTs (0°>90°>/=180°) associated with sensory/attentional IOR. By contrast, when central signals were used, we observed slower 0° relative to 90° and 180° responses (predicted by IOR), but overall fastest 90° responses (predicted by adaptation effects; 0°>90°<180°; 0°>180). Taken together, these results demonstrate different patterns of RTs as a function of signal type, despite a requirement to make metrically identical saccadic responses in both E1 and E2.

Using four target locations, Cowper-Smith et al. previously demonstrated a "U" shaped pattern of RTs when central signals were used to prompt consecutive saccadic or reaching localization responses. Interestingly, when they analyzed RTs in the horizontal and vertical axes separately, saccadic responses exhibited IOR in the horizontal but *not* vertical axis; by contrast, reaching responses did not reveal IOR in either axis. However, when Cowper-Smith and Westwood [49] later tested reaching localization responses using a similar methodology to the present study, they observed evidence of IOR in *both* axes. This suggested that IOR effects may be introduced or magnified when set size is changed from four to two. The results of the present study confirm this idea by demonstrating that IOR is observed in both the horizontal and vertical axes when set size is two (as in E2), but not four [as in 25].

If IOR is introduced when set size changes from four to two, we further predicted that the magnitude of the RT difference between 0°-90° and 0°-180° would increase compared to that observed by Cowper-Smith et al. [29]. However, given that there is no reason to suspect the magnitude of adaptation effects should change as a function of set size, there should be no change in the magnitude of the 90°-180° RT difference when two versus four targets are used on each trial. As predicted, and consistent with the presence of both IOR and adaptation, the magnitude of the RT difference increased for 0°-90° and 0°-180° but not for 90°-180°.

Can IOR Mask Adaptation Effects? Unlike the results of Cowper-Smith and Westwood [49] who observed the 'blended' pattern of RTs (0°>90°<180°; 0°>180°) for consecutive reaching movements across two target locations independent of signal type (central or peripheral), in the present study, the typical pattern of IOR was observed in E1 with peripheral signals (0°>90°>/=180°), while the blended pattern of RTs was observed in E2 with central signals. This observation is consistent with work suggesting that IOR is more pronounced when peripheral stimuli instruct consecutive eye versus arm movements [16,19].

If IOR is more pronounced for eye movements made to peripheral signals, is it possible that IOR masks otherwise present adaptation effects?[22] If so, it is important to note that an *increase* to 0° RTs alone would be insufficient for IOR to mask the overall preference for 90° offsets normally associated with adaptation; rather, for IOR to mask the 90° preference, it would need to *decrease* RTs for 180° offsets. This possibility could be supported by the saccadic momentum phenomenon, which is sometimes debated as a possible explanation of oculomotor IOR [16,51–55].

Saccadic momentum (SM; not to be confused with attentional momentum)[23] refers to a phenomenon where consecutive saccades are more likely to continue

---

[22] Consistent with this idea, across all studies in the present thesis, the magnitude of RT differences between 0°-180° as well as 0°-90° were largest in the in the peripheral-eye condition when set size was two (Appendix A).

[23] Some researchers have suggested that a path of attentional momentum is created when attention is attracted back to fixation from a peripherally cued S1 location [10,59]. This momentum would create a bias for attention to continue moving along the same trajectory toward 180° opposite (previously un-cued) locations. If the attentional momentum hypothesis is correct, un-cued targets that are opposite (180°) from the cued target should exhibit an “opposite facilitation effect” (OFE) where RTs are fastest, e.g., compared to targets aligned orthogonal to the line of attentional momentum. Although OFEs are occasionally observed, when present, OFEs are only observed in a minority of participants and are usually accompanied by an interaction with S1 location. That is, compared with IOR which is robustly observed across participants and target locations, there is no consistent evidence of an OFE, i.e., where 180° RTs are faster than 90° RTs [11,13,60–62]. By contrast, saccadic momentum (SM) effects, referring to a

forward in the same trajectory than they are to change movement trajectories [1,2,51,56,54,57,55,52]. This effect was coined “saccadic momentum” by Smith and Henderson [56] and has been proposed by some scholars to explain specifically the oculomotor form of IOR in the target-target task [16,19,51, but see 52]. The most explicit explanation comes from Wang et al. [51], who suggest that following a saccade, leftover activity in the superior colliculus leads to the facilitation of subsequent saccades made in the same direction and of the same distance [16,51]. Notably, some evidence suggests SM is strongest when peripheral onset stimuli are used to prompt eye movements [52,53]. If eye movements of the same direction and amplitude are facilitated by SM, then in target-target tasks, following the return-to-centre eye movement, S2 responses offset by 180° from S1 would be facilitated. As a result, it is possible that SM masked adaptation effects by decreasing 180° RTs when peripheral stimuli were used in E2. Alternatively, it is possible that adaptation effects are simply absent for saccadic responses to peripheral stimuli. A lack of adaptation effects for saccadic responses to peripheral stimuli could be possible if, for example, visuomotor neurons involved in response generation are somehow immune to adaptation effects that appear to be otherwise present for saccadic responses to central stimuli, as well as for reaching localization responses to both peripheral and central stimuli [29,58].

---

probabilistic bias to repeat the most recent saccadic vector is robustly observed during free search. While SM based facilitation of repeated forward saccades, as determined through RTs remains contentious, a linear pattern of fixation durations is consistently observed in free search (where RTs follow the pattern: 0°>90°>180°) and current evidence suggests that multiple effects, including IOR and SM may contribute to the patterns of RTs observed under different circumstances [51,56,54,55,52].

Wrong Direction Errors. As discussed earlier, the presence of slower 0° relative to 90° and 180° RTs in E2 appeared to be associated with an anticipatory strategy that favored the generation of eye movement programs toward the only other, previously unsignaled, target location. Specifically, in the 0° condition of E2, participants made more directional errors because they were incorrectly moving to a *different* target location rather than correctly moving back to the same location. Notably, the observation of increased wrong-direction errors was unique to E2 and did not occur in either E1 or in any of the four-target experiments conducted by Cowper-Smith et al. [29].

Why would a similar strategy not be used for the four-target experiments conducted by Cowper-Smith et al. [29]? Assuming that only a limited number of eye movements can be prepared in advance (i.e. perhaps only one), then such advance preparation may not be possible when three saccadic responses were possible, as in E2. In this case, participants may simply wait for the presentation of S2 to prepare the signaled eye movement, rather than attempting to anticipate the S2 response; consequently, fewer errors result. While future research may further explore the task conditions that reveal an anticipatory strategy such as that described, we note that the present data indicate such a strategy may be dependent on signal type, given that the same pattern of errors described above for E2 were not observed in E1.

Why would the anticipatory strategy observed in E2 not also be seen for E1 when peripheral signals were used? When peripheral signals were used, because direct visuomotor transformations relating the spatial features of the stimulus to the required motor response are likely, eye movements may be most easily elicited by simply responding to the stimulus event. In other words, it may take more effort to use an anticipatory strategy when peripheral stimuli are used, compared to just responding to the stimuli. In contrast, when central signals were used, it may seem less effortful for participants to use an anticipatory strategy, compared to interpreting the stimulus and generating an appropriate motor response.

6.6 Future Directions

In two experiments and through a direct comparison to the results of Cowper-Smith et al. [29], the present study reveals important differences in the topography of saccadic RTs observed in the target-target task that depend on (1) signal type and (2) set size. Critically, these results demonstrate that an analysis of RTs across only two target locations may lead to over simplified conclusions regarding the nature of the response biases observed, in particular when central signals are used [e.g., 14,16,19–21]. As such, future research in the field should routinely examine RTs across more than two target locations, for example, to explore whether IOR and adaptation-based effects occur in other commonly studied stimulus-response combinations [cf. 14].

6.7 References

[1] J.W. MacInnes, R.M. Klein, Inhibition of return biases orienting during the search of complex scenes, ScientificWorldJournal. 3 (2003) 75–86.

[2] R.M. Klein, W.J. MacInnes, Inhibition of return is a foraging facilitator in visual search, Psychol. Sci. 10 (1999) 346–352.

[3] Z. Wang, R.M. Klein, Searching for inhibition of return in visual search: a review, Vision Res. 50 (2010) 220–8.

[4] R.M. Klein, Inhibitory tagging system facilitates visual search, Nature. 334 (1988) 430–431.

[5] P.J. Bennett, J. Pratt, The spatial distribution of inhibition of return, Psychol Sci. 12 (2001) 76–80.

[6] R.M. Klein, Inhibition of return, Trends Cogn. Sci. 4 (2000) 138–147.

[7] E.A. Maylor, R. Hockey, Inhibitory component of externally controlled covert orienting in visual space, J. Exp. Psychol. Hum. Percept. Perform. 11 (1985) 777–787.

[8] J. Pratt, R.A. Abrams, Inhibition of return to successively cued spatial locations, J. Exp. Psychol. Hum. Percept. Perform. 21 (1995) 1343–1353.

[9] J. Pratt, J., Adam, J.J., McAuliffe, The Spatial Relationship between Cues and Targets Mediates Inhibition of Return, J. Exp. Psychol. 52 (1998) 213–216.

[10] J. Pratt, T.M. Spalek, F. Bradshaw, The time to detect targets at inhibited and noninhibited locations: Preliminary evidence for attentional momentum, J. Exp. Psychol. Hum. Percept. Perform. 25 (1999) 730–746.

[11] J.J. Snyder, A. Kingstone, W.C. Schmidt, Attentional momentum does not underlie the inhibition of return effect, J Exp Psychol Hum Percept Perform. 27 (2001) 1420–1432.

[12] M.I. Posner, R.D. Rafal, L.S. Choate, J. Vaughan, Inhibition of return: Neural basis and function, Cogn. Neuropsychol. 2 (1985) 211–228.

[13] M.I. Posner, Y. Cohen, Components of visual orienting, in: H. Bouma & D.G. Bouwhuis (Eds.) Attention and performance X, Amsterdam: North-Holland, 1984, pp. 243-258.

[14] T.L. Taylor, R.M. Klein, Visual and motor effects in inhibition of return, J Exp Psychol Hum Percept Perform. 26 (2000) 1639–1656.

[15] H.F. Neyedli, T.N. Welsh, The processes of facilitation and inhibition in a cue-target paradigm: insight from movement trajectory deviations., Acta Psychol. (Amst). 139 (2012) 159–65.

[16] Z. Wang, J. Satel, R.M. Klein, Sensory and motor mechanisms of oculomotor inhibition of return., Exp. Brain Res. 218 (2012) 441–53.

[17] G. Berlucchi, Inhibition of return: A phenomenon in search of a mechanism and a better name., Cogn. Neuropsychol. 23 (2006) 1065–74.

[18] M.D. Hilchey, R.M. Klein, J. Satel, Returning to “inhibition of return” by dissociating long-term oculomotor IOR from short-term sensory adaptation and other nonoculomotor “inhibitory” cueing effects., J. Exp. Psychol. Hum. Percept. Perform. 40 (2014) 1603–1616.

[19] J. Satel, Z. Wang, Investigating a two causes theory of inhibition of return, Exp. Brain Res. 223 (2012) 469–478.

[20] A.B. Chica, T.L. Taylor, J. Lupiáñez, R.M. Klein, Two mechanisms underlying inhibition of return., Exp. Brain Res. 201 (2010) 25–35.

[21] A.R. Hunt, A. Kingstone, Inhibition of return: Dissociating attentional and oculomotor components, J Exp Psychol Hum Percept Perform. 29 (2003) 1068–1074.

[22] J. Satel, Z. Wang, T.P. Trappenberg, R.M. Klein, Modeling inhibition of return as short-term depression of early sensory input to the superior colliculus., Vision Res. 51 (2011) 987–96.

[23] A.R. Hunt, A. Kingstone, Inhibition of return: dissociating attentional and oculomotor components, J. Exp. Psychol. Hum. Percept. Perform. 29 (2003) 1068–1074.

[24] M.H. Fischer, J. Pratt, S.F. Neggers, Inhibition of return and manual pointing movements, Percept. Psychophys. 65 (2003) 379–387.

[25] A.B. Chica, R.M. Klein, R.D. Rafal, J.B. Hopfinger, Endogenous saccade preparation does not produce inhibition of return: failure to replicate Rafal, Calabresi, Brennan, and Sciolto (1989)., J. Exp. Psychol. Hum. Percept. Perform. 36 (2010) 1193–206.

[26] E. Birmingham, T.A.W. Visser, J.J. Snyder, A. Kingstone, Inhibition of return: unraveling a paradox, Psychon Bull Rev. 14 (2007) 957–963.

[27] S.P. Tipper, B. Weaver, L.M. Jerreat, A.L. Burak, Object-based and environment-based inhibition of return of visual attention, J Exp Psychol Hum Percept Perform. 20 (1994) 478–499.

[28] S.P. Tipper, B. Weaver, F.L. Watson, Inhibition of return to successively cued spatial locations: commentary on Pratt and Abrams (1995), J. Exp. Psychol. Hum. Percept. Perform. 22 (1996) 1289–1293.

[29] C.D. Cowper-Smith, J. Harris, G.A. Eskes, D.A. Westwood, Spatial interactions between successive eye and arm movements: signal type matters., PLoS One. 8 (2013) e58850.

[30] S. Funahashi, C.J. Bruce, P.S. Goldman-Rakic, Neuronal activity related to saccadic eye movements in the monkey's dorsolateral prefrontal cortex, J. Neurophysiol. 65 (1991) 1464–1483.

[31] S. Barash, R.M. Bracewell, L. Fogassi, J.W. Gnadt, R.A. Andersen, Saccade-related activity in the lateral intraparietal area. II. Spatial properties, J Neurophysiol. 66 (1991) 1109–1124.

[32] A. Fanini, J.A. Assad, Direction selectivity of neurons in the macaque lateral intraparietal area, J. Neurophysiol. 101 (2009) 289–305.

[33] P. Thier, R.A. Andersen, Electrical microstimulation distinguishes distinct saccade-related areas in the posterior parietal cortex, J. Neurophysiol. 80 (1998) 1713–1735.

[34] B. Amirikian, A.P. Georgopoulos, Modular organization of directionally tuned cells in the motor cortex: is there a short-range order?, Proc. Natl. Acad. Sci. USA. 100 (2003) 12474–12479.

[35] A.P. Georgopoulos, J.F. Kalaska, R. Caminiti, J.T. Massey, On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex, J Neurosci. 2 (1982) 1527–1537.

[36] A.P. Georgopoulos, A.B. Schwartz, R.E. Kettner, Neuronal population coding of movement direction, Science. 233 (1986) 1416–1419.

[37] B. Amirikian, A.. Georgopulos, Directional tuning profiles of motor cortical cells, Neurosci. Res. 36 (2000) 73–79.

[38] C.J. Bruce, M.E. Goldberg, Primate frontal eye fields. I. Single neurons discharging before saccades, J. Neurophysiol. 53 (1985) 603–635.

[39] J. Lee, H. Choi, S. Lee, B.H. Cho, K. ha Ahn, I.Y. Kim, K.M. Lee, D.P. Jang, Decoding saccadic directions using epidural ECoG in non-human primates, J. Korean Med. Sci. 32 (2017) 1243–1250.

[40] D.A. Robinson, Eye movements evoked by collicular stimulation in the alert monkey, Vis. Res. 12 (1972) 1795–1808.

[41] P.H. Schiller, M. Stryker, Single-unit recording and stimulation in superior colliculus of the alert rhesus monkey, J. Neurophysiol. 35 (1972) 915–924.

[42] G.D. Horwitz, W.T. Newsome, Target selection for saccadic eye movements: direction-selective visual responses in the superior colliculus, J. Neurophysiol. 86 (2001) 2527–2542.

[43] P.H. Schiller, S.D. True, J.L. Conway, Deficits in eye movements following frontal eye-field and superior colliculus ablations, J. Neurophysiol. 44 (1980) 1175–1189.

[44] C. Lee, W.H. Rohrer, D.L. Sparks, Population coding of saccadic eye movements by neurons in the superior colliculus, Nature. 332 (1988) 357–360.

[45] C.D. Cowper-Smith, E.Y.Y. Lau, C.A. Helmick, G.A. Eskes, D.A. Westwood, Neural coding of movement direction in the healthy human brain., PLoS One. 5 (2010) e13330.

[46] M. Eisenberg, L. Shmuelof, E. Vaadia, E. Zohary, Functional Organization of Human Motor Cortex : Directional Selectivity for Movement, Life Sci. 30 (2010) 8897–8905.

[47] A. Afshar, G. Santhanam, B.M. Yu, S.I. Ryu, M. Sahani, K. V Shenoy, Single-trial neural correlates of arm movement preparation., Neuron. 71 (2011) 555–64.

[48] M.M. Churchland, G. Santhanam, K. V Shenoy, Preparatory activity in premotor and motor cortex reflects the speed of the upcoming reach., J. Neurophysiol. 96 (2006) 3130–46.

[49] C.D. Cowper-Smith, D.A. Westwood, Motor IOR revealed for reaching., Atten. Percept. Psychophys. 75 (2013) 1914–22.

[50] M.D. Hilchey, R.M. Klein, J. Ivanoff, Perceptual and motor inhibition of return: components or flavors?, Atten. Percept. Psychophys. 74 (2012) 1416–29.

[51] Z. Wang, J. Satel, T.P. Trappenberg, R.M. Klein, Aftereffects of saccades explored in a dynamic neural field model of the superior colliculus, J. Eye Mov. Res. 4 (2011) 1–16.

[52] W.J. MacInnes, A.R. Hunt, M.D. Hilchey, R.M. Klein, Driving forces in free visual search: An ethology, Attention, Perception, Psychophys. 76 (2014) 280–295.

[53] T.J. Smith, J.M. Henderson, Does oculomotor inhibition of return influence fixation probability during scene search?, Attention, Perception, Psychophys. 73 (2011) 2384–2398.

[54] T.J. Smith, J.M. Henderson, Looking back at Waldo: Oculomotor inhibition of return does not prevent return fixations, J. Vis. 11 (2011) 3–3.

[55] I.T.C. Hooge, E.A.B. Over, R.J.A. Van Wezel, M.A. Frens, Inhibition of return is not a foraging facilitator in saccadic search and free viewing, Vision Res. 45 (2005) 1901–1908.

[56] T.J. Smith, J.M. Henderson, Facilitation of return during scene viewing, Vis. Cogn. 17 (2009) 1083–1108.

[57] I.T. Hooge, M.A. Frens, Inhibition of saccade return (ISR): spatio-temporal properties of saccade programming., Vision Res. 40 (2000) 3415–26.

[58] C.D. Cowper-Smith, G.A Eskes, D.A Westwood, Motor inhibition of return can affect prepared reaching movements, Neurosci. Lett. 541 (2013) 83–86.

[59] T.M. Spalek, S. Hammad, Supporting the attentional momentum view of IOR: is attention biased to go right?, Percept Psychophys. 66 (2004) 219–233.

[60] J.W. Harris, C.D. Cowper-Smith, R.M. Klein, D.A. Westwood, Further evidence against a momentum explanation for IOR, PLoS One. 10 (2015).

[61] J.J. Snyder, W.C. Schmidt, A. Kingstone, There's little return for attentional momentum, J. Exp. Psychol. Hum. Percept. Perform. 35 (2009) 1726–37.

[62] L. Machado, R.D. Rafal, Inhibition of return generated by voluntary saccades is independent of attentional momentum, Q. J. Exp. Psychol. A, Hum. Exp. Psychol. 57 (2004) 789–796.

CHAPTER 7: GENERAL DISCUSSION

7.1 Summary of Results

The original goal of the present dissertation was to explore whether behavioural correlates of directionally selective neural adaptation could be revealed when consecutive eye or arm movements are made. Of particular interest was comparing the pattern of RTs across more than 2 target locations when central versus peripheral stimuli instructed target responses in the centre-out task. Observing clear evidence of an adaptation-based motor response bias would challenge the idea that a single form of IOR operates in the in the centre-out task (e.g., when eye movements are made, [cf.1]) and behoove future research to examine RTs across more than two target locations. The second and related goal of this dissertation was therefore to test competing predictions regarding the pattern of RTs observed, emerging from prior research on neural adaptation and IOR (Table 1.1). Specifically, if IOR was present, we expected to observe the well-established monotonic pattern of RTs (0°>90°>/=180°) associated with IOR. By contrast, if the Adaptation Hypothesis was correct, we expected to observe fastest RTs for 90° offsets and relatively slower RTs for 0° and 180° offsets (0°>90°<180°).

Study 1 (Chapter 2) revealed different patterns of RTs in the center-out task that depended on signal (central/peripheral) but not response (saccade or manual-localization) type. The pattern of RTs observed for central signals was consistent with distribution of RTs predicted by the Adaptation Hypothesis (0°>90°<180°) while the pattern of RTs observed with peripheral signals replicated the well-established distribution of IOR (0°>90°>/=180°).

Studies 2 and 3 (Chapters 3 and 4 respectively) attempted to eliminate possible adaptation effects, which are likely to affect motor preparation, by allowing participants to fully prepare their saccadic or manual localization response in advance of response execution. Remarkably, when responses were prepared in advance of the movement execution signal, the hallmark pattern of IOR (0°>90°>/=180°) was nonetheless observed. This suggested that an IOR-like pattern of RTs can emerge during late-stage motor execution processes.

In order to rule out potential inhibitory effects created by the requirement to prepare but suppress a response until an execution signal was provided, in Study 4 (Chapter 5), the preparation signal was eliminated and the chances of revealing IOR were optimized by presenting only 2 possible target locations while separately presenting 90° and 180° offsets on different trials. Under similar task circumstances, IOR has been well documented for consecutive saccadic responses [1–3]; however, due to the use of peripheral stimuli in prior study designs, it is possible that a motor form of IOR had not previously been demonstrated within the reaching control system. Interestingly, independent of signal type, a unique pattern of RTs was observed (0°>90°<180°; 0°>180°) where 0° responses were slowest (consistent with IOR), 180° responses were intermediate, and 90° responses were fastest (consistent with motor adaptation effects). This result, combined with the results of Studies 1-3, suggests the possibility that both adaptation and IOR may affect RTs for consecutive reaching movements [c.f. 4].

If Study 4 revealed a combined pattern of adaptation and IOR, the same pattern of RTs (0°>90°<180°; 0°>180°) should be observed within the oculomotor system where the control of movement direction is similarly encoded. Consistent with this prediction, when central signals were used in Study 5 (Chapter 6), a ‘blended’ pattern of RTs predicted by a combination of IOR and adaptation effects was observed (0°>90°<180°; 0°>180°). However, unlike Study 4, but consistent with the pattern expected for oculomotor IOR (0°>90°>/=180°), a preference for 90° was not observed when peripheral signals were used in Study 5.

7.2 Multiple Response Biases Can Shape Behaviour

Together, the results of Studies 1-5 demonstrate for the first time that different spatial distributions of RTs can emerge in the center-out task depending on (1) signal type, (2) set size, and (3) the stages of information processing involved (i.e., whether response execution was separated from response preparation). The present thesis highlights the importance of examining each of these factors when attempting to elucidate the potential mechanisms underlying various response biases, including IOR and neural adaptation. Each of these factors is discussed in turn below.

7.3 The Importance of Signal Type.

There is a key difference between movements elicited by peripheral versus central signals, even if the responses to each signal type exhibit metrically identical profiles (e.g., in terms of direction, amplitude, and velocity). In particular, it is well established that the visuomotor transformations relating the stimulus to the response are quite different depending on the type of signal employed. When peripheral onset signals are used, a delay in response times could be associated with (1) the processing of sensory/attentional information at the peripheral location; (2) the visuomotor integration of sensory information driving motor responses[24]; or, (3) motor planning and execution processes [5–10]. In contrast, a delay in sensory/attentional or visuomotor processing is not possible when central arrowheads are used, because these signals instruct the appropriate motor response from a common spatial coordinate (fixation) and, as such, the potential to reveal a spatially localized form of IOR is eliminated [2,3,5]. Given the differences in how responses are generated to peripheral versus central stimuli, the use of peripheral signals confounds the ability to determine whether sensory/attentional, visuomotor, motor, or some combination of these processes are affected by IOR [2,3,5].

The Oculomotor Hypothesis. Despite the potential differences in the way that peripheral and central signals can elicit movements, Taylor and Klein's [1] study of IOR in 24 different stimulus-response conditions suggested that the oculomotor form of IOR occurs whenever eye movements are made, *independent* of signal type (see discussion of the Oculomotor Hypothesis in the Introduction together with a comparison of the present results to Taylor and Klein in Appendix E) [1,11–14]. However, given that Taylor

---

[24] When peripheral stimuli are used, a direct relationship between the spatial features of the stimulus and the required motor response enables the response to be controlled by neural structures containing integrated sensory and motor maps such as those found in the superior colliculus and parietal cortex [5,6,27–29]. In other words, when peripheral stimuli are used, a direct visuomotor transformation is possible, allowing the spatial features of the stimulus to help drive the appropriate motor response.

and Klein [1] measured IOR using a target array consisting only of two possible target locations, aligned to the left and right of central fixation, the conclusion that the motor form of IOR occurs whenever saccades are made was derived from the simple presence or absence of IOR under different task circumstances. While these data provide a valuable basis for examining whether IOR *might* occur under different circumstances, the presence or absence of an inhibitory cueing effect[25] may be insufficient to make strong conclusions regarding the nature of the underlying response bias. For this reason, it may have been somewhat premature for Taylor and Klein [1] to conclude that a single oculomotor form of IOR was observed across the different stimulus-response conditions whenever an eye movement was made. Indeed, if the two types of movements (generated from central and peripheral stimuli) elicit a common form of oculomotor IOR, e.g., to promote visual search, then the patterns of RTs observed for both central and peripheral stimuli should be similar across a broader range of spatial offsets than studied by Taylor and Klein [1].

Suggesting that different response biases are generated as a function of signal type, in Studies 1 and 5 of the present thesis, the pattern of RTs across 0°, 90°, and 180° offsets varied depending on whether central or peripheral stimuli were used to prompt responses. That different patterns of RTs were observed as a function of signal type is inconsistent with the notion, suggested by the Oculomotor Hypothesis [1], that a single

---

[25] The term inhibitory cueing effect (ICE) has been used by Hilchey et al. [18,59] to refer to delayed RTs in a more theoretically neutral way, when the presence of a true IOR mechanism is uncertain. While the ICE terminology was not applied throughout the present thesis, it's use may be warranted to help distinguish between IOR and other RT biases that do not share the same characteristics or likely underlying mechanisms as IOR.

motor-based response bias might operate when eye movements are made, independent of signal type.

Sensory/Attentional and Motor IOR can Combine in the Target-Target Task. Further evidence against a strict version of the Oculomotor Hypothesis was revealed by Wang, Satel, and Klein [3] who reported the simultaneous presence of both sensory/attentional and oculomotor IOR affecting consecutive saccadic responses. Departing from the assumptions offered by the Oculomotor Hypothesis, Wang et al. [3] proposed that the execution of a saccade to S1 may be necessary to generate oculomotor IOR[26]. Notably, if saccades are required to generate oculomotor IOR, then it should only be possible to observe sensory/attentional IOR (if generated by peripheral stimuli) in cue-target tasks when no saccade is made to the cue. Finally, if the two forms of IOR are generated via distinct mechanisms (i.e., the presentation of a peripheral stimuli and the execution of a saccadic eye movement), then assuming that sensory/attentional and motor-based IOR emerge at different levels of response processing, it should be possible to invoke both sensory/attentional and motor effects to additively slow RTs [3,15].

To test whether sensory/attentional and motor IOR can additively slow RTs, Wang et al. [3] required participants to execute consecutive saccades to either central or peripheral stimuli, similar to the tasks used in the present thesis. As described by

---

[26] In contrast, the Oculomotor Hypothesis forwarded by Taylor and Klein [1] did not require the motor form of IOR be generated by a saccade to S1, as discussed in the introduction. Rather, a saccadic response to either S1, S2 or both would result in observing the oculomotor rather than sensory/attentional form of IOR.

Wang et al. [3], when arrowhead stimuli were used to prompt consecutive saccades, "the IOR effect…is purely motor because no peripheral stimulation is involved" (p. 445); hence, this task was labelled the motor (M) task. However, when peripheral stimuli were used to prompt consecutive saccades, the task was labelled sensory-motor (SM) because to complete the task successfully, participants were required to first detect a spatially localized peripheral signal, then execute a corresponding saccade. Because this task involves both the detection of peripheral sensory information and the execution of consecutive saccades, IOR could arise from both sensory/attentional and motor-based processes. Finally, Wang et al. [3] examined RTs in a cue-target "sensory" (S) task using peripheral stimuli while requiring a saccade to S2 but not S1. In the cue-target task, because a saccade was not made to S1, only the sensory/attentional form of IOR should be revealed.

In direct contrast with the Oculomotor Hypothesis, and consistent with the idea that both sensory/attentional and oculomotor IOR can affect consecutive saccades made to peripheral stimuli, the magnitude of IOR in the SM task was equal to approximately the sum of IOR effects observed in the separate S and M tasks. From these observations, Wang et al. [3] advanced their 2-mechanism theory of IOR, which in contrast with the Oculomotor Hypothesis allowed both the sensory/attentional and oculomotor forms of IOR to be co-activated in the target-target task, provided consecutive saccades were made to peripheral stimuli[27].

---

[27] Wang, Satel, and Klein restrict the scope of their 2-mechanism theory, suggesting that the sensory/attentional form of IOR can be activated whenever peripheral S1 and S2 stimuli are used, while

Is there similar evidence that both sensory/attentional and motor IOR can affect responses when consecutive saccades are required to peripheral stimuli in the present thesis? The results of a supplementary analysis of the magnitudes of IOR observed in Study 4 (Appendix A) appears to provide mixed results. To best compare the results of the present thesis with those of Wang et al. [3] who used two targets offset by 180°, only two-target experiments (Studies 4 and 5) were considered to examine possible differences in the magnitude of IOR (0°-180° RTs) when central versus peripheral signals were used. Interestingly, as shown in Appendix A, a significantly larger magnitude of IOR was observed for peripheral versus central stimuli when reaching but not saccadic eye movements were required. How can one reconcile the observation of greater IOR for consecutive saccades in the SM task described above [2,3] with the data of the present thesis, which like Taylor and Klein [1], did not reveal greater IOR for saccades to peripheral versus central stimuli?

Cue-back Stimuli May Reduce Sensory/Attentional IOR. Wang, Satel, and Klein [3] argued that the sensory/attentional form of IOR can be encoded in retinotopic coordinates (e.g., because of reduced visual input strength to the SC [cf. 15])[28]; if this is

---

the oculomotor form of IOR occurs in any of the saccade-saccade response conditions. Conditions outside of these parameters (e.g., the other conditions tested by Taylor and Klein [1]) are not explained by the 2-mechanism theory, leaving open the possibility that other forms of IOR can operate under different task circumstances (e.g., when IOR is based in environmental [71] or object-based coordinates).

[28] Notably, some lines of evidence suggest spatiotopic but not retinotopic IOR occurs when an eye movement intervenes the cue and target [17,71]. However, other evidence suggests peripheral stimuli generate both retinotopic and spatiotopic IOR [72]. Retinotopic IOR has also been demonstrated in non-human primates and is linked to a reduction of sensory input processing within the superior colliculus [16].

the case, responses to peripheral S2 stimuli will be inhibited provided a prior S1 was presented in the same retinotopic coordinates. Furthermore, if an eye movement is made to a peripheral S1, and a cue-back stimulus is subsequently presented at fixation, then upon returning the eyes to center, S2 stimuli appearing 180° opposite of S1 will be inhibited by sensory/attentional IOR due to the fact that the cue-back and S2 stimuli appeared in the same retinotopic coordinates. Correspondingly, the use of a cue-back presented at fixation may reduce the magnitude of IOR observed for consecutive saccadic responses to peripheral stimuli[29]. As such, Wang and colleagues [2,3] eliminated the cue-back commonly used in other studies [1,8,17–21], which appears to have allowed for the observation of the full magnitude of combined sensory/attentional and motor IOR.

If the cue-back explanation above is correct, peripheral S2 responses offset specifically by 180° and not 90°, should be inhibited because the former but not the latter would share the same retinotopic coordinates as the cue-back once the eyes are returned to center. Correspondingly, when peripheral stimuli were used to prompt eye movements, 180° RTs may have been significantly faster than (rather than equivalent to) 90° RTs if a cue-back had not been used in the present thesis. In other words, in the absence of a cue-back, the magnitude of IOR observed for peripheral versus central stimuli might have been significantly larger in Study 5, consistent with the results of Wang and colleagues [2,3]. Future research may be informative in this regard.

---

[29] As noted in Study 1 (see Experiment 2 Discussion), the use of a cue-back is unlikely to affect responses made to central stimuli.

Combined Sensory/Attentional and Motor IOR Affecting Reaching Movements. An additional discrepancy between the results of the magnitude analysis in Appendix A and those of Wang and colleagues [2,3] surrounds the nature of IOR for consecutive manual responses. As discussed, the analysis in Appendix A reveals a larger magnitude of IOR for consecutive arm but not eye movements made to peripheral versus central stimuli. Notably, because no eye movements were made when reaching responses were required in Study 4, the cue-back and 180° S2 targets would be presented in different retinotopic coordinates. As a result, the cue-back would not be expected to reduce the magnitude of sensory/attentional IOR in Study 4, thereby explaining why a larger magnitude of IOR was observed for consecutive reaching responses to peripheral versus central stimuli. However, in sharp contrast with the analysis in Appendix A, Satel and Wang [2] failed to observe a larger magnitude of IOR when consecutive manual rather than saccadic responses were required to peripheral stimuli. From their failure to observe additive effects for manual responses to peripheral stimuli, Satel and Wang [2] concluded that different motor mechanisms underlie the IOR effect for consecutive eye and arm movements. In short, they argued that if IOR in the M task was caused by the same motor mechanism for eye and arm movements, additivity should have been observed in the SM task for both saccadic and manual responses. Critically however, like many IOR studies [e.g., 1,3,16,17], Satel and Wang [2] relied upon the use of spatially compatible button presses rather than manual localization (e.g., reaching or pointing) responses.

An understated or implicit assumption pervading much of the IOR literature is the idea that saccadic and manual discrimination or detection responses can be equated in their *potential* ability to generate or reveal the motor form of IOR [1,3,22–25]. However, whereas saccadic responses are usually spatially directed to ultimately fixate on the precise *location* of the indicated target, manual discrimination and detection responses are usually not. Manual discrimination and detection responses are typically made on a keyboard aligned adjacent and orthogonal to the display screen. Correspondingly, while these types of button presses may be spatially compatible or congruent with the target stimuli, unlike eye movements, they do not typically require that the movement directly *localize* the target, e.g., by moving the arm to point at or touch the precise target location [11,26][30]. Notably however, Khatoon et al. [8] have demonstrated that the onset of IOR is delayed and further, that the magnitude of IOR is decreased as the stimulus-response mapping becomes more arbitrary or indirect.

Considering the key differences between spatially congruent versus localization responses outlined above, it is perhaps not surprising that Satel and Wang [2] failed to

---

[30] This distinction is often either overlooked [e.g., 73] or blurred by the use of misleading response-type labels [1,2,22,59] in the absence of complete definitions [but see 11,26]. For example, given the widespread use of ‘saccadic localization response’ in reference to a spatially directed saccade, the use of the term ‘manual localization response’, or the suggestion that manual responses are made ‘toward’ a stimulus location, may easily imply the use of spatially directed localization response when in fact a spatially congruent or compatible discrimination response has been used. For these reasons, the terminology used to refer to different manual response types should be more carefully selected and applied in the literature. For example, “spatially congruent” responses can appropriately be used to refer to a lateralized response that corresponds with, but is not made to or toward the location as the visual stimulus itself. However, the present thesis submits that the use of the term “localization response” should be restricted to movements that are made toward the precise location of the visual stimulus, e.g., to fixate, point at, or touch the stimulus.

observe additive effects for manual responses in their SM task. For example, to observe additive effects in their SM task, it may be that the peripheral stimulus needs to be able to invoke visuomotor control mechanisms, allowing the desired response to be driven or defined by the spatial properties of the stimulus [5,6,8,27–29]. When button press responses are made on a keyboard orthogonal to the display screen, this kind of visuomotor control of action is unlikely. Whatever the cause, that the magnitude of IOR may be larger for peripheral versus central stimuli when saccadic [2,3] and manual localization (Study 4) responses are required, suggests that the use of a true localization response [4,11,26] may be required to simultaneously invoke sensory/attentional and motor based IOR. Future work examining the possible additivity of sensory/attentional and motor IOR should further explore the pattern of results revealed for spatially congruent versus localization responses, for example, to explore whether additivity in the SM task is only present when visuomotor control of action is possible.

Signal Type Matters. Taken together, the results of the present thesis illustrate that signal type plays an important role in shaping the nature of the response biases observed when both saccadic and manual localization responses are required. Interestingly, the pattern of RTs observed as a function of signal type was similar for both eye and arm movements (with one exception in Study 4 discussed below), suggesting both systems are subject to similar response biases. In addition to the effect of signal type, the patterns of RTs observed were different as a function of set size, i.e., whether two or four targets were possible on each trial.

7.4 The Importance of Set Size.

While two distinct patterns of RTs were revealed in Study 1, a third 'blended' pattern of RTs demonstrating characteristics of both adaptation and IOR was observed in Studies 4 and 5. This suggests that set size can impact the nature of the response bias observed. For convenience, the patterns of RTs observed across set size in Studies 1, 4, and 5, are presented together for eye and arm movements in Appendix C.

Combined Adaptation and IOR effects. In Study 5, when consecutive eye movements were made to central stimuli, Cowper-Smith et al. [in preparation] predicted and observed a 'blended' pattern of adaptation and IOR effects where RTs were slowest for 0° offsets, intermediate for 180° offsets, and fastest for 90° offsets. Notably, the magnitude of IOR effects (i.e., the difference between 0°-90° and 0°-180°) increased as set size decreased while the magnitude of the adaptation effect (i.e., the difference between 90°-180°) was insensitive to set size. This observation suggested that IOR may be increased or introduced to the pattern of RTs predicted by neural adaptation effects when set size is changed from four to two.

In order to determine if similar magnitude effects were observed as a function of set size for reaching movements to central stimuli, a supplementary analysis comparing Study 1 (four-target) with Study 4 (two-target) was completed in Appendix A. Interestingly, although the overall patterns of RTs observed between studies was different (a significant IOR effect was observed in Study 4 but not Study 1; see also Appendix C), no significant magnitude differences were observed a function of set size.

What might explain the increased magnitude of IOR for eye but not arm movements as set size is decreased from four to two? As discussed in Study 5, there were significantly more wrong-direction errors in the 0° (5% of all trials) compared to the 90° (0.4%) and 180° (0.2%) offset conditions, suggesting the presence of a response strategy where participants preferentially generated motor programs toward the only different (previously un-signaled) target location. However, as shown in Appendix B, wrong-direction error rates did not exceed 1% in any offset condition for consecutive reaching movements, suggesting the response strategy described above may be unique to eye movements. If so, the utilization of such a response strategy may explain why an increased magnitude of IOR was observed for eye but not arm movements as set size was changed from four to two.

Are Adaptation Effects Stronger for Reaching Movements? Across Studies 1, 4 and 5, evidence of adaptation (i.e., a RT preference for 90°) was observed whenever central signals were used. By contrast, evidence of IOR but *not* adaptation was observed whenever peripheral signals were used, with one exception.

When peripheral signals were used to prompt manual localization responses in Study 4, a RT preference for 90° offsets was observed. The preference for 90° offsets observed with peripheral signals might arise as the consequence of a shift in the relative contribution of IOR and neural adaptation, where for some reason, adaptation-based effects were increased or IOR based effects were decreased. One possibility is that the absence of saccadic momentum (see discussion, Study 5) or any analogous phenomenon in the reaching control system allowed adaptation effects to be revealed.

However, if this is the case, it is unclear why evidence of adaptation effects were not revealed when reaching movements were made to peripheral stimuli in Study 1. While it remains unclear why a shift in the contributions of IOR and adaptation effects might occur, the present results suggest set size may affect the relative contributions of different response biases when reaching movements are made to peripheral stimuli.

Taken together, the results of Studies 1, 4, and 5 suggest that set size plays an important role in shaping the nature of the response bias observed. Most notably, when set size is decreased from four to two, a unique response bias was observed that appears to be predicted by a combination of IOR and adaptation-based effects.

7.5 Stage of information processing.

In an effort to eliminate possible adaptation effects, Studies 2 and 3 replicated the central signal conditions of Study 1 but allowed participants to fully prepare their saccadic or manual localization response in advance of the S1 and S2 movement-execution signals. To our surprise, although the “U” shaped pattern observed in Study 1 was partially eliminated, IOR was nonetheless observed ($0^\circ > 90^\circ >/= 180^\circ$). As discussed below, these results suggest that separate inhibitory effects can slow responses to targets offset by 0° and 180° (e.g., in Study 1); one which slows motor preparation for 180° responses (which was eliminated in Studies 2-3) and another that slows response execution to 0° targets (presumably present in Studies 1-3).

Considering the results of Studies 1-3 together, the “U” shaped pattern of RTs ($0^\circ > 90 < 180^\circ$; $0^\circ = 180^\circ$) observed in Study 1 could be explained by a combination of IOR and neural adaptation effects, where IOR inhibits 0° responses while adaptation effects are only observed for 180° responses. Certainly, slowing responses to previously cued locations fits the typical RT pattern observed in IOR; however, can a delay of 180° and not 0° responses be explained by neural adaptation? If one assumes that IOR and adaptation have different time courses, such an explanation is plausible.

While the time course of IOR is well established, typically commencing around 300 ms and lasting as long as 3 seconds [17,30,31], the time course for the possible adaptation effects observed has not been established. Moreover, although IOR is thought to serve an adaptive function (for example to aid in visual search) and appears to have a cognitive mechanism that may extend its time course [3,18,31], neural adaptation effects may be an epiphenomenon of way in which the motor system controls movement direction. Accordingly, and consistent with the observation that residual excitatory activity in the superior colliculus decays rapidly following a saccade (i.e., within less than 270 ms [32]), one might expect the subsequent adaptation effects to also have a short time course[31]. If so, because responses to S2 are closer in time to the return to center movement than the original response to S1, it may therefore be that adaptation effects were overcome for 0° but not 180°. If this was the case, then 0° RTs for central stimuli might be explained by IOR (alone), while 180° RTs would be explained by neural adaptation.

---

[31] Consistent with the view that adaptation effects may have a short time course, Neyedli and Welsh [4] previously demonstrated that the trajectory of reaching movements is biased away from previously cued locations, possibly due to the inhibition of direction encoding neurons representing movements toward the cued location, at 850 ms but not 350 ms or 1100 ms SOAs. However, because Neyedli and Welsh [4] used a cue-target paradigm with peripheral signals, it is difficult to directly compare their results to those of the present thesis. Different time courses of adaptation effects may have been observed in the present thesis when consecutive movements were required in the target-target task.

Why would IOR but not adaptation-based effects be present in Studies 2-3? Given that the specification of movement direction occurs during movement preparation [33–40], and evidence that participants prepared their movement responses in Studies 2-3, it is reasonable to suspect that the preparatory period allowed participants to overcome adaptation effects. However, if IOR is implemented as a late-stage execution bias [41,42], or alternatively, if IOR is cognitively mediated [3,18,31] and slows motor outputs via projections from a centralized mechanism, then IOR would survive the preparation period provided in Studies 2-3.

7.6 Why Aren't Adaptation Effects Observed in Free Search?

During free search of a complex visual array, several studies have demonstrated that the duration of fixations are slowest when consecutive eye movements reverse movement vectors compared to when eye movements repeat movement vectors along the same trajectory [43–48]. A similar observation has been made in the random-walk paradigm where a continuous series of saccades are made to targets randomly presented to the left or right of the current fixation point [49,50]. During free search, the facilitation of RTs for repeated saccades in the same direction is accompanied by the observation that saccades are most likely to continue in the same direction, compared to all other possible movement directions [43–45,47,48,51]. While the debate continues regarding whether this is caused by IOR or saccadic momentum [43–47], no RT benefit for 90° versus 180° offsets is observed during free search. This observation might appear to conflict with a preference for 90° offsets observed present thesis. Notably however, during free visual search, almost all consecutive saccades are made within 300 ms or less [43,44]. As such, saccades in the forward direction are likely to be facilitated by residual excitatory activity, for example, that expected in the superior colliculus following the execution of an eye movement [3,32]. Given that adaptation effects are not expected until *after* cellular activity associated with movement execution has dropped below resting state, a failure to observe evidence of adaptation during free search is not surprising. However, assuming neural fatigue is involved in adaptation effects [c.f. 52], future research may investigate whether adaptation effects eventually accumulate during free search or in the random walk paradigm (e.g., after many consecutive saccades are made in the same direction) [49,50].

7.7 Limitations and Future Research

Underlying Neural Substrates. Like any investigational approach relying on mental chronometry to understand human information processing, in the absence of concurrent neuroimaging, it is difficult to make strong conclusions regarding the underlying neural mechanisms of behavior. As such, while the present results reveal different spatial response biases under various conditions, and although in many cases the patterns of RTs observed are predicted by known neurophysiology, it is not possible to make strong conclusions regarding the underlying neural mechanisms. Further research is needed to establish the neural correlates of the response biases observed herein [c.f. 53].

Set Size. While the present study derived much of its strength from systematically analyzing RTs across four rather than two target locations aligned in the horizontal axis, it is possible that other patterns of RTs could be observed with different set sizes. For example, while the Adaptation Hypothesis assumes that 90° offsets will be overall fastest, additional research is needed to test intermediate offsets (e.g., between 0° and 90° and 90° and 180°) to validate this possibility.

Time Course. Studies 1, 4 and 5 relied upon a single SOA of 2300 ms, while Studies 2 and 3 relied upon SOAs of 2000, 2300, and 2600 ms. While IOR is generally expected across these SOAs, both the magnitude and spatial distribution of IOR appear to be sensitive to SOA [30,54]. Furthermore, although the time course of possible adaptation effects has not been established in the centre-out task, based on a study reporting reaching trajectory deviations that might arise from the inhibition of direction encoding neurons, there is reason to believe that adaptation effects may be restricted to a narrow range of SOAs [4]. Future research is needed to determine if the patterns of RTs observed herein vary by SOA.

Isolation of Motor Effects. While the present thesis relied upon the use of central arrows to eliminate potential sensory/attentional effects associated with the presentation of peripheral stimuli, it is noteworthy that several lines of research suggest the act of programming a spatially directed motor response is tightly linked with the deployment of spatial attention toward the intended movement endpoint [55–58]. In fact, after being instructed to prepare an eye movement, visuospatial attention appears to be deployed toward, then pinned at the precise location of the saccade target; as a result, the detection or discrimination of sensory events more than even a degree of visual angle away from the target are severely impaired until the planned saccade is complete. A similar deployment of spatial attention occurs during the programming of reaching localization responses, although notably, unlike when eye movements are made, attention can be shifted away from the target before the reaching movement is completed [56]. Thus, while the detection of arrows do not require peripheral sensory processing and therefore eliminate most concerns that inhibition is attached to the peripheral target, it is likely that there was a shift of attention toward the target location when arrows were used to prompt responses herein. Importantly however, as noted earlier, it is clear that the presentation of an arrow does not independently generate IOR; rather, for IOR to be observed when arrows are presented, a response must be associated with the arrow [1,59]. This observation suggests that when central stimuli were used in the present studies, the effects observed were more closely related to the generation of motor outputs, rather than earlier sensory/attentional processing of the imperative stimulus.

External Validity. By providing new evidence of unique response biases in a variant of the basic paradigms commonly used in both the IOR [1–3,17,18,23,60–62] and movement direction [36,63–67] literature, the present thesis highlights the need to expand methodologies, in particular, as they relate to set size and signal type, in order to further characterize the response biases observed. However, as with any tightly controlled study, the present thesis is constrained in its external validity, and until further work can validate the effects are observed in other tasks, caution should be taken in interpreting the results. For example, it is possible that the patterns of RTs observed are unique to the center-out paradigm used [cf. 56]. To eliminate this concern, future research needs to look at these response biases in other paradigms e.g., using the random walk paradigm [49,50], during visual search [43,44,48,51], in forward-only reaching tasks [4,69,70], and with reaching movements toward real-world objects.

7.8 Conclusions

In an effort to reveal behavioural correlates of neural adaptation effects, the present thesis set out to examine the spatial distribution of RTs for consecutive eye and arm movements in the center-out task. Competing predictions emerging from the IOR and neural adaptation literature regarding the expected patterns of RTs were tested. The results collectively suggest that (1) spatially defined RT biases consistent with both IOR and adaptation can emerge from the simple execution of a prior movement made with the same effector; (2) that the relative contribution of IOR and adaptation effects to the pattern of RTs observed varies as a function of signal type and set size; (3) that these RT biases can occur outside of the oculomotor system; and (4) that IOR can affect late-stage motor execution processes.

7.9 References

[1] T.L. Taylor, R.M. Klein, Visual and motor effects in inhibition of return, J. Exp. Psychol. Hum. Percept. Perform. 26 (2000) 1639–1656.

[2] J. Satel, Z. Wang, Investigating a two causes theory of inhibition of return, Exp. Brain Res. 223 (2012) 469–478.

[3] Z. Wang, J. Satel, R.M. Klein, Sensory and motor mechanisms of oculomotor inhibition of return, Exp. Brain Res. 218 (2012) 441–53.

[4] H.F. Neyedli, T.N. Welsh, The processes of facilitation and inhibition in a cue-target paradigm: insight from movement trajectory deviations, Acta Psychol. (Amst). 139 (2012) 159–65.

[5] T.L. Taylor, R.M. Klein, On the causes and effects of inhibition of return, Psychon. Bull. Rev. 5 (1998) 625–643.

[6] J.D. Schall, Neural Basis of Target Selection, Rev. Neurosci. (1995) 63–85.

[7] L.H. Snyder, A.P. Batista, R.A. Andersen, Coding of intention in the posterior parietal cortex, Nature. 386 (1997) 167–170.

[8] S. Khatoon, K. a Briand, A.B. Sereno, The role of response in spatial attention: direct versus indirect stimulus-response mappings, Vision Res. 42 (2002) 2693–708.

[9] A. Battaglia-Mayer, S. Ferraina, A. Genovesio, B. Marconi, S. Squatrito, M. Molinari, F. Lacquaniti, R. Caminiti, Eye-hand coordination during reaching. II. An analysis of the relationships between visuomanual signals in parietal cortex and parieto-frontal association projections, Cereb. Cortex (New York, NY 1991). 11 (2001) 528–544.

[10] W. Werner, Neurons in the primate superior colliculus are active before and during arm movements to visual targets, Eur J Neurosci. 5 (1993) 335–340.

[11] M.H. Fischer, J. Pratt, S.F. Neggers, Inhibition of return and manual pointing movements, Percept. Psychophys. 65 (2003) 379–387.

[12] A.B. Chica, T.L. Taylor, J. Lupiáñez, R.M. Klein, Two mechanisms underlying inhibition of return, Exp. Brain Res. 201 (2010) 25–35.

[13] A.R. Hunt, A. Kingstone, Inhibition of return: Dissociating attentional and oculomotor components, J Exp Psychol Hum Percept Perform. 29 (2003) 1068–1074.

[14] M.D. Hilchey, R.M. Klein, J. Ivanoff, Perceptual and motor inhibition of return: components or flavors?, Atten. Percept. Psychophys. 74 (2012) 1416–29.

[15] S. Sternberg, The discovery of processing stages: extensions of donders' method, Acta Psychol. (Amst). 30 (1969) 276–315.

[16] M.C. Dorris, R.M. Klein, S. Everling, D.P. Munoz, Contribution of the primate superior colliculus to inhibition of return., J. Cogn. Neurosci. 14 (2002) 1256–63.

[17] M. Posner, Y. Cohen, Components of visual orienting, in: H. Bouma, D.G. Bouwhuis (Eds.), Atten. Perform. X, Amsterdam: North Holland, 1984: pp. 531–556.

[18] M.D. Hilchey, R.M. Klein, J. Satel, Returning to "inhibition of return" by dissociating long-term oculomotor IOR from short-term sensory adaptation and other nonoculomotor "inhibitory" cueing effects, J. Exp. Psychol. Hum. Percept. Perform. 40 (2014) 1603–1616.

[19] A. Bourgeois, A.B. Chica, R. Migliaccio, M.T. de Schotten, P. Bartolomeo, Cortical control of inhibition of return: Evidence from patients with inferior parietal damage and visual neglect, Neuropsychologia. 50 (2012) 800–809.

[20] K.R. Dukewich, Reconceptualizing inhibition of return as habituation of the orienting response., Psychon. Bull. Rev. 16 (2009) 238–51.

[21] J.J. Snyder, A. Kingstone, W.C. Schmidt, Attentional momentum does not underlie the inhibition of return effect, J. Exp. Psychol. Hum. Percept. Perform. 27 (2001) 1420–1432.

[22] D.J. Prime, L.M. Ward, Cortical expressions of inhibition of return, Brain Res. 1072 (2006) 161–174.

[23] A.R. Hunt, A. Kingstone, Inhibition of return: dissociating attentional and oculomotor components, J. Exp. Psychol. Hum. Percept. Perform. 29 (2003) 1068–1074.

[24] A.B. Chica, R.M. Klein, R.D. Rafal, J.B. Hopfinger, Endogenous saccade preparation does not produce inhibition of return: failure to replicate Rafal, Calabresi, Brennan, & Sciolto (1989)., J. Exp. Psychol. Hum. Percept. Perform. 36 (2010) 1193–206.

[25] B. Avery, C.D. Cowper-Smith, D.A. Westwood, Spatial interactions between consecutive manual responses, Exp. Brain Res. 233 (2015) 3283–3290.

[26] T.N. Welsh, J. Pratt, Inhibition of return in cue-target and target-target tasks., Exp. Brain Res. 174 (2006) 167–75.

[27] Y.E. Cohen, R.A. Andersen, A common reference frame for movement plans in the posterior parietal cortex, Nat Rev Neurosci. 3 (2002) 553–562.

[28] L.H. Snyder, A.P. Batista, R.A. Andersen, Coding of intention in the posterior parietal cortex, Nature. 386 (1997) 167–170.

[29] M.A. Goodale, A.D. Milner, Separate visual pathways for perception and action, Trends Neurosci. 15 (1992) 20–25.

[30] A.G. Samuel, D. Kat, Inhibition of return: A graphical meta-analysis of its time course and an empirical test of its temporal and spatial properties, Psychon. Bull. Rev. 10 (2003) 897–906.

[31] R.M. Klein, Inhibition of return, Trends Cogn. Sci. 4 (2000) 138–147.

[32] Z. Wang, J. Satel, T.P. Trappenberg, R.M. Klein, Aftereffects of saccades explored in a dynamic neural field model of the superior colliculus, J. Eye Mov. Res. 4 (2011) 1–16.

[33] B. Amirikian, A.P. Georgopoulos, Modular organization of directionally tuned cells in the motor cortex: is there a short-range order?, Proc. Natl. Acad. Sci. USA. 100 (2003) 12474–12479.

[34] A.P. Georgopoulos, J.F. Kalaska, R. Caminiti, J.T. Massey, On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex, J Neurosci. 2 (1982) 1527–1537.

[35] R. Caminiti, P.B. Johnson, C. Galli, S. Ferraina, Y. Burnod, Making arm movements within different parts of space: the premotor and motor cortical representation of a coordinate system for reaching to visual targets, J Neurosci. 11 (1991) 1182–1197.

[36] S. Kakei, D.S. Hoffman, P.L. Strick, Muscle and movement representations in the primary motor cortex, Science 285 (1999) 2136–2139.

[37] P.A. Fortier, J.F. Kalaska, A.M. Smith, Cerebellar neuronal activity related to whole-arm reaching movements in the monkey, J Neurophysiol. 62 (1989) 198–211.

[38] A.P. Georgopoulos, A.B. Schwartz, R.E. Kettner, Neuronal population coding of movement direction, Science 233 (1986) 1416–1419.

[39] T. Naselaris, H. Merchant, B. Amirikian, A.P. Georgopoulos, Large-scale organization of preferred directions in the motor cortex. I. Motor cortical hyperacuity for forward reaching, J Neurophysiol. 96 (2006) 3231–3236.

[40] B. Amirikian, A.. Georgopulos, Directional tuning profiles of motor cortical cells, Neurosci. Res. 36 (2000) 73–79.

[41] C.D. Cowper-Smith, G.A. Eskes, D.A. Westwood, Saccadic inhibition of return can arise from late-stage execution processes, Neurosci. Lett. 531 (2012) 120–4.

[42] C.D. Cowper-Smith, G.A. Eskes, D.A. Westwood, Motor inhibition of return can affect prepared reaching movements, Neurosci. Lett. 541 (2013) 83–86.

[43] W.J. MacInnes, A.R. Hunt, M.D. Hilchey, R.M. Klein, Driving forces in free visual search: An ethology, Attention, Perception, Psychophys. 76 (2014) 280–295.

[44] T.J. Smith, J.M. Henderson, Looking back at waldo: oculomotor inhibition of return does not prevent return fixations, J. Vis. 11 (2011) 3–3.

[45] T.J. Smith, J.M. Henderson, Facilitation of return during scene viewing, Vis. Cogn. 17 (2009) 1083–1108..

[46] I.T.C. Hooge, E.A.B. Over, R.J.A. Van Wezel, M.A. Frens, Inhibition of return is not a foraging facilitator in saccadic search and free viewing, Vision Res. 45 (2005) 1901–1908.

[47] T.J. Smith, J.M. Henderson, Does oculomotor inhibition of return influence fixation probability during scene search?, Attention, Perception, Psychophys. 73 (2011) 2384–2398.

[48] R.M. Klein, W.J. MacInnes, Inhibition of return is a foraging facilitator in visual search, Psychol. Sci. 10 (1999) 346–352.

[49] A.J. Anderson, H. Yadav, R.H.S.S. Carpenter, Directional prediction by the saccadic system, Curr. Biol. 18 (2008) 614–618.

[50] S.A.H. Jones, C.D. Cowper-Smith, D.A. Westwood, Directional interactions between current and prior saccades, Front. Hum. Neurosci. 8 (2014) 1–10.

[51] J.W. MacInnes, R.M. Klein, Inhibition of return biases orienting during the search of complex scenes, Sci. World J. 3 (2003) 75–86.

[52] K. Grill-Spector, R. Henson, A. Martin, Repetition and the brain: neural models of stimulus-specific effects, Trends Cogn Sci. 10 (2006) 14–23.

[53] M.D. Hilchey, D. Dohmen, N. Crowder, R.M. Klein, When is inhibition of return input- or output-based? It depends on how you look at it, Can. J. Exp. Psychol. 70 (2016) 325–334.

[54] B. Wang, C. Yan, R.M. Klein, Z. Wang, Inhibition of return revisited: Localized inhibition on top of a pervasive bias, Psychon. Bull. Rev. (2017) 1–7.

[55] H. Deubel, W.X. Schneider, Saccade target selection and object recognition: evidence for a common attentional mechanism., Vision Res. 36 (1996) 1827–37.

[56] H. Deubel, W.X. Schneider, Delayed saccades, but not delayed manual aiming movements, require visual attention shifts, Ann. N. Y. Acad. Sci. 1004 (2003) 289–296.

[57] C. Umilta, L. Riggio, I. Dascola, G. Rizzolatti, Differential effects of central and peripheral cues on the reorienting of spatial attention, Eur. J. Cogn. Psychol. 3 (1991) 247–267.

[58] G.C. Tipper, S.P., Lortie, C., Baylis, Selective Reaching: Evidence for Action-Centered Attention, J. Exp. Psychol. Hum. Percept. Perform. 18 (1992) 891–905.

[59] M.D. Hilchey, J. Satel, J. Ivanoff, R.M. Klein, On the nature of the delayed “inhibitory” cueing effects generated by uninformative arrows at fixation, Psychon. Bull. Rev. (2013).

[60] M.I. Posner, R.D. Rafal, L.S. Choate, J. Vaughan, Inhibition of return: Neural basis and function, Cogn. Neuropsychol. 2 (1985) 211–228.

[61] E. Birmingham, T.A.W. Visser, J.J. Snyder, A. Kingstone, Inhibition of return: unraveling a paradox, Psychon Bull Rev. 14 (2007) 957–963.

[62] J.J. Snyder, W.C. Schmidt, A. Kingstone, There’s little return for attentional momentum., J. Exp. Psychol. Hum. Percept. Perform. 35 (2009) 1726–37.

[63] A.. Georgopoulos, Neural integration of movement: role of motor cortex in reaching, FASEB J. 2 (1988) 2849–2857.

[64] P.A. Fortier, A.M. Smith, J.F. Kalaska, Comparison of cerebellar and motor cortex activity during reaching: directional tuning and response variability, J Neurophysiol. 69 (1993) 1136–1149.

[65] A.P. Georgopoulos, J.F. Kalaska, R. Caminiti, J.T. Massey, On the Relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex, J. Neurosci. 11 (1982) 1527–1537.

[66] C.D. Cowper-Smith, E.Y.Y. Lau, C.A. Helmick, G.A. Eskes, D.A. Westwood, Neural coding of movement direction in the healthy human brain, PLoS One. 5 (2010) e13330.

[67] S. Fabbri, A. Caramazza, A. Lingnau, Tuning curves for movement direction in the human visuomotor system, J. Neurosci. 30 (2010) 13488–13498.

[68] J. Hiltz, The effect of predictable reflxation on inhibition of return, Dalhousie University, 2015.

[69] T.N. Welsh, D. Elliot, Effects of response priming and inhibition on movement planning and execution., J. Mot. Behav. 36 (2004) 200–11.

[70] L. Tremblay, T.N. Welsh, D. Elliott, Between-trial inhibition and facilitation in goal-directed aiming: manual and spatial asymmetries, Exp. Brain Res. (2005) 79–88.

[71] E.A. Maylor, R. Hockey, Inhibitory component of externally controlled covert orienting in visual space, J. Exp. Psychol. Hum. Percept. Perform. 11 (1985) 777–787.

[72] A. Sapir, A. Hayes, A. Henik, S. Danziger, R. Rafal, Parietal Lobe Lesions Disrupt Saccadic Remapping of Inhibitory Location Tagging, J. Cogn. Neurosci. 16 (2004) 503–509.

[73] R.D. Rafal, P.A. Calabresi, C.W. Brennan, T.K. Sciolto, Saccade preparation inhibits reorienting to recently attended locations, J Exp Psychol Hum Percept Perform. 15 (1989) 673–685.

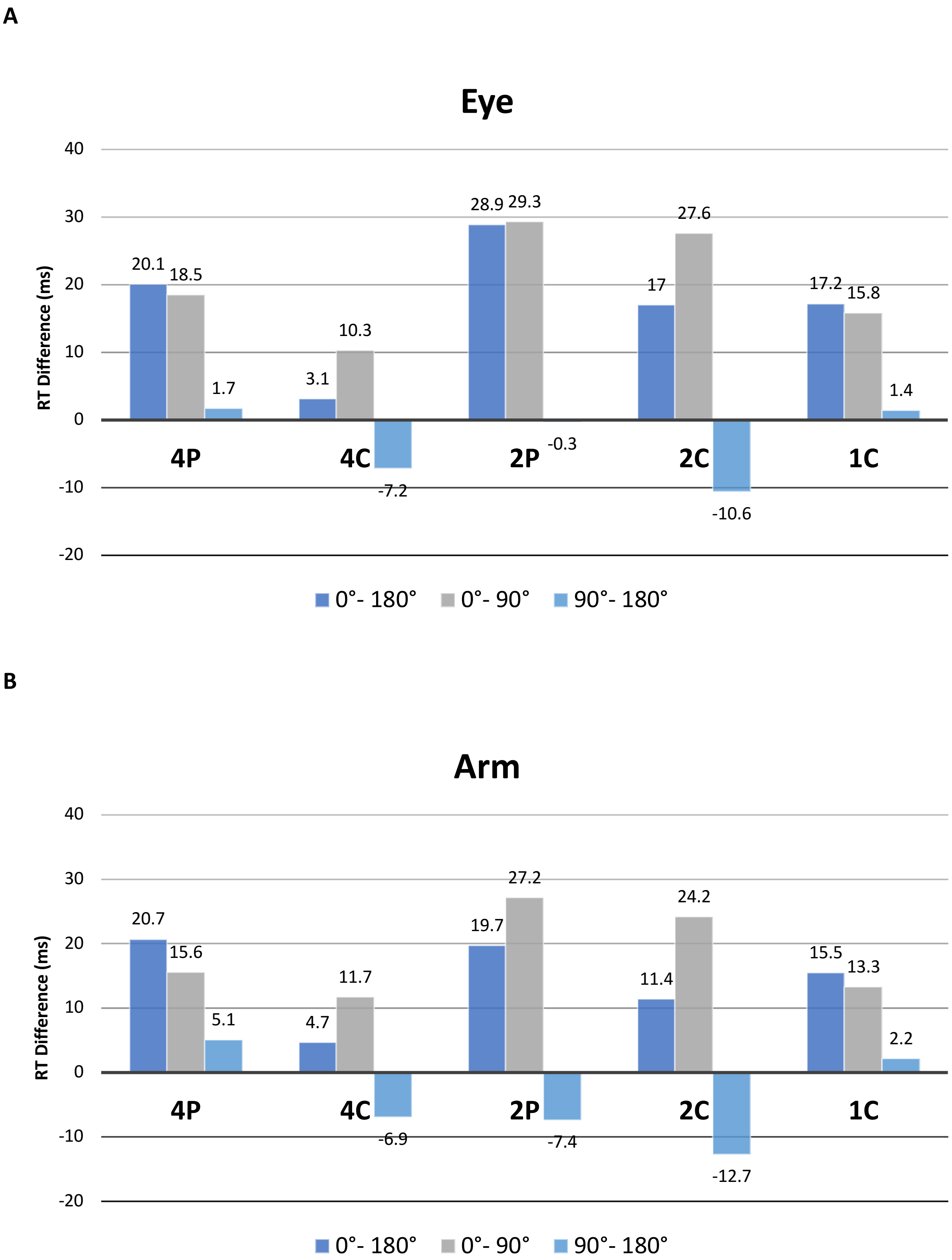
Appendix A: Magnitude Effects

As described in the general discussion and further below, various supplementary analyses were conducted on the magnitudes of RT differences between and within Studies.

Magnitude of IOR for Peripheral Versus Central Signals. In order to determine if the magnitude of IOR is greater when peripheral rather than central signals prompted responses, the RT difference between 0°-180° was compared across signal types in Studies 4 and 5. The magnitude of IOR (0°-180°) was greater when peripheral versus central signals were used to prompt reaching, F(1,20) = 7.19, $p < 0.05$, but not eye movements, F(1,16) = 2.79, $p = 0.11$.

Magnitude of the Adaptation Effect for Reaching Movements. In order to compare the magnitudes of RT differences for reaching responses to central signals across set sizes of four and two, a 2x3 mixed ANOVA with factors of set size (two or four) and offset-magnitude (0°-90°, 0°-180°, and 90°-180°) was conducted. A significant main effect of offset-magnitude, $F(2,40) = 31.38$, $p < 0.001$ but not set size, $F(1,20) = 0.69$, $p < 0.001$ was observed. No interaction between set size and offset-magnitude was observed, $F(2,40) = 2.16$, $p = 0.13$. Planned pairwise comparisons revealed no differences in magnitude across set sizes for 0°-90° ($F(1,20) = 1.79$, $p = 0.20$), 0°-180° ($F(1,20) = 0.84$, $p = 0.37$) or 90°-180° ($F(1,20) = 2.12$, $p = 0.16$).

Figure 7.1. Magnitude of RT differences between 0°-180°, 0°-90°, and 90°-180° offsets in all experiments of the present dissertation. Set size and signal type are combined in column headings as follows: 4-target-peripheral (4P); 4-target-central (4C); 2-target-periperal (2P); 2-target-central (2C); 1-target-central (Studies 3 and 4; 1C). Studies 3 and 4 are considered to present a set size of one because participants knew the required S2 target response with 100% certainty on each trial.


A
Eye
RT Difference (ms)
40
30
20
10
0
-10
-20
4P
4C
2P
2C
1C
20.1
18.5
1.7
3.1
10.3
-7.2
28.9
29.3
-0.3
17
27.6
-10.6
17.2
15.8
1.4
■ 0°- 180°
■ 0°- 90°
■ 90°- 180°
B
Arm
RT Difference (ms)
40
30
20
10
0
-10
-20
4P
4C
2P
2C
1C
20.7
15.6
5.1
4.7
11.7
-6.9
19.7
27.2
-7.4
11.4
24.2
-12.7
15.5
13.3
2.2
■ 0°- 180°
■ 0°- 90°
■ 90°- 180°

Appendix B: Directional Errors

Table 2: Directional error rates in all experiments of the present dissertation. Set size and signal type are combined in column headings as follows: 4-target-peripheral (4P); 4-target-central (4C); 2-target-periperal (2P); 2-target-central (2C); 1-target-central (Studies 3 and 4; 1C). Studies 3 and 4 are considered to present a set size of one because participants knew the required S2 target response with 100% certainty on each trial. Note that wrong-direction error rates were not analyzed if they did not exceed 1% in any offset condition because of an insufficient sample size to calculate reliable statistical differences [cf. 48].

Eye					
Offset	**4P**	**4C**	**2P**	**2C**	**1C**
0°	0.27%	0.76%	1.00%	4.98%	0%
90°	0.78%	1.30%	0.76%	0.42%	0%
180°	0.33%	0.89%	0.25%	0.19%	0%
	Not analyzed	No significant differences	Not analyzed	0>180* 0>90*	Not analyzed
Arm					
Offset	**4P**	**4C**	**2P**	**2C**	**1C**
0°	0.54%	0.42%	0.19%	0.98%	0%
90°	0.54%	0.24%	0.25%	0.50%	0%
180°	0.71%	0.35%	0.12%	0.25%	0%
	Not analyzed	Not analyzed	Not Analyzed	Not Analyzed	Not analyzed

Appendix C: Supplementary Analysis of Set Size

To examine the effect of set size for arm movements across Studies 1 and 4, separate 2x3 mixed ANOVAs were conducted for each signal type, with factors of set size (two or four) and offset (0°, 90°, and 180°). For peripheral signals, a significant main effect of offset was observed, $F(2,30) = 42.14$, $p < 0.001$, and a significant interaction between set size and offset was observed, $F(2,30) = 5.34$, $p < 0.01$. For central signals, significant main effects of set size, $F(1,18) = 6.35$, $p < 0.05$, and offset were observed, $F(2,36) = 31.95$, $p < 0.001$ and an interaction between set size and offset verged on significance at the $p < 0.1$ level, $F(2,36) = 2.4$, $p = 0.10$.

For convenience in comparing the pattern of RTs observed across Studies 1, 4, and 5, reaction times for 0°, 90°, and 180° offset conditions are presented for arm and eye movements in Figure 7.2 and Figure 7.3 respectively.

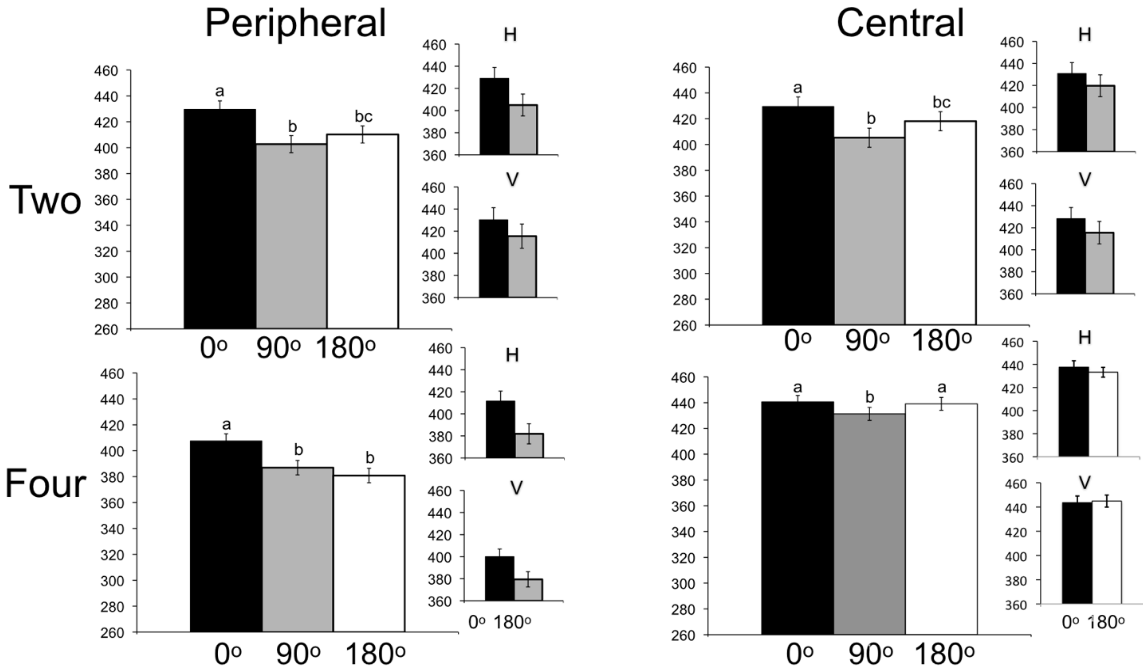


Figure 7.2. Manual reaction times for responses to the second signal (S2) in each offset condition (0°, 90°, and 180°). Results from Study 1 are presented in the bottom row (4-target) while results from Study 4 are presented in the top row (2-target). Within-subjects 95% confidence intervals were generated as described by Masson [11] using the Offset × Subject MSE term.

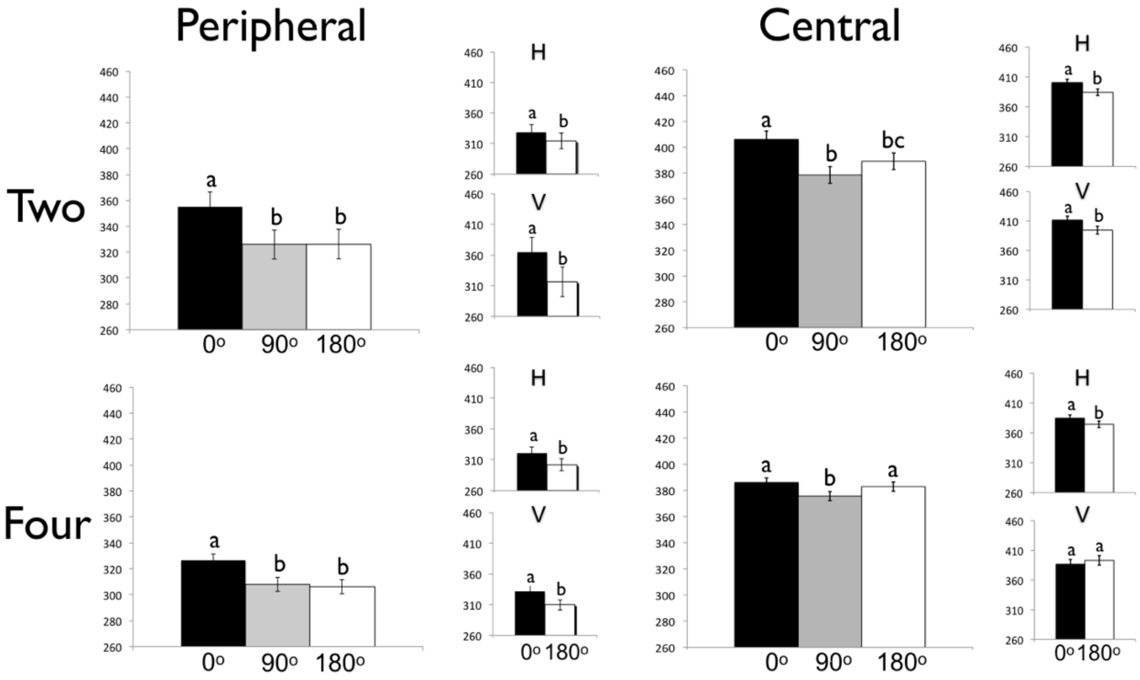


Figure 7.3. Saccadic reaction times for responses to the second signal (S2) in each offset condition (0°, 90°, and 180°). Results from Study 1 are presented in the bottom row (4-target) while results from Study 5 are presented in the top row (2-target). Within-subjects 95% confidence intervals were generated as described by Masson [11] using the Offset × Subject MSE term.

Appendix D: Reaction Times in the Horizontal and Vertical Axes in Studies 3 and 4

In Study 1, when central signals were used and eye *or* arm movements were required, evidence of IOR was discovered in the horizontal but not vertical axis. In order to further compare the results of Studies 2 and 3 to Studies 1, 4 and 5, trials where S1-S2 responses were restricted to the horizontal (left or right) and vertical (up or down) axes were extracted from the Study 2 and 3 datasets and separately analyzed. Zero-degree offset responses were significantly slower than 180° offset responses within both the horizontal, F(1,14) = 6.79, $p < 0.05$ and vertical F(1,14) = 9.02, $p < 0.01$ axes for eye movements (Study 2). Similarly, zero-degree offset responses were significantly slower than 180° offset responses within both the horizontal, F(1,16) = 14.94, $p < 0.001$ and vertical F(1,16) = 15.65, $p < 0.001$ axes for arm movements (Study 3).

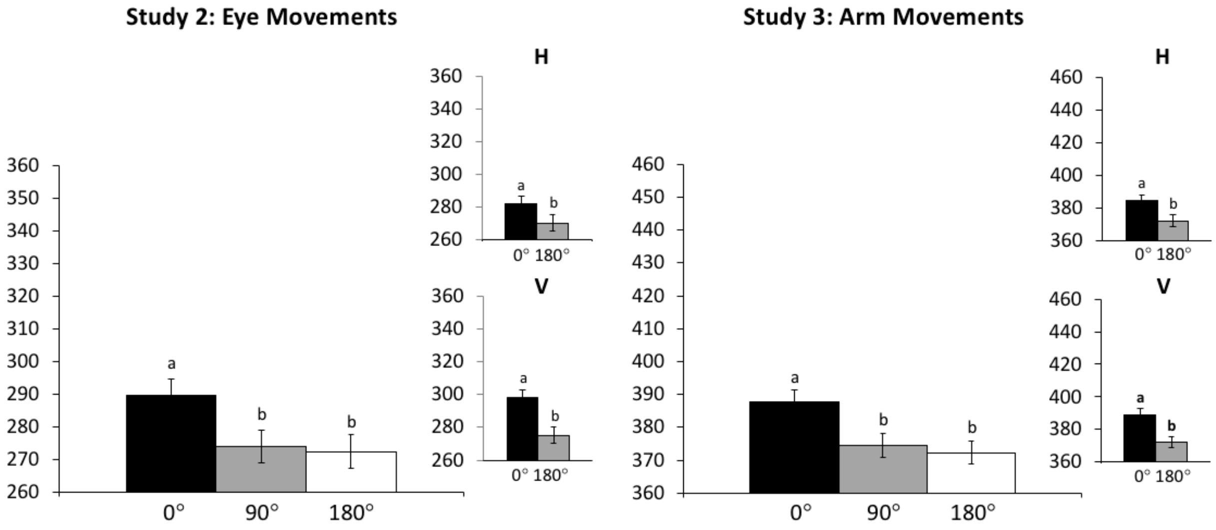


Figure 7.4. Supplementary analysis examining reaction times in the horizontal and vertical axis for Studies 2 and 3. As expected, IOR was present in both the horizontal and vertical axis in both studies.

Appendix E: Comparison of Magnitude Effects with Taylor and Klein (2000)

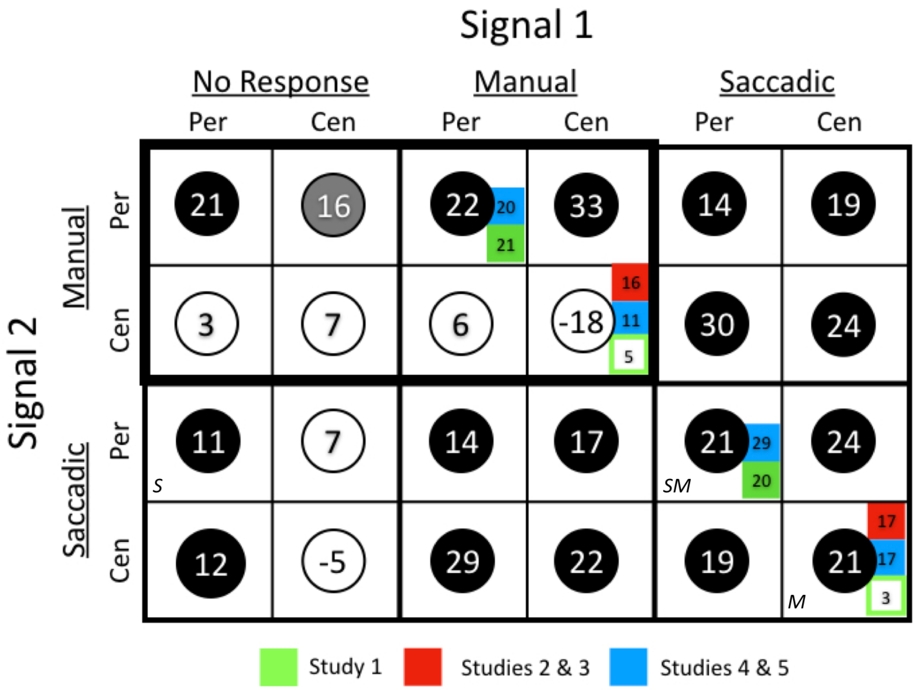


Figure 7.5. The magnitudes of IOR (0°-180° RTs) observed in the present thesis compared to those observed by Taylor and Klein [1]. For a description of Taylor and Klein's study see the General Introduction and Figure 1.3. Numbers within each circle represent the magnitude of IOR (0°-180° RTs) observed by Taylor and Klein. Numbers within each green, red, and blue square represent the magnitude of IOR (0°-180° RTs) observed in Studies 1-5 of the present thesis. Filled circles and squares represent a significant IOR effect; unfilled circles and squares represent a non-significant IOR effect. In contrast with Taylor and Klein, a significant IOR effect was observed in Studies 3 and 4 of the present thesis when consecutive reaching responses were required to central stimuli. Furthermore, in the present thesis, evidence of adaptation rather than IOR was observed when consecutive saccades or reaching movements were made and four rather than two target locations were presented on each trial.

BIBLIOGRAPHY

R. S. Abrams, R. A., Dobkin, Inhibition of Return: Effects of Attentional Cueing on Eye Movement Latencies, J. Exp. Psychol. Hum. Percept. Perform. 20 (1994) 467–477.

A. Afshar, G. Santhanam, B.M. Yu, S.I. Ryu, M. Sahani, K. V Shenoy, Single-trial neural correlates of arm movement preparation, Neuron. 71 (2011) 555–64.

B. Amirikian, A.P. Georgopulos, Directional tuning profiles of motor cortical cells, Neurosci. Res. 36 (2000) 73–79.

B. Amirikian, A.P. Georgopoulos, Modular organization of directionally tuned cells in the motor cortex: is there a short-range order?, Proc. Natl. Acad. Sci. USA. 100 (2003) 12474–12479.

S. Barash, R. M. Bracewell, L. Fogassi, J.W. Gnadt, R.A. Andersen, Saccade-related activity in the lateral intraparietal area. II. Spatial properties, J Neurophysiol. 66 (1991) 1109–1124.

A. Bastian, G. Schöner, A. Riehle, Preshaping and continuous evolution of motor cortical representations during movement preparation, Eur. J. Neurosci. 18 (2003) 2047–2058.

A. Battaglia-Mayer, S. Ferraina, A. Genovesio, B. Marconi, S. Squatrito, M. Molinari, F. Lacquaniti, R. Caminiti, Eye-hand coordination during reaching. II. An analysis of the relationships between visuomanual signals in parietal cortex and parieto-frontal association projections, Cereb. Cortex (New York, NY 1991). 11 (2001) 528–544.

A.V. Belopolsky, J Theeuwes, When are attention and saccade preparation dissociated? Psychol. Sci. 20 (2009) 1340-1347.

P.J. Bennet & J. Pratt, The spatial distribution of inhibition of return, Psychol. Sci. 12 (2001) 76-80.

A. Berger, A. Henik, R. Rafal, Competition between endogenous and exogenous orienting of visual attention, J. Exp. Psychol. Gen. 134 (2005) 207–221.

G. Berlucchi, Inhibition of return: A phenomenon in search of a mechanism and a better name, Cogn. Neuropsychol. 23 (2006) 1065–74.

E. Birmingham, T.A.W. Visser, J.J. Snyder, A. Kingstone, Inhibition of return: unraveling a paradox, Psychon Bull Rev. 14 (2007) 957–963.

A. Bourgeois, A.B. Chica, R. Migliaccio, M.T. de Schotten, P. Bartolomeo, Cortical control of inhibition of return: Evidence from patients with inferior parietal damage and visual neglect, Neuropsychologia. 50 (2012) 800–809.

K. A. Briand, A.L. Larrison, A.B. Sereno, Inhibition of return in manual and saccadic response systems, Percept. Psychophys. 62 (2000) 1512–1524.

C.J. Bruce, M.E. Goldberg, M.C. Bushnell, G.B. Stanton, Primate frontal eye fields. II. Physiological and anatomical correlates of electrically evoked eye movements, J. Neurophysiol. 54 (1985) 714–734.

C.J. Bruce, M.E. Goldberg, Primate frontal eye fields. I. Single neurons discharging before saccades, J. Neurophysiol. 53 (1985) 603–635.

R. Caminiti, P. B. Johnson, A. Urbano, Making arm movements within different parts of space: dynamic aspects in the primate motor cortex, J Neurosci. 10 (1990) 2039–2058.

R. Caminiti, P. B. Johnson, C. Galli, S. Ferraina, Y. Burnod, Making arm movements within different parts of space: the premotor and motor cortical representation of a coordinate system for reaching to visual targets, J Neurosci. 11 (1991) 1182–1197.

A.B. Chica, J. Lupiáñez, P. Bartolomeo, Dissociating inhibition of return from endogenous orienting of spatial attention: Evidence from detection and discrimination tasks, Cogn. Neuropsychol. 23 (2006) 1015–34.

A.B. Chica, R.M. Klein, R.D. Rafal, J.B. Hopfinger, Endogenous saccade preparation does not produce inhibition of return: failure to replicate Rafal, Calabresi, Brennan, & Sciolto (1989), J. Exp. Psychol. Hum. Percept. Perform. 36 (2010) 1193–206.

A.B. Chica, T.L. Taylor, J. Lupiáñez, R.M. Klein, Two mechanisms underlying inhibition of return, Exp. Brain Res. 201 (2010) 25–35.

M.M. Churchland, G. Santhanam, K. V Shenoy, Preparatory activity in premotor and motor cortex reflects the speed of the upcoming reach, J. Neurophysiol. 96 (2006) 3130–46.

M.C. Cirstea, A.B. Mitnitski, A.G. Feldman, M.F. Levin, Interjoint coordination dynamics during reaching in stroke, Exp. Brain Res. 151 (2003) 289–300.

F. Clarac, D. Cattaert, D. Le Ray, Central control components of a “simple” stretch reflex, (2000) 199–208.

Y.E. Cohen, R. A. Andersen, A common reference frame for movement plans in the posterior parietal cortex, Nat. Rev. Neurosci. 3 (2002) 553–562.

R.G. Cook, J.S. Katz, A.P. Blaisdell, Temporal properties of visual search in pigeon target localization, J. Exp. Psych.: Animimal Behavior Processes (2012) Epub.

C.D. Cowper-Smith, D.A. Westwood, Motor IOR revealed for reaching, Atten. Percept. Psychophys. 75 (2013) 1914–22.

C.D. Cowper-Smith, E.Y.Y. Lau, C.A. Helmick, G.A. Eskes, D.A. Westwood, Neural coding of movement direction in the healthy human brain, PLoS One. 5 (2010) e13330.

C.D. Cowper-Smith, G.A. Eskes, D.A. Westwood, Motor inhibition of return can affect prepared reaching movements., Neurosci. Lett. 541 (2013) 83–86.

C.D. Cowper-Smith, G.A. Eskes, D.A. Westwood, Saccadic inhibition of return can arise from late-stage execution processes., Neurosci. Lett. 531 (2012) 120–4.

C.D. Cowper-Smith, G.A. Eskes, D.A. Westwood, Motor inhibition of return can affect prepared reaching movements, Neurosci. Lett. 541 (2013) 83–86.

C.D. Cowper-Smith, J. Harris, G.A. Eskes, D.A. Westwood, Spatial interactions between successive eye and arm movements: signal type matters., PLoS One. 8 (2013) e58850.

T.B. Crapse, M.A. Sommer, Frontal eye field neurons with spatial representations predicted by their subcortical input, J. Neurosci. 29 (2009) 5308–5318.

M. Davare, A. Zénon, M. Desmurget, E. Olivier, Dissociable contribution of the parietal and frontal cortex to coding movement direction and amplitude, Front. Hum. Neurosci. 9 (2015) 1–12.

M. Desmurget, D. Pélisson, Y. Rossetti, C. Prablanc, From eye to hand: planning goal-directed movements, Neurosci. Biobehav. Rev. 22 (1998) 761–88.

H. Deubel, W.X. Schneider, Saccade target selection and object recognition: evidence for a common attentional mechanism, Vision Res. 36 (1996) 1827–37.

H. Deubel, W.X. Schneider, Delayed saccades, but not delayed manual aiming movements, require visual attention shifts, Ann. N. Y. Acad. Sci. 1004 (2003) 289–296.

J. Diedrichsen, R. Shadmehr, R.B. Ivry, The coordination of movement: optimal feedback control and beyond, Trends Cogn. Sci. 14 (2010) 31–39.

M.C. Dorris, R.M. Klein, S. Everling, D.P. Munoz, Contribution of the primate superior colliculus to inhibition of return, J. Cogn. Neuro. 5 (1994) 1256-1263.

M.C. Dorris, R.M. Klein, S. Everling, D.P. Munoz, Contribution of the primate superior colliculus to inhibition of return, J. Cogn. Neurosci. 14 (2002) 1256–63.

M.C. Dorris, T.L. Taylor, R.M. Klein, D.P. Munoz, Influence of previous visual stimulus or saccade on saccadic reaction times in monkey, J Neurophysiol. 81 (1999) 2429–2436.

K.R. Dukewich, Reconceptualizing inhibition of return as habituation of the orienting response, Psychon. Bull. Rev. 16 (2009) 238–51.

M. Eisenberg, L. Shmuelof, E. Vaadia, E. Zohary, Functional organization of human motor cortex: directional selectivity for movement, Life Sci. 30 (2010) 8897–8905.

S. Fabbri, A. Caramazza, A. Lingnau, Tuning curves for movement direction in the human visuomotor system, J. Neurosci. 30 (2010) 13488–13498.

A. Fanini, J.A. Assad, Direction selectivity of neurons in the macaque lateral intraparietal area, J. Neurophysiol. 101 (2009) 289–305.

J.H. Fecteau, D.P. Munoz, Correlates of capture of attention and inhibition of return across stages of visual processing, J. Cogn. Neurosci. 17 (2005) 1714–1727.

M.H. Fischer, J. Pratt, S.F. Neggers, Inhibition of return and manual pointing movements, Percept. Psychophys. 65 (2003) 379–387.

P.A. Fortier, A.M. Smith, J.F. Kalaska, Comparison of cerebellar and motor cortex activity during reaching: directional tuning and response variability, J Neurophysiol. 69 (1993) 1136–1149.

P.A. Fortier, J.F. Kalaska, A.M. Smith, Cerebellar neuronal activity related to whole-arm reaching movements in the monkey, J Neurophysiol. 62 (1989) 198–211.

S. Funahashi, C. J. Bruce, P.S. Goldman-Rakic, Neuronal activity related to saccadic eye movements in the monkey's dorsolateral prefrontal cortex, J. Neurophysiol. 65 (1991) 1464–1483.

A.P. Georgopoulos, Neural integration of movement: role of motor cortex in reaching, FASEB J. 2 (1988) 2849–2857.

A.P. Georgopoulos, On reaching, Annu Rev Neurosci. 9 (1986) 147–170.

A.P. Georgopoulos, H. Merchant, T. Naselaris, B. Amirikian, Mapping of the preferred direction in the motor cortex, Proc. Natl. Acad. Sci. USA. 104 (2007) 11068–11072.

A.P. Georgopoulos, A.B. Schwartz, R.E. Kettner, Neuronal population coding of movement direction, Science. 233 (1986) 1416–1419.

A.P. Georgopoulos, J.F. Kalaska, R. Caminiti, J.T. Massey, On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex, J Neurosci. 2 (1982) 1527–1537.

A.P. Georgopoulos, J.F. Kalaska, J.T. Massey, Spatial trajectories and reaction times of aimed movements: effects of practice, uncertainty, and change in target location, J. Neurophysiol. 46 (1981) 725–743.

A.P. Georgopoulos, R.E. Kettner, A.B. Schwartz, Primate motor cortex and free arm movements to visual targets in three-dimensional space. II. Coding of the direction of movement by a neuronal population, J Neurosci. 8 (1988) 2928–2937.

M.A. Goodale, A.D. Milner, Separate visual pathways for perception and action, Trends Neurosci. 15 (1992) 20–25.

K. Grill-Spector, R. Henson, A. Martin, Repetition and the brain: neural models of stimulus-specific effects, Trends Cogn Sci. 10 (2006) 14–23.

K. Grill-Spector, R. Malach, fMR-adaptation: a tool for studying the functional properties of human cortical neurons, Acta Psychol. 107 (2001) 293–321.

J.W. Harris, C.D. Cowper-Smith, R.M. Klein, D.A. Westwood, Further evidence against a momentum explanation for IOR, PLoS One. 10 (2015).

I. Havsteen, A. Ohlhues, K.H. Madsen, J.D. Nybing, H. Christensen, A. Christensen, Are movement artifacts in magnetic resonance imaging a real problem?-a narrative review, Front. Neurol. 8 (2017) 1–8.

D.J. Herzfeld, Y. Kojima, R. Soetedjo, R. Shadmehr, Encoding of action by the Purkinje cells of the cerebellum, Nature. 15 (2015) 439–442.

M.D. Hilchey, D. Dohmen, N.A. Crowder, R.M. Klein, When is inhibition of return input- or output- based? It depends on how you look at it. Can. J. Exp. Psych. 70 (2016) 325-334.

M.D. Hilchey, R.M. Klein, J. Ivanoff, Perceptual and motor inhibition of return: components or flavors?, Atten. Percept. Psychophys. 74 (2012) 1416–29.

M.D. Hilchey, R.M. Klein, J. Satel, Returning to “inhibition of return” by dissociating long-term oculomotor IOR from short-term sensory adaptation and other nonoculomotor “inhibitory” cueing effects., J. Exp. Psychol. Hum. Percept. Perform. 40 (2014) 1603–1616.

M.D. Hilchey, J. Satel, J. Ivanoff, R.M. Klein, On the nature of the delayed “inhibitory” cueing effects generated by uninformative arrows at fixation, Psychon. Bull. Rev. (2013).

N. Hogan, E. Bizzi, F. Mussa-Ivaldi, T. Flash, Controlling multijoint motor behaviour, Exerc. Sport Sci. Rev. 15 (1987) 153–190.

I.T. Hooge, M.A. Frens, Inhibition of saccade return (ISR): spatio-temporal properties of saccade programming, Vis. Res. 40 (2000) 3415-3426.

I.T.C. Hooge, E.A.B. Over, R.J.A. Van Wezel, M.A. Frens, Inhibition of return is not a foraging facilitator in saccadic search and free viewing, Vision Res. 45 (2005) 1901–1908.

G. D. Horwitz, W.T. Newsome, Target selection for saccadic eye movements: direction-selective visual responses in the superior colliculus, J. Neurophysiol. 86 (2001) 2527–2542.

L.A. Howard, J. Lupiáñez, S.P. Tipper, Inhibition of return in a selective reaching task: an investigation of reference frames, J. Gen. Psychol. 126 (1999) 421–42.

A.R. Hunt, A. Kingstone, Inhibition of return: dissociating attentional and oculomotor components, J. Exp. Psychol. Hum. Percept. Perform. 29 (2003) 1068–1074.

S. Kakei, D.S. Hoffman, P.L. Strick, Direction of action is represented in the ventral premotor cortex, Nat. Neurosci. 4 (2001) 1020–5.

S. Kakei, D.S. Hoffman, P.L. Strick, Muscle and movement representations in the primary motor cortex, Science (80-.). 285 (1999) 2136–2139.

J. M. Karl, I.Q. Whishaw, Different evolutionary origins for the reach and the grasp: an explanation for dual visuomotor channels in primate parietofrontal cortex, 4 (2013) 1–13.

S. Khatoon, K. a Briand, A.B. Sereno, The role of response in spatial attention: direct versus indirect stimulus-response mappings, Vision Res. 42 (2002) 2693–708.

A. Kingstone, J. Pratt, Inhibition of return is composed of attentional and oculomotor processes, Percept Psychophys. 61 (1999) 1046–1054.

R.M. Klein, Inhibition of return, Trends Cogn. Sci. 4 (2000) 138–147.

R.M. Klein, Inhibitory tagging system facilitates visual search, Nature. 334 (1988) 430–431.

R.M. Klein, M.D. Hilchey, Oculomotor inhibition of return, in: S. Liversedge, I. Gilchrist, S. Everline (Eds.), Oxford Handb. Eye Movements, Oxford University Press, London, UK, 2011: pp. 471–492.

R.M. Klein, W.J. MacInnes, Inhibition of return is a foraging facilitator in visual search, Psychol. Sci. 10 (1999) 346–352.

B.M. Koeppen, B.A. Stanton, Berne and Levy physiology e-book, Elsevier Health Sciences, 2017.

B. Krekelberg, G.M. Boynton, R.J. van Wezel, Adaptation: from single cells to BOLD signals, Trends Neurosci. 29 (2006) 250–256.

G. Kuhn, A. Kingstone Look away! Eyes and arrows engage oculomotor responses automatically, 71 (2009) 314–327.

J. Laczko, M.L. Latash, Progress in motor control: theories and translations, Springer International Publishing, 2016.

J. Lee, H. Choi, S. Lee, B.H. Cho, K.H. Ahn, I.Y. Kim, K.M. Lee, D.P. Jang, Decoding saccadic directions using epidural ECoG in non-human primates, J. Korean Med. Sci. 32 (2017) 1243–1250.

C. Lee, W.H. Rohrer, D.L. Sparks, Population coding of saccadic eye movements by neurons in the superior colliculus, Nature. 332 (1988) 357–360.

R.N. Lemon, P. A. Kirkwood, M.A. Maier, K. Nakajima, P. Nathan, Direct and indirect pathways for corticospinal control of upper limb motorneurons in the primate, Prog. Brain Res. 143 (2004) 263–279.

J. Lupiáñez, Inhibition of return, in: H. Nobre, J.T. Coull (Eds.), Atten. Time, 2010: pp. 17–34.

J. Lupiáñez, C. Decaix, E. Siéroff, S. Chokron, B. Milliken, P. Bartolomeo, Independent effects of endogenous and exogenous spatial cueing: inhibition of return at endogenously attended target locations., Exp. Brain Res. 159 (2004) 447–57.

L. Machado, R.D. Rafal, Inhibition of return generated by voluntary saccades is independent of attentional momentum, Q. J. Exp. Psychol. A, Hum. Exp. Psychol. 57 (2004) 789–796.

W.J. MacInnes, A.R. Hunt, M.D. Hilchey, R.M. Klein, Driving forces in free visual search: An ethology, Attention, Perception, Psychophys. 76 (2014) 280–295.

J.W. MacInnes, R.M. Klein, Inhibition of return biases orienting during the search of complex scenes, ScientificWorldJournal. 3 (2003) 75–86.

A. Marotta, J. Lupiáñez, M. Casagrande, Investigating hemispheric lateralization of reflexive attention to gaze and arrow cues, Brain Cogn. 80 (2012) 361–6.

E. Martín-arévalo, A. Kingstone, J. Lupiáñez, Is “Inhibition of Return” due to the inhibition of the return of attention?, Q. J. Exp. Psychol. 66 (2013) 347–359.

M.E. Masson, G.R. Loftus, Using confidence intervals for graphically based data interpretation, Can. J. Exp. Psych. 57 (2003), 203-220.

E.A. Maylor, R. Hockey, Inhibitory component of externally controlled covert orienting in visual space, J. Exp. Psychol. Hum. Percept. Perform. 11 (1985) 777–787.

P.A. McCormick, R. Klein, The spatial distribution of attention during covert visual orienting, Acta Psychol. (Amst). 75 (1990) 225–242.

A.D. Milner, M.A. Goodale, The visual brain in action, 2nd ed., Oxford University Press, New York, NY, US, 2006.

J. Morimoto, M. Kawato, Creating the brain and interacting with the brain: an integrated approach to understanding the brain, J. R. Soc. Interface. 12 (2015) 20141250–20141250.

D.P. Munoz, M.S. Dorris, M. Paré, S. Everling, On your mark, get set: brainstem circuitry underlying saccadic initiation, Can. J. Phys. Pharm. 78 (2000), 934-944.

T. Naselaris, H. Merchant, B. Amirikian, A.P. Georgopoulos, Large-scale organization of preferred directions in the motor cortex. I. Motor cortical hyperacuity for forward reaching, J Neurophysiol. 96 (2006) 3231–3236.

H.F. Neyedli, T.N. Welsh, The processes of facilitation and inhibition in a cue-target paradigm: insight from movement trajectory deviations, Acta Psychol. (Amst). 139 (2012) 159–65.

M.J.L. Perenboom, M. Van De Ruit, J.H. De Groot, A.C. Schouten, C.G.M. Meskers, Evidence for sustained cortical involvement in peripheral stretch reflex during the full long latency reflex period, Neurosci. Lett. 584 (2015) 214–218.

M.I. Posner, Chronometric explorations of mind, Hillsdale (N.J.) : Erlbaum, 1978.

M.I. Posner, Timing the brain: Mental chronometry as a tool in neuroscience, PLoS Biol. 3 (2005) 0204–0206.

M.I. Posner, Y. Cohen, Components of visual orienting, in: H. Bouma & D.G. Bouwhuis (Eds.) Attention and performance X, Amsterdam: North-Holland, 1984, pp. 243-258.

M.I. Posner, R.D. Rafal, L.S. Choate, J. Vaughan, Inhibition of return: neural basis and function, Cogn. Neuropsych. 2 (1985) 211-228.

J. Pratt, R.A. Abrams, Inhibition of return to successively cued spatial locations, J. Exp. Psychol. Hum. Percept. Perform. 21 (1995) 1343–1353.

J. Pratt, J., Adam, J.J., McAuliffe, The spatial relationship between cues and targets mediates inhibition of return, J. Exp. Psychol. 52 (1998) 213–216.

J. Pratt, B. Neggers, Inhibition of return in single and dual tasks: examining saccadic, keypress, and pointing responses, Percept. Psychophys. 70 (2008) 257–265.

J. Pratt, T.M. Spalek, F. Bradshaw, The time to detect targets at inhibited and noninhibited locations: Preliminary evidence for attentional momentum, J. Exp. Psychol. Hum. Percept. Perform. 25 (1999) 730–746.

D.J. Prime, L.M. Ward, Cortical expressions of inhibition of return, Brain Res. 1072 (2006) 161-174.

R.D. Rafal, P.A. Calabresi, C.W. Brennan, T.K. Sciolto, Saccade preparation inhibits reorienting to recently attended locations, J. Exp. Psychol. Hum. Percept. Perform. 15 (1989) 673–685.

R. Rafal, R. Egly, D. Rhodes, Effects of inhibition of return on voluntary and visually guided saccades, Can. J. Exp. Psychol. 48 (1994) 284–300.

J. Ristic, A. Kingstone, Attention to arrows: pointing to a new direction, Q. J. Exp. Psychol. (Hove). 59 (2006) 1921–1930.

J. Ristic, A. Wright, A. Kingstone, Attentional control and reflexive orienting to gaze and arrow cues, Psychon. Bull. Rev. 14 (2007) 964–969.

J. Ristic, A. Wright, A. Kingstone, The number line effect reflects top-down control, Psychon. Bull. Rev. 13 (2006) 862–868.

G. Rizzolatti, L Riggio, I Dascola, C Umilta, Reorienting of attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention, Neuropsych. 25 (1987), 31-40.

D.A. Robinson, Eye movements evoked by collicular stimulation in the alert monkey, Vis. Res. 12 (1972) 1795–1808.

A.G. Samuel, D. Kat, Inhibition of return: A graphical meta-analysis of its time course and an empirical test of its temporal and spatial properties, Psychon. Bull. Rev. 10 (2003) 897–906.

A. Sapir, A. Hayes, A. Henik, S. Danziger, R. Rafal, Parietal Lobe Lesions Disrupt Saccadic Remapping of Inhibitory Location Tagging, J. Cogn. Neurosci. 16 (2004) 503–509.

J. Satel, M.D. Hilchey, Z. Wang, C.S. Reiss, R.M. Klein, In search of a reliable electrophysiological marker of oculomotor inhibition of return, Psychophysiology. 51 (2014) 1037–1045.

J. Satel, Z. Wang, Investigating a two causes theory of inhibition of return, Exp. Brain Res. 223 (2012) 469–478.

J. Satel, Z. Wang, T.P. Trappenberg, R.M. Klein, Modeling inhibition of return as short term depression of early sensory input to the superior colliculus, Vis. Res. 51 (2011), 987-996.

J.D. Schall, Neural Basis of Target Selection, Rev. Neurosci. (1995) 63–85.

P.H. Schiller, M. Stryker, Single-unit recording and stimulation in superior colliculus of the alert rhesus monkey, J. Neurophysiol. 35 (1972) 915–924.

P.H. Schiller, S.D. True, J.L. Conway, Deficits in eye movements following frontal eye-field and superior colliculus ablations, J. Neurophysiol. 44 (1980) 1175–1189.

W. Schneider, VAM: A neuro-cognitive model for visual attention control of segmentation, object recognition, and space-based motor action, Vis. Cogn. 2 (1995) 331–376.

A.B. Schwartz, R.E. Kettner, A.P. Georgopoulos, Primate motor cortex and free arm movements to visual targets in three-dimensional space. I. Relations between single cell discharge and direction of movement, J Neurosci. 8 (1988) 2913–2927.

A.B. Sereno, C.B. Jeter, V. Pariyadath, K. Briand, Dissociating sensory and motor components of inhibition of return, ScientificWorldJournal. 6 (2006) 862–887.

T.J. Smith, J.M. Henderson, Does oculomotor inhibition of return influence fixation probability during scene search?, Attention, Perception, Psychophys. 73 (2011) 2384–2398.

T.J. Smith, J.M. Henderson, Facilitation of return during scene viewing, Vis. Cogn. 17 (2009) 1083–1108.

T.J. Smith, J. M. Henderson, Looking back at waldo: oculomotor inhibition of return does not prevent return fixations, J. Vis. 11 (2011) 3–3.

D.T. Smith, T. Schenk, The premotor theory of attention: time to move on? Neuropsychol. 50 (2012), 1104-1114.

L.H. Snyder, A.P. Batista, R.A. Andersen, Coding of intention in the posterior parietal cortex, Nature. 386 (1997) 167–170.

J.J. Snyder, W.C. Schmidt, A. Kingstone, There's little return for attentional momentum, J. Exp. Psychol. Hum. Percept. Perform. 35 (2009) 1726–37.

J.J. Snyder, A. Kingstone, Inhibition of return at multiple locations in visual search: when you see it and when you don't, Q. J. Exp. Psychol. 54 (2001) 1221–1237.

J.J. Snyder, A. Kingstone, W.C. Schmidt, Attentional momentum does not underlie the inhibition of return effect, J. Exp. Psychol. Hum. Percept. Perform. 27 (2001) 1420–1432.

E.N. Sokolov, Higher nervous functions: the orienting reflex, Annu. Rev. Physiol. 25 (1963) 545–580.

J.H. Song, R.D. Rafal, R.M. McPeek, Deficits in reach target selection during inactivation of the midbrain superior colliculus, PNAS 108 (51) (2011) E1433–E1440.

T.M. Spalek, S. Hammad, Supporting the attentional momentum view of IOR: is attention biased to go right?, Percept Psychophys. 66 (2004) 219–233.

T.M. Spalek, S. Hammad, The left-to-right bias in inhibition of return is due to the direction of reading, Psychol. Sci. 16 (2005) 15–18.

S. Squatrito, M.G. Maioli, Encoding of smooth pursuit direction and eye position by neurons of area MSTd of macaque monkey, J. Neurosci. 17 (1997) 3847–3860.

R. Quian Quiroga, Movement intention is better predicted than attention in the posterior parietal cortex, J. Neurosci. 26 (2006) 3615–3620.

T. Ro, J. Pratt, R.D. Rafal, Inhibition of return in saccadic eye movements, Exp. Brain Res. 130 (2000), 264-268.

S. Sternberg, The discovery of processing stages: extensions of donders' method, Acta Psychol. (Amst). 30 (1969) 276–315.

P. Sumner, P. Nachev, N. Vora, M. Husain, C. Kennard, Distinct cortical and collicular mechanisms of inhibition of return revealed with S cone stimuli, Curr. Bio. 14 (2004) 2259-2263.

A. Tankus, Y. Yeshurun, T. Flash, I. Fried, Encoding of speed and direction of movement in the human supplementary motor area, J. Neurosurg. 110 (2009) 1304–1316.

T.L. Taylor, R. M. Klein, On the causes and effects of inhibition of return, Psychon. Bull. Rev. 5 (1998) 625–643.

T.L. Taylor, R.M. Klein, Visual and motor effects in inhibition of return, J. Exp. Psychol. Hum. Percept. Perform. 26 (2000) 1639–1656.

P. Thier, R.A. Andersen, Electrical microstimulation distinguishes distinct saccade-related areas in the posterior parietal cortex, J. Neurophysiol. 80 (1998) 1713–1735.

G.C. Tipper, S.P., Lortie, C., Baylis, Selective Reaching: Evidence for Action-Centered Attention, J. Exp. Psychol. Hum. Percept. Perform. 18 (1992) 891–905.

S.P. Tipper, B. Weaver, L.M. Jerreat, A.L. Burak, Object-based and environment-based inhibition of return of visual attention, J. Exp. Psychol. Hum. Percept. Perform. 20 (1994) 478–499.

S.P. Tipper, B. Weaver, F.L. Watson, Inhibition of return to successively cued spatial locations: commentary on Pratt and Abrams (1995), J. Exp. Psychol. Hum. Percept. Perform. 22 (1996) 1289–1293.

L. Tremblay, T.N. Welsh, D. Elliott, Between-trial inhibition and facilitation in goal-directed aiming: manual and spatial asymmetries, Exp. Brain Res. (2005) 79–88.

C. Umilta, L. Riggio, I. Dascola, G. Rizzolatti, Differential effects of central and peripheral cues on the reorienting of spatial attention, Eur. J. Cogn. Psychol. 3 (1991) 247–267.

Z. Wang, R. M. Klein, Searching for inhibition of return in visual search: a review, Vision Res. 50 (2010) 220–8.

Z. Wang, J. Satel, R.M. Klein, Sensory and motor mechanisms of oculomotor inhibition of return., Exp. Brain Res. 218 (2012) 441–53.

Z. Wang, J. Satel, T.P. Trappenberg, R.M. Klein, Aftereffects of saccades explored in a dynamic neural field model of the superior colliculus, J. Eye Mov. Res. 4 (2011) 1–16.

B. Wang, C. Yan, R.M. Klein, Z. Wang, Inhibition of return revisited: localized inhibition on top of a pervasive bias. Psychon. Bull. Rev. (2017) 1-7.

T.N. Welsh, D. Elliot, Effects of response priming and inhibition on movement planning and execution, J. Mot. Behav. 36 (2004) 200–11.

T.N. Welsh, J. Pratt, Inhibition of return in cue-target and target-target tasks, Exp. Brain Res. 174 (2006) 167–75.

W. Werner, Neurons in the primate superior colliculus are active before and during arm movements to visual targets, Eur J Neurosci. 5 (1993) 335–340.

Y. Zhao, D. Heinke, J. Ivanoff, R.M. Klein, G.W. Humphreys, Two components in IOR: evidence for response bias and perceptual processing delays using the SAT methodology, Atten. Percept. Psychophys. 73 (2011) 2143–59.