THE EFFECT OF PREDICTABLE REFIXATION ON INHIBITION OF RETURN

by

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ABSTRACT

Inhibition of Return (IOR) refers to slowed responding to stimuli appearing at recently attended locations, and it has been reported for simple detection responses but also saccadic eye movements and even reaching movements (Klein, 2000). Most research studying IOR for consecutive saccades has utilized a task structure requiring a predictable refixation between the saccade creating IOR and the one seeking to reveal it (Taylor and Klein, 2000). Predictable refixation is unlike natural visual searching, so the present study sought to determine if IOR is modified or indeed dependent upon the predictability of refixation events. Participants made sequences of three saccades beginning from the center of a horizontal seven-target array in four conditions. In all conditions, the directions of the first and third saccades were unpredictable (left or right), but in separate blocks of trials the second saccade either predictably returned to the central target location (predictable conditions; all trials matched the classical refixation sequence) or unpredictably signaled a leftward or rightward saccade (unpredictable conditions; 50% of saccade sequences randomly matched the classical refixation sequence). Also in separate blocks of trials, saccade direction could be signaled by peripheral target onsets (exogenous conditions) or arrows located at the currently fixated location (endogenous conditions). These two signal types were chosen to add an additional investigation of whether the effect of refixation varied by modality (sensory or motor). Predictability and stimulus type were crossed with each other to create four experimental conditions. In order to compare equivalent events between conditions, IOR was assessed only for sequences involving refixation and was calculated as reaction time for the final saccade as a function of its direction relative to the first saccade (same direction versus opposite direction). Significant IOR was observed in all conditions except the condition with unpredictable refixation directed by centrally presented arrows. These results indicate that response predictability is a key component of the IOR phenomenon for saccades driven by endogenous signals, but not for saccades driven by peripheral stimulus events. This adds to a growing body of evidence suggesting that IOR arises from different mechanisms depending upon how responses are elicited.

LIST OF ABBREVIATIONS USED

ANOVA Analysis of Variance

IOR Inhibition of Return

RT Reaction Time

SRT Saccadic Reaction Time

ACKNOWLEDGMENTS

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CHAPTER 1 INTRODUCTION

Inhibition of return (IOR) is an important phenomenon that can be informative about the mechanisms and deployment of attention and the neural control of eye movements. IOR is a reluctance to return to previously attended areas of space compared to novel areas (Klein, 2000; Posner & Cohen, 1984). This is manifested in behavioral experiments as slowed reaction times to stimuli presented in a previously attended area of space (Posner & Cohen, 1981, 1984). In Posner and Cohen's experiment (1984), participants were instructed to fixate at a central point and were then cued to the left or right in their periphery. The cue consisted of a brightening of one of the boxes adjacent to fixation. Participants were instructed to ignore the cue, and respond (via button press) as quickly as possible to a target that followed, which appeared either at fixation, to the left, or to the right. The authors found that participants were faster to respond to the second stimulus (i.e., the target) when it was presented in the opposite location to the initial stimulus as compared to when it appeared in the same location as the first. This led the authors to the conclusion that the cue causes sensory inhibition at its location, thus resulting in slower reaction times to targets presented at that location later.

Inhibition of return has been studied predominantly within the parameters of a stimulus array distributed about a central fixation location, a precedent set by Posner and Cohen (1984) with their original study design. In this original study, participants maintained gaze at the central location at least until the onset of the target stimulus, thereby ensuring control over the retinal locations of the cue and target events. In subsequent studies involving saccadic responses to both the cue and target events (e.g., Maylor and Hockey, 1985) it was necessary to return the eyes to the central location after

the first eye movement to ensure that the next target could appear at random to a variety of locations distributed about the central fixation location. In four different experiments, Maylor and Hockey (1985) investigated if IOR differed based on whether a response was made to one or both of the stimuli presented. Each experiment examined different pairings of response requirements (no response, manual and saccadic) using LED stimuli as peripheral signals. The authors found slowed responses to stimuli presented in locations that had previously been attended to compared to stimuli presented in the opposite location (IOR).

There are only a handful of saccadic IOR studies that have used the target-target task structure (e.g., Taylor and Klein, 2000; Cowper-Smith et al., 2013; Welsh and Pratt, 2006) and all incorporate a completely predictable refixation event between the first and final saccade. The potential role of the refixation movement in the IOR phenomenon is generally disregarded, with the resulting IOR typically interpreted as arising from the relationship between the first and final target rather than the return-to-center movement between them.

The study of Taylor and Klein (2000) is particularly influential in the field of IOR as it explicitly tested the role of sensory and motor mechanisms in the phenomenon. This study used a variety of methodologies used to investigate IOR and also compared IOR generated and revealed by both exogenous signals (peripheral target onsets) and endogenous signals (arrows). Exogenous signals are those that appear outside of the fixated field of vision and capture attention and result in an almost reflexive saccade in the direction of the signal. Endogenous signals operate by appearing within fixation, and direct saccades by way of interpreting the signal, for example an arrow, which points in a

specific direction (Taylor and Klein, 1999; 2000).

Of relevance to the present study is the saccadic-saccadic experiment from Taylor and Klein (2000) in which eye movements were made to consecutive targets separated by a refixation saccade. In this experiment, on randomly intermixed trials, the first and final eye movements were either directed by peripheral onsets or arrow signals. Participants fixated at the center of the target array until the appearance of a signal, upon which they directed their eyes to the location of the target (exogenous) or to the location pointed to by the arrow (endogenous). A flash at the central location then attracted a refixation saccade, and the next eye movement was signaled using an exogenous or endogenous stimulus. The results of the study showed that IOR could be generated by exogenous signals (IOR = 21 ms), comparable to the 24 ms observed by Abrams and Dobkin (1994) who used cue-target methods in which eye movements were only made to the final stimulus. However, the magnitude of endogenous IOR (21 ms) differed from Abrams and Dobkin's cue-target study (9 ms). This suggests that different mechanisms might underlie the creation and revelation of IOR when endogenous eye movements are used.

Based on their comprehensive series of experiments, Taylor and Klein (2000) concluded that the nature of IOR varies with the type of response made to the first and second stimuli but also the type of signal used to elicit the response. In general, they concluded that there are two broad forms of inhibition, one that affects peripheral visual processing and arises when eye movements are *not* engaged in the task, and a second form that affects motor responding and arises when the eyes *are* engaged.

Returning to the issue of predictable refixation events in the traditional IOR task structure, one might assume that IOR would be absent in tasks that do not require a

refixation between consecutive saccades if IOR was merely an artifact of the return-to-center movement. However, a number of studies have used sequential saccade paradigms without predictable refixation events and nevertheless report evidence that saccades are slower when they return gaze to previously inspected locations (Klein and Macinnes, 1999; McCarley et al., 2003; Anderson et al., 2008; Jones et al., 2014).

Of particular relevance is a study by Anderson, Yadav and Carpenter (2008) in which participants completed a long series of saccades to targets along the horizontal axis where each saccade was triggered in turn by a peripheral target onset to the left or right of the currently fixated location on a random basis. They reported evidence that saccadic RT was reduced when a previous saccade had been completed in the same direction as the current movement (saccade n), whether that saccade was the immediately preceding movement (n-1), or a number of saccades ago (n-x where x could be 2 or more saccades).

For the n-1 comparison, this result is consistent with IOR because a saccade in the same direction as a previous one brings the eyes to a new location compared to an old location. Indeed, this relationship between consecutive saccades predicts that refixation events in the typical IOR task sequence might be important for observing fast saccadic RTs. Interestingly, however, the observation of a 'same direction benefit' for saccades at n-2 and higher levels is broadly *inconsistent* with a mechanism like IOR, since these comparisons considered all saccade sequences such that the saccade(s) occurring between n and n-x could be in any combination of directions. In other words, the same direction benefit did not simply arise because the eyes were moving to new versus old locations, but instead it seemed to reflect a historical benefit due to the direction of the eye movements themselves.

Anderson et al.'s results suggest that the IOR reported in experiments using refixation tasks (e.g., Taylor and Klein, 2000) could be an epiphenomenon of the cumulative, historical benefits of the directions of prior saccades rather than an inhibitory "tag" residing at the location of recent fixations. In other words, the slower RT for "old" target sequences in refixation tasks (e.g., an R-L-R sequence) might arise because the final saccade and its predecessor are in opposite directions, whereas they are in the same direction for "new" targets (e.g., an L-R-R sequence). However, this speculation disregards the role that predictability might play in refixation tasks; after all, a key feature of Anderson et al.'s task was that the direction of every saccade in the sequence was random whereas the direction of the penultimate saccade is 100% predictable in refixation tasks.

There are a number of methodological differences when comparing the task used by Anderson, Yadav, and Carpenter (2008) and that typically used when investigating IOR. The authors used a single subjects design, with a small number of participants, large number of trials, and single subject statistical analyses. Those who participated in the study were the authors themselves, and thus familiar with the design, hypotheses and expectations. In comparison, IOR studies are typically conducted using a group approach, smaller number of trials, subjects that are relatively unfamiliar with the research area, and within-subject/mixed statistical analyses.

A study by Jones et al. (2014) sought to reconcile some of the differences between the sequential saccade study of Anderson, Yadav, and Carpenter (2008) and traditional studies of IOR. This was done by preserving the random, sequential aspect of Anderson et al.'s task while reducing the number of trials and increasing the number and

naïveté of participants. The experiment also investigated the effect of visually persistent placeholders and the potential difference between exogenous (peripheral target onsets) and endogenous (arrow) signals. There were three separate within-subjects conditions in the experiment: peripheral targets with and without placeholders, and a condition with placeholders that used centrally presented arrows to direct eye movements. In each of the conditions, participants made a sequence of ten consecutive saccades, twenty times, with each group of ten saccades beginning from the central fixation location to ensure continued accuracy of eye-tracking.

The Jones et al. (2014) study revealed a same-direction benefit at the n-1 level (i.e., immediately consecutive saccades) for the peripheral-no placeholders condition and the central arrows condition, with faster reaction times for saccades in the same direction as the preceding one. This pattern matches what would be expected if IOR was operating since it creates a benefit for pairs of consecutive eye movements that bring the gaze to new rather than old locations. Unlike the results of Anderson et al., however, the same direction benefit was not robust when considering saccades beyond the immediately preceding one. Indeed, in some conditions an opposite direction benefit was observed for certain n-back levels. Jones et al.'s results suggest a complex pattern of inhibitory and facilitatory effects that might arise in sequences of eye movements, and challenge the simple model of accumulated historical saccade direction effects proposed by Anderson et al. Nevertheless, the finding of a same direction benefit for two consecutive saccades with unpredictable directions reinforces the need to determine whether the predictability inherent in refixation tasks contributes in any meaningful way to the magnitude of the observed inhibition of return or if the effect is simply the accumulated result of the

specific sequence of eye movements executed, whether or not the directions were predictable.

So why might predictability matter? Although the first and final movement directions are unpredictable in a refixation task, once the initial target is presented the participant knows the second movement will return to the central position. As such, the two movements could be programmed as a single event rather than two movement plans executed sequentially. Research on the concept of a "one-target advantage" (Henry and Rogers, 1960; Khan et al., 2008) suggests that when a movement to two targets is required, especially when the second movement is a reversal, these movements are organized together in the motor system, thus requiring greater neural resources. Preparing the refixation saccade with the first saccade would require twice the preparation of simply preparing one saccade. It is possible that this joint preparation of the first and second saccades might produce the inhibitory effect associated with the return to the initial target's location.

Further complicating the issue of refixation is the use of peripheral stimuli (visual onsets) to return attention and/or gaze to the center position. This creates the possibility of altered sensory processing of subsequent visual stimuli that share the same retinal location as the refixation stimulus. For example, for a sequence R-L-L, the refixation stimulus and the final target stimulus both appear at the same (leftward) retinal location, whereas they are in opposite locations for a sequence like R-L-R (see Figure 1.1). The result of this "extra" stimulation may induce asymmetrical activation of the superior colliculus, the area of the brain containing a retinal map, and part of the neural pathway responsible for the generation of saccades and subsequently a potential site for inhibition

of return to arise (Wang, Satel, & Klein 2012). However, this is only an issue when the stimulus is exogenous, and not an issue when using endogenous stimuli, since endogenous stimuli are typically centrally presented and do not involve a sensory change outside of the fixation area.

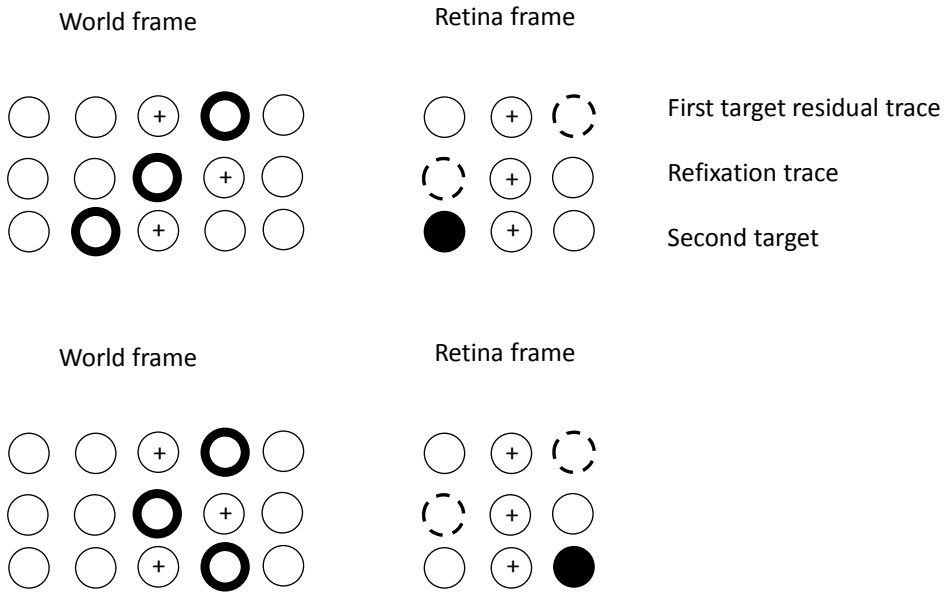

Figure 1.1 The left two panels show the sequence of events during a trial with exogenous stimuli. The panels on the right depict the resultant stimulation of retinal areas. The top panels demonstrate the case where the refixation movement leads to a refixation trace that is in the same location as the final stimulus. The bottom two panels demonstrate the case where the refixation trace is in the opposite location of the final trace.

The purpose of the present study is to explore the independent effect that directional predictability has on the magnitude of IOR observed in saccade-refixation-saccade tasks that have been used in studies such as Taylor and Klein (2000) that have strongly shaped current understanding of IOR. The study brings together the traditional target-refixation-target IOR task and the novel random-walk paradigm introduced by

Anderson et al. (2008). Studies using the random walk paradigm eliminated predictable refixations and showed evidence consistent with IOR, but they provide no insight into the possible role that predictability might play in the magnitude of IOR observed in previous target-refixation-target tasks.

Thus, the present study directly compares sequences of three eye movements that match the target-refixation-target task structure under conditions where the direction of the refixation saccade is either predictable (i.e., opposite in direction to the first saccade 100% of the time) or unpredictable (i.e., opposite in direction to the first saccade only 50% of the time). If predictability was a relevant factor in the observation of IOR in previous refixation tasks, then IOR should be reduced (or eliminated) in the unpredictable conditions. If, however, the IOR observed previously was simply due to the cumulative effects of the individual events in the refixation task structure (either the directions of the saccades, or the locations to which they were directed), then the magnitude of IOR should be the same in predictable and unpredictable conditions. In order to address the possibility that there might be different mechanisms of IOR engaged depending on the stimuli used to elicit saccades (e.g., Cowper-Smith et al., 2013; Jones et al., 2014; Taylor and Klein, 2000), patterns of IOR were compared for peripheral target onsets (exogenous conditions) compared to central arrows (endogenous conditions).

Rationale

The purpose of the present study is to move the field of IOR research into a method of studying the phenomenon that is more naturalistic. This was partially attempted by Anderson (2008), however the study lacked any experimental condition that connected the random walk paradigm to the original cue-target paradigm of Posner and

Cohen (1984). The current study incorporates aspects of both of these experimental approaches in a way that allows direct comparison of the two methods. Of particular interest is the concept of predictability in the two paradigms.

The two independent variables being manipulated in the current study are predictability and cue type. There are two levels of the predictability variable, predictable and unpredictable, and two levels of the cue type variable, endogenous and exogenous. Saccadic reaction time is the dependent variable being measured. In one level of the predictability variable, the second saccade in every sequence has a 100 percent probability of being in the opposite direction to the first saccade. In the other level of the predictability variable, the second saccade in every sequence has a 50 percent probability of being in the opposite direction of the initial saccade, and a 50 percent probability of being in the same direction as the initial saccade.

There are two levels of the cue type variable, endogenous cues and exogenous cues. In the endogenous level, saccades will be directed by arrow cues, and in the exogenous level, saccades will be directed by a peripheral onset (an adjacent placeholder in the stimulus array will become bold for an instant). The cue type manipulation is included because the type of cue used to generate IOR influences whether the IOR observed is of a sensory or motor nature. Endogenous cues rely on signal interpretation and are thus subject to top-down influences, but do not involve differences in retinal stimulation (no sensory change). Exogenous cues drive sensory stimulation and are thus bottom-up influenced, creating changes on the retina altering sensory processing. The potential effects of the independent variable manipulations are outlined below.

Study design and limitations

The study was designed to create patterns of eye movements similar to the target-refixation-target studies described above however, in one case the refixation event is predictable and in the other it is unpredictable. One can then elucidate if IOR appears equally in both cases, or if it increased or decreased when refixation is made unpredictable. Trials involved patterns of three eye movements, with identical sequences of leftward and rightward saccades used in both conditions. The first and final saccade directions were always equally random, but the predictability of refixation in the second saccade varied by experimental condition – either it was assured (predictable condition) or unpredictable. Identical sequences of eye movements from both cases (e.g. LRL) were then matched, where in one case the refixation (rightward eye movement in the example) is predictable (one hundred percent probable) and in the other case refixation occurred by chance. The study involved comparisons of the reaction times to the final target locations under each of the four experimental conditions: Predictable endogenous, unpredictable endogenous, predictable exogenous, and unpredictable exogenous. To determine if IOR was elicited, reaction times (latency to make a saccade) from "old" location sequences (e.g. LRL, RLR) were compared to those from "new" location sequences (e.g. LRR, RLL). To determine if there was a difference in saccadic reaction times due to predictability, the reaction times for the final saccade in the 3-saccade sequence from the predictable conditions were used to build a comparison to those of the unpredictable conditions. In order for this comparison to be made, a subset of saccade sequences from the unpredictable condition that matched the sequences of the predictable condition had to be chosen. The overall design consisted of the following factors: cue type (endogenous

versus exogenous), predictability (second eye movement predictable versus unpredictable), final saccade direction (left versus right), and initial saccade direction (same as final saccade, or opposite to final saccade).

Research questions and hypotheses

The primary research question of the current thesis was to investigate if the predictability of a refixation event affects the presence of IOR as measured in sequences of three saccades that match traditional target-target task paradigms. Two hypotheses are proposed. First, because IOR has been reported in tasks that do and do not require refixation, IOR appears to depend merely on the directions of the sequential eye movements and should be unaffected by the predictability of those movements; in other words, equivalent IOR should be seen regardless of the predictability of the refixation saccade. Second, because predictable movement sequences allow for advance preparation of multiple movement elements, it is possible that the effects on subsequent movements might differ in important ways such that IOR might be greater, or possibly smaller, for predictable as compared to unpredictable refixation conditions.

The second research question addresses the possibility that the relationship between refixation predictability and IOR is different for exogenous stimulus conditions as compared to endogenous stimulus conditions. Although IOR has been reported for both types of stimuli in refixation task structures (e.g., Taylor and Klein, 2000; Cowper-Smith et al., 2013), it has been argued that the IOR might arise from different sensory and motor mechanisms (e.g., Cowper-Smith et al., 2013; Jones et al., 2014). Earlier it was argued that refixation predictability might matter for IOR because it allows the preparation of compound movement sequences (versus single movements). If the IOR

observed for a particular type of stimulus (i.e., endogenous stimuli) arises from motor mechanisms rather than sensory mechanisms, then it is possible that refixation predictability will have a greater impact on the IOR observed for that stimulus type as compared to the other (i.e., exogenous stimuli) which might arise from sensory processes.

CHAPTER 2: METHODS

The present study investigated the role of refixation predictability within the inhibition of return phenomenon. This was done by inducing sequences of three eye movements that are found in traditional target-refixation-target IOR tasks: "old location sequences" of Left (L) Right (R) Left (L), and RLR, and "new location sequences" of LRR, and RLL. However, in some conditions the direction of the second movement was entirely predictable leading to refixation 100% of the time, like traditional target-refixation-target tasks, and in the other conditions the direction of the second movement was unpredictable, only resulting in a refixation movement 50% of the time. Participants were presented with stimuli on a computer screen and responded with eye movements that were tracked by a head mounted eye-tracking system. Additionally, two types of stimuli were used to guide eye movements: exogenous (peripheral target onsets) and endogenous (arrowheads presented at the location of gaze).

2.1 PARTICIPANTS

A total of 32 undergraduate students (24 female, 8 male) were recruited from the Psychology Participant Pool at Dalhousie University. Participant ages ranged from 18 to 27 with an average of 20.88 (SD = 1.82). These participants all visited the lab for a 60-minute experimental session and received one full credit point. All participants had normal, or corrected-to-normal vision and no history of neurological deficits as determined by a self-administered, pre-screening questionnaire.

2.2 APPARATUS

Stimuli were presented on a 32-inch Tyco Electronics computer monitor. An IBM computer running Experiment Builder software, controlled the presentation of trials, and

a separate IBM computer controlled the eye-tracking device. Eye movements were recorded using the EyeLink II from SR Research.

2.2.1 Eye tracking using infrared technology (EyeLink II)

The Eye Link II is a head mounted eye tracking device that uses infrared (IR) cameras (925 nm wavelength) to detect participants' pupil location. This is done with a binocular sampling rate of 250 Hz. The accuracy of the EyeLink II is 0.5^{o}, and the precision is 0.01^{o}. The EyeLink II is able to track the position of participants' eyes by using pupil location and corneal reflectance. A calibration procedure is used to convert eye position from the eye-tracker's frame of reference (i.e., camera) to the user's frame of reference (i.e., viewing screen).

2.3 PROCEDURE

Each experimental session was conducted in a small, quiet laboratory in the Psychology department at Dalhousie University with minimal distractions. Participants began by completing an informed consent form outlining their rights and offering general background information about the experiment. Following this they completed the pre-screening questionnaire to ensure no history of neurological deficit.

After providing informed consent participants were fitted with the eye-tracking device and seated in front of the computer monitor at a viewing distance of 57 cm. Figure 2.1 shows what the actual EyeLink II device looks like.

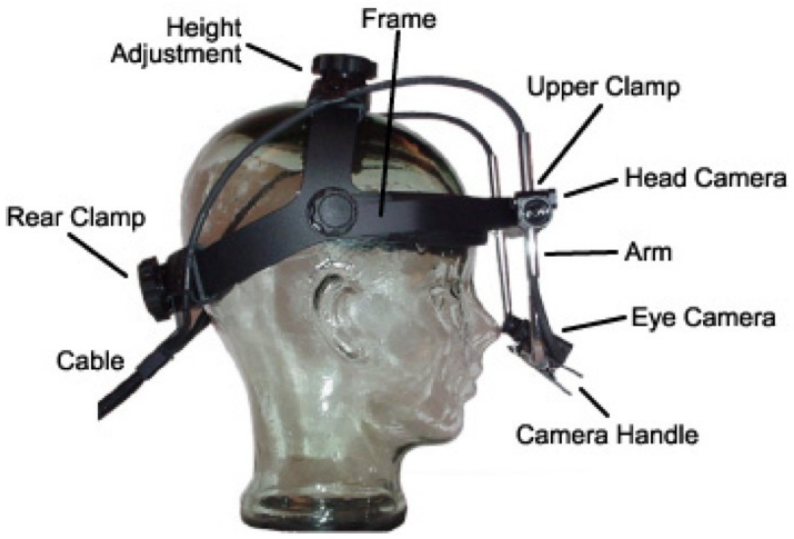

Figure 2.1. The EyeLink II eye-tracking device. From EyeLink II User Manual version (07/02/2006) © 2002-2006 SR Research Ltd.

The system was then calibrated to ensure accurate tracking of the participant's eye movements. The calibration procedure consisted of a nine-dot sequence, where the participant made an eye movement to nine separate dots that appeared on the screen. Repeating the sequence then validates the calibration, and the computer compares where participants' eyes are looking, to where the system predicted the eyes were looking based on the calibration. Figure 2.2 shows an image of what the infrared camera sees, alongside what the computer sees when the calibration is successful.

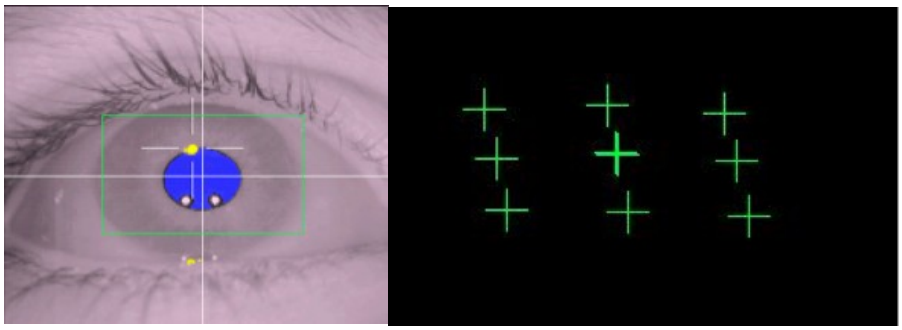

Figure 2.2. An image representing the EyeLink II camera view of the eye on the left, and the computer view of a successful calibration on the right. The green crosses correspond to the nine positions the participant looks at while performing the calibration. From EyeLink II User Manual version (07/02/2006) © 2002-2006 SR Research Ltd.

There were four conditions in the experiment, formed from crossing the independent variables of refixation predictability (predictable versus unpredictable) and stimulus type (exogenous versus endogenous). The predictability variable differed in terms of whether the second saccade in the sequence was in the refixation direction 100% of the time (i.e., always opposite to the first saccade) or only 50% of the time. With regard to the stimulus type variable, the endogenous level uses arrow signals presented at the currently fixated location to direct saccades, and the exogenous level uses peripheral onsets at the target's location to direct saccades. Figure 2.3 shows a breakdown of how these variables are manipulated, and shows the structure of each of the four conditions.

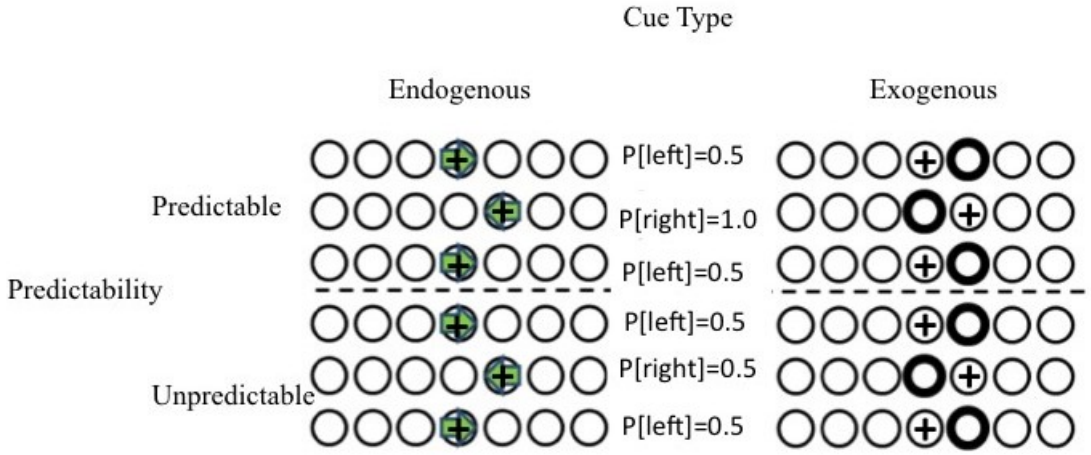

Figure 2.3. A breakdown of the manipulations of the independent variables, and the structure of each of the four conditions. The '+' indicates the current fixation location throughout a trial.

Each participant took part in all of the conditions in one of four random orders (Appendix 2). These orders ensured that participants completed the conditions with all of one cue type before moving to the next, either all of the exogenous trials before endogenous, or vice versa. Within each cue type, predictability was blocked to isolate the effects of cue type.

There were 40 trials in the predictable conditions, allowing for ten repetitions of the four possible combinations (LRL, LRR, RLR, RLL) of the two horizontal directions (left and right). There were 80 trials in the unpredictable conditions, allowing for ten repetitions of the eight possible combinations (the four 'refixation' sequences of primary interest: LRL, LRR, RLR, RLL, and four additional non-refixation sequences necessitated by the unpredictable direction of the second movement: LLL, LLR, RRL, RRR) of the two horizontal directions. The dependent variable of interest for the primary hypothesis was reaction time for the final saccade in the sequence

Figures 2.4-2.6 show timelines with specific timing details of how individual

trials progressed in each of the conditions. Each trial began with a drift correct at the center of the screen (the same location as the fourth circle in the stimulus array); the participant fixated this location and pressed the spacebar until the system determined that the eye was stable at the required location. This reoriented the computer's tracking system to ensure it had a precise location for the participant's eyes. For all trials, a seven-circle stimulus array appeared indicating the start of the trial. Participants were required to maintain fixation for 1000 ms at the central circle until a saccade was signaled by the onset of a stimulus.

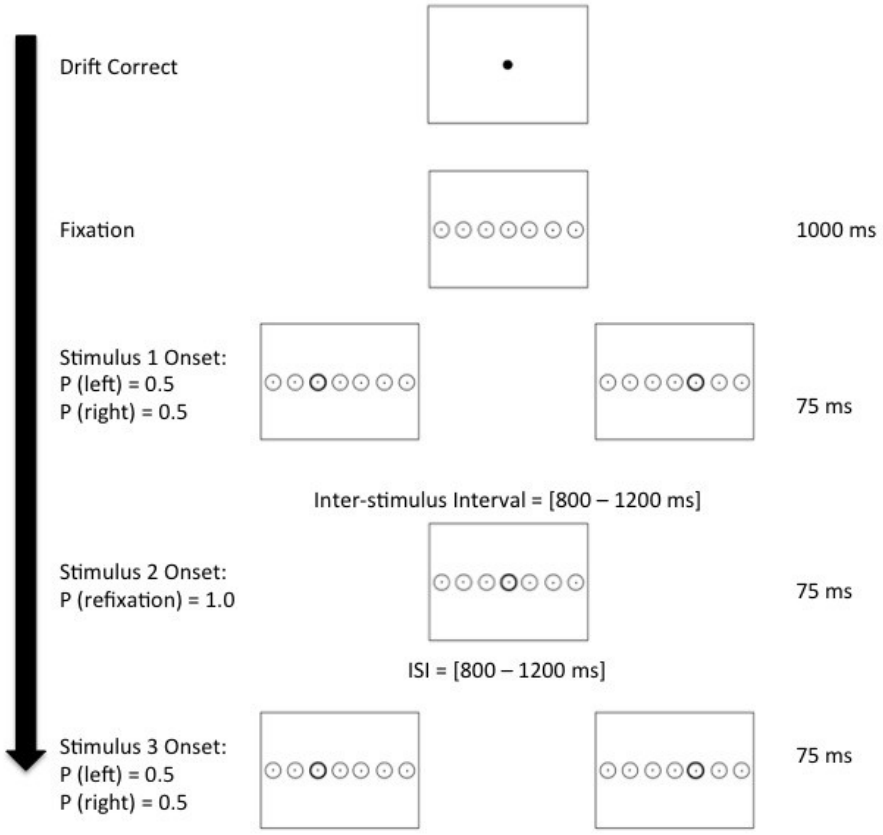

Figure 2.4. Timeline of events during a trial in the predictable exogenous condition.

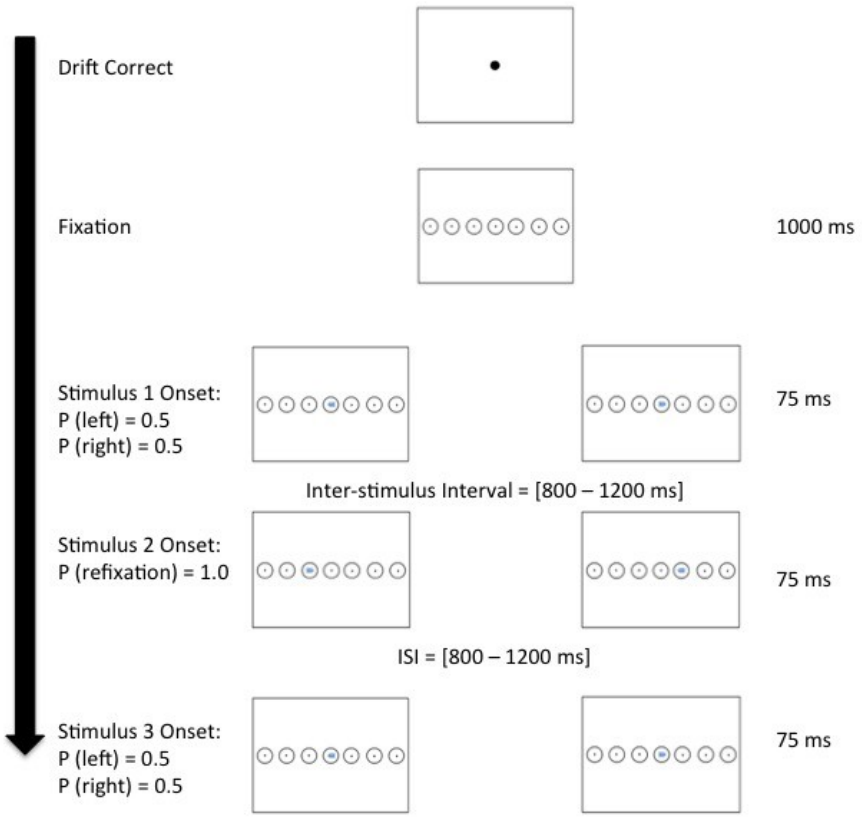

Figure 2.5. Timeline of events in the predictable endogenous condition.

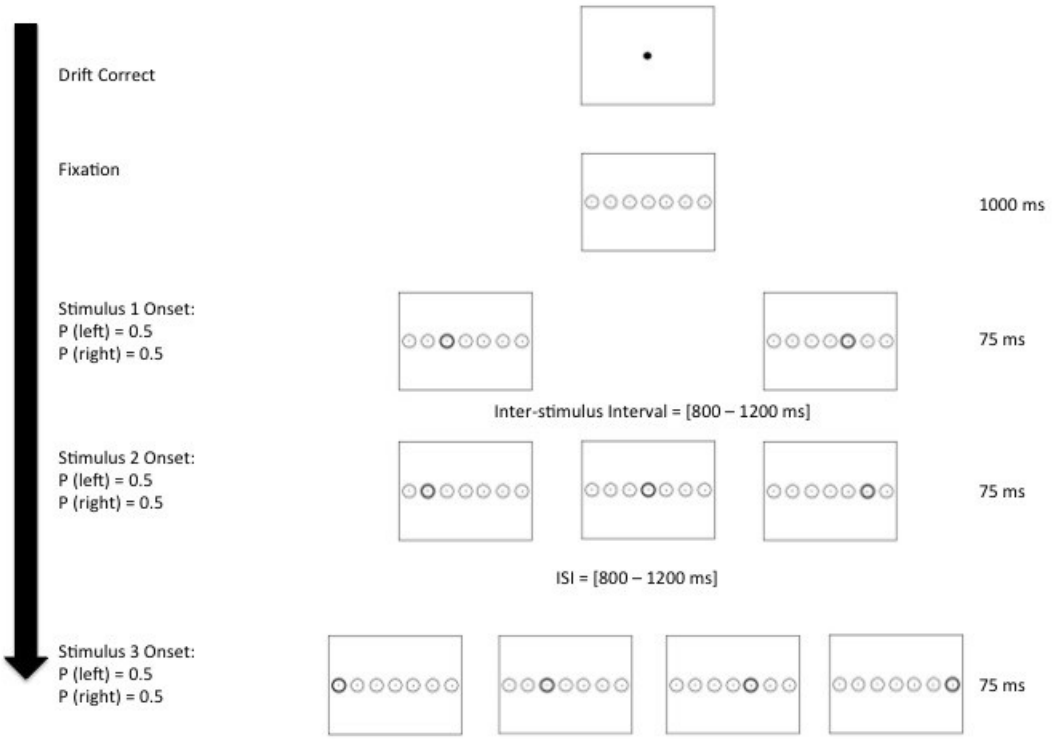

Figure 2.6. Timeline of events in the unpredictable exogenous condition. Sequence and timing details were identical for the unpredictable endogenous condition.

In the exogenous condition the boldening of an adjacent circle to the left or right (each with a probability of 0.5) indicated the first target stimulus, which was illuminated for 75 ms. The stimuli were black and presented against a grey background. Once the participant made an eye movement to the target they were required to maintain their gaze at this location until the onset of the next target, the duration of this inter-trial interval varied from 800 ms – 1200 ms. In the predictable condition, the next target was always located in the central location, therefore engaging a refixation movement in exactly the opposite direction to the first movement each time. However, in the unpredictable condition the target to the left or right of the current fixation point could be boldened,

therefore requiring a refixation of the central target only 50% of the time on an unpredictable basis. After the participant made the second eye movement, they maintained fixation at this location until the third and final target stimulus appeared. This inter-trial interval also varied from 800 ms – 1200 ms. In both the predictable and unpredictable conditions there was an equal likelihood that this movement would be to the left or right; however, because the starting location for this final saccade could vary in the unpredictable trials (i.e., 50% of the time it would begin from the central location like in all the predictable trials, but it could also begin from the left [25%] or right [25%] of center on some trials), the absolute location of the target varied accordingly. The successful completion of this final eye movement signaled the end of the trial as indicated by an onscreen message. The participant then returned to the drift correct screen and began the next trial. In the predictable conditions (exogenous and endogenous) there were four possible types of trials defined by the sequence of eye movements (LRL, LRR, RLR, RLL) with ten repetitions each for a total of 40 predictable trials. In the unpredictable condition there were a total of eight trial types (LRL, LRR, RLR, RLL, LLR, LLL, RRL, RRR) with ten repetitions each for a total of 80 unpredictable trials. Therefore the entire experiment consisted of 240 trials for each participant.

2.4 STATISTICAL ANALYSIS

To test the primary hypothesis, four separate ANOVAs were conducted, one for each of the experimental conditions. Note that only trial sequences consisting of refixation-type sequences (LRL, LRR, RLR, RLL) were included in this analysis, to ensure that equivalent events were compared for predictable and unpredictable conditions. Each of these was a two (final saccade direction: left/right) by two (initial

saccade direction: same or different from final saccade direction) ANOVA. All analyses were tested for significance at an alpha level of 0.05. The data were normally distributed, and sphericity was assumed since there were only two factors involved. Analyses were tested for significance at an alpha level of 0.05.

2.5 ERROR ANALYSIS AND DATA CLEANING

Error trials were excluded from all analyses prior to calculating reaction time means/standard deviations. Participants were eliminated based on high numbers of error trials and eliminating outlier reaction times. If a participant had a total error count for a condition that was greater than three standard deviations from the average number of errors for that condition, they were excluded. The average number of errors for each condition is shown in Table 2.1. Errors included anticipatory eye movements to any of the presented signals (participant moved prior to signal presentation), eye movements in the wrong direction (opposite to the direction indicated by the signal), eye movements that were too slow (timeout), and blinks, on a saccade-by-saccade basis.

Table 2.1

The percentage of error trials on which each error type occurred for each experimental condition. A timeout error is defined as a failure to respond quickly enough to the presentation of the signal (arrow or peripheral brightening) and an anticipation error is defined as initiating a saccade prior to the presentation of the signal.

Experimental condition	Error types					
	Fixation Error (%)	S1 Timeout (%)	S2 Timeout (%)	S3 Timeout (%)	S2 Anticipation (%)	S3 Anticipation (%)
Predictable endogenous	1.51	0.70	0.12	0.12	9.68	6.64
Predictable exogenous	1.94	0.31	0.00	0.05	7.26	3.02
Unpredictable endogenous	3.43	0.26	0.26	0.22	5.12	8.06
Unpredictable exogenous	2.95	0.45	0.00	0.08	5.40	9.13

The total number of error-free trials for each participant was calculated and an average number of errors across all trials for each of the four experimental conditions was generated (predictable endogenous, predictable exogenous, unpredictable endogenous, and unpredictable exogenous), this is shown in Table 2.2.

Table 2.2.
The average number of errors in each of the experimental conditions as a percentage of the number of trials in each condition. The absolute number of errors is shown in parentheses.

Experimental Condition	Average number of errors
Predictable exogenous	20% (8)
Predictable endogenous	13% (5)
Unpredictable exogenous	18% (14)
Unpredictable endogenous	18% (14)

If a participant's total number of error trials for a given condition was greater than three standard deviations away from the mean number of error trials for a given condition, they were excluded, as per the above reasons. This process led to the elimination of two participants from the predictable exogenous condition, one participant from the predictable endogenous, two from the unpredictable exogenous, and three from the unpredictable endogenous condition.

Reaction times for the final saccade in a trial sequence were processed on an individual rather than group basis, where if a given reaction time for a participant was greater than three standard deviations away from the participant's own mean, the reaction time was not included. The reaction time was not included, as it does not reflect performance typical of the participant, and was likely the result of one of the erroneous eye movements as described above. Additionally, only those trials in which all three eye movements were error free were included in the analysis and the lower bound for reaction times was set at 100 ms, meaning for a reaction time to be included it had to at least be

greater than 100 ms. Eye movements faster than 100 ms are the result of an anticipatory eye movement, as they are too fast to be in response to the onset of the signal. This led to a mean retention of 80 percent of trials for the predictable exogenous condition, 82 percent trials for the unpredictable exogenous condition, 87 percent for the predictable endogenous condition, and 82 percent for the unpredictable endogenous condition. To summarize, these percentages reflect the proportion of the total number of trials that were used for the analysis and were free from errors, outlier reaction time values, or anticipatory eye movements.

CHAPTER 3: RESULTS

3.1 REACTION TIME ANALYSIS: REFIXATION SEQUENCES

Refixation sequences are those where the second saccade was a return to center, and thus was always opposite in direction to the initial saccade. These are the sequences that offer a direct comparison to how inhibition of return is predominantly studied in the literature. This means that for the following analyses only the following sequences of saccades are included, regardless of predictability: LRL, LRR, RLR, and RLL. All of the sequences in the predictable conditions were composed of one of these combinations. Shown in Table 3.1 is a summary of the reaction times and accompanying standard deviations used for the primary analysis.

Table 3.1. *A summary of the reaction times (ms) used in the primary analysis, with standard error of the mean in parentheses.*

	Exogenous condition		Endogenous condition	
	Same	Different	Same	Different
Predictable	250. (9.0)	237 (9.0)	349 (10)	338 (9.4)
Unpredictable	246 (8.6)	235 (8.9)	341 (8.5)	341 (9.3)

3.1.1 Predictable exogenous

Shown in Figures 3.1 and 3.2 is a summary of the results, collapsed over final saccade direction (left/right), showing only the effect of the relative direction between the first and final saccades (same/different), from the predictable conditions of the experiment. To determine if significant inhibition of return occurred in a condition, a 2 (s1s3 offset: same or different) by 2 (s3 direction: left or right) ANOVA was conducted with saccadic

reaction times (SRT) to the third stimulus as the dependent variable: IOR should appear as a significant main effect of s1s3 offset with RT greater for 'same' compared to 'different' trials. A main effect of s1s3 offset was found, $F(1, 29) = 14.5$, $p = 0.001$, $MSE = 4480$, demonstrating that there was a significant difference between the SRTs of same (249 ms) and different direction (237 ms), such that SRTs to the same location were significantly slower than those to different locations, as predicted. A marginally significant main effect of s3 direction was also found $F(1, 29) = 4.09$, $p = 0.052$, $MSE = 18142$, indicating that SRTs were faster when they were rightward (231 ms) compared to leftward (255 ms). No significant interaction was found, $F(1, 29) = 0.010$, $p = 0.923$, $MSE = 3.03$.

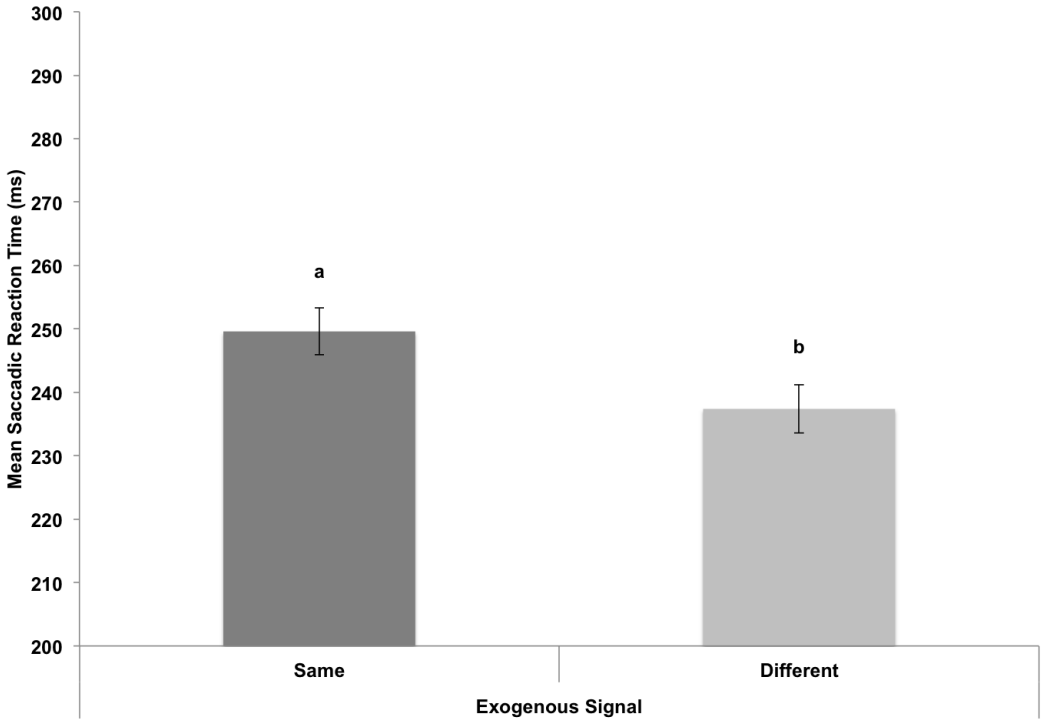

Figure 3.1. The mean saccadic reaction time (SRT) in milliseconds broken down by the offset between the first and final saccade directions (same versus different) for the predictable exogenous condition. Differing letters indicate conditions with a significant difference between same and different RTs, thus demonstrating inhibition of return (IOR). There is a significant IOR of 12.2 ms, error bars represent standard error of the mean.

3.1.2 Predictable endogenous

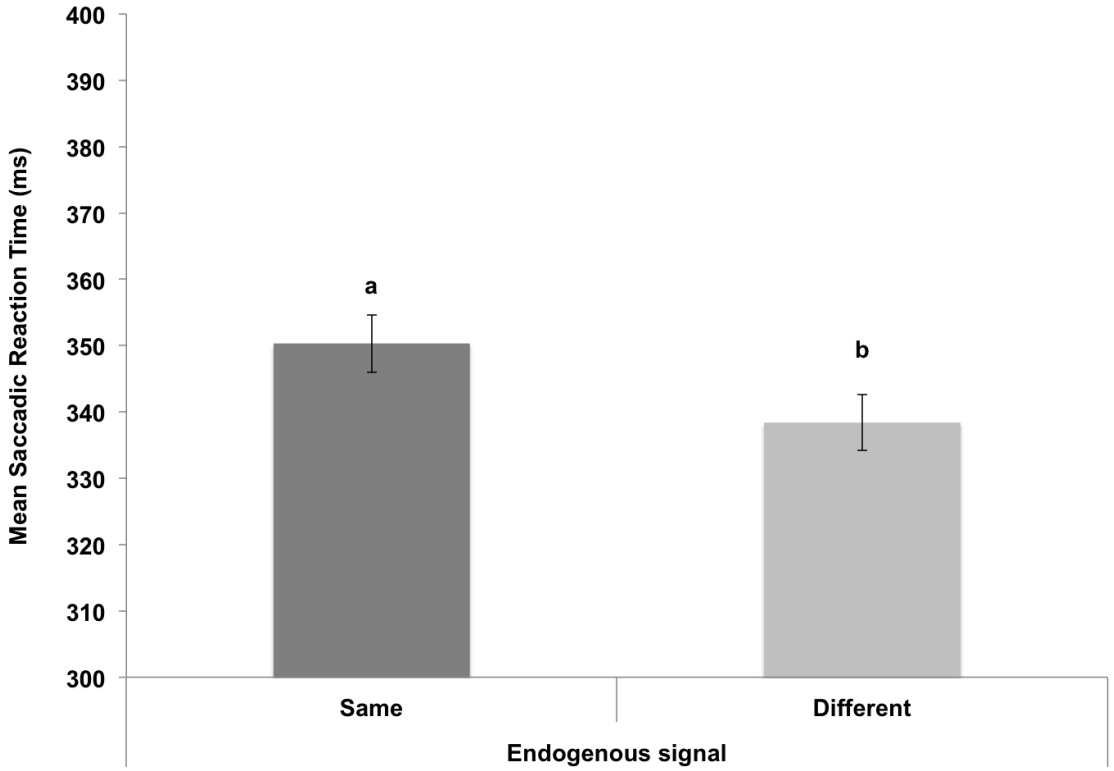

Figure 3.2. The mean saccadic reaction time (SRT) in milliseconds broken down by the offset between the first and final saccade directions (same versus different) for the predictable endogenous condition. Differing letters indicate conditions with a significant difference between same and different RTs, thus demonstrating inhibition of return (IOR). There is a significant IOR 11.9 ms, error bars represent standard error of the mean.

For the predictable endogenous condition a 2 (s1s3 offset: same or different) by 2 (s3 direction: left or right) repeated measures ANOVA was conducted using SRTs to the third stimulus as the dependent variable. A significant main effect of s1s3 offset was revealed, $F(1, 30) = 4.18$, $p=0.050$, $MSE = 3930$ showing that SRTs were faster for different (338 ms) directions compared to same (349 ms). There was no significant main effect of s3 direction, $F(1, 30) = 0.0480$, $p= 0.827$, $MSE = 140$, and no significant interaction, $F(1, 30) = 0.032$, $MSE = 13.8$.

3.1.3 Unpredictable exogenous

Figures 3.3 and 3.4 depict the mean saccadic reaction times from the unpredictable conditions of the experiment. It is important to note that this analysis only includes the half of completed trials with sequences matching those of the refixation trials, consistent with how the predictable condition was analyzed.

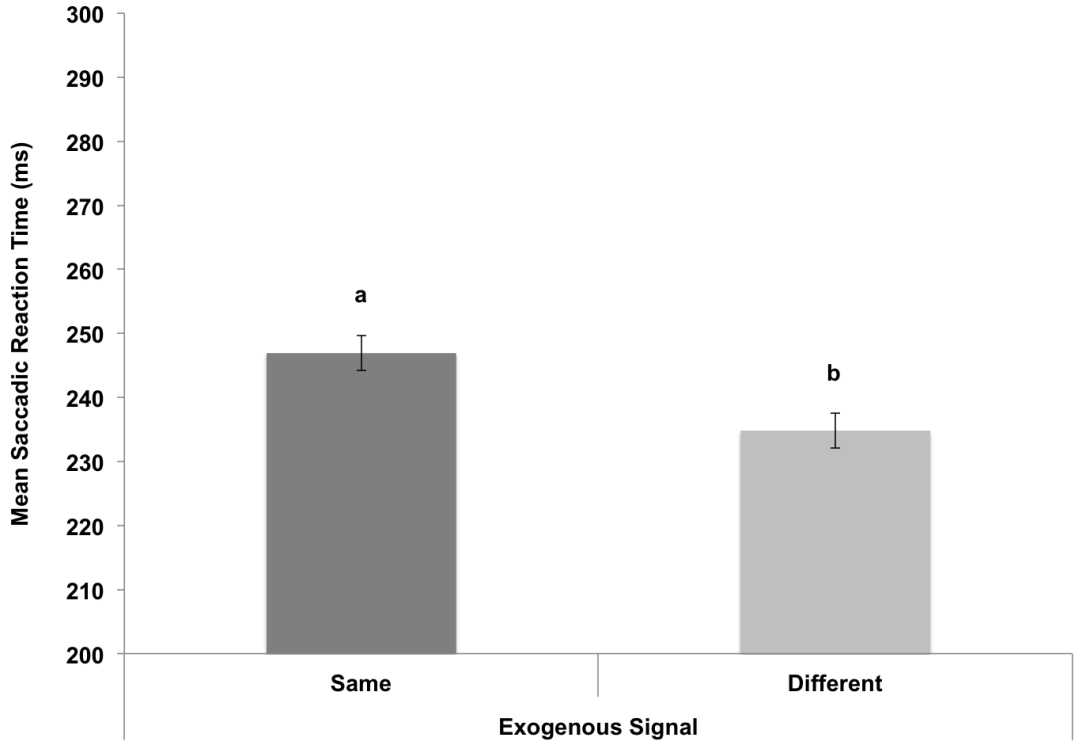

Figure 3.3. The mean saccadic reaction time (SRT) in milliseconds broken down by offset between the first and final saccade directions (same versus different) for the unpredictable exogenous condition. Differing letters indicate conditions with a significant difference between same and different RTs, thus demonstrating inhibition of return (IOR). Using exogenous signals there is a significant IOR of 12.1 ms. Error bars represent standard error of the mean.

A 2 (s1s3 offset: same or different) by 2 (s3 direction: left or right) ANOVA was conducted with SRTs to the third stimulus as the dependent variable for the unpredictable exogenous condition. A main effect of s1s3 offset was found $F(1, 29) = 13.5$, $p= 0.001$, $MSE = 4390$, demonstrating a significant difference between reaction times for same

(247 ms) and different directions (235 ms). This showed that SRTs in the same direction were significantly slower than those in different directions. No main effect of s3 direction was found, $F(1, 29) = 0.015$, $p = 0.905$, $MSE = 9.06$ and no significant interaction, $F(1, 29) = 2.74$, $p = 0.109$, $MSE = 721$.

3.1.4 Unpredictable endogenous

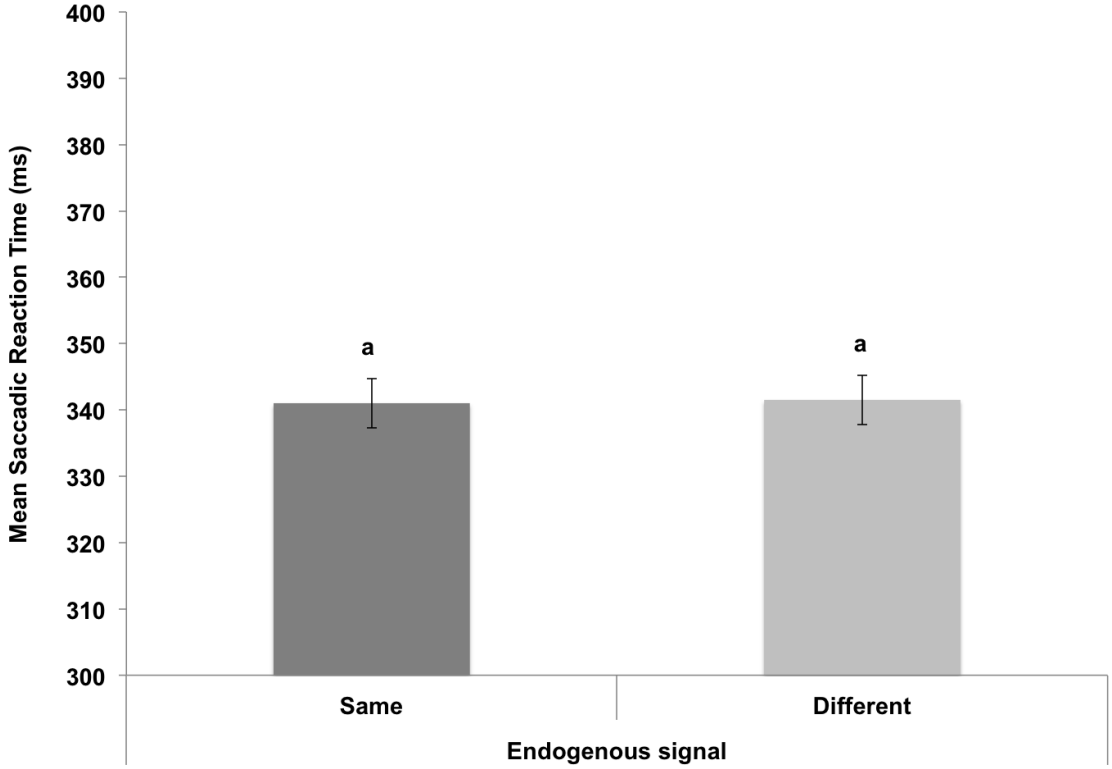

Figure 3.4. The mean saccadic reaction time (SRT) in milliseconds broken down by offset between the first and final saccade directions (same versus different) for the unpredictable endogenous condition. Identical letters indicate conditions with no significant difference between same and different RTs. Error bars represent standard error of the mean.

A 2 (s1s3 offset: same or different) by 2 (s3 direction: left or right) repeated measures ANOVA was conducted with SRTs to the third stimulus for the unpredictable endogenous condition. There was no significant main effect of s1s3 offset, $F(1, 28) =$

0.013, p= 0.910, MSE = 7.41, s3 direction, F(1, 28) = 0.214, p= 0.647, MSE = 188, and no significant interaction, F(1, 28) = 2.09, p= 0.159, MSE = 3320.

3.2 REACTION TIME ANALYSIS: 1-BACK SEQUENCES

Further analyses were conducted (on unpredictable trial sequences only) to determine if saccade SRT was affected by the direction of the immediately preceding saccade (second in the sequence). This was done as a means of comparing results with Anderson, Yadav and Carpenter's (2008), and Jones et al.'s (2014) studies that looked at consecutive saccades in unpredictable directions. Data were cleaned consistent with the above-described procedure (see section 3.2), and errors were dropped based on the same criteria. A total of 80 trials were considered for each participant with 82 percent trials for the unpredictable exogenous condition, and 82 percent for the unpredictable endogenous included in the analysis after cleaning. This analysis considered all trial types of all directions, regardless of whether the second saccade was the same or opposite to the first. Thus it was different than the analysis in section 3.2 which only considered trial sequences with a second saccade that was opposite to the first.

A 2 (s1s2 offset: same or different) by 2 (s2 direction: left or right) repeated measures ANOVA was conducted for the exogenous experimental condition, the results of which are shown in Figure 3.5. This showed a significant main effect of s2 direction, F (1,29) = 7.19, p = 0.012, MSE = 3200, such that leftward saccade RT (241 ms) was slower than rightward saccade RT (231 ms). There was also a significant main effect of s1s2 offset, F (1,29) = 16.8, p <0.001, MSE = 4930. When a saccade was made in the same direction (243 ms) as the preceding one it was slower than a saccade made in the

opposite direction (229 ms). A significant interaction between s2 direction and s1s2 offset was also found, F (1, 29) = 4.40, p = 0.045, MSE = 516.

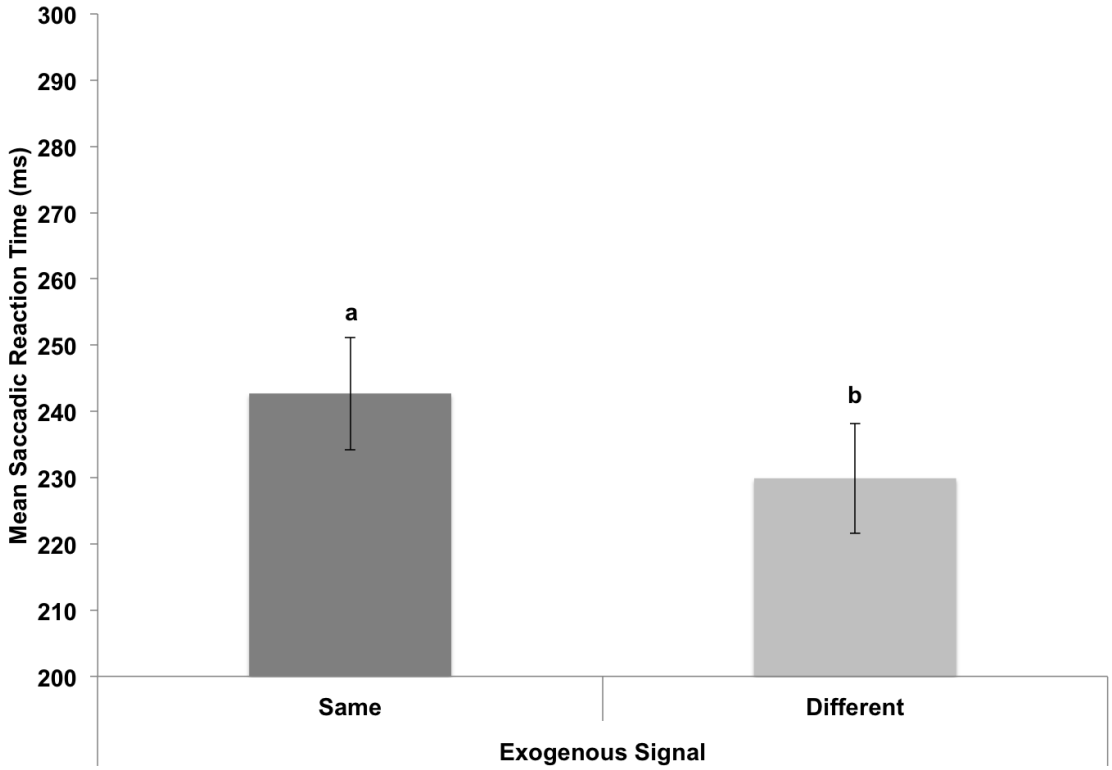

Figure 3.5. The mean saccadic reaction time (SRT) in milliseconds broken down by offset between the first and second saccade directions (same versus different) for the exogenous conditions. Different letters indicate conditions with a significant difference between same and different RTs. Error bars represent standard error of the mean.

A 2 (s2s3 offset: same or different) by 2 (s3 direction: left or right) repeated measures ANOVA was conducted for the exogenous experimental condition; these results are shown in Figure 3.6. This showed no significant main effect of s2s3 offset, F (1,29) = 0.166, p = .687, MSE = 71.8, and no significant main effect of the direction of the final saccade, F (1,29) = 3.67, p = 0.065, MSE = 1160; the interaction between these two variables was also not significant, F(1,29) = 0.276, p = 0.603, MSE = 53.5.

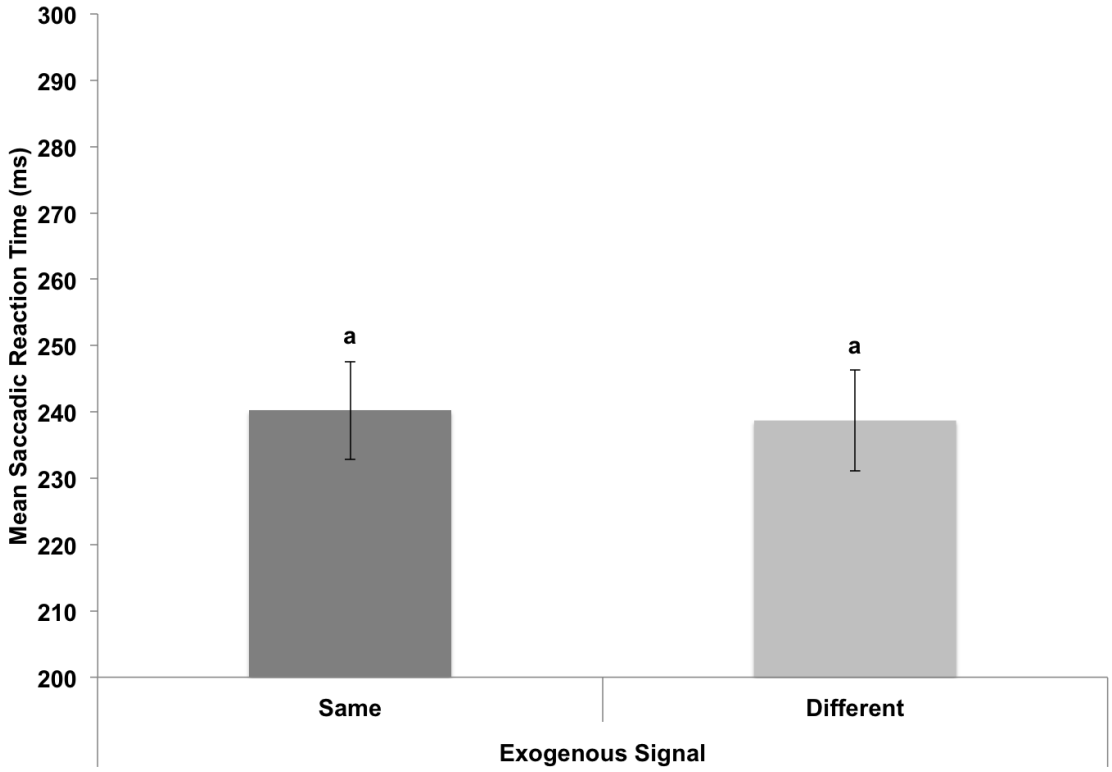

Figure 3.6. The mean saccadic reaction time (SRT) in milliseconds broken down by offset between the second and final saccade directions (same versus different) for the exogenous conditions. Identical letters indicate conditions with no significant difference between same and different RTs. Error bars represent standard error of the mean.

The 2 (s1s2 offset: same or different) by 2 (s2 direction: left or right) repeated measures ANOVA for the endogenous condition showed no significant main effect of s1s2 offset, $F(1,28) = 0.834$, $p = 0.369$, $MSE = 3650$, and no main effect of s2 direction, $F(1, 28) = 0.039$, $p = 0.845$, $MSE = 23.6$. No significant interaction was found, $F(1,28) = 0.629$, $p = 0.434$, $MSE = 105$. These results are shown in Figure 3.7.

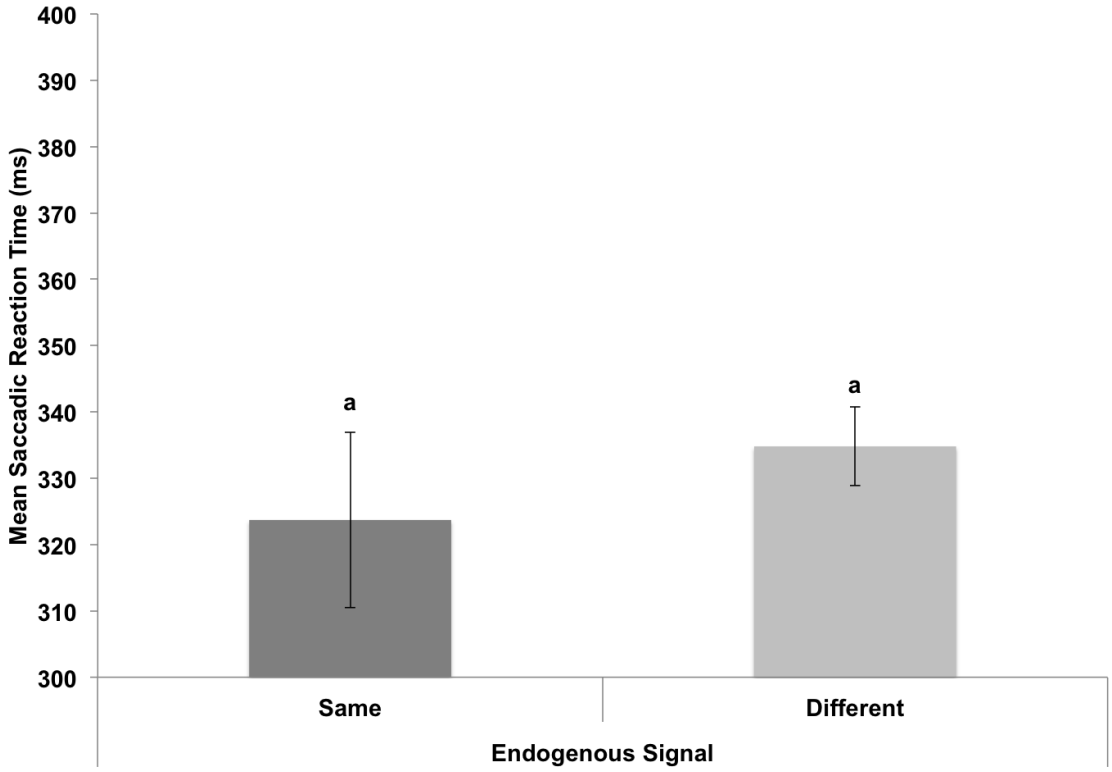

Figure 3.7. The mean saccadic reaction time (SRT) in milliseconds broken down by offset between the first and second saccade directions (same versus different) for the endogenous condition. Identical letters indicate conditions with no significant difference between same and different RTs. Error bars represent standard error of the mean.

The 2 (s2s3 offset: same or different) by 2 (s3 direction: left or right) repeated measures ANOVA for the endogenous condition showed no significant main effects of s2s3 offset, $F(1,28) = 1.08$, $p = 0.307$, $MSE = 251$, or s3 direction $F(1,28) = 0.687$, $p = 0.414$, $MSE = 355$, and no significant interaction, $F(1,28) = 0.328$, $p = 0.572$, $MSE = 86.4$. Figure 3.8 shows these results.

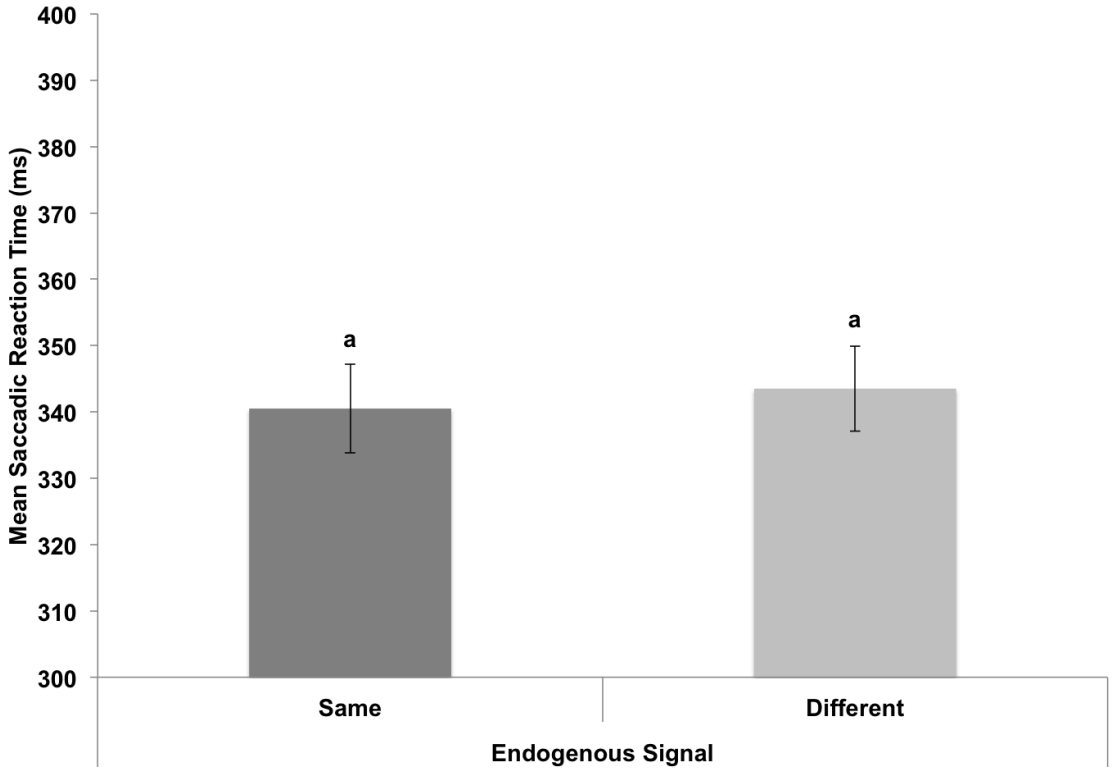

Figure 3.8. The mean saccadic reaction time (SRT) in milliseconds broken down by offset between the second and final saccade directions (same versus different) for the unpredictable endogenous condition. Identical letters indicate conditions with no significant difference between same and different RTs. Error bars represent standard error of the mean.

3.3 REACTION TIME ANALYSIS: 2-BACK SEQUENCES

An analysis of the effect of the offset between the first and final saccade and the final saccade direction on SRTs to the final stimulus was also conducted, with all trials included regardless of whether the second saccade was opposite in direction to the initial saccade. This means that in addition to the IOR-like sequences mentioned above, this analysis considered 100 percent of the trials in the unpredictable condition, including LLL, LLR, RRR, and RRL. That is to say, this analysis examined trials where the first and third saccade could be in the same direction and to the same location, and also trials where the first and third saccade could be in the same direction but to a different location.

Unlike the “same direction” trials considered in section 3.2 where return to center was always part of the trial sequence, these “same direction” trials also included those where all three saccades could be in the same direction.

A 2 (s1s3 offset: same or different) by 2 (s3 direction: left or right) repeated measures ANOVA was conducted for the exogenous experimental condition. This showed a significant main effect of s1s3 offset, $F(1,29) = 4.23$, $p < 0.049$, $MSE = 1400$, with SRTs slower when the first and final saccades were in the same direction (242 ms) compared to opposite direction (235 ms). A significant main effect of final saccade direction was also found, $F(1,29) = 36.9$, $p < 0.001$, $MSE = 8650$, such that leftward saccades (248 ms) were slower than rightward (230 ms). However the interaction between s1s3 offset and s3 direction was not significant, $F(1,29) = 0.133$, $p = 0.718$, $MSE = 23.6$. Figure 3.9 shows these results.

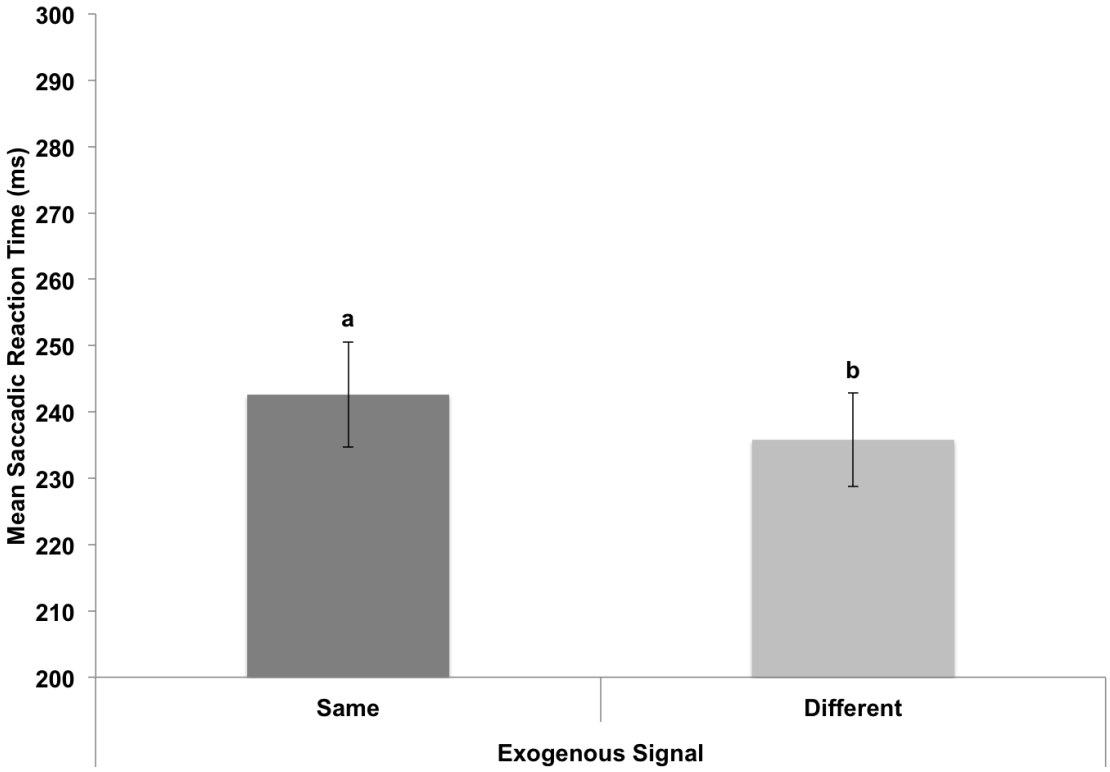

Figure 3.9. The mean saccadic reaction time (SRT) in milliseconds broken down by offset between the first and final saccade directions (same versus different) for the exogenous conditions. This analysis was inclusive of all trials and saccade sequences. Significant differences are indicated by different letters. Error bars represent standard error of the mean.

The 2 (s1s3 offset: same or different) by 2 (s3 direction: left or right) repeated measures ANOVA for the endogenous condition showed no significant main effects of s1s3 offset, $F(1,28) = 0.685$, $p = 0.415$, $MSE = 262$, or final saccade direction, $F(1,28) = 1.07$, $p = 0.309$, $MSE = 394$, and no significant interaction, $F(1,28) = 0.243$, $p = 0.626$, $MSE = 84.6$. These results are shown in Figure 3.10.

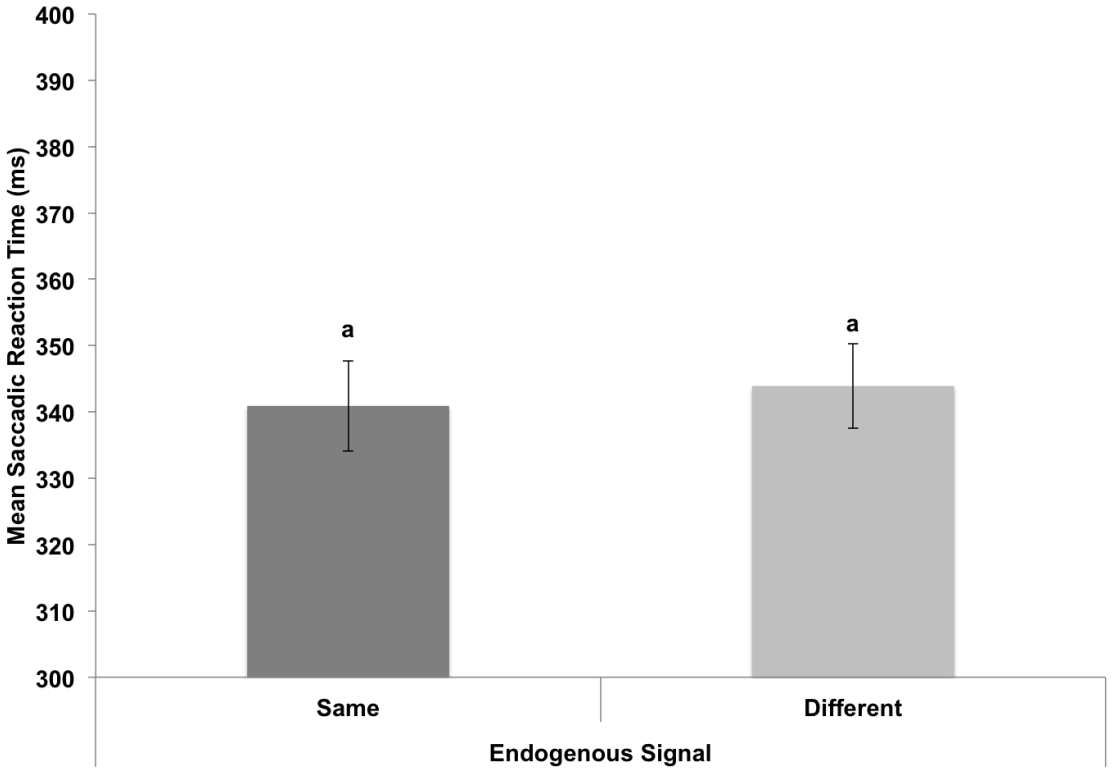

Figure 3.10. The mean saccadic reaction time (SRT) in milliseconds broken down by offset between the first and final saccade directions (same versus different) for the endogenous conditions. This analysis was inclusive of all trials and saccade sequences. Significant differences are indicated by different letters. Error bars represent standard error of the mean.

CHAPTER 4: DISCUSSION

The main objective of the present experiment was to investigate whether the predictability of a refixation event affects the presence and/or magnitude of IOR as measured in sequences of three saccades that match traditional target-target task paradigms. Since IOR has been observed in tasks that do and do not require refixation, IOR may only depend on the directions of the sequential eye movements involved, and thus would be similarly observed under both predictable and unpredictable refixation conditions. Two experimental conditions tested this predictable task structure, one using exogenous stimuli (bold peripheral stimulus) and the other endogenous stimuli (arrows presented at the fixated location). Two additional experimental conditions tested the scenario in which predictability was removed, with the second saccade no longer a consistent refixation. Instead, the second saccade in the sequence was just as likely to be in the same, or opposite direction to the first saccade.

4.1 IOR IS OBSERVED IN PREDICTABLE REFIXATION TASK STRUCTURES

The primary analysis of the predictable experimental conditions revealed a significant main effect of the offset between the first and final saccades for both the exogenous and endogenous conditions, consistent with IOR: saccadic reaction times to the final stimulus were significantly slower when they were in the same direction as the first stimulus. This result demonstrates that the present study was successful in replicating past research (Cowper-Smith et al., 2013; Maylor and Hockey, 1985; Taylor and Klein, 2000), generating IOR with both exogenous and endogenous stimuli. The current study can be framed as a target-target study, meaning each signal is itself a target or directs a movement to a target, as opposed to a cue-target study. In cue-target studies,

the first and often second signals do not require movement. As this experiment is target-target, it offers some comparison with experimental conditions used by Taylor and Klein (2000) and Cowper-Smith et al (2013).

The target-target task used by Taylor and Klein (2000) where peripheral onsets signaled target location, revealed IOR with a magnitude of 21 ms. When central arrows were used to signal target location, IOR with a magnitude of 21 ms was found. These magnitudes are somewhat greater than those observed in the present study, which revealed IOR magnitudes of ~12 ms for both exogenous and endogenous signals. Of note though is a difference in the return to center signal. In the present study, the return to center signal matched the stimulus type of the relevant experimental condition. That is to say, in the endogenous condition where arrows were used to direct saccades to the target location, an arrow was also used to direct the eyes back to center. Consistent with this, in the exogenous condition, the signal to return to center was the central placeholder becoming bold. These return to center signals contrast with those used by Taylor and Klein (2000), since in their experiment when arrow signals were used for target-target trials, the return to center was always directed by a flash at central fixation. Therefore, although both studies revealed IOR using arrow signals, it is likely that the present study revealed a primarily motor IOR, whereas Taylor and Klein (2000) revealed an IOR consisting of motor effects from the execution of the saccades, but also sensory effects due to the central flash.

A comparison of the IOR scores between these two studies supports this sensory and motor distinction. The magnitude of IOR for the exogenous condition of Taylor and Klein's (2000) target-target study was 21 ms and their endogenous condition of the same

experiment produced IOR with a magnitude of 21 ms also. In the present study the magnitude of IOR for both the exogenous and endogenous predictable conditions was approximately 12 ms.

The experiment by Cowper-Smith et al. (2013) also distinguished between exogenous and endogenous effects in a target-target task. Their method involved movements in four directions, however upon extracting the comparison between their 0 degree and 180 directions (in the horizontal plane), an exogenous IOR of approximately 20 ms was revealed, and an endogenous IOR of approximately 10 ms. The endogenous results are comparable to that of the current study, although the exogenous results differ. Some of these apparent discrepancies in the two effects are likely attributable to the difference in the return to center signal and subsequently the forms of IOR generated, if said return to center signal combined sensory and motor traits. The difference highlights one of the ways that the return to center saccade can interfere and influence IOR, although there is a possibility that the differences in IOR magnitude could also be attributed to timing or stimulus differences, as well as differences in the stimulus array (the current study used a horizontal array covering a wider area of visual angle than the horizontal and vertical array of Cowper-Smith et al. (2013) that was centrally presented).

Taylor and Klein (2000) used the oculomotor readiness hypothesis to explain the inhibition of return they observed. This hypothesis postulates that IOR will be the same, regardless of signal type provided that the eyes move. The present results contradict this and imply that signal type plays an important role in the type and magnitude of IOR that will be observed by an experiment. Were the oculomotor hypothesis correct, the current study would have shown similar IOR regardless of signal type. Instead, the present

results demonstrate that in the absence of predictability, different signal types reveal different effects. Cowper-Smith et al. (2012) also showed differences between IOR revealed by exogenous in comparison to endogenous signals, further supporting the notion that endogenously generated IOR has a greater sensitivity to predictability.

4.2 IOR IN UNPREDICTABLE REFIXATION TASKS

The results of the present study demonstrate that predictable refixation saccades can have an effect on the type and duration of IOR that is observed depending on the signal type used. In the unpredictable condition, using exogenous signals, saccadic reaction times were significantly faster when the eyes were moving in a different direction for the final saccade compared to the first. This effect is not remarkably different than that seen in the predictable condition, indicating the presence of IOR. However, when endogenous signals are used to direct eye movements, reaction times were not statistically different, regardless of whether the first and final saccades are in the same or in different directions; in other words, IOR was not observed.

Since the two unpredictable conditions were methodologically identical except for the nature of the signal used to direct saccades, the absence of inhibition of return in the endogenous condition is unique to endogenously guided saccades. The type of IOR that manifests in tasks involving endogenous saccades is therefore sensitive to predictability. This finding reveals an important distinction between the form of IOR that is observed when using exogenous compared to endogenous signals. The current results showing different effects of IOR under exogenous versus endogenous conditions, is consistent with much of the present literature, which generally demonstrates differences in IOR for these two stimulus types. The foundation of this IOR is where the results diverge. Some

(Taylor and Klein, 2000) maintain that IOR is the same regardless of signal type, provided the eyes move. IOR elicited by endogenous signals is purported by others (Cowper-Smith et al., 2012, 2013) to be a motoric effect, and based on the present study, this motoric effect is reliant on the presence of predictability. Such a finding indicates a necessary reevaluation of previous studies that use endogenous signals to direct saccades and include a return to center as part of the task structure (e.g. Abrams and Dobkin, 1994; Copwper-Smith et al., 2012; 2013) This study sets a precedent for the role of predictability in studies of inhibition of return, and studies of IOR that utilize endogenous signals.

The role of predictability has potential implications for a study by Cowper-Smith, Eskes, and Westwood (2012). Their experiment was specifically designed to determine if inhibition of return was present after all sensory events and motor preparation had occurred. Each saccade in the study by Cowper-Smith, Eskes, and Westwood (2012) was completely predictable at the time of execution because participants were informed of the required movement direction before the signal to move was given. Thus, any delays observed in the resulting movement could not be due to processing delays related to processing of the stimulus or selection/preparation of the required movement. In each trial, saccade direction was signaled by centrally presented arrows, but participants were instructed not to initiate the saccade until a subsequent "go" signal. Once the signal to go was given, indicated by the central placeholder changing color, the participant could make the saccade in the signaled direction. This method ensured that participants' eye movements were prepared and ready to execute in advance of the "go" signal.

The authors successfully revealed IOR within the paradigm and proposed that IOR may be either the result of a motor execution bias or a delay in late-stage attentional processing, since it was revealed independently of sensory detection and saccade preparation. They proposed that were their effect a motor execution bias, this bias could arise from a small selection of neural substrates involved in motor execution. Any structure must necessarily be downstream from the superior colliculus, which has a firmly established role in saccade programming (Munoz, Dorris, Pare, and Everling, 2000). The authors also ruled out any mechanism at the level of ocular muscles since these muscles have long been shown to be fatigue resistant (Fuchs and Binder, 1983). The results of the present study diverge from those reported by Cowper-Smith et al. (2012), since if IOR is simply the result of motor execution processes, predictability should not matter. The current results demonstrate that predictability does matter, particularly when endogenous signals are involved. Taken together, the two studies imply that IOR may only be one effect, but it arises for different reasons under different task conditions.

The alternative proposal of Cowper-Smith, Eskes and Westwood (2012) implicating attentional processes opens up a greater realm of possible neural substrates responsible for IOR in their study. These include the superior colliculus itself, posterior parietal cortex, or the prefrontal cortex. The posterior parietal and prefrontal cortex are areas are used for higher cognitive functions and are implicated in the control of attention (Kolb and Whishaw, 2009), suggesting that IOR elicited by endogenous signals is subject to top-down influences such as predictability. If IOR were attached to predictability itself, one would expect to see it at all processing stages that are subject to said predictability,

from sensory detection to motor execution, inclusive of saccade preparation. IOR is clearly a complicated phenomenon that has now been shown to affect various processing stages based on task and signal type. The results of the present study suggest that predictability may modulate endogenously elicited IOR, since in the absence of predictability, IOR is also absent. The absence of IOR in the unpredictable endogenous condition may be the result of eliminating this top-down influence. One way to further determine the role of predictability in endogenous orienting would be to conduct an experiment similar to that of Cowper-Smith, Eskes, and Westwood but have an additional condition that lacks a predictable return to center saccade. If such a study were to reveal a deficit in IOR using endogenous signals after eliminating the sensory and saccade preparation stages of processing, this would lend credence to the crucial role of predictability in endogenous IOR.

Also among the studies affected by a potential variation in IOR observed using endogenous signals is an experiment by Fecteau et al. (2004). This study is important to note as it uses an alternative endogenous signal (colors) to indicate saccade direction as well as a prosaccade/antisaccade task, to investigate alternation advantage. Alternation advantage is the tendency for participants to respond faster to a signal when the response requirement is opposite in direction to the previous one. It is a similar phenomenon, if not identical to inhibition of return, so it represents an additional area of scientific literature that may be impacted by determining the influence of predictability on IOR. The task used by the authors only involved one saccade per trial, however in order to move from trial to trial, a return to the central fixation area was required. In their purely exogenous task that used only prosaccades, participants maintained fixation and then moved their

eyes in response to the onset of a visual signal either to the left or right of fixation. This was the reaction time measured, and then participants moved their gaze back to central fixation to begin the next trial. The following trial could then involve an alternation response, or the same response. The authors found that participants′ responses were quicker when the response was alternating from the previous response. However, this is not a true alternation, since returning to center between trials is an alternation response inherent in the task structure. The results of the present study do not portend this finding, however they may cause the results of the prosaccade/antisaccade task to be questioned. This task involved interleaved trials of saccades to the visually presented target (prosaccades) that were signaled by red central light, and saccades in the opposite direction of the visually presented target that were signaled by a green central light. The nature of the target in the antisaccade task is not stated. The authors found that alternation advantage was based on the location of the previous target, and not due to the direction of the previous saccade. They therefore concluded that the difference in the two saccade types (prosaccades and antisaccades) was attributable to a sensory and not a motor effect. The results of the present study bring doubt to this conclusion, since a return to center was required between trials. This return to center may have had undue influence on their results, since it is predictable. They were only accounting for the direction of the previous prosaccade or antisaccade, and not for the direction of the saccade required to bring gaze back to center, which would also vary from trial to trial. The return to center saccade would also be classified as a form of endogenous saccade response, since it was a rule-based part of the task, meaning that they were testing a greater number of endogenous trials than they were accounting for. To further solidify their conclusions, a study

including a condition of multiple saccades within a trial without a return to center would be ideal. If the results of such an experiment still showed alternation advantage that was based on the location of the previous target, and not the direction of the previous saccade, this would lend support to their claim of a sensory basis of the effect.

A study by McInnes, Kruger, and Hunt (2015) demonstrated a dichotomy between motor and attentional IOR, and the results of their saccadic experiment contrast with those of the current study. By defining different saccades as either "independent" or "parallel", the authors showed that when saccades were programmed in parallel, IOR was not present whereas independent saccades were subject to IOR. For comparison, the parallel sequences of McInnes, Kruger and Hunt are like those in the predictable condition of the present study, thus the results are opposite. The methodology of their study involved an endogenous-like task where participants fixated peripheral targets as either an independent saccade, or in parallel with another saccade. Starting at a fixation point, participants' saccades were directed by instructions of which color targets (e.g. red, then blue) in a six-target array to look at. The saccadic latency to each of the targets was measured using eye-tracking technology. As mentioned, these latencies demonstrated an opposite effect to that seen in the current study. There was a marked reduction in IOR for saccades that were programmed in parallel, and robust IOR for saccades prepared independently. Of note though, are methodological differences between the two studies, including a lack of a return to center saccade throughout. The current study used clearly distinguishable signals to direct all eye movements throughout the tasks (arrows and peripheral onsets). McInnes et al.'s study used a task that combined features of exogenous and endogenous signals. The color component of the task used for the first saccades was

endogenous, however the final target used to probe for IOR was presented peripherally, and thus an exogenous component. These methodological differences make it difficult to ascertain whether the same effects are being considered. A hybrid of the two studies, where the two methodologies could be compared to one another may offer more clarity on how the effects in each of the studies truly compare.

The findings of the present study also have relevance and implications for Anderson, Yadav, and Carpenter's (2008) original study using the random walk paradigm. Their primary finding was that saccadic reaction time was affected by the direction of a preceding saccade, and this effect diminished over time. They found that if a saccade followed a saccade of the same direction, it was faster than one that had been preceded by a saccade of the opposite direction. This effect was also seen when comparing saccades that were separated by an intervening saccade of either direction. Anderson and his colleagues' methodology was significantly different than that of the current experiment, and thus the present study serves to further connect the findings of the random walk study with the inhibition of return literature. The findings of the two studies differ though when examining the unpredictable conditions of the present study at the n-1 level. Anderson, Yadav, and Carpenter (2008) noted a significant reduction in saccadic latency for successive eye movements in the same direction, whereas the current results showed a significant reduction in saccadic latencies for successive eye movements in opposite directions. This finding, distinguishes the present study from that of Anderson, Yadav and Carpenter, and is limited to saccades driven by exogenous signals. When the current study expanded the paradigm to include endogenous signals, no significant effect of prior saccade direction was revealed. Since exogenous-driven

saccades were subject to effects based on prior saccade direction, it is of interest to determine how that effect arises. According to Anderson, Yadav and Carpenter (2008) the reduction in saccadic latency to targets in the same direction is due to repeated inputs to the superior colliculus. The superior colliculus is a likely candidate as a source for this effect due to its structural organization, and the basic behavior of neurons (repeated input lowering the threshold to fire). There are other structures that may be implicated though when predictable saccades or volitional saccades are involved (Cowper-Smith, Eskes, and Westwood, 2012).

Anderson, Yadav, and Carpenter (2008) also included a condition where they tested saccadic latencies in a refixation (also known as a return to center) task. They found that the latency of saccades returning gaze to center (refixation saccades) had an impact on the latency of the final saccade in the sequence of three saccades, such that it appeared to cancel out any potential additive effect of repeated saccades. The overall effect found was that of weak inhibition of return. The present experiment also found shorter IOR latencies than that typically seen in the literature (e.g. Taylor and Klein, 2000). It is possible that both effects are the same, but the limitations of Anderson, Yadav, and Carpenter's (2008) task led them to even shorter latencies. Their limited participant pool (the three authors) and the lack of placeholders may be contributing factors in these shorter reaction times. The absence of placeholders in their study is a limitation for ecological relevance, since objects that humans saccade to in everyday life tend to persist in their locations and not disappear as the next object appears to us.

A study by Jones, Cowper-Smith, and Westwood (2014) examined the effect of the presence or absence of placeholders within a random walk task. In fact, the study was

also the first to explicitly use the random walk paradigm in an investigation of inhibition of return, particularly in a group design. Jones et al. (2014) found a significant IOR-like effect in a condition that lacked placeholders for targets, maintained placeholders for targets, and for a condition that used central arrows to signal saccade direction. Jones et al. (2014) labeled the IOR-like effect a "same direction benefit", since the effect was consistent with IOR, but did not involve a refixation event. The level at which the same direction benefit was revealed varied by condition. In the condition with placeholders, a same direction benefit was only revealed when measuring the latency of saccades separated by two or three intervening saccades. For the condition without placeholders, a same direction benefit was revealed when measuring the latency of the immediately preceding saccade, two, and three saccades previous. This supports Anderson, Yadav, and Carpenter's (2008) assertion of a saccade history affect, albeit diminishing. Their results may differ from Jones, Cowper-Smith and Westwood (2014) because of differences between the individual and group designs, but the effect remains similar.

The 2-back results (final saccade versus two saccades back) of Jones, Cowper-Smith and Westwood (2014) do not correspond with those of the present study. The advantage of the present study is that it offers a direct comparison of tasks using predictable refixation, and tasks that do not. The present study found inhibition of return in the unpredictable exogenous condition (nearly identical to that of Jones, Cowper-Smith, and Westwood's peripheral targets with placeholders) when comparing final saccade direction with initial saccade, and yet the other study found no such effect. However, the primary analysis of the present experiment was restricted to refixation sequences, whereas that of Jones et al. (2014) incorporated all sequences. When

comparing similar conditions, Jones et al. (2014) only revealed a same direction benefit for saccades that were three back. The results of the present study also diverge from Jones et al. (2014) at the n-1 level, as an opposite direction benefit was seen at this level, in contrast to a same direction benefit. The two studies also differed in the endogenous signal conditions. Both studies used centrally presented arrows to signal saccade direction and therefore the difference cannot be attributed to the nature of the signal. Without a return to center signal, the present study did not reveal inhibition of return at any level. However, Jones, Cowper-Smith, and Westwood (2014) did reveal inhibition of return when comparing saccades that were one back, two back, and three back from the saccade of interest. Ultimately this indicates that a great deal of research is still required to reconcile the difference between saccadic effects that occur when using signals of varying types, and whether a refixation saccade is required as part of the task structure.

4.3 LIMITATIONS AND FUTURE DIRECTIONS

The present findings are limited in their scope of relevance and practicality. In terms of functioning in everyday life, one typically moves their eyes in multiple directions, and not just horizontally. The present results only directly measure saccades made along a horizontal axis, limiting their applicability, yet the random nature of the task brings it closer to human behavior. Tasks that use a return to center saccade after each saccade in a trial are not accounting for how we may unpredictably move our eyes, so this study takes us in a direction that will help improve the understanding of said (un)predictability. Future studies should investigate this further by including additional directions within a random saccade task structure. The present study (and also that of Anderson, Yadav, and Carpenter, 2008) does not account for the direction of the

intervening saccade, merely whether it is predictable or unpredictable, and the number of intervening saccades. Future studies may reveal additional details about the above-discussed effects if the number of intervening saccades of each direction was measured. This may offer insight into the hypothesis of Anderson et al. (2008) that saccades of opposite directions will cancel their respective latencies. The results are also limited by the richness of the testing environment. The stimuli presented in the current study were simplistic and not reflective of the diversity of our everyday environment. As this study moved inhibition of return research away from the refixation "fixation", future studies should continue to move towards testing with more diverse stimuli, up to and including dynamic stimuli. With regards to stimuli, it would also be of value to investigate the effects of predictability using endogenous stimuli other than arrows, to determine if the effects seen in the endogenous condition of the present study are replicable under such circumstances. Once sufficient evidence is established that indicates how IOR manifests in the brain at the neural level, it may also be of interest to upregulate or downregulate particular pathways to determine what influence, if any, this would have on IOR. Such an undertaking would assist in the understanding of the underling processes that give rise to IOR, and its potential purpose.

Aside from its scientific merit, and contribution to the IOR literature, the present study does have certain broad applications. The study increases our understanding of IOR, and this can inform a number of different fields. By understanding how eye movements are executed, and how attention is allocated, we can potentially influence where and how people move their eyes. This knowledge could help marketers to develop ways of highlighting their products, and even provide greater evidence for why it is

important to keeps ones eyes on the road while driving, since looking away from the road will delay reaction times to events occurring on the road. This research could also lead to the development of specific search strategies, designed to reduce the number of items that go undetected in any number of fields where searching is required.

4.4 CONCLUSION

The present study is the first to directly examine the effect of predictability in the target-refixation-target task structure that is so commonly used to study IOR. Using the principles of Anderson, Yadav, and Carpenter's (2008) random walk paradigm, it was found that under conditions involving a predictable return to center saccade, inhibition of return is can be generated and revealed using both exogenous and endogenous signals. However, using endogenous signals, inhibition of return was not generated under unpredictable conditions. Saccades in response to exogenous signals are robust, sensory driven events and not easily influenced by top-down effects such as the presence or absence of predictability. Saccades in response to endogenous signals however, can be affected by top-down influences such as predictability. In such cases, when predictability is not incorporated, inhibition of return is not present, suggesting that predictability may modulate the role of inhibition of return in volitional orienting. The results of the present experiment support the distinction between two distinct types of IOR: one that is sensory based and resistant to the effect of predictability, and one that is motor based, and attenuated by the absence of predictability.

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APPENDIX 1: REVIEW OF THE LITERATURE

When interacting with the environment, humans predominantly rely on visual information to guide their behaviors. Vision is one of the most widely and thoroughly studied senses, and yet there are still many mechanisms that operate within the visual domain that are poorly understood. One such mechanism is inhibition of return (IOR), a neural mechanism that promotes visual inspection of novel areas (Klein, 2000). This mechanism has many interactive effects, and involves multiple systems including sensation, perception, attention, and motor control.

Vision

The visual system captures light from the environment and transduces it into electrical and chemical energy that is then interpreted by the various visual areas of the brain (Goldstein, 2010). The retina functions as the first point of contact of light energy with the nervous system. The light causes chemical reactions in the rod and cone photoreceptors, and these chemical reactions eventually lead to the transduction of electrical energy down the optic nerve. The optic nerves of each eye then meet at the optic chiasm where the majority of the fibers decussate. After crossing at the optic chiasm the fibers form the optic tract which projects to the lateral geniculate nucleus of the thalamus, which has a regulatory role in the relay of information to primary visual areas (V1) of the cortex in the occipital lobe.

The primary visual cortex is retinotopically mapped. Each area of the visual cortex corresponds to a specific part of the retina, and subsequently, a specific area of the visual field (Goldstein, 2010). The fovea is the area of the retina that consists

predominantly of cones and is responsible for the highest acuity vision. Subsequently, the fovea has the greatest representation in the primary visual cortex, and with greater retinal eccentricity (meaning further away from the fovea) there is less visual cortex devoted to areas of the visual field (*cortical magnification factor*). Another characteristic of the primary visual cortex is due to the crossing of fibers at the optic chiasm; objects that appear in the left visual field are inverted and represented in the right visual cortex, and objects appearing in the right visual field are inverted and represented in the left visual cortex.

Certain extra-striate areas (near the primary visual cortex) project to areas of the frontal lobe responsible for eye movement control. The eye movement control system (or oculomotor system) is housed in the Frontal Eye Fields, Supplementary Eye Fields, and Superior Colliculus (Luna & Sweeney, 1999). Together these brain structures form a neural network that is responsible for the planning, initiation, suppression, and regulation of eye movements.

The Oculomotor System

The oculomotor system is responsible for the control of eye movements. The eye is capable of making many different types of movements, including pursuit eye movements, fixation, and saccades. Saccades are the most relevant eye movement type for the present study. They are quick, direct eye movements, and are often reflexive. The purpose of saccades is to bring the fovea to a specific area of interest. The fovea is the area of the retina that has the highest density of cone photoreceptors, which are responsible for the highest acuity vision (Goldberg, 2010). Eye movements involve the rotation of the eye in three axes, and are controlled by six extraocular muscles. The

medial and lateral recti are responsible for eye movements along the horizontal plane (abduction and adduction). The remaining four muscles are the inferior and superior recti and the inferior and superior oblique muscles. These allow the eye to perform elevation and depression movements, as well as intorsion and extorsion (see *Figure A.1*).

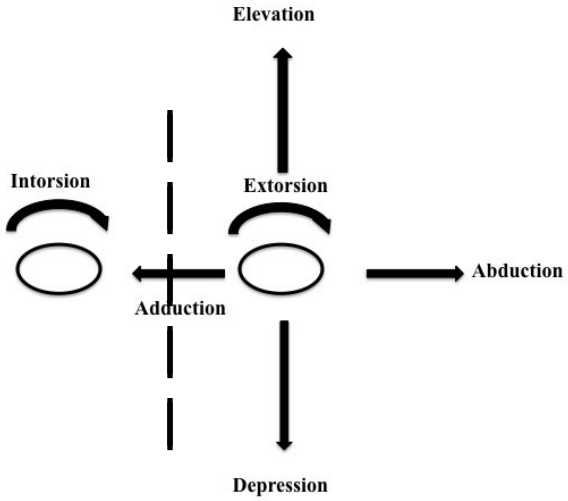

Figure A.1. A depiction of the various eye movement possibilities. See text for information regarding muscular control.

A variety of brain areas are responsible for the neural control of eye movements. First and foremost there are three cranial nerves that innervate the extraocular muscles. These cranial nerves are regulated by cranial nerve nuclei and some are under cerebral control. Important areas within the brain for eye movements include the frontal and supplementary eye fields, lateral interparietal area, and the superior colliculus. The superior colliculus is of specific importance in the control of saccades as it has a spatially coded map of space that helps direct eye movements. The superior colliculus contains both fixation and burst neurons (Munoz and Wurtz, 1993; 1995). Fixation neurons are

responsible for maintaining gaze at a specific location, and when burst neurons reach a higher threshold than these fixation neurons, a saccade is initiated.

Eye movements that are initiated voluntarily are defined as endogenous and are representative of a motor process. Exogenous saccades are different in that they involve an initial reflexive capturing of attention prior to the execution of the motor process. This indicates that exogenous saccades are useful when studying attentional and sensory processes, whereas endogenous saccades are relevant when studying purely motor processes.

Attention

Attention is the means by which information is selected from the environment for processing, and can be conceptualized as a filter. Attention functions within multiple modalities and filters extraneous information from the environment so that the most relevant and salient information is readily available. Sensory processes detect stimuli in the environment and then attention regulates what is perceived. These sensory processes are an example of how bottom-up processing can affect perception by way of attention. Highly relevant stimuli in the environment have the capacity to capture attention and draw sensory systems to detect them; this is also known as covert attention. On the other hand, overt attention relies more on strategy and top-down processing. Overt attention is essentially directed attention, and the observer is actively allocating their attention to a specific stimulus. This typically requires head or eye movements to direct vision, since it is the most dominant sensory modality. Attention links sensory and perceptual processing and is subject to regulation by both top-down and bottom-up processing.

Not only does attention link sensory, perceptual, and motor processes, but it also shares neural substrates with these functions, as explained by the premotor theory of attention (Rizzolatti et al., 1987). According to the premotor theory of attention, attention does not require its own system in the brain. Since attention operates within the sensory and motor domain it simply makes use of those systems that are already available. Attention is typically allocated on a spatial basis, and can be endogenously or exogenously activated. Endogenous spatial attention involves actively directing sensory processes to a specific stimulus in space. Most times this means performing a head or eye movement in an effort to foveate the target. The observer directs an eye or head movement so that there is maximal visual acuity. Exogenous spatial attention is different as it involves activation of the eye movement system but through attentional capture processes. In order to activate exogenous spatial attention there needs to be a change in sensation to draw attention to a stimulus. This is often described as a reflexive eye movement. Both types of attention involve activation of the oculomotor system to produce eye movements, however one acts on bottom-up processing and the other on top-down processing.

Traditional studies of IOR

While initially studying the mechanisms of peripheral orienting, Posner and Cohen (1984) noticed a significant increase in reaction time when participants were required to respond to a target in a previously cued location. This was measured using a spatial cueing paradigm where participants were required to maintain fixation while viewing a central box. Two additional boxes flanked this, one to the left, and one to the right. A trial in the experiment consisted of one of the boxes being cued (the box would

flash) followed by a target (a small black box would appear inside one of the other boxes). Figure 2 shows this trial sequence graphically. On any given trial, any of the three boxes could be the cue, target, or both. Sequences where the cue and target were both either central, left or right can be considered "same" trials, and sequences where the cue appears in one box, and the target appears in another can be considered "different" trials. When the cue appeared during a trial participants were not required to make any response. The target would then appear (at variable intervals of 0, 50, 100, 200, 300, or 500 ms, following the cue) and participants indicated detection of the target via button press response. Participants were instructed to respond to the detection of the target as quickly as possible, and not to remove their gaze from fixation.

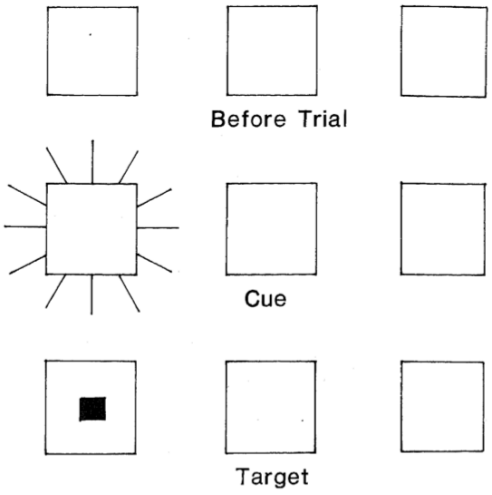

Figure A.2. A graphical representation of the cuing paradigm used by Posner and Cohen (1984). Taken from Posner and Cohen (1984).

The results showed that when the interval between the cue and the target was short (~150 ms) there was a facilitation of reaction time when the target appeared at the same location as the cue had. At longer intervals (200+ ms) however, the results shifted and there were slower reaction times to targets that appeared at the same location as the cue, and

participants were faster to report detection of the target when it was in a different location than the cue had been. Figure A.3 summarizes the main findings from the study (from Klein, 2000).

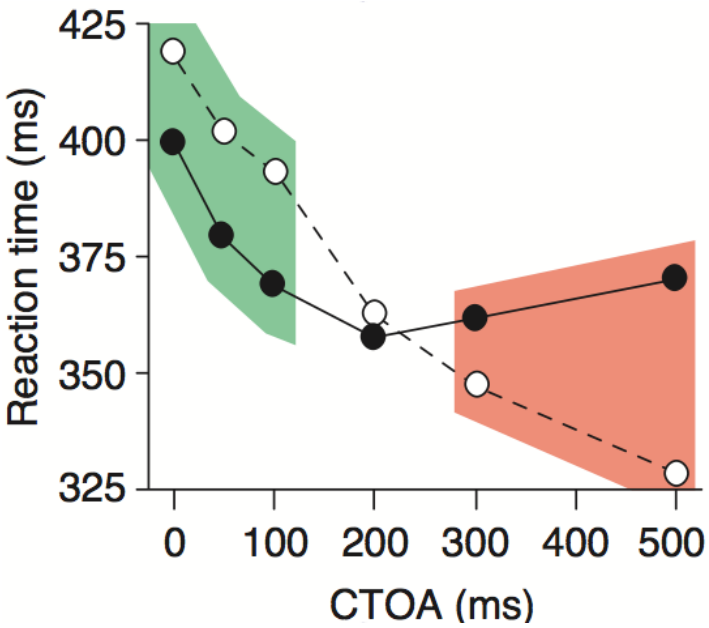

Figure A.3. A summary of the primary results from Posner and Cohen's (1984) study that demonstrates an initial facilitation of reaction times followed by an inhibition. (Cue target onset asynchrony (CTOA) is the time difference between the onset of the cue and the onset of the target).

Similar results were also found when, in a second experiment, the center was cued between the cue and the target. This essentially created a cue-cue-target sequence. The central cue was introduced to remove attention from the initially cued location so that it was in a neutral location before a non-central target appeared. This also meant that they could create shifts of attention without manipulating the probability of each location being the target.

However, each of these experiments was conducted while participants maintained fixation. Posner and Cohen were curious as to whether the inhibitory effect that they were

observing was due to the suppression of eye movements, and thus monitored eye movements during experimental paradigms such as those described above as well as in other cuing paradigms. The inhibitory effect was present both when measuring manual (button press) response times, and eye movement reaction times. This lead to an entire area of research investigating the inhibitory effect, now termed inhibition of return, and its relation to both attention and eye movements.

Sensory and motor forms of IOR

Posner and Cohen (1984) also reported using central arrow cues to elicit inhibition of return. The effect that they observed was different however, than the effect observed when non-central cues (i.e. peripheral flashes) are used. When a central arrow cue indicated the location of an upcoming target, manual responses were not subject to the same inhibitory effect. It then became unclear as to whether there was an effect of cue type, as well as target type, and response requirement on inhibition of return. A study by Taylor and Klein (2000) addressed these questions.

Taylor and Klein (2000) were interested in determining whether IOR represented either a perceptual or a motor bias. That is to say, does IOR operate within the visual domain by inhibiting the visual detection of targets ("blinding"), or does it operate in the motor domain by inhibiting the preparation of eye movements to targets ("paralyzing")? What they termed the *oculomotor readiness hypothesis* was able to frame the basic predictions of their experiments. The hypothesis postulates that after the appearance of a stimulus at a given location, the oculomotor system is engaged to produce an eye movement to the location of that stimulus. This eye movement (or planned eye movement) is responsible for the creation of inhibition of return. Inhibition of return is

then revealed through any task that requires information from the stimulus location. They developed an experimental paradigm to optimize control over the events occurring within a trial sequence that could be varied in terms of stimuli and responses. The cue is responsible for generating IOR, and was termed S1, and the target (responsible for revealing IOR) was termed S2. The authors manipulated both the type of S1 and S2, and the response required upon the appearance of the target.

S1 and S2 could either be a central arrow or a peripheral onset. A peripheral onset is simply a perceptual change at a location outside of fixation. These onsets were horizontally arranged with the central fixation point keeping everything along one axis. A variety of responses could be required to both S1 and S2. These included no response to S1 and a manual response (button press) to S2, a button press to both S1 and S2, an eye movement (saccade) to S1 and a button press to S2, no response to S1 and a saccade to S2, a button press to S1 and a saccade to S2, and finally a saccade to both S1 and S2. A visual depiction of these combinations is provided in Figure A.4.

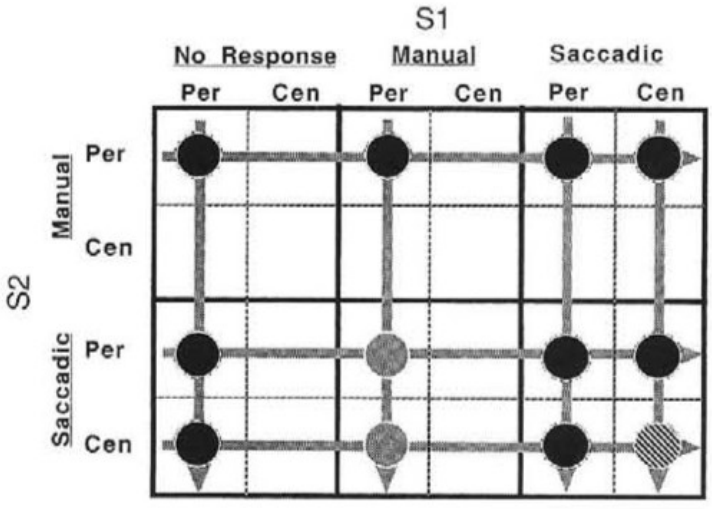

Figure A.4. A graphical representation of the experimental conditions tested in Taylor Klein (2000). Taken from Taylor and Klein (2000). The black circles

indicate specific S1 and S2 combinations that have previously demonstrated IOR in the literature. The vertical arrows show S1 stimulus-response conditions (none, manual or saccadic) that are predicted by the motor view to generate IOR, and the horizontal arrows are S2 stimulus-response conditions (manual or saccadic) predicted by the motor view to reveal IOR. Empty cells indicate conditions under which IOR would not be predicted to occur, whereas intersecting lines (gray circles) indicate conditions predicted to demonstrate IOR, but have not been shown in the literature.

Taylor and Klein proposed that IOR could only be generated on trials with an S1 of a specific nature. These included no response to a peripheral onset, manual detection of a peripheral onset, saccadic response to a peripheral onset, and saccadic response to a central arrow cue. These conditions were believed to generate IOR based on a motor planning perspective of IOR. Their stance was that IOR was generated whenever an eye movement was prepared to a location, regardless of whether or not it was executed (motor hypothesis). Based on the motor hypothesis, IOR may be generated but not always revealed, depending on how a person is expected to respond to S2. IOR should be revealed by S2 when S2 is a peripheral onset and the response is either manual or a saccade. S2 will also reveal IOR if it is a central cue and the response required is a saccade. On the other hand, IOR will not be revealed if manual detection of a central S2 is the task. Figure 3 depicts the predictions that stem from the oculomotor readiness hypothesis. The black circles indicate task conditions that have been used in previous studies and have found significant IOR, and the gray circles indicate where the hypothesis would expect to also find IOR, given specific task conditions and these

conditions are outlined by the horizontal and vertical arrows. The vertical arrows represent the S1 conditions that would lead to a generation of IOR; the S2 conditions required to reveal IOR are represented by the horizontal conditions.

These predictions were tested in their entirety using a simple experimental paradigm. Participants would stare at a fixation point flanked by two boxes. These two flanking boxes could be cued peripherally (they would flash), or centrally as indicated by an arrow at the center pointing in the direction of the box that was the target. After the initial cue (S1) the central box would flash returning the participants' attention to center. The second event would then occur (S2) and this could again be either a peripheral onset or a central cue direction. The predictions described above mostly held true based on the results of the study. Contrary to the predictions though, IOR was still observed in the condition where central arrows (to which no response was required) were presented as S1, and manual detection was required to peripheral S2s. Together these results were taken as evidence that when the eyes do not move during a trial (i.e. S1s not requiring a manual or saccadic response), the oculomotor system is "disengaged" and target information is suppressed at the cued location, generating a perceptual form of IOR, thus affecting responses that require manual and saccadic responses. However, when the eyes move during a task, a motor form of IOR is generated, and any response to S2 that requires spatial information about the target is impeded (i.e. slower saccadic reaction times).

A recent study by Chica and colleagues (2010) sought to support the distinction between sensory and motor IOR. Their experiment was designed to demonstrate that the motor form of IOR was due to activation of the oculomotor system (generated by

planning and executing a saccade) and had no effect on sensory processes or attention (therefore not impede ability on a discrimination task). In their first experiment, participants were required to make a saccade to a peripheral target, and then return their eyes to center. This was followed by a second target to which participants either pressed a button upon detection of the target (Experiment 1A), or pressed one of two possible buttons corresponding to the color of the target (Experiment 1B). The results showed that manual response times for the detection task showed a typical IOR pattern: when the final target appeared in the same location as the first, there was a slower response time compared to when the final target appeared in a different location. Response times did not show an IOR pattern for the discrimination portion of the task though. Instead, a speed-accuracy tradeoff was observed, where response times were affected by IOR, but facilitation was found in accuracy.

In a second and third experiment of the same study, Chica et al. (2010) also manipulated the presence of a cue-back/refixation signal in their task, and whether or not eye movements were required or restricted during a trial. Experiment 1 had required refixation in each trial but it was not cued. Experiment 2 revisited the detection task; in Part A, eye movements were restricted, and Part B eye movements were required. Experiment 3 utilized the discrimination task, and in Part A eye movements were restricted and in Part B they were required. The combined results showed that when the sensory form of IOR is generated (eye movements restricted), performance as measured by response time was impeded on the discrimination task and not the detection task – opposite to the effect of motor IOR seen in Experiment 1. The results of their experiment demonstrate that when the motor form of IOR is generated, attentional/perceptual

processes are spared, and motor execution is impaired. When eye movements are restricted and sensory IOR is generated, perceptual/attentional processes are impaired, and motor processes are spared. These results corroborate the sensory/motor IOR distinction postulated by Taylor and Klein (2000).

The aforementioned studies are able to demonstrate the behavioral impact of inhibition of return through psychophysical experiments. These studies also offer a theoretical basis for why and how inhibition of return is generated and measured. Based on the robust findings of these studies of inhibition of return, there must be an organic basis to IOR that can be revealed through techniques that measure brain function at the neural level.

Neurophysiology of IOR

Since sensation and motor control both have underlying causal neural mechanisms, it follows that phenomenon that affect these processes (such as IOR) also have neural mechanisms. Dorris and colleagues (2002) looked for such a mechanism for IOR in a primate closely related to humans. The study involved single cell recordings from the superficial and intermediate layers of the superior colliculus of the monkey. The superior colliculus (SC) is an important brain structure involved in the execution of saccades, and is spatiotopically mapped. The recordings were taken while the monkey went through a basic IOR paradigm. The monkey fixated at the center of the stimulus array after the presentation of a fixation point. Following this a stimulus was presented (the cue), and the monkey was trained to make no response to this stimulus, and continue to maintain fixation. The final target either appeared at the same or different location to the cue, and the monkey was required to saccade to this target. The time between the first

and final target was kept at greater than 200 ms to ensure sampling was done inside of the inhibition rather than the facilitation range of the IOR time course.

The results showed varying neural activity and response times based on whether the cue and target were appearing at either the same or different location. Neurons of the superior colliculus had an initial reaction associated with the visual detection of the cue when it appeared in the neuron's receptive field, and a second associated with the initiation of a saccade to the target. For example, in a given trial the cue appeared and the neuron of interest had a response related to this onset. Following this, the target appeared and the neuron responded to the onset, and then responded based on the initiation of a saccade to the target. When the cue appeared opposite to a neuron's receptive field, this neuron had no response to the cue. With regards to response times for initiating a saccade to the target, saccades in the "same" condition were delayed compared to the "different" condition, a classic IOR response. However, when looking at the neuron's response to the onset of the target, the magnitude of neuronal firing was less in the "same" condition than in the "different" condition. The magnitude of neuronal firing due to saccade initiation was unaffected by the location of the previous cue. A second difference between the two groups was observed in neurons during the interval between the cue and the target. Neurons of the superior colliculus would fire at a higher rate during this interval in the "same" condition. This indicates an overall excitability of superior colliculus neurons following a stimulus, and no active inhibition within it. The authors concluded that the inhibition responsible for IOR must not come directly from the superior colliculus itself, but rather somewhere upstream from it. However, the superior colliculus is where the result of the upstream inhibition will manifest itself. The authors suggest that the

posterior parietal cortex may be the site of upstream inhibition, and that from here the inhibition can be to either an object or location. The superior colliculus is then responsible for creating the appropriate saccadic behavior.

The results from the study by Dorris et al. (2002) contrast with those in the literature that demonstrate the superior colliculus is the site of IOR (Sapir et al., 1999). Sapir et al. (1999) studied a patient with damage to the right superior colliculus following a spontaneous hemorrhage in the right side of the midbrain. This patient represented the ideal participant for such a study, to examine asymmetry between responses to stimuli presented in different visual fields. The researchers presented stimuli to one eye at a time and controlled which part of the visual field it was in, either nasal (part of the field closest to the nose) or temporal (part of the field closest to the temple). Since the visual system is lateralized, information from different visual fields crosses over and is processed in opposite hemispheres of the brain, and they had the unique opportunity of dissociating between fields where IOR would be expected or not. Stimuli presented in visual fields that projected to the damaged portion of the patient's superior colliculus (right side) were not expected to generate IOR. However, stimuli that were presented in visual fields that projected to the intact portion of the superior colliculus (left side) were expected to generate IOR.

These hypotheses were tested using a cue-target paradigm while the patient viewed the stimuli through one eye. The patient fixated on the center of a screen, a cue came on either to the left or right (to which they made no response), and then a target would appear and the patient would respond via key-press. Sapir et al. (1999) failed to find IOR in portions of the visual field that projected to the damaged, right superior

colliculus. Conventional IOR was found in portions of the visual field that projected to the intact, left superior colliculus, that is to say response times were slower to targets appearing in previously cued locations (when that location was part of a visual field projecting to the intact portion of the superior colliculus). The authors took these results as neurological evidence that IOR required the superior colliculus and is the site of IOR.

Alternatively however, one can align these of the later study by Dorris et al. (2002). They hypothesize based on their results that IOR is generated in brain regions upstream from the superior colliculus, and that the superior colliculus is simply the means by which that inhibition is realized and implemented. This reasoning can account for the dissociation seen by Sapir et al. (1999). IOR might have been generated in the patient based on cues presented in any portion of the visual field, but damage to the right superior colliculus prevented that inhibition from being manifested behaviorally.

Moving beyond refixation

To research the fundamental aspects of IOR it is important to use the very basic and replicable paradigm described above. However, there are many subtle ways that this paradigm can be manipulated to produce changes in the IOR that is observed. This can be done in an effort to see how IOR is affected by what is being inhibited (location versus object), memory and IOR, as well as randomness and IOR.

A study by Tipper, Driver and Weaver (1991) looked at whether IOR was affecting responses to objects or locations. To do this they had a typical experimental display of three boxes along a horizontal axis - a central box and a box flanking it on either side. Either the left or the right box would be cued, and then the outer boxes would rotate in an imaginary circle around the central box. The target would then appear and

reaction times were measured. This experimental set-up is depicted in Figure A.5.

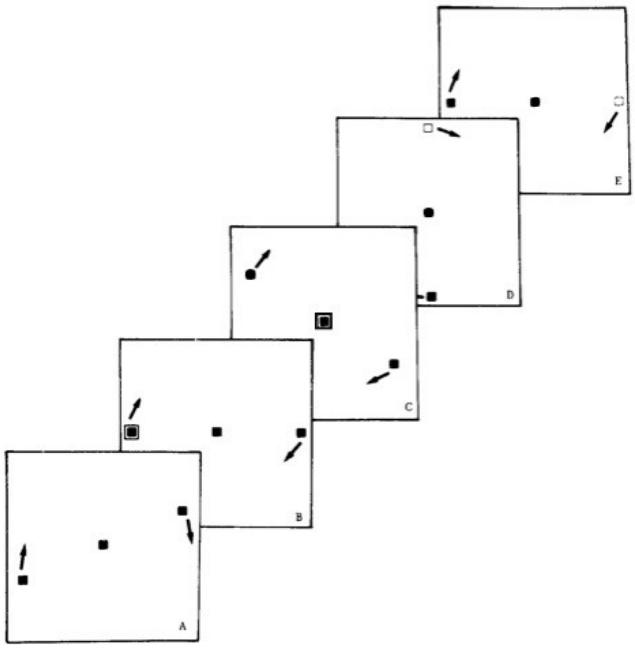

Figure A.5. A depiction of the experimental set-up used by Tipper, Driver, and Weaver (1991). Beginning in Panel A, participants fixated, followed by the cue onset (B), cued refixation (C), rotation of stimulus array (D), and finally the target appeared (E). Taken from Tipper, Driver and Weaver (1999).

They found IOR at the box that had been initially cued, even if it had moved to the new location, and the location the cue had originally appeared lacked IOR. This was one of the first studies to look at IOR that wasn't location based, and operated within a pseudo-dynamic paradigm that involved motion.

Visual search paradigms are another way that IOR can be studied, moving away from the traditional three-box set up. Klein and MacInnes (1999) monitored participants' eye movements as they explored a scene searching for Waldo. Participants began with their eyes fixated at a specific point on an otherwise blank screen. A "Where's Waldo?"

image would then appear and participants were required to locate Waldo, and then the wizard. After a random amount of time, a target appeared at some point within the scene. Figure A.6 shows what the participant would experience throughout a trial.

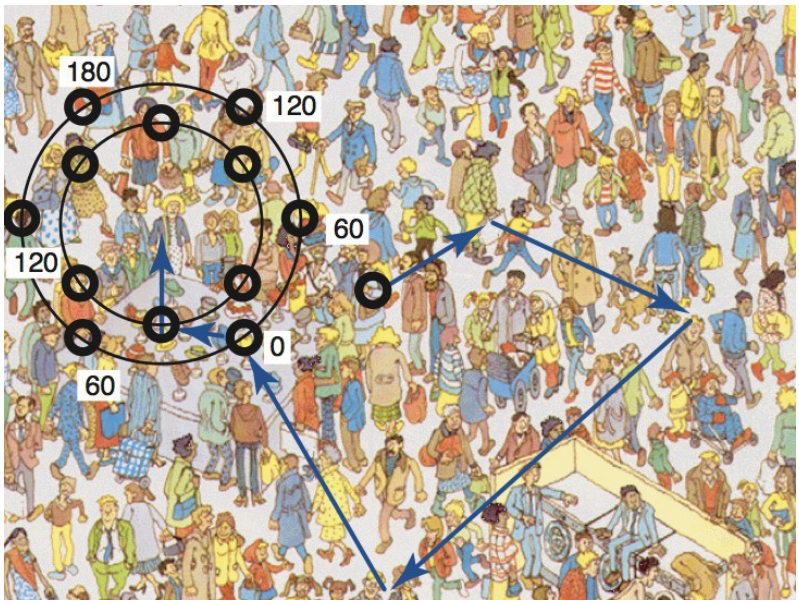

Figure A.6. A depiction of what participants would experience while performing the "Where's Waldo" task. The black circle at the center of the array shows where a participant began. The arrows show a potential search pattern, ending in the appearance of a target. The target could appear in any of the potential locations indicated. Image from Klein (2000).

The location that the probe appeared was contingent upon the gaze of the participant. The locations at which it was programmed to appear were arranged to test for IOR, so sometimes fixation appeared at a location that hadn't been searched, and other times it appeared exactly where the participant had just removed their gaze from. The results demonstrated a typical IOR effect was occurring while participants searched the visual scene. They were slower to look back at fixation disks that appeared where they had looked compared to new locations where they were looking.

Interestingly, a variation of the task by Klein and MacInnes (1999) involved the removal of the image simultaneous with the appearance of the target. IOR was not found when the image was removed and the participant was required to locate the target. This means that the inhibition had attached to the objects located in the scene being searched, similar to the way that the inhibition had followed the box in the study by Tipper, Driver and Weaver (1991). The authors also observed an overall bias of eye movements during the search to be in the same direction, rather than to go back in the opposite direction of the search. These results support the view of IOR as a mechanism to aid in the search for novelty.

Another important aspect of visual search is the role that memory plays in it. By definition IOR is a memory-based phenomenon keeping previous locations (or objects) in a buffer and remembering not to return to those locations. This was the idea investigated by McCarley and his colleagues (2003). They were interested in finding out the memory capacity of oculomotor search. To do this they designed a task where participants began with their eyes at fixation and to then move their eyes to stimuli that would appear in a specific sequence. Each trial consisted of a series of events where participants would move their eyes to the stimulus, and at the third event, two stimuli would appear and the participant would be required to choose which object to move their eyes to. Once they decided and moved their eyes, two new alternative stimuli appeared and the participant made another decision. This sequence continued to a maximum of 11 eye movements to a new location.

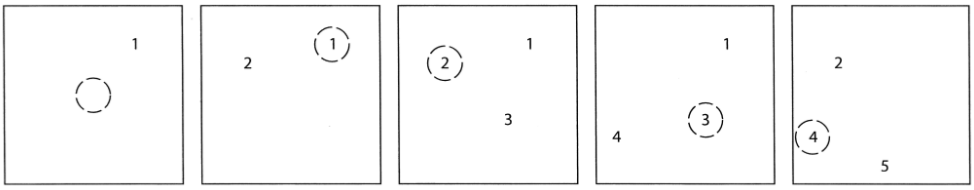

Figure A.7. Sequence showing how participants progressed through a trial, dashed circle indicates gaze location. From McCarley et al. (2003).

It was found that there was a "search history" of three to four items. This was determined by looking at the likelihood that participants chose to return to objects already seen compared to new ones. The authors therefore demonstrated the memory component of IOR, and its potential impact in visual search.

As demonstrated by the aforementioned studies, IOR is a phenomenon that exists outside of the refixation paradigm that it was first discovered in. This is an indication that if a greater understanding of IOR is to be garnered, the manner in which it is studied needs to be shifted away from tasks that use refixation. Refixation tasks are useful for demonstrating the basic presence of IOR, but lack the relevance to a naturalistic environment that is less predictable. An inherent restriction on refixation tasks is the predictability component that is built in. Studies that eliminate refixation are able to demonstrate a more dynamic form of IOR that is more like the IOR that likely operates within individuals on an everyday basis.

One such study that doesn't use refixation saccades is by Anderson, Yadav, and Carpenter (2008). They used a random walk paradigm to study what effect the removal of the refixation event would have on saccadic reaction times. They identified the confound of many IOR studies where every eye movement made away from the central point is

followed by an eye movement back to that same center point every time. Their study design circumvented this problem by implementing a "random walk". Participants moved their eyes along a horizontal axis following a dot that moved either immediately left or right of its current position. They engaged in a continuous series of saccades (200 in total), and each upcoming saccade had an equal probability of either being leftward or rightward, a fundamental difference from the typical IOR refixation task. By removing predictability from the task, the authors were hoping to isolate the effect of saccadic direction.

One can then analyze the authors' data, looking for sequences of three saccades, with an intervening second saccade opposite to the initial saccade. These are the types of eye movement sequences that most closely match typical IOR task eye movements. The saccadic latencies resulting from such an analysis demonstrate a small, but significant IOR effect, where eye movement sequences that require the eyes to move back to a location recently visited are slower than those to new locations. The effect of previous saccades on any given saccade was also found to decrease as the number of intervening saccades increased, but still having an effect of increased latency (regardless of direction) from as far back as five saccades

An IOR-like effect was also seen between any given saccade and the immediately preceding saccade. In sequences of eye movements where a leftward saccade was preceded by a left, this leftward saccade was faster than if a right preceded the leftward saccade. This pattern was seen for rightward saccades as well; rightward saccades preceded by right saccades were faster than rightward saccades preceded by left saccades. In an IOR framework, moving left and then left again means moving to a new location

and thus towards novelty. Moving left and then right means moving back towards a previously viewed location, which is inhibited.

Several issues arise from the limitations of Anderson, Carpenter and Yadav's (2008) experiment however. The use of the moving black disk as the stimulus means that only peripheral events were studied, potentially involving both sensory and motor IOR. This is because when the black disk appears at a new location, there is both the change in retinal stimulation based on its new location, but also the motor response due to the saccade to the disk. As a result of this, the authors are potentially not fulfilling their goal of isolating saccadic direction effects, because there is an inherent perceptual change involved as well. Second, there were only three participants (two were authors), and thus they were not naïve to the purpose of the experiment and likely had more practice with such experimental paradigms. This familiarity with the task also meant they were in a unique position to remain vigilant during a task requiring 200 trials such as theirs did. Additionally, the study completely eliminates the refixation movement from the procedure and lacks a control condition that compares reaction times when the refixation is present to see how it differs. Even when isolating sequences of three saccades to examine the effect of the first in the sequence on the final, the intervening saccade in the sequence is unpredictable, unlike in a typical IOR study where the sequence would involve an initial unpredictable saccade, followed by a predictable saccade, ending with an unpredictable saccade. Furthermore, their task involves tracking a black dot that disappears from its current location before appearing in a new location. This is unlike visual search in the natural world, because objects remain in their place after being scanned and do not disappear. The study by Anderson, Carpenter and Yadav (2008) was

important insofar as it provides a launching point for the investigation of the effect of the cue-back used in traditional IOR paradigms. This launching point highlights an important gap in the IOR literature that can be addressed by a study combining elements of both the random walk paradigm and refixation tasks to isolate the effect of predictability on IOR.

Rationale

The purpose of the present study is to move the field of IOR research into a method of studying the phenomenon that is more naturalistic. This was partially attempted by Anderson (2008), however the study lacked any experimental condition that connected the random walk paradigm to the original cue-target paradigm of Posner and Cohen (1984). The current study incorporates aspects of both of these experimental approaches in a way that allows direct comparison of the two methods. Of particular interest is the concept of predictability in the two paradigms.

The two independent variables being manipulated in the current study are predictability and cue type. There are two levels of the predictability variable, predictable and unpredictable, and two levels of the cue type variable, endogenous and exogenous. Saccadic reaction time is the dependent variable being measured. In one level of the predictability variable, the second saccade in every sequence has a 100 percent probability of being in the opposite direction to the first saccade. In the other level of the predictability variable, the second saccade in every sequence has a 50 percent probability of being in the opposite direction of the initial saccade, and a 50 percent probability of being in the same direction as the initial saccade.

There are two levels of the cue type variable, endogenous cues and exogenous cues. In the endogenous level, saccades will be directed by arrow cues, and in the

exogenous level, saccades will be directed by a peripheral onset (an adjacent placeholder in the stimulus array will become bold for an instant). The cue type manipulation is included because the type of cue used to generate IOR influences whether the IOR observed is of a sensory or motor nature. Endogenous cues rely on signal interpretation and are thus subject to top-down influences, but do not involve differences in retinal stimulation (no sensory change). Exogenous cues drive sensory stimulation and are thus bottom-up influenced, creating changes on the retina altering sensory processing. The potential effects of the independent variable manipulations are outlined below.

Posner and Cohen's (1984) original cue-target paradigm (which consequently is the most frequently used method in the literature) involves a sequence of three events. A participant begins with their eyes at a central fixation point, and then after a predetermined duration there is the onset of a stimulus. The nature of this stimulus can vary, as can the response to this stimulus. For example the stimulus can be the onset of a cue in the periphery, and there can either be no response requirement, or the participant may make a manual or saccadic response. In either event, it is assumed that the peripheral stimulus draws attention to itself from the center. A refixation of attention then occurs, to return the focus of attention to the center. If the initial response was a saccade, this means that the refixation involves a saccade back to the center. The final event in the sequence is then the onset of a stimulus to which the participant makes their final response. The literature has shown that the magnitude of IOR is less when using exogenous cues than endogenous cues (Taylor & Klein, 1998, 2000) and that difference will be replicated in the present study.

Refixation often involves being cued back to the central fixation point, and therefore involves both sensory and motor processes (Taylor and Klein, 2000). The sensory change is the appearance of a stimulus, and there can be a motor component if the initial response was to move the eyes away from center. This is important because how IOR is generated will determine how it can be revealed. Having refixation is necessary to make the paradigm work in many cases (to control for retinal eccentricity) but only really necessary when there is no response to the initial stimulus. However it is still frequently incorporated into experimental tasks, possibly confounding or altering the IOR effect. The refixation movement is never really measured or examined since it is typically the first and third eye movements in an IOR trial sequence that are of interest, and only the reaction time of the third eye movement is analyzed. The relationship that is formed between the location of the first and final events (same/different) was of more importance in early studies than the direction of the eye movement. Even if the refixation saccade were analyzed it would have little meaning on its own since it is always predictable and to the same spatial location, and thus there is nothing different to compare it to. The timing of refixation is also predictable/programmed in most tasks, thus placing restrictions on possible reaction times. Based on the predictable nature of refixation it is possible that there is a separate control mechanism responsible for it. Predictable saccades fall more under endogenous control, and are more internally driven. This means they are probably regulated through a top-down attentional mechanism. The planning of the refixation movement may also vary, and it is unknown whether it is prepared on its own, or possibly in conjunction with either the initial or final saccade. This could influence IOR, since IOR is generated by the initial saccade, and then revealed

in the reaction time of the final saccade. Depending on which saccade it is prepared with, it may influence input processes or output processes with regards to the superior colliculus. Most studies typically use a visual stimulus to direct attention or saccades back to fixation as well, meaning that in many cases the central location is receiving extra retinal stimulation that is unaccounted for, and affecting processes within the superior colliculus. An increase in retinal stimulation leads to an increase in visual input that has been shown to increase sensory IOR (Wang, Satel & Klein, 2012). A study by Satel and Wang (2012) used an auditory stimulus instead of a visual stimulus to drive the refixation saccade, and also included an experiment that lacked a stimulus to drive refixation. When the auditory stimulus was used to direct refixation, IOR was not found to be different from when it is visually different. The auditory cue was still a sensory event though, so it may not have been expected to differ, since there are auditory connections to the superior colliculus (Goldstein, 2010). In the experiment that removed the refixation signal altogether, the IOR pattern still did not change. Notably though, the removal of the refixation signal does not mean the removal of the refixation event, nor the predictability associated with the refixation event.

If predictability of the second eye movement in the trial sequence does have an affect on IOR, it may change all present understanding of the effect. The movement itself introduces a confound into every trial sequence. The random concept used by Anderson, Carpenter and Yadav (2008) allows for identical sequences to occur in a trial (for example left, right, left) but the predictability of the second movement in the sequence can be manipulated. This creates a scenario where the effect of predictability can be isolated. The present study will bridge the gap between the body of literature that uses the

refixation paradigm and the random walk paradigm of Anderson, Carpenter, and Yadav (2008) that provides a more naturalistic approach to the study of IOR.

If IOR is affected by manipulating predictability it may either increase or decrease the magnitude of IOR. Anderson, Carpenter and Yadav (2008) found a reduced IOR effect in sequences of two saccades, when removing predictability from the scenario. When their data are analyzed in blocks of three saccade sequences there is also a smaller than typical IOR magnitude found. If a similar result were found in the present study it would lend support to Anderson's findings, and indicate that the IOR effect observed when using refixation paradigms may be stronger than that occurring in the natural world.