INHIBITORY CONSEQUENCES OF GRASPING MOVEMENTS: IS GRASPING THE SAME AS REACHING?

by

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ABSTRACT

Studies have shown that past actions can impact present and future actions. More specifically, inhibition of return (IOR) is a phenomenon in which participants respond slower to previously attended areas compared to novel locations (Posner & Cohen, 1984). IOR has been shown for eye movements, key presses and reaching but until now has not been investigated for grasping despite the prevalence of these actions. In this study, participants were asked to reach out and grasp a small or large block following the presentation of a central arrowhead cue indicating which direction to make a movement, while the eyes remained fixated centrally. Results showed slower reaction times for grasping movements made in the same direction as a preceding movement, demonstrating an IOR like effect. The grip scaling function however was not affected which adds to the growing body of evidence that IOR serves a broader function than facilitating visual search behaviour.

LIST OF ABREVIATIONS USED

IORInhibition of ReturnRTReaction TimePGAPeak Grip Aperture

CTOA Cue Target Onset Asynchrony
OMRH Oculomotor Readiness Hypothesis

IREDs Infra Red Emitting Diodes

PLATO Portable Liquid-Crystal Apparatus for Tachistoscopic Occlusion

LGN Lateral Geniculate Nucleus
V1 Primary Visual Cortex
EOG Electrooculograph
ANOVA Analysis of Variance

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CHAPTER 1 INTRODUCTION

1.1 Background

It is essential for humans to interact with their environment to survive. Humans possess the ability to perform a large array of actions ranging from something as simple as picking up a glass of water to something much more complicated, such as playing a musical instrument. Effective movement depends upon accuracy and precision, based on information about the objects that are targets of action (Goodale, Milner, Jakobson, & Carey, 1991). In virtually all environments, however, there are non-target objects present and the motor system must ensure that these non-target objects do not lead to unintentional motor plans.

The ability to minimize the contribution of non-target objects is done through selective information processing; this is commonly referred to as attention (Goodale et al., 1991). Attention selectively filters out irrelevant information from the environment to ensure only the information needed is processed. However, evidence suggests that even non-target objects can sometimes influence movement (Wolfe, 1994; Castiello 1996).

The need for selective attention in action systems was nicely demonstrated by Castiello (1996) who studied the effect of interference on grasping movements to a target object presented alongside distractor objects. In his study, participants were asked to reach out and grasp a piece a fruit located in their central view. At the same time they were also asked to count the number of light flickers, which were being displayed on a second piece of fruit located laterally. They were instructed to keep their gaze located on the central piece of fruit. Results showed that the grip aperture while picking up the

central fruit was affected by the size of the lateral piece of fruit despite the fact that it was not a target and that participants did not look at it. This study demonstrated how interference could occur between target and non-target objects, and that selection for action does not preclude the motor system from engaging in movement planning for non-target objects.

Attention is typically thought of as a sensory phenomenon where incoming information is filtered out to enhance perceptual function, and it has been widely studied from this perspective. According to the premotor theory of attention, sensory and motor attention overlap with each other in terms of anatomical location and function (Rizzolatti, Riggo, Dascola, & Umilta, 1987) in the sense that movements of spatial attention might require the engagement of eye movement programming systems. While this theory might imply that knowledge about the operation of sensory attention might inform us about the nature of motor attention, relatively little research has focused on motor attention so the similarity between sensory and motor attention is not at all clear.

1.2 Selection for Action

Motor attention is required when the environment provides more than one potential target for an action or when movement plans require more than one action in a sequence. Indeed, many of the actions humans perform are made up of combinations of several components. For example, it order to enjoy a cup of coffee one must pick up a cup, pour the coffee from the pot into the cup, pick up the cream and pour it into the coffee, place the cream back down and again pick up the cup and bring it to your lips. In doing this, a sequence of actions is performed. Motor attention works to filter out movement plans to non-target objects as well as ensure that the correct action is executed first.

Henry and Rogers (1960) conducted a series of experiments made up of different sequences of movements to better explore motor attention. Participants performed sequences of one to three discrete movements in length and results showed that the reaction time (RT) to the first movement increased with sequence length. This is also known as the "one target advantage". These results suggest that when a sequence of movements is performed, attention is focused on the movement as a whole rather than several individual steps. Despite the fact that participants are clearly engaging in some level of advance preparation of upcoming movements in the sequence, participants still executed the actions in the correct order indicating that the filtering of action plans must be taking place.

More recent studies went on to investigate how the presence of non-target objects impact actions toward the target object, more specifically grasping actions (LeBlanc & Westwood, 2016). This was done as an extension of Henry and Rogers (1960) work on action sequencing, looking at how effective selective attention is for movements.

Participants were presented with two small blocks, one placed directly in front of the other. They were instructed to pick up the block located in front and place it in a designated spot. They were then instructed to just grasp the second block, make a perceptual judgment about the blocks size or ignore it. The second task to be performed was known to participants before beginning the trial. Results showed that when the participant was told they would be grasping the second block there was no effect on the initial grasping but when they knew they would have to make a judgment about the size of the second block the initial grasping movement was affected. This finding indicates that when the task at hand was a sequence of two actions there was no interference showing effective motor attention. However, the interference seen for an action followed

by a perceptual judgment shows that attention is not as good between perceptual and motor systems. This suggests that sensory and motor attention is different.

Since many of our daily activities involve sequences of individual actions it is important to understand how past and future actions and objects may impact the present ones. Action sequence research has looked at how *future* actions affect current ones. Inhibition of Return (IOR) is a phenomenon providing evidence of how *past* behavior can create a bias for future behavior. Participants have been shown to be significantly slower to respond to location in which they previously attended compared to a novel location. IOR represents a form of selective attention because it biases the selection of information for elaborated processing; however, it is not clear if IOR is a form of sensory attention, motor or attention, or perhaps both.

1.3 Inhibition of Return

Posner and Cohen (1984) were the first to discover inhibition as a consequence of orienting. In their initial study, participants were presented with a display of three boxes. While maintaining central fixation, the brightening of one of the boxes in the periphery of the display would occur. This would be the initial cue. No response was required to the cue. There would then be varying intervals between onset of the initial cue and presentation of the target. The target would be presented at the previously cued area or the uncued area. The participant was asked to make a detection response as soon as they were able to locate the target. Reaction time to the target object was measured. According to the results of this study, participants were initially faster responding to the cued locations compared to the uncued locations, showing a facilitation response. However, if 300 ms or time more elapsed between the cue and target onsets, this facilitation turned into an inhibitory response and participants showed slower responses to targets in the cued

locations compared to those in the uncued locations. The first event, or the cue, draws spatial attention to its location. Participants then return attention to centre because the cue does not predict where the target will appear. The withdrawal of attention from the cue leaves behind an inhibitory trace that discourages attention from returning when future events, such as the target, appear in that location.

This initial study was the first to document and also explore inhibition of return and its key characteristics. It employed a traditional cue-target paradigm in which participants were presented with peripheral cue (which required no response and that did not predict the future location of the target), followed by a peripheral target (requiring a response) located in the same or opposite location as the cue. Upon further investigation, it was shown that inhibition was not seen when the same procedure was repeated using a central arrow cue that actually predicted the target's location. In this case, participants were motivated to move their attention to the cued location but they had no incentive to withdraw attention back to the center since the target was most likely to appear at the cued location. Based on these findings, it was proposed that IOR had a function and it was to discourage attention from being reoriented to locations from which attention had recently been withdrawn, presumably to encourage the exploration of novel locations (Posner & Cohen, 1984).

Many studies went on to define the properties of IOR and to further investigate when and why it occurred. A dominant question related to the locus of the inhibitory effect; specifically, was the delayed response to previously attended locations due to the suppression of sensory information arising from locations in space (i.e., a 'sensory' mechanism) or from the suppression of motor commands planning movements in certain directions (i.e., a 'motor' mechanism)? It was unclear from Posner and Cohen's original

study if IOR arose from sensory inhibition or response suppression. Taylor and Klein (2000) addressed this more specifically and looked for the presence of IOR using a target-target task paradigm in which stimuli and responses were modified to emphasize sensory or motor processes. Unlike the cue-target task typically used to study IOR, which requires the participant to withhold a response to the first stimulus (i.e., "ignore the cue"), target-target tasks require the participant to make responses to the first and second stimuli. The initial targets were either peripheral onsets or central arrows, and participants made either no response, a saccadic eye movement, or a manual key press response to the first target followed by either a saccadic or manual response to the second target. Six experiments were performed consisting of all combinations of these first and second target response combinations. Within each experiment, the first and second targets were independently randomized to be peripheral onsets (emphasizing sensory processes related to detecting and locating the target) or central arrows (emphasizing response preparation and execution without the need to detect the target's location).

Results showed inhibition in all conditions in which eye movements were prepared for the first or second target, whether or not they were executed, regardless of the nature of the response used for the second target. The authors proposed that this was evidence of a sensory form of IOR arising from activation of the oculomotor system, and that this was the type of IOR documented in prior cue-target paradigms (Posner & Cohen 1984; Posner, Rafal, Choate, & Vaughn, 1985; Rafal, Calabresi, Brennan, & Sciolto, 1989). The authors also reported evidence of inhibition in conditions that did not require eye movement preparation, but this inhibition was specific to the type of response made to the second target. This observation implied a motor form of IOR that was related to the preparation of specific responses (Klein, 2000), and that could only be isolated using

central arrow stimuli that did not automatically elicit eye movement preparation. As mentioned previously, Posner and Cohen did not find any signs of inhibition in their experiments utilizing a central arrow cue but this was because the arrow cues used in that experiment predicted the future location of a target with high probability, whereas in Taylor and Klein the arrows simply instructed a response and there was no predictive relationship to the location of the subsequent target.

Based on these findings, it was suggested that two different forms of IOR potentially existed, a sensory form and a motor form, and these were related to whether or not eye movements were activated in the task. The potential presence of IOR following manual key pressing actions was also explored by Taylor & Klein (2000) to investigate if IOR was primarily restricted to the oculomotor system. Participants performed a central-target task experiment in which the cue and target signaled a manual key pressing movement. Results did not show any inhibition occurring in response to these movements suggesting that motor IOR is restricted to the oculomotor system.

Several studies went on to explore the presence of IOR for reaching movements (i.e., Fischer, Pratt and Neggers (2003), Pratt & Neggers (2008); Neyedli & Welsh (2012)). While these studies found that IOR could be revealed in reaching movements, it was not possible to conclude that this was a form of *motor* IOR because peripheral stimuli were used for cues and also sometimes also for targets. This is problematic because Taylor and Klein (2000) already showed that a sensory form of IOR arises when peripheral cues are used, due to the automatic engagement of eye movement preparation. As such, subsequent manual responses to peripheral targets could well be reflecting a sensory rather than motor form of attention, such that participants might simply have been slow to detect the target's onset. Thus, previous studies could not confirm a specifically

motor form of IOR arising from and affecting manual responses. To isolate motor mechanisms, central arrows must be used to enable movements to be made without the confounding effect of automatic eye movement preparation and subsequent sensory IOR.

Cowper-Smith and Westwood (2013) were the first to investigate the presence of IOR for reaching movements using a central-central target paradigm similar to the paradigm used by Taylor and Klein (2000). While the eyes remained fixated in a central location, participants were instructed to make a reaching movement in the direction of a central arrow cue and again in the direction of the central target. Results showed the presence of IOR-like phenomena for the reaching movements in a central target task.

This study was the first to demonstrate conclusive a specifically motor form of inhibition related to arm movements. The findings called into question the idea that all forms of IOR were primarily about enhancing visual search performance since eye movements and searching were not a part of the experiment (Cowper-Smith & Westwood, 2013). It also added strength to the argument that motor and sensory forms of IOR are different, because the pattern of spatial inhibition for the reaching task was quite different from what has been reported for classical 'sensory' forms of IOR involving peripheral stimulation. It was suggested that the inhibition observed for arm movements was qualitatively different from IOR per se, arising instead from inhibitory after-effects located within neurons encoding movement directions (Cowper-Smith & Westwood, 2013).

According to Georgopolous, Schwartz and Kettner (1986), the final direction of a limb movement is determined by the collective activity of an entire population of individual neurons each with a preference for movements in a certain direction.

Individual direction-encoding neurons demonstrate maximum firing rates in a preferred

direction, with decreasing firing rates as the direction of movement deviates from that preference. When a reaching movement is made in a specific direction (e.g., in the direction of an arrow cue), the neurons that encode this preferred direction could become fatigued or adapted because of the high firing rate. Subsequent movements in the same, or very similar, direction would engage the same neurons again and thus be impacted by the prior adaptation resulting in slowed reaction time. Because the consecutive movement task also requires a return movement to the central location (of necessity, 180 degrees in opposition to the first cued movement), residual adaptation would leave both the initial and opposite directions of movement subject to delayed reaction time. Movements at 90 degrees to the initial movement direction are least affected by the inhibition arising from the cued and return to centre movements due to the tuning curves for individual directionencoding neurons, with the result that reaction times are fastest when the final movement is 90 degrees opposed to the initial movement direction, and relatively slower for movements in the same (0 degree) or opposite (180 degree) directions. Although speculative and without neurophysiological support at this time, such a model could explain the unique "U-shaped" spatial distribution of inhibitory effects for reaching movements (Cowper-Smith & Westwood, 2013).

To date, current studies investigating motor forms of inhibition have focused on movements that depend solely on location information, such as saccades, key pressing or reaching. However, many human actions depend on the manipulation of objects and thus require information about the form or shape of the object in addition to its location. It is not clear whether actions that require processing of object form will be affected by motor inhibition in the same way as simple reaching movements given the assumption that the inhibition observed to date arises from spatial information (i.e., movement direction).

1.4 Prehension

Prehension is defined as reaching out and grasping an object (Jeannerod, 1984). When the arm reaches out to pick up an object the shape, size and orientation of the hand opening will be altered to match that of the target object. This occurs soon after the reaching movement is initiated. It is referred to as preshaping and is dependent on visual information gathered from the object of interest. The index finger and thumb are responsible for forming the grip portion of prehension. Peak grip aperture (PGA) is the maximum distance attained between the index finger and the thumb during preshaping and it typically occurs at 60-70% of the duration of the reach. Peak grip aperture is strongly correlated with size of the target object although it invariably exceeds the size of the object by 10-20% in order to facilitate enclosure of the object without unintended contact (Jackobson & Goodale, 1991).

Reaching and grasping actions both require visual processing. Reaching to touch depends on location information whereas reaching to grasp depends on location information but also shape and size information, along with coordination between the reach component and the grasp component. To date, no studies have sought evidence for motor inhibition in grasping actions despite the prevalence of such movements in our daily behavior.

To better understand motor IOR, it is important to further investigate its characteristics and its presence within different motor-based processes. Motor IOR has been shown, (via the use of central – central tasks) for eye movements (Posner & Cohen, 1984; Taylor & Klein 2000), key pressing movements (Taylor & Klein, 2000) and reaching movements (Cowper-Smith & Westwood, 2013). However, there are some important differences between reaching and grasping, so it is not certain that IOR would

affect both.

Studying the presence of inhibition for grasping would add to our knowledge of motor inhibition in several different ways. It would add a new form of action to be studied in terms of inhibitory processing and would provide us with the ability to investigate how object shape processing might be affected by motor inhibition.

1.5 Purpose

The purpose of this study was to explore the effects of prior grasping actions on current grasping actions using a consecutive movement paradigm with central arrows instructing each movement. In particular, the study focused on two aspects of grasping:

(i) Is the time to initiate a grasping action (reaction time) affected by the direction of the preceding gasping action? (ii) Is the grasping component of prehension affected by prior grasping movements, more specifically is the timing to achieve peak grip aperture affected, and is the scaling of the grip size to the object size affected?

In order to investigate these questions, a target-target task paradigm was employed using central arrows to direct grasping movements to target objects (Taylor & Klein, 2000; Cowper-Smith & Westwood, 2013). Given that this research is exploratory, distinctly different predictions can be made based on the existing body of literature.

1.6 Hypotheses

There are three broad theoretical positions that allow for predictions to be made about which, if any, aspects of prehension might be affected by IOR-like phenomena.

The first theoretical position is that motor inhibition is a subset of a general phenomenon (inhibition of return) and this phenomenon arises from a mechanism that operates on searching or exploratory behaviours to discourage returning to previously searched places (Klein & MacInnes, 1999). Because manual prehension is not an

exploratory behaviour, reflecting in contrast the decision to act upon an object *after* it has been found, it should not fall prey to inhibition in the way that simple reaching movements and eye movements do. If this set of proposals is correct, then no inhibition should be observed for the time to initiate the action, or for the timing or scaling of the grasp. Although prior studies have shown reaching movements to be subject to IOR it remains a common idea in the literature that IOR is related to efficient visual search.

A second theoretical position is that is that motor inhibition is fundamentally different to inhibition of return, arising instead from residual suppression within direction-encoding neurons in the motor system after response execution (Cowper-Smith et al., 2013). According to this view, inhibition should be observed for the reaching component of prehension (i.e., reaction time to initiate the movement) since this depends on location or direction information (Jeannerod 1984), but not the grasping component (i.e., peak grip aperture or the timing of peak grip aperture) since this depends instead on form and size information.

A third theoretical position exists but lacks precedent in the existing literature. It is possible the motor inhibition is a general mechanism that discourages the repetition of prior movements in favor of novel ones. According to this perspective, the inhibition observed in prior studies of repeated movements is not specific to the *directional* aspects of the movements per se, but instead affects a more comprehensive representation of *all* features of the movement, directional or otherwise. Because prior studies considered only movements that depended upon location or directional information (i.e., reaches, key presses, or saccades), it is not clear if inhibition might extend beyond the processing of spatial information to other features of movement. By studying prehension, it is now possible to look at the directional component of the movement (the reach) as well as the

non-directional component (the grasp). In contrast to the second theoretical position outlined above, this theory predicts that both the reaching AND grasping aspects of prehension will show evidence of inhibition; specifically, RT will be longer for repeated movement directions, grip aperture will be smaller and occur later in time, and perhaps the scaling of grip size to object size might have reduced slope.

Chapter 2 Literature Review

As human beings we interact with objects as part of our daily lives. These interactions range from simple actions, such as picking up a glass of water to more complex actions with multiple steps, such as preparing a meal. We depend on motor control to help us carry out these actions. Our brains must successfully communicate with our musculoskeletal system while incorporating sensory information about the environment to activate the muscles needed to perform a specific action (Rosenbaum, 1991).

Attention acts as a selective filter, which allows us to process only the relevant information for a specific task (i.e., to pick up a coffee cup and not a water glass when having a cup of coffee). Attention is typically thought of as being a sensory phenomenon but it is also important to consider the motor component of attention, which allows us to pick and choose the movements we make. Motor attention filters movement plans to ensure the correct actions are performed for a specific task. Humans' daily activities are made up of different combinations of individual actions. Motor attention filters out unwanted movement plans to ensure that the right action is executed at the right time. To have a better understanding of movement it is important to know how past and future actions will impact present ones. This has been studied in the literature by looking at Inhibition of Return (IOR), which is a phenomenon providing evidence of how past behavior can create a bias for future behavior.

2.1 Inhibition of Return

Inhibition of return (IOR) is a phenomenon characterized by impaired perceptual and/or motor performance at the location of a previously stimulated area, compared to the original location (Posner & Cohen, 1984; Posner et al., 1985). This phenomenon is

thought to reflect a selective processing bias created by prior sensory and/or motor events (Taylor & Klein, 2000).

2.1.1 Basic Mechanism and Early Research in IOR

Posner & Cohen (1984) were the first to discover an inhibitory effect in orienting tasks. Experiments were performed in which participants were presented with a set of three sequential boxes in a display. In the first procedure, a brightening of one of the peripheral boxes would occur as the cue. Following the cue, a target would appear in the center box (0.6 probability), on the left side (0.1), right side (0.1) or not at all (0.2)(Figure 2.1). The second procedure involved the flashing of a peripheral cue followed by the brightening of the central fixation box prior to the presentation of the target in one of the three boxes. In both of these procedures participants were required to respond to the target by pressing a key and reaction time of target detection was measured. Results of these studies showed that participants had a faster reaction time to targets displayed in cued locations versus non-cued locations for the first 150ms following the onset of the cue. This was described as facilitation (Posner, 1980; Jonides, 1981). After 200-300ms following the cue onset, the pattern reversed and participants showed slower reaction times to targets in the cued locations versus the non-cued locations. This was referred to as inhibition (Posner & Cohen, 1984). As hypothesized by Posner & Cohen, inhibition could be occurring because only two alternative positions were used. It has been shown in other two-alternative RT tasks that alternations have faster RTs than repetitions (Posner & Cohen, 1984). It could also be due to the fact that once attention is removed from the cued location and returned back to fixation it takes longer to re-attend to the already viewed area (Posner & Cohen, 1984).

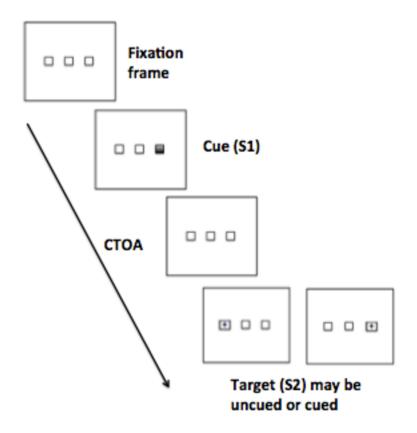


Figure 2.1 Representation of cuing paradigm used by Posner and Cohen (1984). The fixation frame is followed by the initial cue (S1), the brightening of one of the boxes in the periphery of the display. Following the cue, there occurs varying time intervals (CTOA- cue target onset asynchrony) followed by the presentation of the target (S2). The target is presented at the cued (right) or uncued (left) location. Participants must make a detection response as soon as they detect the target.

Separate experiments were done to explore these hypotheses and further investigate why inhibition was occurring. The first experiment eliminated the factor of only having two alternative target locations. As mentioned above it was hypothesized that the reason for the inhibition may be due to the fact that only two target locations were possible. To eliminate this, four peripheral boxes surrounding a central box in a display were presented to participants. The cue and target were displayed in one of the five boxes and the same initial procedure was performed. Results showed facilitation occurring initially followed by inhibition, after a 200-300ms delay as seen in the previous experiments. The position of the boxes in the display had no impact on the results and all of the uncued peripheral locations were faster than the cued locations (Posner & Cohen, 1984). Therefore, inhibition was still occurring with more than two alternative boxes and was seen in other positions in the visual field.

The next set of experiments involved the brightening and dimming of cues to investigate the involvement of sensory factors on inhibition and determine if the brightening of the peripheral boxes was the crucial factor. They looked to find a different way to capture attention that was not only the brightening of a box to see if the same effect was still present. The cues used were either the brightening or dimming of one of the peripheral boxes and the same procedure was repeated. Results of this experiment showed that the regardless of whether the cue was a brightening or dimming of the peripheral boxes, the result was the same. This showed that the facilitation is not solely a product of the brightness enhancement as initially presumed and what was in common between the two was a general attention capture (Posner & Cohen, 1984).

In the original experiment, Posner and Cohen used peripheral cues that were not predictive of target location. The cue automatically drew attention to the peripheral box,

but attention was eventually disengaged from this location and moved back to center since the target could appear on either side. According to Posner and Cohen, it was the removal of attention that created the inhibition. To further test this theory the same procedure was repeated using a predictive central cue rather than the traditional peripheral cue.

The cue in this experiment was a small central arrow displayed just above the central fixation box providing directional information. The arrow pointed to the left or right side indicating where the participant should look. In 50% of trials the target appeared 450ms after the arrow either in the cued location (0.8) or uncued location (0.2). If however, after 600ms the target did not appear the center box was brightened to reset attention to the fixation location. A target would then appear in the center box (0.6), the left side (0.2) or the right side (0.2). Results showed facilitation following the arrow cue but no inhibition was displayed in these trials following the return of attention to the center.

The cue used in this experiment informed participants of exactly where the target was to appear, therefore not only was it centrally located but also predictive of target location. Participants had a reason to shift their attention in the direction of the arrow and keep it there. It was hypothesized that IOR was not found because once attention was shifted in the direction of the arrow it was never withdrawn as it was with the peripheral cue because the target would soon appear in that exact location.

This study concluded that inhibition was present following a non-predictive peripheral cue. However, when a predictive central arrow cue was used the same result was not found.

Further work done by Posner et al. (1985) explored what would happen when the

eyes made a movement to the initial central arrow cue and refixated before responding to the target. In this study, a small arrow was displayed in central fixation. The arrow indicated to the participant to make a saccade movement in that direction and read a small number appearing in the target box. They then refixated back at the central location and a key pressing response was required in the direction of the target. When the initial central arrow caused the participant to make a saccade to the direction in which it was pointing, followed by refixating centrally before responding to the target, IOR was found to be present.

The results from Posner and Cohen's work posed many questions related to the effect that cue-type, target-type and required response had on IOR. They suggested that IOR was a result of a sensory process because it was found following a non-predictive peripheral cue but not a predictive central cue. It was also suggested that it occurred because eye movements were being programmed to look in that direction. This can be referred to as the Oculomotor Readiness Hypothesis, OMRH (Klein, 1980). A stimulus will cause the oculomotor system to become engaged to produce an eye movement to the location suggested by the stimulus.

2.1.2 Signal Types and Orienting

The use of different signal types in IOR studies is based on the existence of two very different forms of spatial orienting. Reflexive orienting is associated with the presence of peripheral visual onsets, which capture attention via reflexive mechanisms and is demonstrated by showing participants a peripheral cue that bears no predictive relationship to the subsequent location of the target (Taylor & Klein, 2000), this is also known as covert attention (Maylor & Hockey, 1985). In contrast, voluntary orienting occurs when participants are given information about the probable location of an

upcoming target, either via a cue located at the central fixation location (i.e., a "pure" voluntary cue) or via a peripheral cue whose location is consistent with the later target on a majority of trials (i.e., a "mixed" reflexive/voluntary cue). This is also known as overt attention (Maylor & Hockey, 1985).

Orienting is related to the onset of the cue and IOR is related to the withdrawal of attention from the location that was indicated by the cue (Taylor and Klein, 2000). In the case of non-predictive peripheral cues, orienting and IOR are both expected. Orienting is expected due to the capture of attention by the peripheral cue. IOR is expected because attention is removed from the cued location after orienting since the cue's location is not predictive of the target's location. Attention is returned to the central location as targets could appear to the left or right side. For central cues, neither orienting nor IOR are necessarily expected. Orienting will only occur if the central cue accurately predicts the location of the target on the majority of trials, since centrally presented signals do not automatically capture attention. IOR will only occur if participants withdraw attention from the cued location (i.e., this will not normally occur because the cued location is actually where the target will appear); as mentioned previously, Posner and Cohen (1984) showed that IOR does not follow central arrow cues that predict the most likely location of the target.

Based on these predictions of cue-target predictability, Taylor and Klein (2000) went on to further explore the cause of IOR and more specifically if it represented a solely sensory or motor bias in responding. They looked at IOR using manual responses for both peripheral and central cues. This was done using a set of six experiments in which combinations of responses were made. The tasks involved used three different types of responses to the cue (S1); no response, a saccadic response or a manual response

(key pressing). The response to the target (S2) was either a manual key pressing or a saccadic response. The cues could be displayed as either peripheral onsets or central arrows and a flash of light in the center fixation box was used to draw attention back to center between the first and second responses (Figure 2.2). Six experiments were performed using a combination of these response combinations.

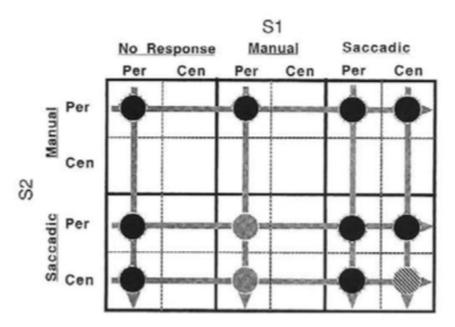


Figure 2.2 Representation of cuing paradigm used by Taylor and Klein (2000). Taken from Taylor and Klein (2000). Vertical arrows represent S1 response conditions that are predicted to show a motor form of IOR. Horizontal arrows represent S2 response conditions predicted to show a motor form of IOR. Black circles are indicative of combinations of S1 and S1 shown in the literature to produce an IOR effect. Gray circles are indicative of conditions predicted to show an IOR effect but had not been shown in the literature. Empty cells are indicative of conditions in which an IOR effect would not be predicted to occur.

Taylor and Klein hypothesized that IOR should be generated when the S1 response is one of the following; no response to a peripheral cue, saccadic response to a central or peripheral cue or manual key pressing response to a peripheral cue. This was believed because all of the listed conditions cause the preparation of eye movements and according to the OMRH a stimulus can cause the oculomotor system to become engaged to produce an eye movement in the location of the stimulus regardless of if the movement is actually executed. However, they believed that IOR would only be revealed under specific S2 conditions. These conditions were a saccadic response to a central target and a manual key pressing or saccadic response to a peripheral onset cue.

Results of these experiments showed the presence of an inhibitory effect for conditions in which when the eyes remained fixated for peripheral signals (i.e., as is true in classic cue-target paradigms in which participants are to ignore a peripheral onset cue). This is similar to the sensory forms of IOR already documented in the literature (Posner & Cohen 1984; Posner et al., 1985; Rafal et al., 1989). Unlike previous studies, however, it was found that inhibition existed when the eyes moved in response to the central or a peripheral cue. A central arrow was used as the cue and participants made a saccadic movement toward the cue direction, they then re fixated back at the center position and the target was the displayed (Klein, 2000). These results demonstrate a bias in responding to the cued location, which is different than the perceptual form of IOR already documented.

According to Taylor and Klein (2000), a perceptual form of IOR exists in which automatic orienting occurs toward the peripheral location and the brain prepares eye movements to that location. Further responses made to targets in that location are inhibited. However, their results suggested a separate motor form of the phenomenon also

existed and was generated by the movement of the eyes in the direction of S1 causing any further response to the target in that direction to be inhibited.

This was the first time a separate form of IOR was shown with eye movements in response to a non-predictive central cue. Other results from this set of experiments showed that manual key pressing responses following a central cue- central target response did not show IOR. These results suggested that motor IOR was restricted to the oculomotor system.

Unlike Posner and Cohen (1984), Taylor and Klein (2000) showed IOR with both central and peripheral cues in many of their experimental conditions. There were two critical differences between the studies. First, Taylor and Klein used non-predictive peripheral and central cues whereas Posner and Cohen's central cues predicted the target's location. Second, in most of their experiments Taylor and Klein required that participants make a spatial response (press a key or make a saccade) to both cues and targets, returning to the central position between responses. Participants were required to orient to the cue and then withdrawal their attention, creating the necessary conditions for IOR

2.1.3 IOR for Reaching Movements

Many studies have been done to investigate the presence of IOR for reaching movements (e.g., Fischer, Pratt & Neggers, 2003; Welsh & Pratt, 2006). Fischer, Pratt and Neggers (2003) compared the effects of peripheral *cues* on manual responses (reaching and key pressing), to peripheral onset or central arrow *targets*. Results clearly indicated that IOR was present for peripheral targets, but not for the central arrow targets. Based on these results, it was concluded that the IOR for manual responses was due to an attentional suppression of the peripheral target and not motor-based effects associated

with performing manual tasks (Fischer et al. 2003). However, in this study, no response was required toward the cue and the cue was always peripheral. As such, the conditions were insufficient to test the possibility that a uniquely motor form of IOR could have been created by performing an actual reaching movement followed by a second response.

Taylor and Klein (2000) argued that under conditions of a peripheral cue, a perceptual form of IOR is created impacting future behavior that requires you to localize a target. So whether it be an eye movement, key pressing movement, or in this case a reaching movement this form of IOR is thought to impact the taking in of new information following a peripheral cue. According to that information, the Fischer et al. (2003), reaching study poses problems because the cues used were peripheral. Therefore, the IOR found in that study was not specific to reaching but rather another demonstration of perceptual IOR.

Cowper-Smith and Westwood (2013) went on to look for the presence of IOR following a reaching movement using a central target paradigm, in which participants were required to make a movement to both the non-predictive central cue and the target. This was similar to the experiments done by Taylor and Klein (2000) but instead had participants making a reaching movement instead of a key pressing movement.

Participants were presented with a display of a central fixation target surrounded by an array of placeholders located 0, 90, 180 and 270 degrees around fixation. A central arrowhead was displayed as the first target indicating to participants to make a reaching movement in the direction of the arrow. The eyes were to remain fixated while the arm reached out to a projected target. Following the onset of the initial target was the return of the hand to the center position and after was the onset of the second target. The second target was again a central arrowhead pointing to one of the four placeholder locations,

unrelated to the direction of the first movement. Participants made a second reaching movement in the direction of the target arrow. In different trials, the target arrow pointed in the same direction as the cue (0 degree offset) or at an angular offset of +/-90 or 180 degrees.

The anlaysis focused on the reaction time to the second target as a function of its direction in relation to the first movement. Results of this study showed slower reaction times for reaching movements made to targets located at the 0 degree offset (same location as the first target) compared to those located at the 90 or 180 offsets. It was also noted that 90 degree offsets were faster than the 180 degree offsets. This provides evidence to support an IOR effect for reaching movements made in response to central stimuli in a target-target paradigm in the sense that reaction times were shorter for movements in the opposite compared to same direction. However, the U-shaped function found here, in which RT for 90 degree offsets were the fastest of all, is not typical of IOR. Cowper-Smith et al. (2013) proposed a unique type of inhibitory interaction between successive movements. They proposed an explanation based upon neural adaptation within direction encoding motor neurons (Georgopoulos et al., 1986).

Direction-encoding neurons show maximal firing rates for a specific preferred direction, and cosine-modulated activity for intermediate directions. When a reaching movement is made in the S1 direction, the neurons that encode that direction become fatigued or inhibited. Therefore, future movements in that direction will be slower as the neurons are fatigued to that direction. This would explain why movements made to the cued location are slower than those made to the uncued location. Since the first movement is always followed by an opposing movement back to the central position, the neurons encoding this 180 degree direction are also fatigued or inhibited, leading to an

increased in RT for this direction as compared to the 90 degree direction which overlap least with the neurons encoding the first and return movement directions. The results of this study are the first in the literature to challenge the idea of motor IOR only being present for the oculomotor system.

reaching and key pressing responses during consecutive movements to similar and different spatial targets signaled by central arrows, much like Cowper-Smith et al., (2013). Taylor and Klein (2000) failed to show the presence of IOR for key pressing movements in their experiments. Their results suggested that motor IOR did not exist for key pressing. This study, however, was done to further explore and understand the properties of motor IOR for key pressing and reaching as it could not be explained why IOR was found for reaching movements but not key pressing movements. Results showed a similar pattern for both the reaching and key pressing responses. Consistent with IOR, reaction time was less when the central target signaled a movement to the opposite spatial location as compared to the same one. It is hypothesized that because similar behavior was evident for both types of manual responses, that a common mechanism could be operating, based on inhibition within neural populations encoding movement direction.

2.1.4 Defining Sensory and Motor IOR

It is important to consider the different parameters used in IOR experiments when differentiating between motor and sensory forms. Most of the studies done have focused on manipulating stimulus onset asynchrony, signal type, or the required mode of responding. However, spatial distribution, or how IOR is distributed across the visual field, for both sensory and motor forms has been less of a focus. This poses the question of how does inhibition vary with proximity to the location of the initial cue or target?

Spatial distribution patterns for IOR using peripheral signals have been investigated by measuring the reaction times to targets across different angular offsets. To better understand and differentiate sensory and motor forms of IOR in a meaningful way, spatial distribution patterns can be created to see if two potentially separate forms of IOR actually map out differently.

Bennett & Pratt (2001) published the first study that examined spatial distribution of IOR over a large area of the visual field. Results of this study showed that IOR affected targets distributed around the location of the cue in a monotonic manner; inhibition was strongest at the exact location of the cue but diminished in a systematic way as the target became further away from the cue, giving way to facilitation in the opposite location of space. This study set out the monotonic pattern of the spatial distribution of IOR with the use of peripheral stimuli; however, as discussed earlier, the cue/target conditions used favored a sensory form of IOR so the spatial characteristics of motoric IOR were not explored.

Cowper-Smith et al. (2013) compared the spatial distribution of IOR using peripheral or central stimuli to further reveal a difference between sensory and motor forms of IOR. They hypothesized that if a similar mechanism of IOR exists when peripheral and central stimuli are used then you would see a similar spatial distribution between the two. If the two types of stimuli, and their forms of IOR are truly different, separate spatial distributions might be possible.

A central signal (a small arrowhead) was used to replace the peripheral signal already demonstrated in the literature. Results showed a distinctly different spatial representation as that seen with the peripheral stimulus. It was demonstrated that 90-degree offsets were faster than the 0 or 180 degree offsets. There was also a significant

difference noted between offsets on the horizontal versus vertical axes. These results show the difference in the sensory and motor forms of IOR using spatial representations based on eye movement recordings.

This particular study also went on to identify the role of the effector system being used by introducing reaching movements into the task and comparing the effect the signal type has on the movement. It was hypothesized that if the spatial distribution of IOR was due to the signal type being used than results would be similar as those seen in the first two experiments. Results showed that the monotonic spatial distribution patterns depended on having a peripheral signal and the non-monotonic pattern was related to the use of a central signal. Introducing the reaching movement had no effect on the spatial distributions (Cowper-Smith et al., 2013).

This work was the first to highlight a non-monotonic spatial distribution using behavioral evidence, of IOR. This poses the question of how motor IOR can impact reaching responses to central stimuli. This study further emphasized the existence of distinct sensory and motor forms of IOR and demonstrated that response-based processes are affected by IOR following a central stimulus. It provided a form of behavioral evidence for motor IOR. It appears that motor IOR is based on using central signals with overt responses. It has been shown to be present for eye movements, as well as arm movements and demonstrates a unique non-monotonic spatial distribution pattern as compared to sensory IOR. These patterns appear to be similar for different effectors (Cowper-Smith et al., 2013; Avery et al. 2015).

2.1.5 Why Does IOR Occur?

Many theories about IOR assume that the phenomenon is related to the need for efficient visual searching behavior, which is a function of the oculomotor system (Posner

& Cohen, 1984; Posner et al. 1985; Klein & MacInnes 1999). Klein and MacInnes (1999) investigated the presence of IOR using a visual search paradigm by examining participants' saccades as they explored a complex scene. Participants where presented with a small black fixation target in the center of a blank screen. A "Where's Waldo?" image was then presented and participants were instructed to locate Waldo. After a random time interval, a fixation stimulus would appear unexpectedly on the screen in a randomized location. The Waldo image was either removed or kept in place. The participants were told to look at the fixation stimulus as soon as it appeared on the screen. This stimulus appeared at different locations in the display in both areas that had already been searched or in those that had not.

Results showed that participants were slower to foveate the fixation stimulus when it was located in areas in which they had previously searched compared to when it was in a new location when the Waldo image was left in place. This shows an IOR-like effect. However, when the Waldo image was removed and participants had to foveate the fixation stimulus with no background image, this same effect was no longer present. This suggests that the inhibition occurring was attached to objects in the search array. These results support the idea that IOR could potentially be occurring to aid in efficient visual search behavior and bias attention away from previously attended areas (Klein & MacInnes 1999).

2.1.6 IOR for Discrimination Tasks

The presence of an IOR effect for discrimination and identification tasks has also been investigated. If IOR acts to bias attention away from previously attended areas, one could predict that it would also be present regardless of if the response required was based on detection or on discrimination. Neill and Valdes (1992), performed a set of

experiments that predicted an IOR effect to be present when participants were required to discriminate between a target and a non-target character in a fixation display. Their results showed significant facilitation for targets that appeared in the same location as the preciously attended targets. Other studies (i.e., Terry et al. 1994; Egly, Rafal & Henik, 1992) went on to look for the presence of IOR in discrimination tasks and were also not successful. More recently Cheal, Chastain & Lyon (1998) showed evidence of an IOR effect in their identification task. Due to the discrepancy in the literature it is unclear how IOR impacts discrimination.

2.1.7 IOR for Grasping Movements

The observation that IOR can affect arm movements implies that the phenomenon might serve a broader purpose than simply guiding visual search. IOR may still aid in visual search behavior when present in the oculomotor system however it may also serve a different more general purpose related to the prevention of repetitive behaviors across motor systems (Cowper-Smith & Westwood, 2013).

To date, motoric IOR has been studied primarily via eye movements, although more recent research has identified similar patterns for reaching movements and manual key pressing (Avery et al., 2015; Cowper-Smith et al., 2013), bringing into question the idea that IOR exists solely as a foraging facilitator. Most actions we perform lead to the manipulation of an object, which emphasizes the importance of better understanding grasping behaviour. IOR has yet to be investigated for grasping actions despite the high prevalence of this action in our behavioral repertoire.

2.2 Prehension

Prehension can be defined as an object directed manual action of reaching out to grasp an object (Jeannerod, 1984 or 1986). The act of picking up an object located on the

table in front of you involves three steps. First is the positioning and moving of the arm toward the target object; this is referred to as the reaching component. Next is the positioning of the hand to match the size and shape of the target object; this is the grasping component. Finally you must physically pick up the object (Jeannerod 1986). Humans engage in these acts of prehension continuously throughout the day and so it is important to have a better understanding of any processes that may impact these actions.

2.2.1 Measuring Prehension

Common kinematic measures of prehension include reaction time, peak grip aperture and time to peak grip aperture (Jeannerod & Prablanc, 1983). Reaction time is the time between the onset of the cue (i.e., central arrow pointing left or right) and the onset of the movement. Peak grip aperture is the maximum distance between the index finger and thumb of the hand performing the grasping action. This is altered by object size; a larger object will have a larger PGA compared to a smaller object. These measures are related to the location of particular points of interest located on the fingers and wrist. These point locations represent sets of 3D coordinates in space and are collected using infrared emitting diodes (IREDS) placed on the wrist and fingertips of the participants. The IRED locations are measured at fast sampling rates and are detected by a set of three infrared detecting cameras.

2.2.2 Grasping

Grasping is a highly evolved object-directed manual action that requires information about object form as well as location (Jeannerod, 1984). There are two main types of grasping motions, the power grip and the precision grip. A power grip occurs when an object is placed between the thumb and all other fingers. A precision grip occurs by grasping an object solely between the thumb and index finger (Napier, 1960). Factors

at play when determining which form of grasping will be executed include the type of object being picked up and how the object will be used.

When reaching out to grasp an object the shape of the hand must be altered to match the shape of the object in which it is reaching for. Studies have shown that the hand will be altered to match the shape and size of the target object soon after the reaching to grasping movement is initiated. This is referred to as "preshaping" (Jeannerod, 1984). This indicates that this action is dependent on the visual information gathered from looking at the object and allows us to properly position the hand to match what is being grasped (Jeannerod et al., 1995). Peak grip aperture (PGA), the maximum distance between the thumb and the index finger, occurs at about 60-70% of the duration of the reach and is highly correlated with target size (Jackobson & Goodale, 1991). Studies have shown that PGA is consistently slightly larger than the size of the target object. However, changes in target size produce a predictable change in PGA (Marteniuk et al., 1990).

According to Jeannerod (1984), the initial reaching movement towards the target object (movement initiation to 70% movement time) occurs at a high velocity. The final movement however, (starting around 70% movement time) occurs with a lower velocity. This low velocity phase continues until the target object is grasped (Figure 2.3). The peak grip aperture is occurring during the fast velocity phase meaning that the hand is taking the shape of the target object early on in the movement. This suggests that the movement depends on visual processing of the object prior to picking it up (Jeannerod, 1984).

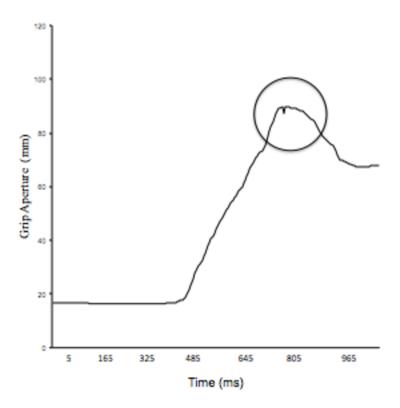


Figure 2.3 Typical grasping profile. A participant's thumb and index finger first pinch together at the start of the movement followed by the opening of hand. The peak grip aperture is illustrated as the circle on the graph. This is the time where the grip aperture is the largest. Following this grip opening is the closing of the fingers around the target object.

Reaching to and picking up a target object requires the processing of visuo-spatial cues in the environment. These cues provide information about object properties such as: how far away the object is located and its size. When viewing an object, each retina receives a slightly different 2-dimensional image. Binocular perception occurs as a result of the sensory fusion of these two images. Binocular single vision provides humans with a sense of depth and has been shown to play an important role in efficient grasping control.

Many studies have been done to demonstrate the role of binocular cues on the performance of reaching and grasping actions (Servos et al. 1992; Marotta et al. 1995; Jackson et al. 1997). More specifically, a study done by Melmoth and Grant (2006) investigated how binocular vision is advantageous in the planning and control of reaching and grasping movements. In their study, participants were seated in front of a table containing two household objects. These objects were placed in one of four locations. Participants wore PLATO translucent glasses, which provided three different viewing conditions: binocular, monocular with the dominant eye and monocular with the nondominant eye. They were instructed to reach out and pick up the object, place it to the side and return their hand to the starting position. Results showed the binocular and monocular conditions were similar in terms of the early phase of the reaching movement by looking at the peak velocity. However, binocular conditions showed significantly faster velocities for the final, low velocity stage of the reaching movement and shorter overall movement times. The grasping action was also affected by the monocular conditions as demonstrated by a significantly wider PGA and a consistent overshooting of the target location. Overall the grasping was much less accurate in the monocular conditions (Melmoth & Grant, 2006).

2.3 Visual Motor Transformation Processing

Visual processing begins when light reflected off of objects is refracted by the surface of the cornea and the lens. This light will travel through the vitreous to the inner layer of the retina and fall on the retinal photoreceptor cells called the rods and cones (Cassin, 1995). Once rods and cones become stimulated, a nerve impulse is generated and travels from these photoreceptor cells to the retinal bipolar cells and finally to the rental ganglion cells. The retinal ganglion cell axons exit the back of eye through the optic nerve. Nasally located retinal fibers cross at the optic chiasm to join the temporally located uncrossed fibers and form the optic tracts. The optic tract travels through the midbrain to the lateral geniculate nucleus (LGN) located in the thalamus. The LGN processes visual information and projects to the primary visual cortex (V1) (Cassin, 1995). From here, the information leaves the primary visual cortex and follows two different streams, the dorsal or ventral stream.

2.3.1 Dorsal and Ventral Streams

The ventral stream follows the path of the inferotemporal cortex, while the dorsal stream follows the posterior parietal cortex (Goodale and Milner, 1992). The ventral stream is considered to be the stream of "vision for perception", while the dorsal stream is considered to be the stream of "vision for action" (Westwood & Goodale, 2011). The input of the ventral stream focuses on perception of the object while the output of the dorsal stream focuses on the intended actions. For example, the ventral stream aids in identifying what an object is and storing that representation, while the dorsal stream aids in localizing the object and extracting shape information from the object in order to initiate the intended action (Westwood & Goodale, 2011).

Studies have been done to demonstrate the difference between these two cortical

visual streams using visual illusions. Aglioti et al. (1995) used the Ebbinghaus illusion to show the distinction between visual perception and control of grasping actions (Figure 2.4). When participants were presented with a 3 dimensional version of the image they reported that the target disk surrounded by smaller circles was actually larger than the same target disk surrounded by larger sized circles. However, when asked to pick up the disks their PGA remained true to the actual size of the target disk. Such an observation is inconsistent with a unitary visual system that mediates *both* perception and action, but is entirely consistent with the proposal and perception and action are generated by distinct cortical visual systems.

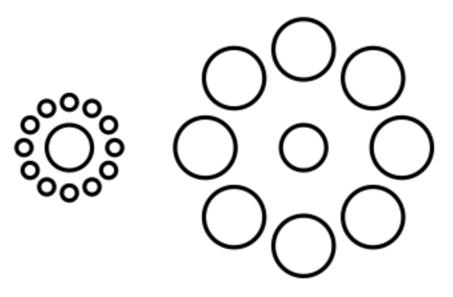


Figure 2.4 Ebbinghaus Illusion. The target center circles appear to be of different sizes although they are identical in size.

2.4 Object Properties

An object's orientation, size, shape and location are all important factors to be considered if that object is a target for grasping. The person picking up the object must determine these parameters prior to picking it up. The visual system works to detect the specific features of the target object. Object features can be classified as intrinsic or extrinsic (Jeannerod, 1984). Intrinsic features are things such as size, shape or color and are present independent of the person picking up the object. Extrinsic features are those relative to the person pick up the object, such as location or orientation. Both of these features are necessary in reaching and grasping, in contrast to reaching which depends entirely upon extrinsic object features. As such, comparisons between simple reaching, and reaching to grasp an object, emphasize the visual processing of object shape information since spatial location is common to both.

As mentioned previously, grasping requires information about form and location of an object. IOR is thought to be a location-based phenomenon that is proposed to discourage the preparation of responses to previously attended areas and objects. It is currently unclear whether this inhibitory activity is restricted to purely spatial representations or if it can also affect the information about object form and the transformation into action. By focusing on grasping, this study will provide information on how locations are inhibited, based on impairments in the initiation of the reach (reaction time), as well as how the inhibition may impact the extraction of object formation from by looking at the relationship between object size and grip opening.

IOR has been studied as a mechanism that improves the efficiency of visual search by acting to bias attention away from previously attended areas (Klein & MacInnes 1999). However, the presence of an IOR effect seen in reaching studies

questions this idea. The IOR found following reaching movements has been thought to be related to the direction encoding of movement leading to a residual inhibition for further movements made in the same direction (Cowper-Smith & Westwood 2013). According to that hypothesis, it is likely that an IOR effect will be present for grasping movement because these movements are also direction based. It is unclear however if this inhibitory effect will impact the grip scaling properties since this has not been explored in the literature.

Chapter 3 Methodology

3.1 Participants

Sixteen participants (n=3 men, n=13 women, ages ranging from 18-32) who fell under the inclusion criteria (see below) were included in this study. The number of participants needed for this research was based on previous work on IOR for reaching movements, which identified significant effects using 16 participants (Cowper-Smith et al., 2013). Two people were recruited by word of mouth and 14 from the SONA undergraduate psychology pool. All participants included in the study had a near visual acuity of 20/20 or better on the Sloan near visual acuity card and had a near stereoacuity of 60" or better on the Frisby stereoacuity test.

Inclusion criteria for this study included that participants be at least 18 years of age, prefer to use their right hand, have normal or corrected to normal near visual acuity of 20/20 (or better) and have normal near stereoacuity of 60" or better as assessed using the Frisby Stereo Test. Exclusion criteria for this study included the presence or history of any neurological challenge or diagnosis affecting coordinated eye movements, visual or cognitive processing skills, head or neck control or upper limb fine motor coordination, or the presence of visual or ocular anomalies such as amblyopia, strabismus, retinal or corneal disease.

It was required that all participants be of at least 18 years of age as this is the age at which the brain is considered mature, and also the age required to provide consent.

Right-handedness was necessary for participation in this study. It has been shown in the literature that those with preference for their left hand are more likely to have atypical cerebral organization compared to those who are right-handed (Ferrari, 2007).

Participants with reported visual abnormalities or disorders were excluded because of the

impact that these conditions can have on perception and localization of targets.

Stereoacuity is known to play a key role in depth perception under binocular conditions.

For this reason, it was necessary that each participant had at least 60" on the Frisby stereoacuity test (Appendix A- Participant Screening Form).

3.2 Ethics

The Dalhousie University Research Ethics Board approved all materials and methods necessary for this study (Appendix B- Ethics Approval Form). All participants included in the study provided informed consent. (Appendix C- Participant Consent Form)

3.3 Equipment

Equipment used in this study included the Optotrak 3020 [™] motion analysis system, Electrooculograph (EOG) eye movement recording system, two pressure sensitive switches, a mounted projection system and a turntable apparatus.

3.3.1 Electrooculograph

Eye movements were monitored using an electrooculograph recording system. Small foam dermal electrode pads were placed on the participants' lateral canthi of the orbits (left and right side), as well as on the forehead for a reference. This system was used to infer eye movements from changes in electrical signals related to movements of the negatively charged retinas, which was necessary to exclude trials in which the participant did not maintain central fixation. Any trial in which an eye movement occurred was eliminated from analysis.

3.3.2 Optotrak 3020TM

The Optotrak 3020TM motion capture system (NDI, Waterloo, ON, Canada) was used to track and record movements of the right hand throughout testing. This system uses infra-red position sensing units to monitor the 3D locations of small infra-red

emitting diodes (IREDs) attached to the skin of the index finger, thumb and wrist of the right hand of each participant using medical Transpore tape (Figure 3.1).

IREDs were connected to a computer-controlled unit via a wire used to control the timing of IRED activation. A position sensor unit consisting of three infrared cameras was used to measure IRED positions using three-dimensional coordinates (Figure 3.2). The system was set to sample three-dimensional positions of each IRED at 200 Hz. Data were stored in text files and processed using a custom PythonTM script.

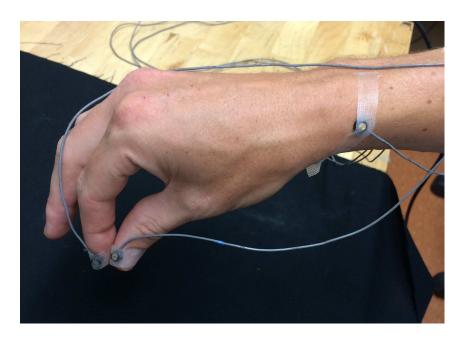


Figure 3.1 Position of infrared emitting diodes on the index finger, thumb and wrist of the participant's right hand.



Figure 3.2 Optotrak 3020 3D motion capture system.

3.3.3 Apparatus

Two sizes of small wooden blocks (4.5 cm X 1cm X 1cm and 5.5cm X 1cm X 1cm) were used as target objects for this study, with four of each to create the necessary stimulus arrays. Blocks were placed atop a black turntable apparatus (30cm X 30cm), consisting of a vertical centerboard fixed in the middle of a horizontally placed turntable creating two separate stimulus display areas that could be shown to the participant by rotating the apparatus (Figure 3.3). Two identical blocks were secured on the left and right side of both display areas prior to beginning each trial, thus creating two identical displays. Blocks were placed 8.7cm on either side of the center of the display area, which was located approximately 50 cm away from the mid-forehead of the participant such that objects were approximately 8 degrees to each side of central fixation (Taylor & Klein, 2000). During trials, a 3.5 cm long arrow stimulus pointing to the left or right object could be displayed at central fixation using an overhead-mounted LCD projector. This arrow was generated and displayed using Experiment Builder.



Figure 3.3 Depiction of experimental set up including the turntable apparatus, starting switch, central arrow and target blocks for grasping.

3.4 Procedure

Data collection and reduction was performed by the principal investigator and took place in the Action Laboratory (Dalplex room 218) at Dalhousie University in Halifax, NS Canada. Participants arrived at the laboratory and were provided with a participant information sheet explaining the inclusion and exclusion criteria of the study. If participants answered yes to any of the exclusion criteria, they were told that they were unable to participate. If they fell under the required inclusion criteria participants were then asked to sign a consent form to participate in the research.

Once consent was provided, best corrected near (40cm) visual acuity was tested using a Sloan near visual acuity card. A Frisby stereoacuity test was then performed to ensure participants had at least 60" stereoacuity. (Appendix D- Participant Information).

Participants were seated comfortably in front of the turntable apparatus under photopic conditions with the pressure sensitive switch located approximately 20 cm in a central position on the table in front of them. The task was then explained to each participant. Participants were told they would be completing 160 trials of picking up one block as indicated by an arrow followed by a rotation of the turntable and picking up a second block as indicated by another arrow while maintaining fixation on a central location. They were told to start the trial by placing their right hand on the pressure sensitive switch in front them while maintaining fixation on the crosshair displayed in their central field of view. They were instructed how to position their hand on the switch so the IREDS could be picked up by the Optotrak motion analysis camera.

When the trial started, a fixation cross appeared centrally for between 500-1000ms. This was followed by the appearance of an arrow located in their central fixation for 2000ms, and this was the cue to grasp a block on either the left or right side of the

turntable (p=0.5), depending on the direction of the arrow. Participants were reminded to maintain fixation on the central arrow during this task. Upon the arrow cue, participants were to then remove the hand from the switch, grasp the indicated block lengthwise, drop the block in a designated position and replace the hand on the switch. Once the hand returned to the switch the turntable was rotated 180 degrees by the principal investigator to reveal the second set of paired blocks. A fixation cross was displayed for between 500 and 1000ms. An arrow pointing to the left or the right (p=0.5, determined separately from the location of the first arrow in the trial) appeared for 2000ms indicating to the participant to grasp the second block (Figure 3.4). After the second grasping movement was complete and the block was placed in the designated area, the trial ended. In between trials, the participant was instructed to position their hand back at the home position and the turntable was reset with the required blocks, which took about 15 seconds. For each trial, the first and second blocks to be grasped were either on the same side of space (left/left or right/right) or on different sides of space (left/right or right/left). For an entire trial all objects were either 4.5cm X 1cm X 1cm or 5.5cm X 1cm X 1cm.

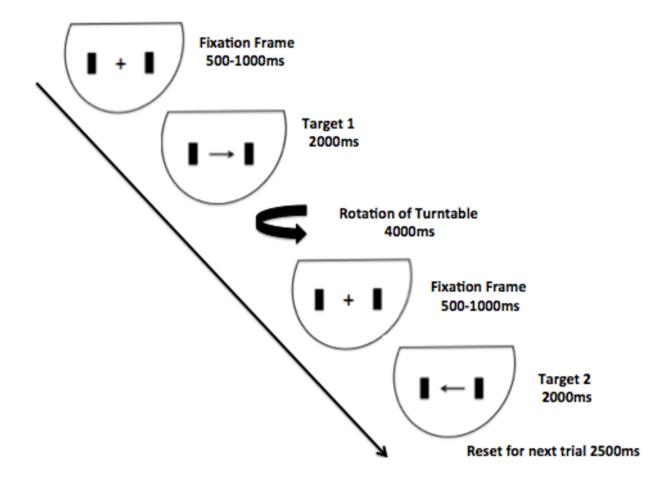


Figure 3.4 Sequence of events during a single trial. At the beginning of a trial the fixation cross was displayed for 500-1000 milliseconds followed by the appearance of the initial target arrow pointing to the left or right (p=0.5). This arrow was displayed for 2000 milliseconds indicating to the participant grasp the block in the direction displayed. Following the grasping of the block the turntable was rotated and a second fixation cross was displayed for 500-1000 milliseconds. The second arrow stimulus then appeared for 2000 milliseconds indicating to the participant to grasp a block on the same side or different side as the initial movement.

Manipulated variables included target size (2: large or small block), direction of the first arrow (2: left or right) and direction of the second arrow (2: left or right). Each participant performed 160 trials made up of twenty repetitions of each of these conditions randomly scattered throughout the experiment. Breaks were provided after every 60 trials and participants were told that they could stop the experiment at any time if additional breaks were needed.

Trials were excluded from data analysis if participants moved their eyes from central fixation as judged by the investigator, or if any instrumentation failure occurred.

3.5 Statistical Analyses

Dependent measures included reaction time for the movement to the second target block (the time between the onset of the central arrow instruction stimulus and the onset of hand movement), peak grip aperture (the maximum distance attained between the participant's index finger and thumb), and time to peak grip aperture (the time it took to reach the peak grip aperture following the start of the movement) for each trial. Note that all of these measures were derived from the second movement in the trial (i.e., in response to the second arrow), thus reflecting the potential influence of a prior action on the current action. Data were analyzed using Statistical Package for the Social Sciences, (SPSS) version 23 TM. Outlier data were excluded for each participant by calculating the mean and standard deviation for each dependent variable across all trials, and eliminating all data from a trial if at least one dependent measure fell outside +/-3 Z-scores.

For the purpose of analysis, the independent variables for direction of the first (left/right) and second arrow (left/right) were recoded into factors of second arrow direction (left, right) and the relationship between the first and second arrows (same, different). Repeated measures ANOVAs were performed for each dependent variable

with factors S2 direction (right or left) X relative direction (same or different) X size (large or small). An alpha of 0.05 was used for all omnibus analyses. (Appendix E-Statistical Data)

A custom PythonTM script was used for the analysis of kinematic data. Using data obtained from the IRED on the wrist, movement onset was defined as the first sample for which speed was greater than 50 mm/s for 5 consecutive samples. Movement offset was defined as the first sample for which speed was less than 50 mm/s for 5 consecutive samples. Since the onset of data collection was synchronized with the presentation of the arrow stimulus, reaction time was thus defined as the time for the movement onset event. Grip aperture was calculated as the vector distance between the finger and thumb IREDs, and peak grip aperture was the largest grip aperture value occurring between movement onset and offset. Interactive graphical analysis was used in cases where the preceding algorithms did not correctly identify the target events due to missing data or irregular kinematic profiles.

Chapter 4 Results

Of the 2560 total trials in this experiment, 92.80% were included in the analysis. Reasons for exclusion of trials included participant failure to maintain central fixation throughout the trial (1.6%), instrumentation and data collection error (3.8%) and Z score exclusion (1.7%) (Appendix- F Eliminated Trials). The analyses included only the trials that had a Z score (based on individual participant data distributions) of less than or equal to 3 for reaction time, peak grip aperture and time to peak grip aperture. Trial data, which had a Z score greater than three, were considered outliers and were not included in the data set.

The dependent measures in this study were reaction time, peak grip aperture and time to peak grip aperture. These measures were analyzed using repeated measures analysis of variance (ANOVA) with factors S2 direction (right or left), relative direction (same or different), and object size (small or large).

4.1 Reaction Time

Reaction time is the time measured between the presentation of the cue and the onset of the movement. We looked at the RT following the second arrow stimulus, which indicated, to participants to pick up the second block. A significant main effect for relative direction (same or different side), F (1,15)=7.40, MSE=15613, p=0.016 was found, indicating a faster mean reaction time for objects located in a different direction (403) versus the same direction (417) as the first movement (Figure 4.1).

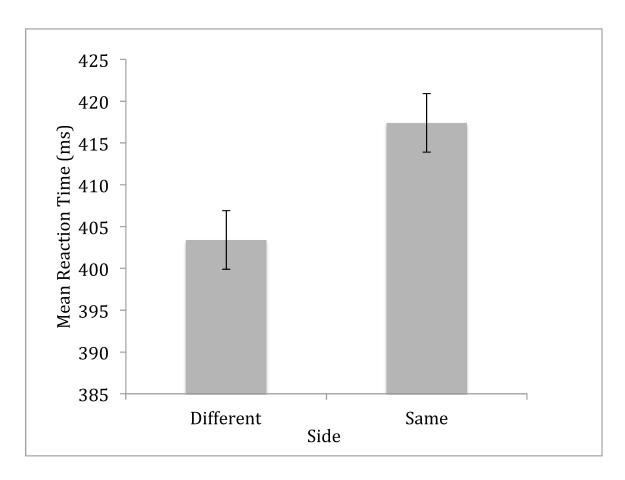


Figure 4.1 Mean reaction times in milliseconds following the second arrow stimulus, to the same or different side as the initial movement. A significant difference was found in the RT's suggesting an IOR-like effect was found. Error bars represent standard error of the mean.

4.2. Peak Grip Aperture

Peak grip aperture is the greatest distance measured between the index finger and the thumb during the grasping action. As expected, a significant main effect for size, F(1,15)=66.1, MSE=270.030, p<.001, showed that the peak grip aperture was significantly larger for the larger sized objects (85) versus for the smaller sized objects (80) (Figure 4.2). However, there was no main effect of relative direction, and no significant interaction was found between object size and relative direction (same or different).

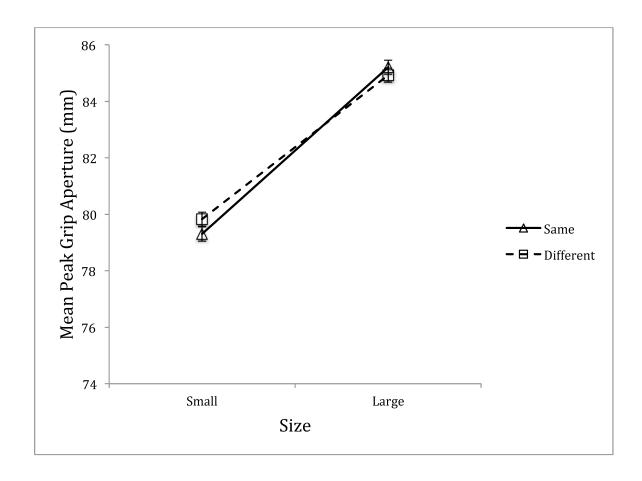


Figure 4.2 Mean peak grip aperture, in millimeters, for small and large sized objects following the second arrow stimulus to the same or different side as the initial movement. Error bars represent standard error of the mean and are smaller than the markers on the figure.

4.3 Time to Peak Grip Aperture

The time to peak grip aperture is the time between movement onset and the moment in time the peak grip aperture occurs. As predicted, a significant main effect for size, F(1,15)=7.0, MSE =3, p=.018 was shown, time to peak grip aperture was significantly larger for the larger sized objects (393 ms) versus for the smaller sized objects (387ms) (Figure 4.3). However, there was no main effect of relative direction and no significant interaction was found between object size and relative direction (same or different).

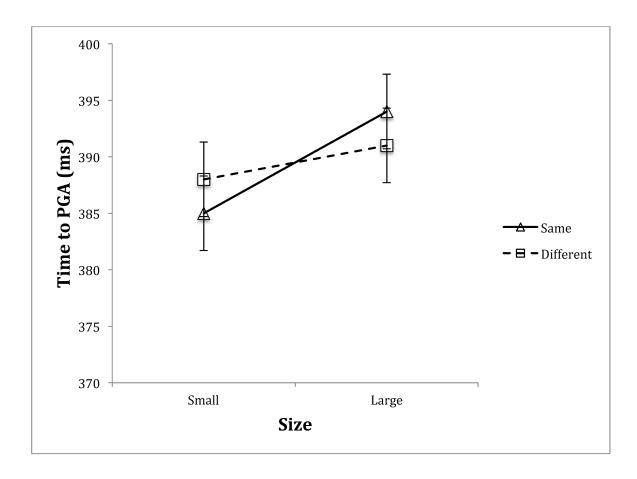


Figure 4.3 Mean time to peak grip aperture, in milliseconds, for small and large sized objects following the second arrow stimulus to the same or different side as the initial movement. Error bars represent standard errors of the mean.

CHAPTER 5 DISCUSSION

This study was the first of its kind to investigate the presence of an IOR effect for grasping movements both in terms of the time to initiate the movement and the scaling of grip opening to object size. Motor IOR has been shown to be present for saccades, key pressing movements and reaching movements but until now has not been investigated for grasping movements despite the prevalence of these actions in our daily lives.

The purpose of this study was to investigate if the time to initiate a grasping action (reaction time) was affected by the relative direction (same or different) of the preceding grasping action. We also looked at the scaling of the grip size to object size and the timing of grip formation. The predictions made in this study were based on different aspects of grasping. We investigated if the starting of the movement (reaction time) was slower when moving to the same direction as preceding movement compared to moving in the opposite direction. We also looked at if the timing and/or scaling of the grip aperture function would be impacted.

More specifically, participants were required to grasp a 4.5cm X 1cm or 5.5cm X 1cm wooden block following the presentation of a central arrowhead cue indicating which block to grasp (left or right), while keeping their eyes fixated centrally. Following the grasping of the first block, a fixation cross appeared in the center followed by a second central arrowhead indicating to the participant to pick up a block either in the same direction or different direction as the first block. Analyses looked at reaction time to the second object, peak grip aperture and time to peak grip aperture. From those measures, different sets of predictions based on three different theories were made.

The first theory in the literature claims that IOR is a mechanism used to facilitate

efficient visual search behavior (Klein & MacInnes, 1999). This visual search theory seems insufficient, however, because many subsequent studies have found IOR for arm movements (Cowper- Smith & Westwood, 2013; Avery et al., 2015), which are not exploratory behaviours and have little if any role in visual search. Nevertheless, the prediction based on this theory was that we would see no IOR effect for reaction time of the movement or on the grip aperture as grasping is simply not a searching movement and therefore would be unaffected by a phenomenon used in visual search.

The second relevant theory is related to the relevance of spatial coding for the IOR phenomenon. If IOR is based on the suppression of direction encoding neurons, as speculated by Cowper-Smith and Westwood (2013), we predicted that only the directional components of the grasp should be affected. Therefore we expected to see slower reaction times for movements made in the same direction as a preceding movement. The grasp, which is not itself a directional movement, would be unaffected and both the scaling of the grip aperture and the time to reach the PGA would show no difference between same and different conditions.

The final relevant theory is related to the idea that IOR and IOR-like phenomenon may arise from the suppression of an entire movement plan in order to avoid repetitive behaviors and promote novelty. If this were true, every aspect of the movement, both the starting of the movement and the grip scaling and timing would be affected and we would likely see a difference in those movements made in the same directions as preceding movements.

5.1 Summary of Results

As predicted based on the spatial encoding hypothesis, reaction times were significantly slower for the grasping of objects in directions in which a preceding

grasping movement was made, consistent with an IOR-like effect. A separate analysis revealed that no IOR-like effect was found for overall PGA (i.e., for 'same' compared to 'different' directions) or for the simple effect of object size on PGA (i.e., grip scaling: a significantly greater PGA was observed for larger than smaller objects, but this was not influenced by the direction of the previous movement). The same patterns were revealed for the time to reach PGA.

With respect to the three sets of predictions, the results are most consistent with the spatial encoding hypothesis because there was a significant difference for the onset of the movement but there was no impact found on the grip aperture functions in the same and different locations.

As outlined earlier, it is unlikely that IOR and IOR-like phenomena serve the sole purpose of facilitating visual search behaviour, since robust motor IOR has been shown for reaching movements and these have no relevance for searching behaviour (Cowper-Smith & Westwood, 2013). It is possible that visual search facilitation is a byproduct of a more general mechanism that inhibits directionally repetitive behaviours as will be discussed later. With reference to the current study, grasping is not a searching behaviour as objects must be located before grasping is initiated otherwise people would waste tremendous time and energy. For example, when you want to pick up your coffee cup off of a table containing multiple items such as a coffee cup, a bowl and a glass of water, you would not pick up the bowl first and to determine if it is the correct object. Rather, you would search the array first to locate the coffee cup and then initiate grasping. Thus, the observation that grasping RT shows an IOR-like pattern is further evidence against the idea that IOR is a tool to promote efficient visual search.

The results support the direction-encoding model of inhibition as proposed by

Cowper-Smith et al. (2013). Here, we found a significant difference in the onset of movements made in the same direction as a preceding movement compared to those made in the opposite direction. According to Georgopolous et al. (1986), the direction of movement is determined by populations of neurons that individually have a preference for a particular direction. These neurons display maximum firing rates in the preferred directions and are reduced when the direction deviates from that preference. According to this idea, we propose that in our study, when an arm movement was made in the direction of the arrow cue, the neurons that encoded that direction became fatigued due to high firing rate. Therefore, future movements made in that direction potentially engaged the same neurons and because of the "fatigue", slower RTs were observed. Based on this theory, once a movement is made in a particular direction, an inhibitory trace potentially gets left behind. When a return movement is made back to the center location after completing the first grasp, a second inhibitory trace is created, discouraging movements in that direction. More specifically, in this study participants made a movement in one direction (left or right) to pick up a block followed by a reach in the counter direction to move their hand back to the center location. This is a similar setup to the study by Cowper-Smith & Westwood (2013), which found an IOR effect for reaching movements.

5.2 Grip Aperture

This study investigated preshaping of the grip aperture, which, unlike reaching, does not have an inherently directional component (Jeannerod, 1984). When making a grasping motion, the hand opens and the thumb moves in an opposite direction of the index finger. It is possible that the coding of the size and shape of the hand is unrelated to the movement direction and therefore was not inhibited by neurons that code for movement direction. As mentioned previously, our third hypothesis was based on the

theory that IOR-like phenomenon could be due to the suppression of an entire movement plan in order to avoid repetitive behaviors. If this were true the entire movement would be affected unlike the direction-encoding model in which only a direction is suppressed. It is important to note that many aspects of movement do not have a spatial component to them and therefore may not be impacted by suppression of direction. One issue with prior research on reaching and eye movements is that it is focused on these directional components (i.e. Posner & Cohen, 1984; Taylor & Klein, 2000). The idea of suppressing an entire movement does not necessarily have to be direction based. Participants are typically asked to make a movement in a direction and come back to center. When an IOR effect is found following these movements, we assume that it is occurring because of repeating a direction but it could be due to something more. It is possible that this inhibition is caused by the repetition of an entire action. This could be direction based, but it is hard to conclude that because it is all that has ever been studied. Another idea is that an inhibitory trace following every movement might serve this purpose. If a reaching movement was made in one direction, the brain would inhibit it from being done again and so you would be faster to reach in the opposite direction, as seen in IOR for reaching studies. The brain is taking the memory of the movement you just made and inhibiting it so it makes it harder or less likely that you will repeat it. If this is happening we would see all aspects of the movement affected.

Although there is no direct evidence to support this idea, it is important to explore. The brain has a memory for things that just happened allowing for easy reactivation of recent events. Priming is an example of how the brain can fall into a repetitive process. (i.e., when a person is shown an object for a second time they are much faster to recognize it) (Ratcliff & McKoon, 1988). If the execution of movements also followed

this pattern it would be very difficult to avoid continuous repetition of the same movements. For example if you just picked up your coffee cup, this movement is now primed and fresh in your mind, ready to be reactivated. The brain must find a way to prevent this from happening over and over again. Priming is beneficial for some things in perception but for accurate motor control you need some kind of mechanism that prevents you from repeating the same things, i.e. something to stop you from picking up the coffee cup again and to do something new. One way to prevent this repetitive behavior is to create an inhibition on whatever was just performed to combat the priming effect.

Inhibition could be a way from preventing people from lapsing into a cycle of repetitive movements. Evidence suggests that the brain is easily primed and so inhibition could be a tool to help promote novel behavior.

The grip aperture component allowed us to investigate if direction or movement suppression was occurring and further distinguish between two hypotheses, the first being that IOR is related to the suppression of direction (Cowper-Smith et al. 2013) and the other being that it is a product of an entire movement suppression. Each theory makes a different prediction about what would happen to the grip aperture if affected by inhibition. The direction-encoding model suggests that grip aperture should not show IOR-like phenomena, whereas the movement suppression model predicts that all aspects of the movement would be suppressed including the grip aperture. Results showed that the grip aperture was not impacted by any IOR effect providing strength in the direction-encoding hypothesis.

5.3 Potential Limitations & Future Studies

In this study, to characterize the grasping component of prehension we made the choice to examine PGA and time to PGA. Much of the literature on reaching and grasping

uses PGA as a measure of the grip component of a movement. However, it is also of interest to discuss other measures of grip aperture, which were not included, i.e. what is happening early on in the movement, compared at the later stages and how they differ.

Glover & Dixon (2013), have argued that choosing PGA as a sole measure to analyze grasping is problematic as it occurs fairly late into the movement. It is suggested that looking at the grip shortly after the movement begins and again later on in the movement and comparing the two is a better representation of the grip profile. Studies using visual illusions have showed that if you look at early stages of movement time, the opening of the hand is affected by the perceptual illusions of size but later stages are not (Glover & Dixon, 2013). This suggests that what you see early on the in grasping movement is a reflection of the brain's planning of the movement while the later movement reflects visual feedback control. Allowing for time to view the object and correct your grip to accurately grasp it. Therefore the PGA, made later on in the movement is artificial because it has already been corrected by visual feedback.

We choose to look at PGA as our main variable because this is what was most common amongst other studies in the field when looking at hand opening. It is possible however that a change in scaling function of the grip may have been present early on in the movement and was later corrected because of visual feedback. When the participant was making a movement toward the object the grip aperture may in fact have been smaller but as the hand got closer to the block and the brain realized the grip was not wide enough to properly pick up the block, it may have been adjusted causing the appearance of the inhibition to go away. However, based on our findings it is not likely that there was any impact of inhibition on the earlier movements because time to PGA was also unaffected. If visual feedback were being incorporated, it would likely cause an increase

in time to reach PGA (to allow for adjustment time).

Future studies could look at the grip aperture measures earlier in time to see if those measures are significantly different from the PGA measures or they could eliminate visual feedback altogether using liquid-crystal occlusion goggles. Once a participant began a movement, the goggles would become opaque eliminating any chance of visual feedback. This was not possible in the current study because of the fixation requirement and the corresponding need to monitor eye movements. The participants were required to be hooked up to an EOG so that eye movements could be monitored throughout the experiment. It was not possible to use both the EOG and goggles at the same time without massive electrical interference. The fixation requirement was necessary in order to exclude the possibility that any IOR-like effects observed were due to eye movements rather than grasping movements. If however, in future studies the fixation requirement was eliminated the occlusion goggles could be put to use. Now that we know the IOR effect is present for grasping, there is no evidence to suggest that eye movements would eliminate this. By repeating the study and allowing eye movements one could investigate if the current pattern still held true with visual feedback eliminated.

Another potential concern about the present study was that the objects used for the first and second targets in a trial were always matched. Allowing different sizes of blocks within a single trial would have complicated the analysis of size scaling because one would need to consider both the repetition of movement direction itself, as well as the repetition (or not) of object size. According to our predictions, if inhibition were happening it would have made the grip aperture smaller regardless of a large or small object being picked up.

We chose to use only two sizes of blocks instead of a larger range of sizes that might have been less perceptually discriminable. However, with only two sizes of objects, it is possible that participants may not have actually used vision of size to guide their actions. They might have simply recognized which object, "big" or "small" was to be picked up and then programmed the required movement from memory. The problem with this is that movements are no longer "visually guided" but instead "memory guided". This could complicate the interpretation of underlying brain mechanisms since it is assumed that visually guided movements are dorsal stream functions and memory guided movements are ventral stream (Westwood & Goodale, 2003).

However, if participants were visually aware of the block size they were picking up, we believe it would not have any impact on the task at hand. The purpose of this study was to investigate if IOR was either direction specific or due to movement suppression. Whether the movement was memory guided or not does not impact our research question. Nevertheless, to eliminate this possibility, future studies could ensure that movements are controlled with vision, using a range of sizes that are not easily recognized so the participant would be required to look at the object to know how to pick it up.

In order to probe the presence of IOR-like phenomena for grasping we chose to manipulate the size of the objects and not the orientation or shape. Size was chosen as a simple mechanism that helped us to answer the research question. Even if orientation or shape of the objects were manipulated instead of the size it would not change our predictions. It can however be argued that orientation has more to do with direction encoding. Our experiment was intentionally designed so that the direction of the reach was orthogonal to the grasping axis of the object to eliminate an overlap between the reaching and grasping movements. Future studies could repeat this experiment and alter

the orientation of the object.

In addition to previously discussed concerns about the limited range of grasping measures used in this study, this experiment could have incorporated measures of the reach component other than using only reaction time. Of course, reaction time was used as it is the primary and often only measure used to document the presence of IOR. It is possible that other aspects of the reach could have been affected by the direction of the movement such as hand speed or direction suppression in hand deviations.

If direction encoding is what is being suppressed there are other factors to investigate such as looking for evidence of direction suppression in hand movements in areas other than left and right. Populations of neurons encode for multiple different directions and so a consequence of inhibition could be for all movements toward the inhibited direction. When a reaching movement is made to the left hand side, that side becomes inhibited for future movements. The ability to make a straight-ahead movement is a reflection of all the neurons in the brain that encode all directions working together and so if some directions (i.e., left side) have suppression you should be slower to go left but it is possible that the ability to go to the left at all may be compromised. This could be investigated using a trajectory study. Past studies have looked the spatial characteristics of aiming a key pressing movement following a non-predictive cue and have found that inhibition is shown in these trajectory measures. According to Neyedli & Welsh (2012), hand trajectories were shown to deviate toward the non-predictive central cue at short CTOA's (100ms) but when the CTOA became longer (850ms) an opposite affect was found. It can be predicted that if suppression were created in a particular direction following an initial reaching movement, the following movement would veer away from that direction.

5.4 Practical Implications for Orthoptic Practice

Relatively little is known about how visual disorders impact functional movements. Many common visual disorders such as strabismus or amblyopia lead to a reduction in, or an elimination of depth perception, which has an impact on how patients make movements but currently this is not measured in an orthoptic setting (Melmoth & Grant, 2006). Interestingly, most of the clinical techniques used to assess binocular depth tend to be of a perceptual nature (i.e., Worth 4 Dot, Titmus stereo test, Frisby stereo test) but very rarely are functional movements assessed. By incorporating an assessment of functional movement clinicians could have a better understanding of how particular visual disorders impact the daily lives of patients.

Knowledge of grasping and the results of this study could be beneficial in the creation of clinical assessment techniques that incorporate grasping as part of a visual assessment. If a standardized assessment of grasping were ever to be a part of clinical visual assessments it is important to realize that processes like IOR may impact what you measure. The findings of this study would alter how a grasping task would be structured in a clinical setting to avoid causing the appearance of a visual abnormality due to slower response times to previously viewed areas.

5.5 Conclusion

This study is the first to look at the presence of an IOR-effect on grasping actions and the effect this has on grip aperture. Using a traditional central target-target task paradigm it was found that grasping movements made in the same direction as a preceding movement were slower compared to those made in a different direction. These findings demonstrate an IOR effect, similar to that found for reaching movements (Cowper-Smith & Westwood, 2013). Results also showed no impact on the size scaling

function of the grip. These results support the idea that IOR may play a different role than facilitating visual search and is associated with direction encoding.

On the global scheme of understanding how people make movements this study has contributed knowledge of how ones previous movement history can impact future movements. Our results support the idea of the presence of an innate brain mechanism that aims to reduce or prevent the likelihood of repeating behaviours, allowing for efficiency in our daily lives.

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APPENDIX A



SCREENING FORM: *Inhibition of return for Grasping Movements.*

If the answer to any of these questions is "YES", you are not eligible to participate in this study.

It is not necessary to disclose which of the questions or conditions applies to you.

- Please inform the investigator you are unable to participate.
- If you have any questions regarding the question or any of the conditions listed below, please ask the investigator.
- 1. Are you under the age of 18?
- 2. Do you prefer to use your left-hand for tasks that require the use of only one hand?
- 3. Have you ever been diagnosed with any form of visual disorder?

Possible examples may include (but are not limited to):

- Amblyopia
- Colour Blindness
- Glaucoma
- Monocular deprivation for an extended period (e.g. eye patching)
- Strabismus
- Uncorrected near- or far-sightedness
- Corneal or Retinal disease
- Cataracts
- 4. Have you ever been diagnosed with any form of neurological challenge or diagnosis which has affected your ability for coordinated eye movements, visual and cognitive processing skills, head and neck control in a seated position, or upper limb fine motor coordination?

Possible examples may include (but are not limited to):

- Acquired Brain Injury as a result of: Trauma, Cerebral palsy, Encephalitis, Hydrocephalus, Meningitis, Stroke, Tumour, etc.
- Developmental Coordinator Disorder
- Learning Disability
- Movement Challenges such as: athetosis, chorea, dystonia, spasticity, rigidity, etc.
- Peripheral neuropathy
- Seizure disorder
- Vestibular disorder
- Progressive conditions such as: Amyotrophic Lateral Sclerosis (ALS), Huntington's, Multiple sclerosis, Parkinson's disease, etc.

APPENDIX B

Social Sciences & Humanities Research Ethics Board Letter of Approval

July 29, 2013

Dr David Westwood Health Professions\Health & Human Performance

Dear David,

REB #: 2013-3051

Project Title: Inhibition of Return for Grasping Movements

Effective Date: July 29, 2013 Expiry Date: July 29, 2014

The Social Sciences & Humanities Research Ethics Board has reviewed your application for research involving humans and found the proposed research to be in accordance with the Tri-Council Policy Statement on *Ethical Conduct for Research Involving Humans*. This approval will be in effect for 12 months as indicated above. This approval is subject to the conditions listed below which constitute your on-going responsibilities with respect to the ethical conduct of this research.

Sincerely,

Dr. Sophie Jacques, Chair

Post REB Approval: On-going Responsibilities of Researchers

After receiving ethical approval for the conduct of research involving humans, there are several ongoing responsibilities that researchers must meet to remain in compliance with University and Tri-Council policies.

1. Additional Research Ethics approval

Prior to conducting any research, researchers must ensure that all required research ethics approvals are secured (in addition to this one). This includes, but is not limited to, securing appropriate research ethics approvals from: other institutions with whom the PI is affiliated; the research institutions of research team members; the institution at which participants may be recruited or from which data may be collected; organizations

or groups (e.g. school boards, Aboriginal communities, correctional services, long-term care facilities, service agencies and community groups) and from any other responsible review body or bodies at the research site

2. Reporting adverse events

Any significant adverse events experienced by research participants must be reported in writing to Research Ethics within 24 hours of their occurrence. Examples of what might be considered ?significant? include: an emotional breakdown of a participant during an interview, a negative physical reaction by a participant (e.g. fainting, nausea, unexpected pain, allergic reaction), report by a participant of some sort of negative repercussion from their participation (e.g. reaction of spouse or employer) or complaint by a participant with respect to their participation. The above list is indicative but not all-inclusive. The written report must include details of the adverse event and actions taken by the researcher in response to the incident.

3. Seeking approval for protocol / consent form changes

Prior to implementing any changes to your research plan, whether to the protocol or consent form, researchers must submit them to the Research Ethics Board for review and approval. This is done by completing a Request for Ethics Approval of Amendment to an Approved Project form (available on the website) and submitting three copies of the form and any documents related to the change.

4. Submitting annual reports

Ethics approvals are valid for up to 12 months. Prior to the end of the project?s approval deadline, the researcher must complete an Annual Report (available on the website) and return it to Research Ethics for review and approval before the approval end date in order to prevent a lapse of ethics approval for the research. Researchers should note that no research involving humans may be conducted in the absence of a valid ethical approval and that allowing REB approval to lapse is a violation of University policy, inconsistent with the TCPS (article 6.14) and may result in suspension of research and research funding, as required by the funding agency.

5. Submitting final reports

When the researcher is confident that no further data collection or analysis will be required, a Final Report (available on the website) must be submitted to Research Ethics. This often happens at the time when a manuscript is submitted for publication or a thesis is submitted for defence. After review and approval of the Final Report, the Research Ethics file will be closed.

6. Retaining records in a secure manner

Researchers must ensure that both during and after the research project, data is securely retained and/or disposed of in such a manner as to comply with confidentiality provisions specified in the protocol and consent forms. This may involve destruction of

the data, or continued arrangements for secure storage. Casual storage of old data is not acceptable.

It is the Principal Investigator?s responsibility to keep a copy of the REB approval letters. This can be important to demonstrate that research was undertaken with Board approval, which can be a requirement to publish (and is required by the Faculty of Graduate Studies if you are using this research for your thesis).

Please note that the University will securely store your REB project file for 5 years after the study closure date at which point the file records may be permanently destroyed.

7. Current contact information and university affiliation

The Principal Investigator must inform the Research Ethics office of any changes to contact information for the PI (and supervisor, if appropriate), especially the electronic mail address, for the duration of the REB approval. The PI must inform Research Ethics if there is a termination or interruption of his or her affiliation with Dalhousie University.

8. Legal Counsel

The Principal Investigator agrees to comply with all legislative and regulatory requirements that apply to the project. The Principal Investigator agrees to notify the University Legal Counsel office in the event that he or she receives a notice of non-compliance, complaint or other proceeding relating to such requirements.

9. Supervision of students

Faculty must ensure that students conducting research under their supervision are aware of their responsibilities as described above, and have adequate support to conduct their research in a safe and ethical manner.

APPENDIX C



CONSENT FORM

Title of Study: Inhibition of return for grasping movements

SSHREB Approval #: 2013-3051

Who is in charge of this study?	Who is involved with this study?
Ms. Kaila Bishop	Dr. David A. Westwood
MSc Student,	Professor
Clinical Vision Science program	Division of Kinesiology
Dalhousie University	Dalhousie University
kaila.bishop@dal.ca	Email: dwestwood@dal.ca
	Phone: 494-1164
	Mr. Kevin LeBlanc
	PhD Student,
	Department of Psychology and Neuroscience
	Dalhousie University

Introduction:

We invite you to take part in a research study run by Kaila Bishop, a Vision Science Masters student. You do not have to take part in this study if you do not want to. It is entirely your choice. Your grades will not be affected if you choose not to take part. Even if you do take part, you may leave the study at any time for any reason. The study is described below. You will learn about the risks, inconveniences, or discomforts that might go along with taking part in the study. There probably will not be a benefit to you from taking part, but what we learn might help other people in the future.

Please ask as many questions as you want from the person running the study today. If you have any questions after you leave feel free to email the principal investigator.

Why are we doing this study?

We want to learn more about how people use their hands to pick up objects. Right now we know very little about how the brain makes this happen. In particular, we want to know if your past movements affect the movements you make next. This study will help us understand movement control better.

What type of study is this?

Everyone in the study will do the same tasks. We will compare how you do the task in slightly different conditions to see which conditions matter.

Who can take part in this study?

Males and females over the age of 18, who are right handed with good visual acuity and 3D vision. You can use glasses or contact lenses if you need to. You cannot take part if you have had any ocular anomalies, neurological disorder, or a history of movement difficulty.

Who is running the study?

This study is being run by Kaila Bishop, a Masters student in the Clinical Vision Science program at Dalhousie University, in conjunction with Dr. David Westwood, a professor of Kinesiology at Dalhousie University.

How many people are taking part in the study?

Overall we hope to have about 16 people take part.

Where is the study being done?

Right here! This is the Westwood Action Laboratory in the Dalplex.

What you will be asked to do:

You will use your right hand to grasp small wooden blocks. You will be seated in front of a turntable where the objects will be put to your left and right side. You will have some time to practice, and to ask questions. We will put small wires on your index finger, thumb, and wrist that let us measure where you hand moves. The system uses special cameras to measure where things are located. The cameras do not take a picture of you but just the little markers on your hands. There are no shocks and the wires do not get warm. We will measure how fast you move your hands to the targets, and how accurate you are. We will compare how you do when two movements are repeated back to back. We will also be monitoring your eye movements. We will put sticky foam pads on your forehead and on the right and left temples, we will attach a small wire to these pads and this will allow us to see where your eyes are looking during the study. You can take breaks as often as you need to. The entire study will take about 90 minutes.

Possible Benefits, Risks and Discomforts:

There are no major risks to taking part in this study. There is nothing that should hurt you. Nothing will touch your eyes. The sensor wires do not shock you or get warm, you might find them a bit annoying because the wires can get tangled sometimes. Your arm might get a bit tired from so many arm movements, but you can take breaks when you need to. There is no real benefit to you for taking part in this study, but you might learn a bit about science and kinesiology. Plus you get to see interesting research equipment.

What will I receive for taking part?

There is no payment for taking part in this study, and we cannot pay for any expenses. If you signed up for this study using the Department of Psychology Participant System (SONA), you will receive two percentage points for taking part in this study.

How will my information be protected?

Your information will be kept safe. We will use a code number, instead of your name, to keep track of your information. This means your name cannot be connected to your information. Only the researchers will know your name and your code number. Your results in the study will be put together with other people who take part. Only this 'group' information will be shared with other scientists. Your personal information will not be shared. These 'group' results might be published in a scientific article. All information from this study will be protected with a code key on computers in our laboratory. We will keep all information for at least five years after the study has been published as a scientific article. Then, we will shred all paper information and erase all computer information. You can choose to remove your information from the study at any point in time, just let us know. Keep this consent form to help you remember taking part in this study.

Can I find out the results of the study?

We cannot give your individual results. But if you are interested, please write your email address on this consent form. We can send you a summary of the results. We can also explain what the study was about, and help you find more to read about the topic if you find it interesting.

What if I start the study but decide not to keep going?

That is no problem at all! You can leave the study at any time, for any reason. There won't be any negative effects from doing this. It will not affect your compensation either.

Questions and Contact Information:

Please keep this letter so you can remember the name of the study and who to contact later if you need to. At any time you can ask questions to the person running the study today. Later you can email Kaila Bishop if you have any more questions. If you know someone who might want to take part in this study, you are welcome to share Kaila Bishops email address with him or her. (kaila.bishop@dal.ca)

Who makes sure this study is run safely?

This research study has been reviewed and approved by the Social Sciences and Humanities Research Ethics Board (SSHREB) at Dalhousie University. It is your choice to take part in the study, or not. You can drop out of the study at any time for any reason. There won't be any negative consequences to you for dropping out of the study.

If you have difficulties with, or wish to voice your concerns about, any aspect of your participation in this study, you may contact the Director, Research Ethics, Dalhousie University, Catherine Connors (ethics@dal.ca, or phone 902-494-1462).

Quick summary of the study:

- This study is about grasping objects.
- It is your choice to take part in this study, or not.
- The study will last 90 minutes.
- You can withdraw from the study at any time, for any reason.
- Ask as many questions as you need to.
- You will pick up wooden blocks with your right hand.
- You can take breaks whenever you need to.
- A motion tracking system will track wires on your right hand to see how you move.
- An eye movement tracking system will track your eye movements using small wires attached to your face and hand.
- There is no payment for taking part in the study.
- Your information will be protected: no one can find out your name and your information.



Title of Study: Inhibition of return for grasping movements.

Principal Investigator:

Kaila Bishop, Clinical Vision Science Masters Student, Dalhousie University, (kaila.bishop@dal.ca)

Research Supervisor:

Dr. David Westwood, Division of Kinesiology, Dalhousie University (dwestwoo@dal.ca, phone# 902-494-1164).

I have read the information consent letter. I meet the requirements to take part in the study as outlined earlier. I have had the opportunity to ask all the questions I needed to. I understand that I can withdraw from the study at any time, for any reason. I understand that I can contact the person in charge of the study even after I leave the laboratory, using the contact information provided above. I understand that this study has been reviewed and approved by the Social Sciences and Humanities Research Ethics Board (SSHREB) at Dalhousie University. If I have any concerns or comments as a result of my participation in this study I may contact Catherine Connors, Director, Research Ethics, Dalhousie University, ph. 494-1462 email: ethics@dal.ca

I agree to participate in this study.

Participant Name (please print)	Participant Signature	Date:
Researcher Name (please print)	Researcher Signature	Date:
I wish to take part as a PARTICIPANT	「(use my data for the study):	
I wish to take part as an OBSERVER ((do not use my data for the study):	
Assigned Participant Code Number	·	
Date of birth:		

APPENDIX D

Participant Information

Participant #	Sex	Age	Near Visual Acuity	Stereoacuity
10	F	19	6/6	40"
11	F	20	6/6	40"
12	F	19	6/6	30"
13	F	19	6/6	30"
15	F	19	6/6	40"
16	M	21	6/6	40"
17	F	28	6/6	30"
18	F	21	6/6	40"
19	M	24	6/6	40"
20	M	32	6/6	50"
22	F	19	6/6	50"
23	F	19	6/6	50'
24	F	19	6/6	40"
25	F	20	6/6	40"
26	F	18	6/6	40"
27	F	19	6/6	40"

APPENDIX E

Statistical Data – Reaction Time

Variable		Df	Mean Square	F	Sig.
S2 Direction	Hypothesis	1	29825.765		
S2 Direction	Error	15.292	3695.540b	8.071	0.012
Relative	Hypothesis	13.292	115486.066	0.071	0.012
Direction	Error	15.068	15613.137c	7.397	0.016
		13.008	85144.677	1.391	0.010
Object Size	Hypothesis	_		4.206	0.056
D 4: : 4	Error	15.054	19819.534d	4.296	0.056
Participant	Hypothesis	15		•	•
	Error	.e			
S2 Direction	Hypothesis	1	6170.054		
*Relative	Error	15.114	9368.848f	0.659	0.43
Direction					
s2 direction*	Hypothesis	1	121951.341		
object size	Error	15.03	35547.657g	3.431	0.084
s2 direction*	Hypothesis	15	3670.456		
participant	Error	7.493	28508.323h	0.129	1
Relative	Hypothesis	1	2852.752		
direction *	Error	15.064	16683.376i	0.171	0.685
object size	Elioi	15.001	10003.3701	0.171	0.002
Relative	Hypothesis	15	15621.928		
direction*	Error	2.164	9590.422j	1.629	0.433
participant	Liioi	2.104	7570. 4 22j	1.02)	0.433
Object size *	Hypothesis	15	19840.28		
participant	Error	10.6	35843.642k	0.554	0.857
s2 direction *	Hypothesis	10.0	6762.721	0.554	0.657
relative	Error	15.065	16453.4971	0.411	0.531
direction*	EHOI	13.063	10433.49/1	0.411	0.331
object size s2 direction *	TT41	1.5	9359.889	0.568	0.057
	Hypothesis	15		0.568	0.857
relative	Error	15	16464.676m		
direction *					
participant	** .1 .	1.5	25612.11		
s2 direction *	Hypothesis	15	35613.11		
object size *	Error	15	16464.676m	2.163	0.073
participant					
Relative	Hypothesis	15	16695.209		
direction *	Error	15	16464.676m	1.014	0.489
object size *					
participant					
s2 direction *	Hypothesis	15	16464.676		
relative	Error	2248	12520.524n	1.315	0.184
direction*					
object size *					
participant					

Peak Grip Aperture

Variable		Df	Mean	F	Sig.
~ · · ·	**		Square		
S2 Direction	Hypothesis Error	1 15.017	110.186 176.758	0.623	0.442
Relative	Hypothesis	13.017	8.95	0.023	0.442
Direction	Error	15.067	45.973	0.105	0.665
				0.195	0.665
Object Size	Hypothesis	1	17853.754	66.115	
D .: .	Error	15.011	270.039	66.115	0
Participant	Hypothesis	15	4740.027	11.510	
	Error	22.04	404.727	11.712	0
S2 Direction	Hypothesis	1	0.355		
*Relative	Error	15.064	48.672	0.007	0.933
Direction					
s2 direction*	Hypothesis	1	286.695		
object size	Error	15.089	34.736	8.254	0.012
s2 direction*	Hypothesis	15	177.157		
participant	Error	14.743	62.754	2.823	0.027
Relative	Hypothesis	1	96.673		
direction *	Error	15.118	26.409	3.661	0.075
object size					
Relative	Hypothesis	15	46		
direction*	Error	12.698	54.403	0.846	0.626
participant	Ellor	12.000	31.103	0.010	0.020
Object size *	Hypothesis	15	270.703		
participant	Error	10.521	40.427	6.696	0.002
s2 direction *	Hypothesis	10.321	5.529	0.090	0.002
relative	Error	15.15	20.729	0.267	0.613
	EHOI	13.13	20.729	0.267	0.013
direction*					
object size	TT 41 .	1.5	40.707	2.255	0.054
s2 direction *	Hypothesis	15	48.707	2.355	0.054
relative	Error	15	20.685		
direction *					
participant					
s2 direction *	Hypothesis	15	34.731		
object size *	Error	15	20.685	1.679	0.163
participant					
Relative	Hypothesis	15	26.381		
direction *	Error	15	20.685	1.275	0.322
object size *					
participant					
s2 direction *	Hypothesis	15	20.685		
relative	Error	2248	36.328	0.569	0.9
direction*					
object size *					
participant					

Time to PGA

Variable		Df	Mean	F	Sig.
Relative	II	1	Square		
Direction	Hypothesis Error	1 15.09	0 0.003b	0.078	0.783
S2 Direction			0.0036	0.078	0.783
S2 Direction	Hypothesis Error	1 15.016	0.203 0.019c	10.861	0.005
Object Size		13.010	0.0196	10.801	0.003
Object Size	Hypothesis Error	15.091	0.023 0.003d	7	0.018
Dantiainant		15.091	0.0034	/	0.018
Participant	Hypothesis Error	2.689	0.778 0.010e	80.098	0.002
G2 D: 4:				80.098	0.003
S2 Direction	Hypothesis	1	0.001	0.145	0.700
*Relative	Error	15.034	0.009f	0.145	0.709
Direction					
Relative	Hypothesis	1	0.005		
direction* object	Error	15.044	0.007g	0.726	0.407
size		1			
Relative	Hypothesis	15	0.003		
direction*	Error	14.453	0.011h	0.289	0.989
participant					
S2 direction *	Hypothesis	1	4.58E-05		
object size	Error	15.072	0.004i	0.011	0.917
S2 direction*	Hypothesis	15	0.019		
participant	Error	10.831	0.009j	2.123	0.108
1 1			,		
Object size *	Hypothesis	15	0.003		
participant	Error	9.169	0.007k	0.471	0.906
s2 direction *	Hypothesis	1	0.006		
relative	Error	15.075	0.0041	1.582	0.228
direction* object					
size					
s2 direction *	Hypothesis	15	0.009	2.186	0.071
relative direction	Error	15	0.004m		
* participant					
r · · · · r · ·					
Relative	Hypothesis	15	0.007		
direction * object	Error	15	0.004m	1.709	0.155
size * participant			0.00	11,705	0.120
participant					
S2 direction *	Hypothesis	15	0.004		
object size *	Error	15	0.004m	1.039	0.471
participant					
L-markanit					
s2 direction *	Hypothesis	15	0.004		
relativedirection*	Error	2260	0.004n	1.078	0.372
object size *					
participant					

APPENDIX F

Eliminated Trials

Participant #	# of trials lost to eye movements	# of trials lost to instrumentation failure	# of trials lost to outliers	# of trials included in analysis	Total # of trials
10	3	10	1	146	160
11	3	5	3	149	160
12	3	4	3	150	160
13	7	13	2	138	160
15	5	19	5	131	160
16	1	4	0	155	160
17	1	5	2	152	160
18	4	8	5	143	160
19	0	1	1	158	160
20	1	0	2	157	160
22	4	12	2	142	160
23	2	0	4	154	160
24	3	7	5	145	160
25	1	2	6	151	160
26	3	6	1	150	160
27	1	2	2	155	160