

Planning Sequential Eye Movements

by

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ABSTRACT

Studies have shown that future actions in a sequence have an effect on both the mechanics and timing of arm movements. In saccadic eye movements, future saccades in a sequence have been shown to impact the reaction time of the first eye movement, suggesting these movements may be planned as an entire sequence (Inhoff, 1986). The aim of the present study was to determine if the location of a second target had an impact on the metrics of the first saccade since research on this question is limited. In Experiment 1, subjects performed either a saccade to a single target, or a sequence of two saccades to two targets. The first target was located 12, 15, or 18 degrees from fixation, and the second target (when present) was located 12, 15, or 18 degrees from the first target. First and second target location, as well as number of targets presented, was randomized on a trial by trial basis. The presence of a second target was found to have a significant effect on the reaction time, amplitude and horizontal end position of the first saccade. Furthermore, the location of the second target was found to have a significant effect on amplitude, horizontal end position and duration of the first saccade. The first saccade was found to have a significantly shorter amplitude the further the second target was from the first target, with other significant saccade metrics following this same pattern. In Experiment 2, two targets were presented on all trials, with target locations as described in Experiment 1. The second target in Experiment 2 was an “x” or a “+”, which was randomized on a trial by trial basis. Three conditions were performed in Experiment 2 in blocked order randomized by participant. In the “look” condition, participants were instructed to look at the first target, and then the second. In the “ignore” condition, participants were instructed to look at the first target only, and ignore the second target. In the “attend” condition, participants were asked to make a perceptual judgement about the second target (whether it was a “+” or an “x”) before looking at the first target only. Once participants moved their eyes away from the fixation target, the second target changed into its masked form (a star, formed by the overlapping of the two possible second target images). The location of the second target was found to have a significant effect on amplitude, horizontal end position and peak velocity of the first saccade. No significant effect of condition was found for any variable except reaction time. Most importantly, no significant interaction was found between second target location and condition. This suggests that task instructions did not have an impact on the effects of second target location on the metrics of the saccade to the first target. This may be the result of the summation of a motor plan to the first target and the inhibition of a motor plan to the second target (or inhibition of head movements), regardless of whether or not subjects were instructed to make a movement to the second target. Another possibility is that the second target changed the perceived visual location of the first target. Further research is required to differentiate between these possibilities.

LIST OF ABBREVIATIONS AND SYMBOLS USED

FEF	Frontal Eye Fields
INC	Interstitial Nucleus of Cajal
LIP	Lateral Intraparietal Area
MVN	Medial Vestibular Nucleus
NPH	Nucleus Prepositus Hypoglossi
PPC	Posterior Parietal Cortex
PPRF	Paramedian Pontine Reticular Formation
riMLF	Rostral Interstitial Nucleus of the Medial Longitudinal Fasciculus
SEF	Supplementary Eye Fields

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CHAPTER 1 INTRODUCTION

1.1 Background

Many activities in our day to day lives require multiple movements in order to complete a goal. Everyday tasks such as getting dressed, preparing a meal, or driving a car require multiple motor actions to take place in sequence. These many sequential movements not only require coordination of limbs to reach, grab, place and manipulate objects, but also sequential eye movements to guide these other motor commands, as described by Land (2006). Throughout a simple task such as making a cup of tea, eye movements are required to locate an object, such as a kettle, mug and milk. Eye movements are then involved in directing the hand to reach for these objects, guiding the kettle to the tap, and the lid to the kettle, and then monitoring the kettle to see if it is done boiling, to name a few.

Evidence that motor actions are planned before they are executed has been predominantly studied in arm movements. This has been demonstrated by the mechanics of a movement, such as in studies of the end-state-comfort effect (Rosenbaum et al., 1990; Rosenbaum & Jorgensen, 1992) that showed that participants performed actions in such a way that the most comfortable final position of a movement was obtained, even if this required initial positions that increase the overall awkwardness of the movement as rated by participants.

1.2 Sequential Movements

Previous research that has looked at whether sequences of movements are planned holistically (all at once) or whether sequential movements are planned individually, has often focused on arm movements. In 1960, Henry and Rogers conducted a study where they had subjects perform movements of various complexities. One movement condition involved subjects simply lifting their finger from a key, the second involved lifting their finger to reach out and then grasping a ball hanging from a string, and the third involved lifting their finger to hit a ball, switching direction and returning towards the start position to press a key, and then returning again towards the balls to hit a second ball. It was found that as the number of movements increased, reaction time (the time before the onset of the movement) increased as well. This increase in reaction time suggests that more time is needed to plan more complex or multi-step movements.

Not only has reaction time been found to be impacted by sequential actions, but so has movement time. The one-target advantage, first discovered by Glencross (1980) has shown that arm movement times are significantly shorter to a target when only a single movement is required, compared to when a second movement to another target is required following this action. As stated by Glencross (1980), one of the effects of having to make a movement to a second target is that the movement to the first target is slowed down. This finding has been repeated in numerous studies (e.g. Adam et al., 2000; Fischman, 1984)

Motor planning in sequences is also demonstrated in studies that looked at the mechanics of a movement. One of these studies, conducted by Haggard in 1998,

inspired by the previously mentioned studies on end-state-comfort effect look to expand this evidence that movements are planned to see if more than a single movement could be planned in advance. In this study, participants were instructed to grasp an octagonal object with 8 different faces, and a single pointer extending from a point between two of the faces. This object was surrounded by an octagonal fence. Each side of the fence had a hole in which the pointer could be inserted, and each side of the fence had a different coloured target. The way in which the participants grasped the object, when no further instructions were given, was recorded as a baseline measurement. Subjects then performed 12 sequences, of either 2, 3 or 5 targets. The target positions were given to the subjects verbally as a list of colours, and then participants were to place the pointer in the target hole in order of the colours specified. Subjects were not to change their grasp or put down the object throughout the sequence. The grasp on the object during these sequence movements was then compared to the baseline grasp. In 81% of sequences a different grip was used compared to the baseline grasp. Haggard discussed that the results of this study show that movement planning extends beyond the immediate action to be taken, and this planning can be significant for the second and third movements in a sequence.

1.3 Sequential Eye Movements

While not as extensive as research on sequential planning of arm movements, studies have been conducted to determine if sequences of saccades are planned

together in advance of the eye movement. Early research on this subject was done by Inhoff in 1986 and Zingale and Kowler in 1987.

In Inhoff's study, subjects began by fixating on a target towards the left of a screen. The fixation target then changed to an X or an O. This indicated when participants were to begin to move their eyes as half of the participants were told to initiate their eye movements when the fixation target switched to an O, and not to move when the fixation target changed to an X. The other half of the participants were given opposite instructions in regard to the X and O. Subjects were instructed prior to each trial to either make 1, 2 or 3 equidistant saccades. In half of the trials an asterisk was present as a cue to mark the saccade targets, and in the other half no cue was present. It was hypothesized that, as demonstrated in arm movement studies (e.g., Henry and Rogers, 1960), as sequence length increased, so would the latency before the eye movements were initiated, indicating more processing time. This was replicated in the findings in this study, as the saccade onset latency significantly increased as the number of saccades to be made in sequence increased. Contrasting evidence came from examination of non-initial saccade latencies. While it had been predicted that these latencies would be shorter than average saccade latencies, as they would be (at least partially) planned before the onset of the first saccade, it was found that these latencies ranged from 196-260ms. These latencies are considered relatively long and consistent with saccade latencies that are programmed online, as opposed to preplanned. Inhoff then conducted a second experiment where the number of saccades to be performed could not be predicted prior to the onset of the choice reaction signal (the changing of

the fixation target to an X or O). In this experiment, the effect of increasing initial saccade latencies with sequence length was found to disappear.

A year later, in 1987, a similar study was conducted by Zingale and Kowler. In this study, subjects were required to make either 1, 2, 3, 4 or 5 saccades. The points to which saccades were made were arranged in the shape of an imaginary pentagon, with the points being located where the vertices of a pentagon would be. Subjects began by fixating a single point that was displayed, and pressed a key to begin the trial. 800ms after this key was pressed, the successive targets were displayed and subjects were instructed to make eye movements to targets in a clockwise direction. Targets were displayed as consecutive points on the pentagon, such that when less than 5 targets were present, no points were skipped. Consistent with the findings of Inhoff's 1986 study, in this study it was also found that the latency of the first saccade in a sequence increased with sequence length, given further evidence of saccades being planned as a sequence. It was also found that the latency of non-initial saccades increased with sequence length. For example, the second saccade in a sequence had a longer latency in a sequence of 5 saccades than a sequence of 3 saccades, potentially giving further indication that saccades are planned in sequence. However, a large problem exists within the methodology of this study. This study consisted of only two participants, one of which, Eileen Kowler, was a principle investigator of the study and not naïve to the purpose of the experiment. This may have greatly impacted the validity of these results.

Conflicting evidence has been found by Pratt in 2004. This study looked at whether or not the one target advantage exists for eye movements. The one target

advantage, previously demonstrated in arm movements and similar to studies on reaction time latency, states that the movement time to a target is shorter when the limb stops on that target compared to when it has to proceed to a second target. In this experiment, there were three different possible conditions for movement instructions. In the one target condition, an eye movement was made from the initial fixation target to a single target and the trial ended. In the two-target reversal condition an eye movement was made from the initial fixation target to a second target and then back to the starting position. In the two target extension condition, an eye movement was made from the fixation target, to the first saccade target, then to a second saccade target. It was found that the one target advantage did not exist for eye movements. Furthermore, the effects on saccade reaction time latency due to the presence of non-initial saccade targets as previously discussed by Inhoff (1986) and Zingale and Kowler (1987) were also not replicated in this study. Both of these findings suggest that saccades are planned individually, as opposed to in sequence. The reason for this conflicting findings is unknown but it was suggested by Pratt that this may be due to his larger sample size (18 participants) compared to previous studies.

1.4 Planning and Saccade Endpoint

While studies looking at reaction times and movement times for sequential saccades provide conflicting evidence as to whether or not saccades are planned in sequence, even less is known about whether or non-initial targets in a series of sequential saccades influence the endpoint of the first saccade made. One study that

has in fact looked at this effect was conducted by McSorley, McCloy, and Williams in 2016. In this study participants made either a single reflexive saccade, a single voluntary saccade, or a sequence of two saccades (reflexive, followed by voluntary, or voluntary followed by reflexive) in each trial. Participants began by fixating a central target, which was a white square with an “X” in the center. In order to signal a voluntary saccade, two lines disappeared from the fixation target to form an arrow in the direction of one of the four stimuli presented at each corner of the screen. A reflexive saccade trial was also initiated by the disappearance of two lines from the fixation target, this time to form an hourglass shape that did not indicate a saccade direction, and the saccade was directed by the onset of a new target point.

This study looked at both saccade latencies and endpoints to help answer the question of whether or not saccades are planned in a sequence. Contrary to previously discussed studies that determined longer first saccade latencies provided evidence to saccade sequence planning, this study found that for 2-target trials, first saccade latencies were actually shorter than corresponding latencies for single target trials. Second saccade latencies, however, did show evidence of sequence planning, as these saccade latencies were significantly shorter compared to single target trials.

Also of great interest in relation to the present study, saccade endpoints were examined. Accuracy of the first saccade was analyzed both for distance and direction. No effect on first saccade amplitude (distance) was found whether the saccade was executed as a single saccade or as the first saccade in a series of two saccades. Direction of the first saccade, was found to be effected by the presence of a second saccade

target. This difference was found to exist only for voluntary saccades that were followed by reflexive saccades in this two target condition. It was found that the first voluntary saccade direction was shifted towards the second reflexive saccade location.

However, in the majority of 2-target trials (91%), the second target location was changed during the first saccade, either in distance or direction from the first target. According to authors, this was done to determine the programming of the second saccade that is done during the first saccade, however this may have confounded effects of planning the second saccade that would have otherwise occurred had this change requiring online control not been induced. In other words, this shift that occurred during the first eye movement may have cancelled out the planned saccade to the original second target location. Another potential issue that arises with this study is that for two target trials, the first saccade target, was located 8 degrees of visual angle away from fixation, but the second target location was located only 3.1 degrees of visual angle from the first target. This distance could be reduced even further to 1.6 degrees of visual angle in conditions in which position shift brought the second target closer to the first by 1.5 degrees. Such small distances between the first and second targets may have caused participants to make a single eye movement that fell in between both targets instead of two distinct eye movements. A distance of only 1.6-3.1 degrees in which the second target is clearly visible from the first target without even having to make a movement to it may have confounded results. A second issue with this study is that one saccade was elicited by reflexive cues, which would elicit exogenous attention, and the other by voluntary cues, which would elicit endogenous attention. The different types of

attention allocated to the different targets could also have influenced results. The exogenous (reflexive) stimuli would have automatically captured attention, whereas the endogenous (voluntary) stimuli would require processing in order to select the target.

1.5 Purpose and Hypothesis

The purpose of this experiment is to determine if the position of the second target in two sequential saccades influences the endpoint of the first saccade. This would provide further evidence of sequences of saccades being planned together. Current research on whether or not saccades are planned together is conflicting, and research on whether or not later targets affect initial saccade endpoint is limited. It is hypothesized that the second target will influence the first saccade endpoint. This can be demonstrated if the endpoint of the first saccade is closer to the second target for greater second target distances, compared to smaller second target distances. It is also hypothesized that reaction times will be longer for two saccade trials, compared to single saccade trials.

CHAPTER 2 LITERATURE REVIEW

2.1 Introduction

An action plan is the steps required to reach a goal. In the motor system, there are several steps that need to be taken to perform even seemingly simple tasks. For example, consider picking up a cup of coffee. The many steps involved in this action are outlined by Steenbergen et al. (2006). First, the cup needs to be seen, and visually processed. Features of the cup, such as its size, shape, and location, form the cup-centric frame of reference, which then needs to be converted into a body-centric frame of reference. This body-centric frame of reference is then used to plan the movement. The way in which the cup is gripped depends on the cup's position and the goal of the action – whether the cup is to be placed upwards on a table or downwards into the dishwasher, for example. Once this grip is planned the movement can then be executed, also taking into account different portions of the body involved in the movements such as the elbow, shoulder, and wrist, and appropriate forces necessary to generate a smooth movement (Steenbergen et al., 2006).

In our day-to-day lives, actions are rarely executed in isolation. Objects in the visual world that are not the immediate target of an action can still have an effect on the present action. Movements are often planned together in order to achieve a goal, such as bringing a fork to a plate and then to one's mouth to eat. In other situations, other objects in the vicinity of a target must be avoided, such as grasping a pen from a desk covered in various office supplies. In order to have optimal accuracy and efficiency of these movements, features of non-target objects must be taken into consideration.

2.2 Motor Control

There are several steps involved in generating a movement in order to achieve a goal. A target of action must be selected, a motor plan must be generated, and the forces required to carry out the objective must be coordinated (Wise & Shadmehr, 2002). In order to achieve this, there must be interaction between the peripheral motor system and the central motor system. The peripheral motor system includes the muscles, motor neurons - which innervate the muscles, and muscle afferents - which send information back to the CNS about muscle length and force. The central motor system includes the spinal cord (which contains motor neurons, the sensory pathway, and the proprioceptive system), the brainstem, hypothalamus, thalamus, cerebral cortex, and basal ganglia (Wise & Shadmehr, 2002).

In the execution of a movement, there are two main forms of control that allow a movement to be carried out efficiently and effectively: planning, and online control. Planning refers to the aspects of motor control that are coordinated before the movement begins, whereas online control refers to the process that occur to optimize a movement while the movement is being executed. Motor planning in response to visual stimuli appears to be mediated by the dorsal premotor cortex. This had been demonstrated by Crammond and Kalaska (2000), who studied the activity in this brain area in monkeys during a task in which monkeys were signalled to move a handle to a target. In some trials, which authors refer to as instructional-delay tasks, the target location was cued with an instructional signal (illumination of a green peripheral target

LED), allowing the monkey to plan for the future movement, which was executed after a “go” signal (illumination of the red LED of the same peripheral target). Conversely, in the second type of trial, which the authors refer to as reaction-time tasks, there was no instructional signal, so the monkey was unable to commence movement planning until the illumination of the “go” signal. It was found that in instructional delay tasks, activity in the dorsal premotor cortex began following the instructional cue, whereas in reaction-time tasks, activity in this area was present following the “go” signal. This suggests that this area is involved in the directional planning of motor tasks (Crammond & Kalaska, 2000).

In humans, research on action planning is often focused on arm movements. Marteniuk et al. (1987) showed that arm movement trajectories differ based on features of the object, as well as how the object to be reached is to be used, by varying movement conditions. In the first experiment, subjects either had to point to a target with their index finger, or grasp it between their thumb and index finger. In the second experiment subjects either had to grasp a fragile object (a light bulb), or a soft, durable object (a tennis ball). In the third experiment subjects had to grasp a disk and then either throw it large box, much bigger than the size of the disk, or place it into a well, with a much smaller diameter, into which the disk would tightly fit. For each experiment it was found that there were significant differences between the conditions (mainly differences in acceleration and deceleration times). As stated by Marteniuk and colleagues (1987), these results show that differences in movement outcome, movement intent, and object properties play a role in the planning of arm movements.

While it could be argued that these differences represent an effect of online control as opposed to planning effects, authors state that when intent was considered as a variable (pointing vs. grasping target), there was an influence on movement trajectory, which represents constraints of the task being considered in the planning process.

Evidence of motor planning is exemplified in work that demonstrates what has been described as the “end-state comfort effect” (Rosenbaum et al., 1990; Rosenbaum & Jorgensen, 1992). When presented with a goal, there are often many different ways in which we could execute a movement to achieve this goal, and the motor system must decide between many different action alternatives. Research on the end-state comfort effect has shown that when presented with an action task, subjects carry out this task in such a way that allows for the most comfortable, or least awkward, final position. For example, Rosenbaum and colleagues (1990) conducted an experiment in which subjects were asked to grab a cylindrical bar, and place a specific end of the bar into a hole on a disk. Prior to performing this task, subjects were also asked to rate all different possible positions that the bar could be held throughout the task in terms of subjective awkwardness. They found that subjects gripped the bar in such a way that minimized awkwardness of the final position, even if this required initial positions that had been rated higher in terms of awkwardness, or positions that increased the mean awkwardness rating for the entire movement. This demonstrates that the motor system takes the final position into consideration in a movement task, which impacts the first movement position, indicating that there is a motor plan at work.

Not only does action planning play an important role in motor control, but movement can also be modulated during its execution. This phenomenon is known as online control. Movement plans can be altered over the course of a movement both with and without sensory feedback as described by Shadmehr et al. (2010). Some movements, such as saccades, taking less than 80 ms, are too fast for visual or proprioceptive sensory information to feedback and alter a motor command. Variability in motor commands, or mechanical perturbations, such as a blink, can impact the accuracy of a saccade. However, in a normally functioning system, the eye still manages to land on target. It has been proposed by Robinson (1975) that this is possible due to an internal feedback process that takes place in the cerebellum. The cerebellum processes the motor command in such a way that predicts the consequence of an action, and then can send out motor commands during the saccade to allow for online correction.

Many other forms of movement, such as arm movements, take much longer than saccades. This allows for sensory information to feedback onto the control of a motor command. However, a delay exists for this sensory feedback information. As a result, sensory feedback information is often limited to peripheral mechanisms such as fast, spinal reflexes, and intrinsic biomechanical properties of the muscles (Shadmehr et al., 2010). As this delay can result in unstable control of a motor command, previously discussed cortical predictions about an action are also involved in longer movements with sufficient time for sensory feedback. Thus, as sensory feedback is integrated into

the predictive forward model of motor control, optimal control of a movement can be achieved (Shadmehr et al., 2010).

Attention also plays an important role in motor control. Visual attention allows for the entire visual scene to be filtered, such that only those parts necessary to achieve a goal are processed (Baldauf & Deubel, 2008). This first step of visual attention is known as “selection for perception”. This is then followed by the second step “selection for action” (Allport 1987). These two steps have been shown to be linked in several studies on saccadic eye movements and attention. One such study, conducted by Hoffman and Subramaniam in 1995, conducted two different experiments in order to demonstrate the link between visual attention for perception and action. In experiment one, an arrow directed subjects to direct a saccade to one of four different rectangular targets. A tone then instructed participants to initiate their saccades 0-100 ms after this tone, a letter appeared in each of the 4 boxes. Three of these letters were “distractor letters” (either an E or an F), and one was the “target letter” (a T or an L). Participants were found to be more accurate in detecting the target letter when it appeared in the same box that an eye movement was made to. Blocks of trials in which an eye movement only, with no target detection was required, or detection only, with no eye movement were also included. (Figure 1.1). Authors described that this suggested the two forms of attention were linked because if they were independent processes, this bias for the saccade target location would not be present. Experiment 2 was then conducted to optimize conditions in which these two forms of attention would be separated, if this was possible. In this experiment, participants were explicitly told to attend to a certain

location. This location may or may not be the same location to which the subsequent saccade was directed. Despite being told to attend to a particular location, this cue was found to have no effect and once again target discrimination was highest when the letter target was in the same location as the saccade target, suggesting that these two forms of attention cannot be separated.

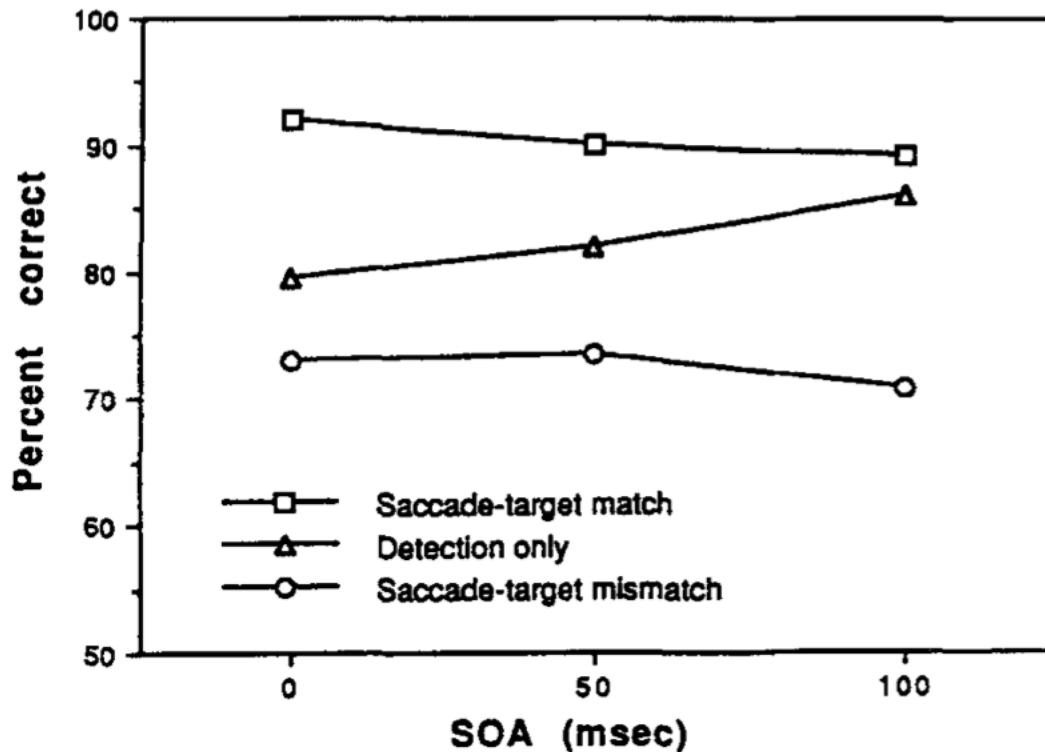


Figure 2.1. Results from Hoffman and Subramaniam (1995) Experiment 1. Correct responses for saccade-target match, mismatch and detection only for each possible stimulus onset time (duration between tone and onset of stimulus). The results show that target detection was greatest when the detection target was located in the same location as the saccade target, suggesting that these two forms of attention are linked. Taken from Hoffman and Subramaniam (1995).

2.3 Saccade Generation

While previous research on motor planning has often focused on arm movements, the eyes also play an important role in motor planning. Before an arm

movement to a target can be planned, the target must first be located. The posterior parietal cortex (PPC) appears to play a particularly important role in locating a target that a movement is to be directed towards. In one area of the PPC, the parietooccipital area, cells respond to visual stimuli, however, their receptive fields do not show any increasing sensitivity towards foveal targets. This is in contrast to most visual areas, which tend to be biased towards foveal representation. This general sensitivity over the entire visual field in this area suggests that this area is involved in the processing of visual information related to movement, as opposed to object features (Wise & Shadmehr, 2002). Another area of the PPC, the lateral intraparietal area (LIP) acts as priority map, and plays an important role both in guiding eye movements, as well as covert attention. This area uses both bottom-up processes, where prominent features in the environment are given priority, as well as top-down processes, where cognitive inputs also direct which areas are given priority. One of these cognitive inputs that influence that lateral intraparietal area is eye movement generation. Eye movement generation itself is also guided by input from the LIP, therefore there appears to be a positive feedback loop where the eye movement target increases activity in the LIP, and the motor response generated feeds back to further increase activity in this area. This serves to ensure that covert attention is allocated to the same location as eye movement generation (Bisley et al., 2011).

Once a target has been located, how is an eye movement generated to this target? One type of eye movement is a saccade. This is a rapid gaze shift that brings an object of interest onto the fovea. These movements can be voluntary or involuntary. Involuntary,

or reflexive saccades may be initiated by localization of a target in the PPC. Other cortical areas involved in the initiation of saccades include the frontal eye fields, which control voluntary saccades, and the supplementary eye fields, which plays a role in motor learning (Gulyàs, 2016).

Signals for saccade generation from the PPC, FEF, or SEF, are projected to the superior colliculus. This brainstem region provides the main input to areas of the pons and midbrain that generate the pulse (the eye movement), and the step (the change in tonic control of eye muscles that maintain the eye in this new position) (Sparks, 2002). For horizontal saccades, the burst neurons are located in the paramedian pontine reticular formation (PPRF). In order for these burst neurons to be activated, a signal must be sent to inhibit the omnipause neurons, also located in the pons, which tonically inhibit the burst neurons. Once the burst neurons have been un-inhibited, the premotor saccade command is sent to the oculomotor nuclei (CNIII, CNVI), to stimulate the primary muscles involved in horizontal saccades, the medial rectus and lateral rectus. (Sparks, 2002; Gulyàs, 2016). The step portion of a saccade, which keeps the eye in their new position, is mediated by the medial vestibular nucleus (MVN) and the nucleus prepositus hypoglossi (NPH), which act as neural integrators (Sparks, 2002).

In a vertical saccade, the same omnipause neurons, must stop inhibiting the burst neurons in order for a saccade to occur. For vertical saccades, these burst neurons are located in the rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF). From the riMLF, signals are sent to the oculomotor nuclei that generate vertical eye movements (CN III, and if the saccade is downward, CNIV), to stimulate the muscles

involved in vertical saccades which include the superior rectus, inferior rectus, superior oblique and inferior oblique. (Sparks, 2002; Gulyàs, 2016). The neural integrator for vertical saccades, which controls the step portion of the saccade, is the interstitial nucleus of Cajal (inC) (Sparks, 2002).

2.4 Action Planning in Sequences: Previous Research

Not only is our motor system capable of making a plan for a single action, but evidence exists that actions can also be planned in sequence. This was first discovered in studies on speech production on coarticulation, where different articulatory goals can be met at the same time through parallel activity (Rosenbaum, 2010, p. 325). In speech production it has been found that actions such as lip rounding (Kozhevnikov, & Chistovich, 1967; Daniloff & Moll 1968), and opening of the velum for nasalization (Moll & Daniloff, 1971), show that later phonemes in speech can affect the actions undertaken in the articulation of current phonemes (Rosenbaum, 2010; Hesse & Deubel, 2010).

From there, many studies on action planning in sequences have explored this phenomenon in reaching and grasping movements. It has been shown that the initial action reflects planning for later actions in an action sequence. For example, Ansuini et al. (2008) performed an experiment in which participants had to reach out and grasp a bottle filled with water. They then either had to simply grasp the bottle (no further action required), or to lift the bottle and then throw it into a container, place the bottle in a drawn circle in a container that matched the diameter of the bottle, pour the water

into a container, or pass the bottle to the experimenter. It was found that the way in which the bottle was grasped, and the duration of the reach, were impacted by the next action in the sequence. This phenomenon is also known as the action context effect, which can be defined as when the “kinematics of a reach-to-grasp movement, performed within an action sequence, vary depending on the action goal and the properties of subsequent movement segments” (Hesse and Deubel, 2010). The action context effect has been demonstrated in several similar studies (eg Haggard 1998; Armbrüster & Spijkers, 2006; Gentilucci et al., 1997; Johnson-Frey et al., 2004; Marteniuk et al., 1987).

While these numerous previous studies have demonstrated that action sequence planning exists, all of these studies have used sequences that involved the same object. Hesse and Deubel (2010) were the first to investigate whether the action context effect exists when different target objects are incorporated into the sequence with several subtasks. This study differed from previous studies on action planning in that movement tasks with the initial target were self-contained before subsequent tasks began. In this experiment, participants first had to grasp a cylindrical object and place it either precisely, or sloppily (depending on the trial condition), and then grasp a target bar, whose orientation varied trial to trial, and place it in the middle of the table (Figure 1.2). They found that the orientation of the bar in the final task impacted the way in which the cylinder was grasped in the first task, even in the cognitively more demanding condition that required accurate placement of the cylindrical target. In a follow-up experiment, placing of the cylindrical target was made even more difficult by increasing

the required accuracy of the placement. In this follow-up experiment, it was found that the final target bar's orientation did not impact the grip placement in the first task, contrary to findings in the first experiment. This suggests that as the task is made more difficult, tasks are planned individually as opposed to holistically (Hesse & Deubel, 2010).

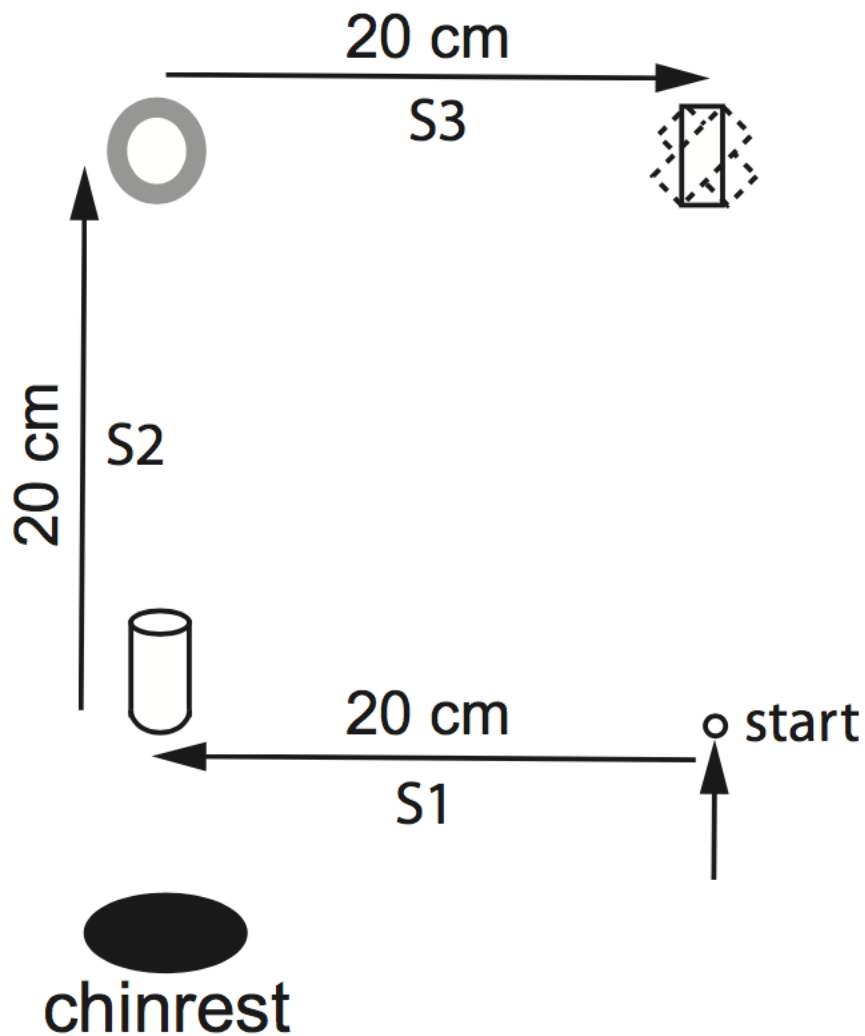


Figure 2.2. The experimental setup used in Hesse and Deubel (2010). In the first phase (S1) participants grasped a cylindrical object, and then placed it into a target area in the second phase (S2). Participants then grasped a cylindrical bar of various orientations (S3). Taken from Hesse and Deuebel (2010).

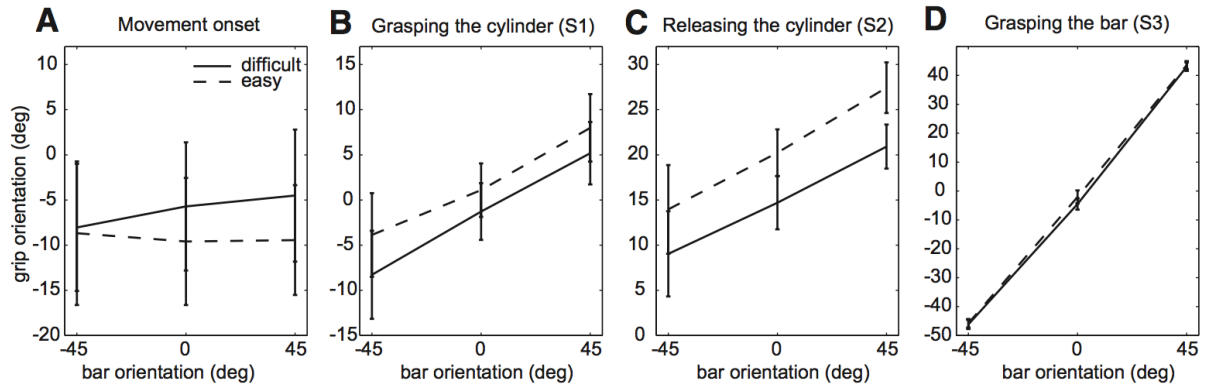


Figure 2.3. Results from Hesse and Deubel (2010) Experiment 1, demonstrating that the orientation of the bar that was to be grasped as the final action impacted grip orientation in earlier movements in the action sequence, on objects unrelated to the final object. Taken from Hesse and Deubel (2010). For both of these task difficulties, the grip orientation was affected by the final bar orientation. In a follow-up experiment (not shown), where the placement of the cylinder was made even more difficult, this effect was not found.

Evidence of action planning comes not only from the mechanics of movements towards a target, or the way in which a target is grasped, but also from reaction time. Several studies have found that more complicated tasks are associated with longer reaction times which indicate that greater motor planning is at work. This was first demonstrated by Henry and Rogers (1960), who had measured reaction times in 3 tasks of increasing complexity, all with the same starting point. In the first task, participants simply had to lift their finger. In the second they had to lift their finger and grasp a ball. In the third task, they were to lift their finger, strike the first ball, press a button, and then hit a second ball. As the number of movement steps increased, so did reaction time. This response complexity effect suggests that the sequences of movements are planned all at once, also known as holistic planning. Similar findings have been replicated several later studies (e.g., Khan et al. 2008).

Taking this concept a step further, in 2010, Khan and colleagues found that not only are reaction times longer in sequential tasks, but so are movement times to the first target. This experiment had 3 conditions. The first condition required participants to move a hand from the start position to only the first target, and the second condition required participants to move a hand to the first target, followed by the second target. In both of these conditions the other hand remained on target 1 throughout the trial. In the third condition participants were instructed to move their hand to the first target, and then their other hand from the first target to the second target. It was found that both reaction time and movement time to the first target was longer for the two target conditions. This finding that movement time was also affected is known as the one-target advantage, and is further evidence that actions in a sequence are not planned individually.

2.5 Evidence of Sequential Planning of Eye Movements

Substantial evidence exists for the concurrent planning of sequential arm movements, however whether or not sequential saccades are planned holistically is less well understood. Early evidence of saccades being planned in sequence come from studies by Inhoff (1986) and Zingale and Kowler (1987).

In 1986, Inhoff conducted a series of experiments in which subjects were to make either 1, 2 or 3 saccades in sequence. It was found that the time before onset of the first saccade increased as the number of saccades a subject was required to make increased, consistent with findings from studies on reaction times in manual reaction

times such as Henry and Rogers (1960). This effect was found to disappear in a second experiment, when subjects were unable to predict how many saccades would be required in an upcoming sequence. It was also found that the later the saccade in a sequence, the shorter its latency, and that the latency of the second saccade was shorter in sequences of only 2 saccades compared to 3 (Inhoff, 1986).

In 1987, Zingale and Kowler conducted further research to determine whether or not saccades are planned in sequence. They had subjects make 1-5 saccades to targets arranged as consecutive points of an invisible pentagon. Similarly to previous research by Inhoff, they also found that latency of the first saccade in a sequence increases with sequence length. Results of this study also found that the latency of saccades in a sequence after the first saccade also increased with sequence length, which agrees with findings from Inhoff (1986).

The increased latency of the first saccade demonstrates the presence of the response complexity effect. This finding in eye movements has also been replicated by Franks and Lajoie (1998), who looked at reaction times in a single eye saccade and compared this to reaction times for a sequence of two saccades, one away from the initial starting point, and a second back to the starting point. This study included conditions in which accurate saccades were required, with both a starting target and a first saccade target visible, as well as a “no accuracy condition” in which only the starting target (towards which the second saccade was made back to) was visible. Results for reaction times were averaged across these two conditions (accuracy/no accuracy) and the response complexity effect was found.

Not only is the latency of the initial saccade used as evidence for holistic planning of saccade sequences but non-initial saccades can also serve as evidence as well. This has been demonstrated by Walker and McSorley (2006). They conducted a study in which subjects made two saccades in sequence. The first saccade was either reflexive (to a target that appeared), or voluntary (an arrow directed towards one of two targets already present on screen). The second saccade was of the opposite type. The latency of the saccades in these sequences were compared to control trials in which subjects made a single reflexive or voluntary saccade. It was found that second saccade latencies were significantly shorter than the same type of saccade when executed as a single saccade. It has been suggested by the authors that this reduced second saccade latency is the result of the fact that the second saccade is partially planned during the time that the first saccade has is also being planned.

However, conflicting research has also given evidence that saccades are not in fact planned together in sequence. As discussed above, the one target advantage has been used as evidence of movements being planned in sequence. In 2004, Pratt and colleagues conducted a study to determine if this phenomenon exists in eye movements. Saccades of either 5 or 15 degrees were made in three different conditions: either to a single target, to an initial target and then to a second target in the same direction, or to an initial target and then back to the starting point (in the opposite direction). The two-target reversal condition was included as this has been found in previous studies to eliminate the one-target advantage. As the two-target, same direction condition failed to create longer movement times to the first target as

compared to the other two conditions, it was concluded that the one-target advantage does not exist in eye movements. Furthermore, this study failed to find the response complexity effect that has been demonstrated in previous studies (i.e., Inhoff, 1986; Zingale & Kowler, 1987) (Figure 1.4). Authors hypothesized that, given the larger sample size in this study compared to previous studies, this effect may not be as robust as previously thought. Walker & McSorley (2006) also failed to replicate the response complexity effect, although, as previously discussed, have nonetheless found evidence of saccades being planned as sequences.

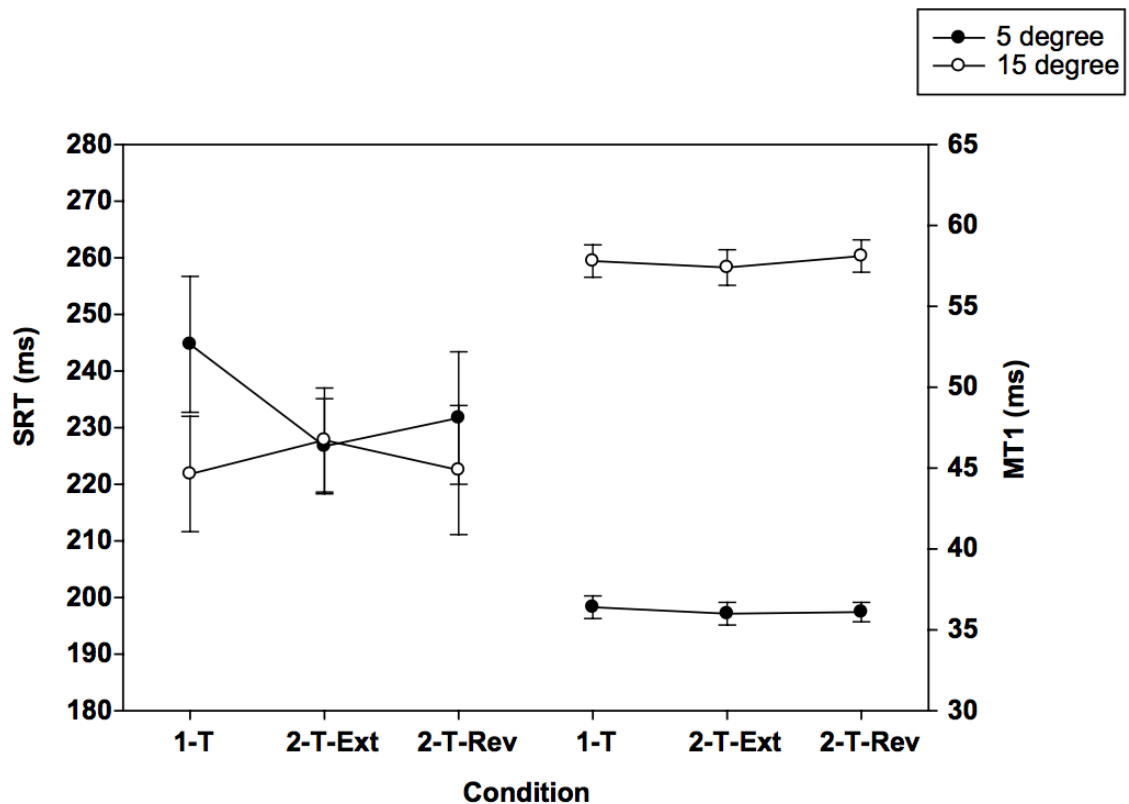


Figure 2.4. A graph of results from Pratt (2004). Reaction times for each of the three instruction conditions and both possible saccade distances (5 or 15 degrees) are shown on the left. Movement times are shown on the right. Taken from Pratt (2004).

Further conflicting research on whether or not saccades are planned in sequence also comes from studies on attention in saccadic sequences. In 2008, Baldauf and Deubel conducted a study in which subjects performed a sequence of two saccades to targets (out of a possible 12) arranged on a circular array. The first movement was directed by an arrow, and the second saccade was to be made to the target two clock numbers away in the clockwise direction. 50ms after participants were directed to move, previously masked characters at each of the 12 possible target locations were revealed. 11 of these characters were “distractors” (either a digital 5 or 2), and one was the critical discrimination target, which was an E or a 3. These characters were masked again before the saccades began. After making the sequence of saccades participants were required to indicate which of the discrimination targets was present. It was found that discrimination accuracy was enhanced for either position in the sequence, while close to chance for positions not in the sequence. This demonstrates that attention is allocated to both target locations in parallel prior to initiation of movement, giving evidence of saccades being planned in sequence.

Another study on attention and saccade sequences provided opposing results. Gersch et al. (2004) presented six targets on a screen and instructed participants to make saccades to every other box in sequence, maintaining a constant direction (either clockwise or counterclockwise). Gabor patches were presented during randomly selected intersaccadic pauses in one of the 6 boxes, and participants were to indicate the orientation (left or right) of the Gabor. Subjects were able to direct saccades to the Gabor patch once it was presented, so all subjects should have been able to foveate the

target. Researchers used the results from this discrimination task to determine that contrast sensitivity for orientation discrimination to be highest when the Gabor was presented at the target for the fixation position and for the immediate next target to be fixated but not for any subsequent targets, suggesting that attention is only allocated to the next saccade target in a sequence of multiple saccades.

2.6 Effect of Saccade Planning on Saccade Endpoint

While findings that look at saccade latencies have found (sometimes controversial) effects of saccades being planned in sequences, it is still unknown whether or not later steps in a sequence of saccades modulate the endpoint of the first saccade. As previously discussed, it has been shown in arm movements that later movements to be made can influence not only the timing of the first movement, but also the way in which the movement is made (e.g., grip orientation). Few studies have looked at whether or not a similar effect exists in eye movements.

In 2016, McSorley, McCloy and Williams conducted an experiment in which participants either had to make a single saccade (either voluntary or reflexive) or a set of two saccades (reflexive, then voluntary, or voluntary, then reflexive). Reflexive saccades were elicited by presenting a new stimulus in the periphery, and voluntary saccades were elicited by removing two of the lines on the fixation target, leaving an arrow pointing towards a target. Additionally, in the majority of trials, the second target was moved slightly in distance (0.75 or 1.5 degrees) towards or away from the first target, or in direction (10 or 20 degrees clockwise or counterclockwise) in order to

determine the preparation of the saccade to the second target that occurred while the first saccade was being prepared and executed. (Figure 1.5)

It was found that when a reflexive saccade followed a voluntary saccade, the distance of the endpoint of the first saccade was not affected, however the direction of the first saccade was, with the first saccade being “pulled” towards the location of the second target. However, a major limitation of this experiment is that while the voluntary targets were 8 degrees of visual angle from the fixation point, only 3.1 degrees of visual angle separated the voluntary and reflexive saccade targets. In some trials there was a shift of the second target of 1.5 degrees towards or away from the second target, further reducing this distance to only 1.6 degrees in some trials. When targets are this close together a saccade can be made between the two targets, instead of to each individual target, while still allowing the participant to see both targets very clearly, which may have skewed results. Furthermore, the use of a voluntary and reflexive saccade in the same sequence of saccades would result in one target eliciting endogenous attention (the voluntary saccade) and the other exogenous (the reflexive saccade) which can also influence results.

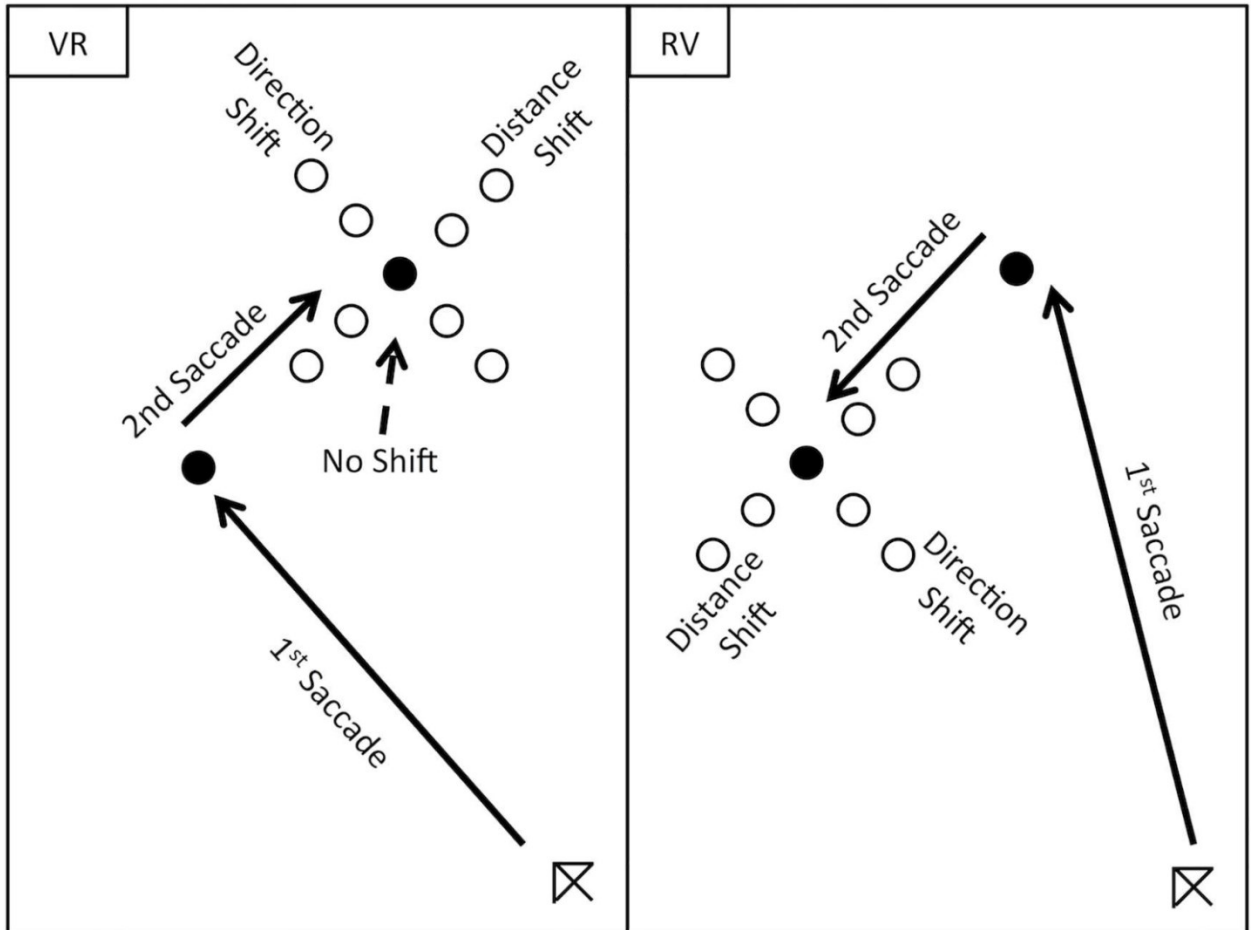


Figure 2.5. Experimental design in McSorley, McCloy, Williams (2016). Reflexive saccades were indicated with the onset of the target and voluntary saccades were indicated with an arrow. 91% of trials involved a shift of the second trial, either in distance or direction during the execution of the first saccade. Taken from McSorley, McCloy, Williams (2016).

Another study that looked at saccadic endpoints and planning was conducted by Bhutani, Ray and Murthy in 2012. They wanted to determine if saccadic averaging was a result of visual processing, or of movement planning. Saccadic averaging is a phenomenon that occurs when an eye movement fall in between two targets, either in the presence of a distractor target (Coren & Hoenig, 1972), or when the target is not

specified (Findlay, 1982). This study differed from previously described studies on movement planning as it was a double-step task, where a second target appears after the first target. In this study, the delay ranged from 50-200 ms. Participants were instructed either to “follow” in which subjects were to make two sequential saccades, one to the first target and one to the second, later-appearing target, or to “redirect”, where subjects were to saccade directly to the later-appearing target, cancelling their saccade to the first target. Single-target saccades or “no-step” trials were also included. There was found to be significantly more midway saccades (that landed between the two targets) in the “follow” condition, and significantly more hypometric saccades (towards the initial target) in the “redirect” condition. Authors conclude that the difference in results for these two conditions suggest that saccadic averaging is a result of movement planning, as if it was solely a result of visual processing alone, both results would have produced midway saccades between the two targets. Furthermore, when midway saccades did occur in the “redirect” condition, the endpoint of these saccades were found to significantly shift towards the final target as the time between the first saccade and the appearance of the second target increased. This shift, while not significant for both task conditions, may suggest that the second target influences the first saccade. However, as this was a double-step task, movement planning to both targets could not truly occur simultaneously, the first saccade was at least partially planned before the onset of the second target.

In summary, there is still more to be learned about the planning and execution of sequential saccades. The response complexity effect, which has been used as

evidence of sequential movements being planned together, has been demonstrated in some studies (Inhoff, 1986; Zingale & Kowler, 1987), but in other studies has not been found (Pratt, 2004). Even less research has been done on how the second target location impacts the first saccade in a sequence. Studies that have done so (McSorley, McCloy, Williams, 2016), have had some experimental design issues such as target locations moving mid-trial, very small distances between targets, and different targets eliciting different forms of attention, which all may have confounded results. The aim of the present study is to resolve some of these questions by examining if the presence, and location of a second target has an impact on the first saccade in a sequence of two saccades.

CHAPTER 3 EXPERIMENT 1

3.1 METHODOLOGY

The first experiment investigated whether the presence and location of a second target influenced the first saccade in a sequence of two saccades. It also investigated whether reaction times were affected by the presence of a second target, as compared to trials in which only a single target was present.

3.1.1 PARTICIPANTS

Eighteen participants (4 male, 14 female) were recruited for Experiment 1. Participants were recruited from the SONA undergraduate participant pool. Participants received one credit point for participating through SONA. Ages ranged from 18 to 22 with a mean age of 19.83 (SD=1.54). (Table 3.1)

Participant	Biological Sex	Age
1	F	19
2	F	21
3	F	18
4	F	19
5	F	24
6	F	20
7	F	19
8	F	18
9	F	20
10	F	18
11	F	19
12	F	20
13	M	21
14	M	20
15	F	19
16	F	19
17	M	21
18	M	22

Table 3.1 Participant characteristics for Experiment 1.

Participants needed to be at least 17 years of age, as this was determined to be the age to give informed consent, and an age at which the brain is considered fully developed. Participants were required to have normal or corrected-to-normal visual acuity with contact lenses, normal ocular alignment and motility, normal visual field, and normal saccadic eye movements. Exclusion criteria included the presence of any known ocular or neurological disease, as these could affect visual processing of visual stimuli and generation of eye movements. These conditions were detected with a self-screening form (Appendix A) Participants who required glasses to achieve normal visual acuity were also excluded as glasses can create issues with glare on the EyeLink II system, and can induce a prismatic effect when viewing peripheral targets.

3.1.2 OCULAR TESTING

Ocular testing was done to ensure that all participants met the inclusion criteria for visual functioning. Visual acuity was tested monocularly using the Sloan near card. Participants were required to have visual acuity of at least $6/6^{-2}$ to meet inclusion criteria. Visual field was tested by having participants fixate on a cross on the left side of their visual field and detect the presence of a visual target, by indicating when they saw a target switch from the white background colour of the screening field, to the black side (Figure 3.1). Spot checks of the visual field were performed every 3 degrees of visual angle up to a total of 36 degrees of the participants right visual field, to simulate target positions in the experimental set up.

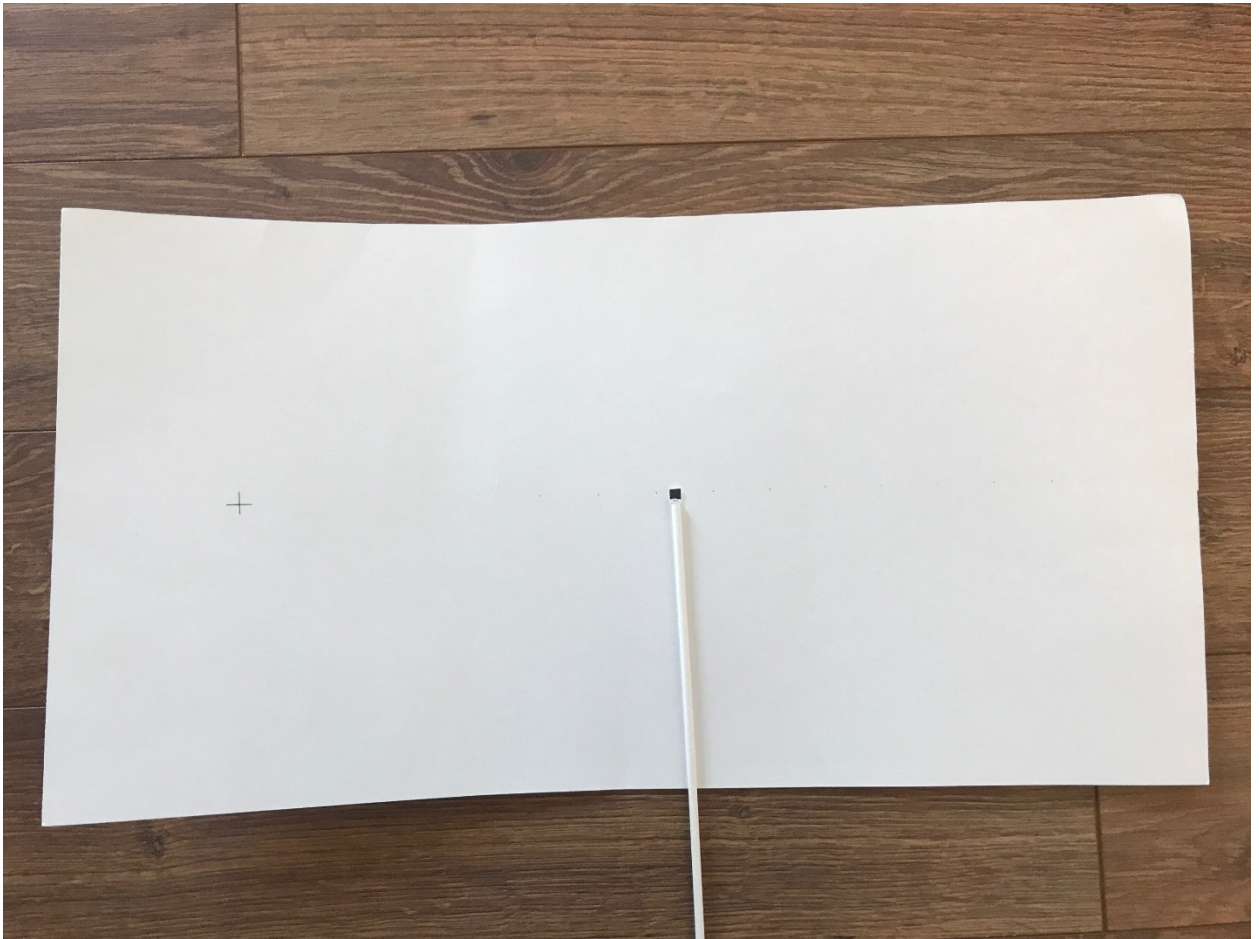


Figure 3.1 Visual field screening equipment. The screening field background and target which was switched from its white side (not shown), which matched the colour of the background, to its black side (shown)

Ocular alignment was testing by performing an alternate prism cover test at near and distance to detect the presence and size of any deviation. Participants with any manifest strabismus, or any vertical deviation, whether phoric or manifest were excluded from the study. In order for an esophoria to be considered within an acceptable range for inclusion in the study, a deviation of less than 10 prism diopters was required (Pratt-

Johnson & Tilson, 1994). For exophorias, the deviation was required to be less than 12 prism diopters (Parks, 1975). Ocular motility was assessed by having the participant look in the field of gaze of each extraocular muscle and any overaction or underaction of the corresponding muscles were noted. If overaction or underaction of a muscle was noted an alternate prism cover test was performed in that field of gaze. If the deviation measured in this position changed compared to the measurement found in primary position, it was considered a true ocular motility abnormality, and the participant was excluded from the study. Horizontal saccades were also assessed by the experimenter by directing the participant to fixate on the experimenter's centrally located finger, and then to make a saccade to the experimenter's finger held in the participant's right field of gaze. Participants were directed to look from the central finger to the peripheral finger several times, and this was then repeated having the participant look from the central finger to a peripheral finger in the participants left field of gaze. The experimenter monitored the participant's saccades for any hypometric or hypermetric saccades. If any saccadic abnormality was detected, the participant was excluded from the study.

3.1.3 ETHICS

Ethical approval was obtained from the Dalhousie University Research Ethics Board (Appendix B). All participants provided informed consent before participating in the experiment. (Appendix C).

3.1.4 APPARATUS

The Eyelink II (SR Research) was used to track participants' saccades. This device was composed of a head mounted infrared camera that tracks pupil movement and corneal light reflectance (Figure 3.2). Due to technical limitations, the pupil only mode was used. This allowed for the pupil to be tracked with an accuracy of 0.5° , a spatial resolution of 0.01° and a sampling rate of 250Hz. The location and orientation of the infrared camera (and subsequently the participant's head) relative to the computer monitor was detected by four sensors on each corner of the computer monitor on which the participant fixated. This allowed for variations in head positioning to be accounted for by the system. The head mounted camera was positioned approximately 57 cm from the monitor and this distance was monitored by the experimenter throughout the experiment. The experiment was presented on a 53 cm by 30 cm Toshiba monitor and the experiment was built and run on a Lenovo computer (Figure 3.3). The display was controlled by a separate Dell computer monitored by the experimenter.



Figure 3.2. The head-mounted Eyelink II eye tracker.



Figure 3.3. Experimental setup as viewed by the participant including display monitor with infrared targets for Eyelink II system and keyboard.

3.1.5 PROCEDURE

The experiment took place in the Action Laboratory (Room 218C) at the Dalhousie University Dalplex. Participants were first given a screening form with exclusion criteria for the study (Appendix A). If participants met any of the exclusion criteria, they were unable to participate in the study. If participants met study criteria, they were then asked to read a consent form and informed consent was obtained. Once consent was obtained,

ocular testing was performed as described above to ensure participants met ocular inclusion criteria. Participants were then asked to fill out a demographic form. (Appendix D).

Participants were then seated approximately 57 cm from the computer monitor, and the Eyelink II was placed and secured on their head. Once securely fastened the Eyelink II was then calibrated by having the participant fixate on targets around the perimeter of the screen, and validated by repeating this process once more.

Instructions were given to participants both on screen and verbally before the experiment began. Participants were asked to make a saccade from the fixation target to the leftmost (center) target, then to the next target, on the right for trials in which two targets were present (two target trials). When only one target appeared on screen (single target trials), participants were asked to simply look at the single (centrally located target). To begin the experiment and each subsequent trial, participants hit the spacebar. When the space bar was pressed, a drift correct procedure would occur to correct for any slippage of the eye tracker on the head between trials. Participants' head position and fixation could be monitored by the experimenter throughout each trial (Figure 3.4). After pressing the spacebar and performing the drift correction, the trial began. At this point, a fixation target appeared to the left of the screen. After a time interval of either 1000, 1250, or 1500 ms, which were randomized to prevent predictability, either one or two targets appeared to the right of the fixation target. The fixation and saccade targets were all 0.5 degrees of visual angle in size, as this size has been used on previous studies on eye movement planning. Six practice trials were done

before data recording began. The position of the first saccade target was 12, 15, or 18 degrees of visual angle from the fixation target with position randomized for each trial to prevent predictability (Figure 3.5). These first target positions will be referred to as the near, middle, and far positions respectively. The second saccade target, when present, was located 12, 15, or 18 degrees from the location of the first saccade target. (Figure 3.6). These second target locations will be referred to as the near, middle and far positions respectively. The variability of this target location was used to determine if second target location has an impact on first saccade endpoint. Single target trials were included to compare the effects on saccade endpoint and latency to two-target trials. The location of both saccade targets were randomized on a trial by trial basis, along with target onset time, for a total of 27 possible combinations for two target trials (3 first target positions x 3 second target positions x 3 onset times), and 9 for single target trials (3 target positions x 3 onset times). Each two target trial combination was repeated 4 times, for a total of 108 two target trials, and each single target trial combination was repeated 12 times in order to also have 108 single target trials, for an overall total of 216 trials. It was important to equate the total number of single and double target trials so that the probability of preparing a sequence of two saccades was the same as that of preparing only a single saccade (i.e., 50%), thus enabling a measurement of reaction time to be used to infer the cost of preparation rather than the expectation of whether or not planning would be required. At the end of the experiment participants were provided with a debriefing form (Appendix E) and the purpose of the experiment was explained to them. Participants were also given the opportunity to ask any questions

they may have before leaving the lab.

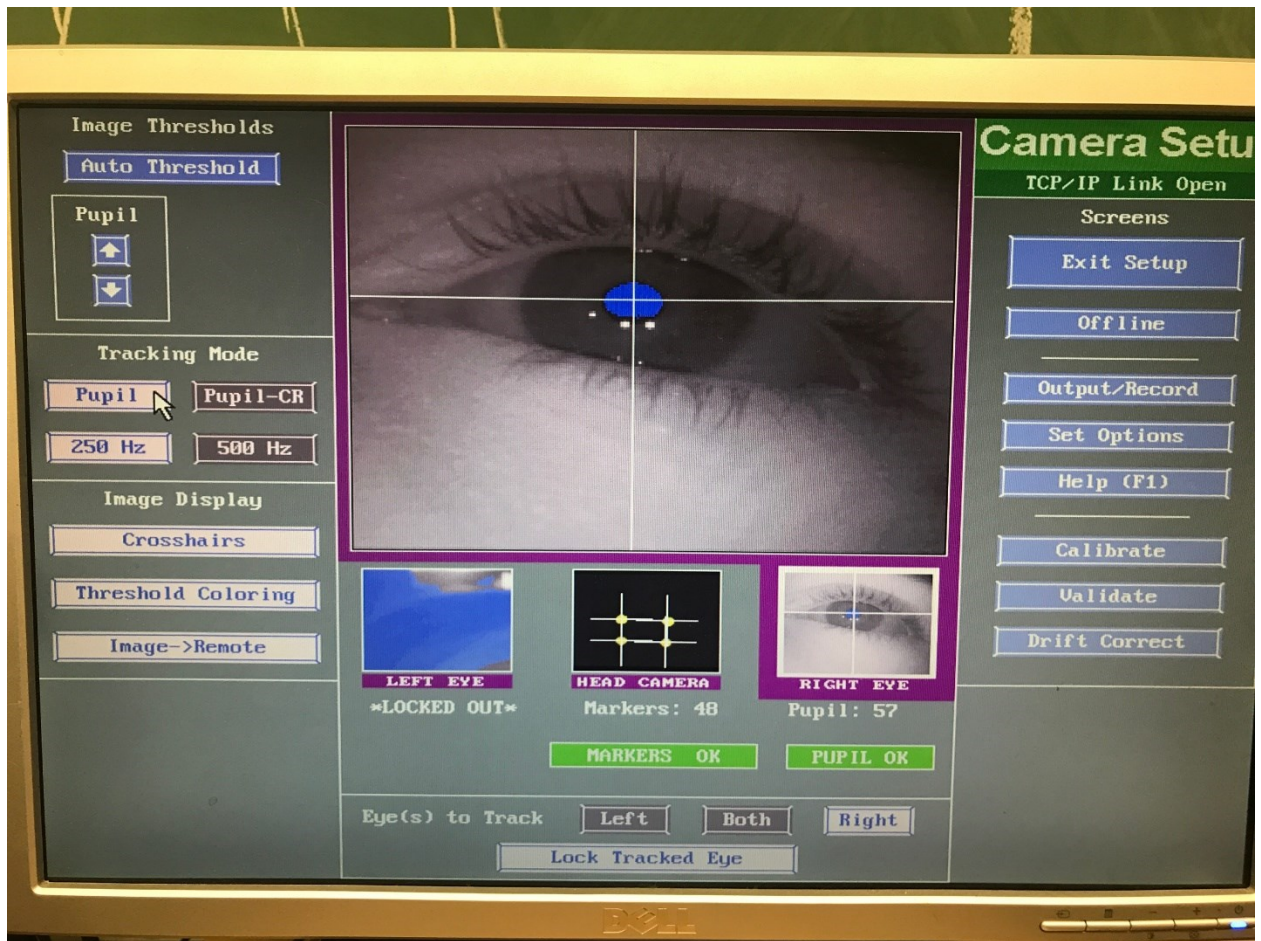


Figure 3.4 View of the experimental monitoring display. This display allowed for the experimenter to monitor participant's distance from the monitor, ensure the pupil was being tracked, and monitor fixation throughout the trial

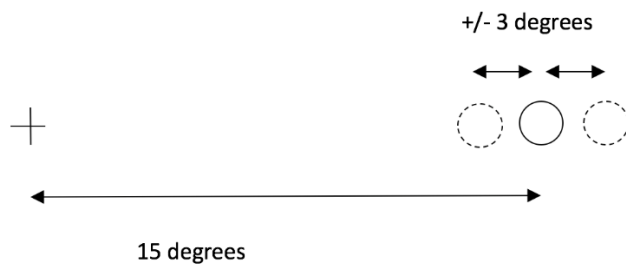


Figure 3.5. The experimental design for single target trials.

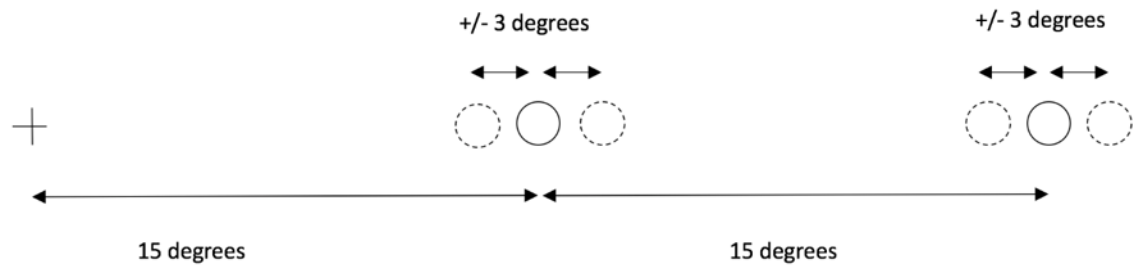


Figure 3.6. The experimental design for two target trials. (Note: The second target was located either 12, 15 or 18 degrees from the *first target position* for that trial (shown here in a solid outline target). Shown here are all three possible first target locations, and only possible second target locations for a first target that is located 15 degrees from fixation).

3.1.6 STATISTICAL ANALYSIS

Data was analyzed using Data Viewer (SR research) to extract information about the amplitude, end horizontal position (note: end position was not redundant with amplitude because not all saccades were initiated from precisely the same initial location given the size of the fixation stimulus), duration, peak velocity, and reaction time of the participant's primary saccade. The primary saccade was defined as the first saccade greater than 2 degrees in amplitude initiated from the fixation location after the onset of the targets. If no saccades greater than this minimum amplitude were detected the trial was not analyzed. Error trials were then removed from analysis, which consisted of participants who did not make the correct number of saccades for a trial. Outlier data were also removed by removing any saccade data that was more than 3 SD from the participant's own mean for any parameter analyzed; for outlier detection, trial averages were generated per target 1 location (near, middle, far) to ensure that data

ranges were not affected by variation in saccade parameters naturally arising from target position.

Data analysis was done using SPSS Statistics (v24, IBM). Each dependent variable (amplitude, end horizontal position, peak velocity, duration, and reaction time) was analyzed separately using a repeated measures ANOVA. For amplitude, horizontal end position, peak velocity and duration, factors included first target location (near, middle, far) and second target location (near, middle, far). Single and double target trials were analyzed separately because single-target trials did not have the factor of second target location. Amplitude, horizontal end position, peak velocity, and duration, this time also with reaction time was analyzed again, this time with factors first target location (near, middle, far), and trial type (single vs. double target) to look for an effect of the presence of multiple targets on reaction time. All analyses were tested for significance at an alpha level of 0.05. Variability is indicated by standard error of the mean.

3.2 RESULTS

Experiment 1 consisted of a total of 3888 trials across all participants. Of the 3888 trials, 3318 (85.3%) were used in the final analysis and 570 (14.7%) were excluded as follows. Reasons for exclusion were no sufficiently large primary saccade (0.6%), incorrect number of saccades made (2.5%), improper fixation at trial onset (7.7%), and outlier data (3.9%) (Appendix F). One participant had a particularly large number of excluded trials so a group-wise outlier procedure was used based on the range of trials included for all participants the experiment. This single participant fell outside 3

standard deviations of the group mean and thus constituted a legitimate outlier. Results were analyzed with and without this participant's trials included and since the results were similar in both cases the reported statistics include that individual's data. Only significant effects are reported, except in cases that are relevant to the experimental hypothesis. Analysis of double target trials is shown below, followed by analysis of single and double target trials.

3.2.1 Analysis of Double Target Trials

3.2.1.1 Amplitude

Saccade amplitude is the length in degrees of the primary saccade from its starting position to its end position. As expected, there was a significant main effect of first target location $F(2,36)=1136.3$, $MSE=4.043$, $p<0.001$, indicating that as the first target location shifted further away from the fixation point, saccade amplitude increased. (Table 3.2) Of greater relevance to the experimental hypothesis, a significant main effect was found for second target location $F(2,37)=7.4$, $MSE=2.078$, $p=0.002$ (Figure 3.7). In contrast to the predicted direction of this effect, however, the further away the second target position, the *smaller* the amplitude of the first saccade.

First Target Distance from Fixation (degrees)	Mean Saccade Amplitude (degrees)
12	10.9
15	13.9
18	16.9

Table 3.2. Mean saccade amplitudes for double target trials for each first target location.

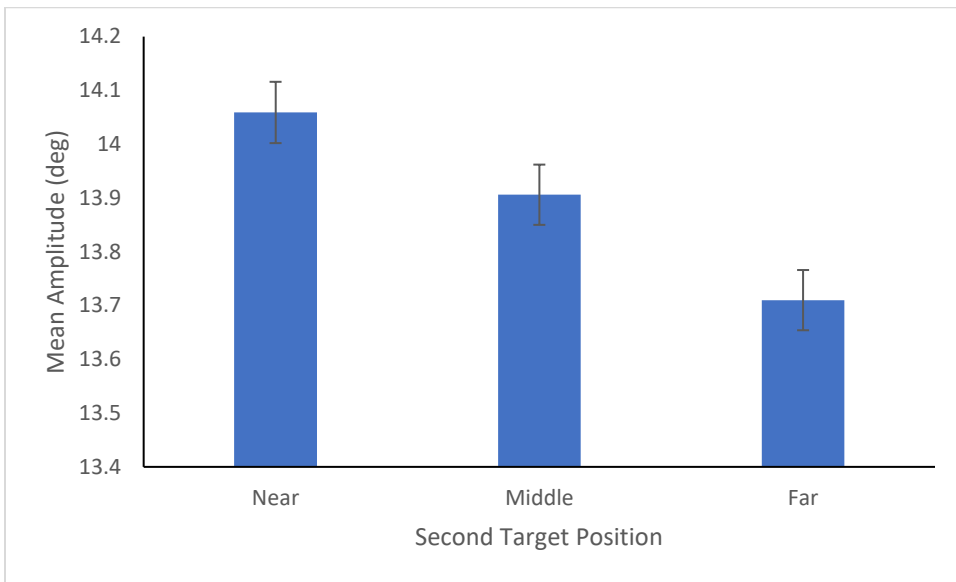


Figure 3.7. Mean amplitude (in degrees) of the first saccade, split by second target position (near, middle and far). A significant difference was found for second target position on first saccade amplitude. Error bars represent standard error of the mean.

3.2.1.2 Horizontal End Position

The horizontal end position of the primary saccade is the location, in on-screen pixel co-ordinates, at which the first saccade lands. As noted earlier, this parameter is not entirely redundant with saccade amplitude because the starting position of each saccade can vary slightly due to the size of the fixation point. There was a significant main effect found for first target location, as expected, $F(2,35)=977.8$, $MSE=2014.234$, $p<0.001$, which indicated that as the first target location shifts further from the fixation

point, so does the horizontal end position of the first saccade. Consistent with findings from saccade amplitude, there was a significant main effect of second target location as well, $F(2, 37)=6.4$, $MSE=1001.512$, $p=0.004$, indicating that as second target position was shifted further from the fixation target (right), the primary saccade end position was located closer to the fixation target (left) (Figure 3.8).

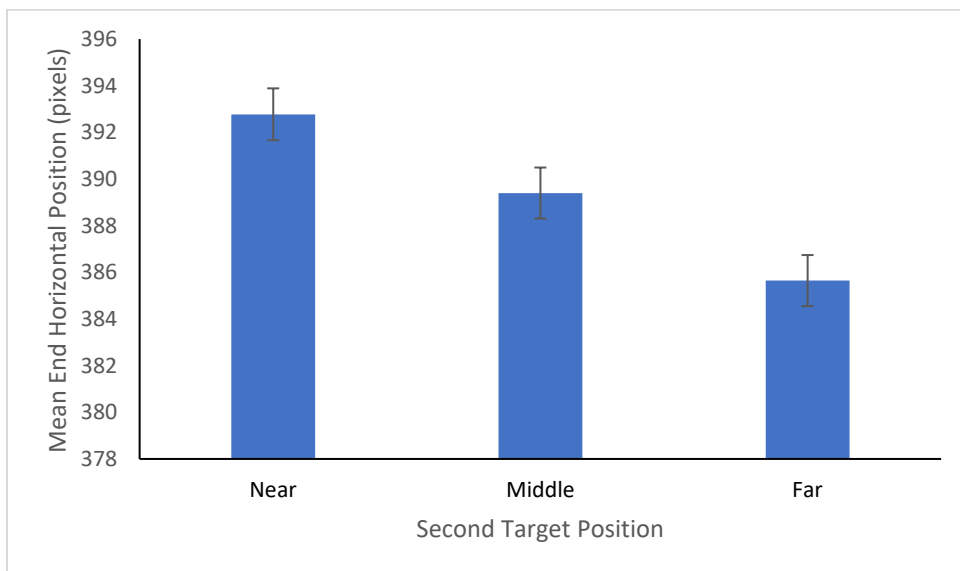


Figure 3.8. Mean horizontal end position (in pixels) of the first saccade, split by second target position (near, middle and far). A significant difference was found for second target position on first saccade horizontal end position. Error bars represent standard error of the mean.

3.2.1.3 Duration

Saccade duration is the length of time taken from the onset of the saccade to its end. There was a significant main effect found for first target location $F(2,35)=46.1$, $MSE=423.761$, $p<0.001$, which in accordance with amplitude, indicates that as the first target location was shifted further away from the fixation point, the length of time to

get to complete the saccade increased. A significant main effect of second target location was found $F(2,45)=4.3$, $MSE=36.748$, $p=0.019$, which, consistent with the significant effect found for saccade amplitude, indicated that as second target location shifted further from the first target location, first saccade duration decreased (Figure 3.9).

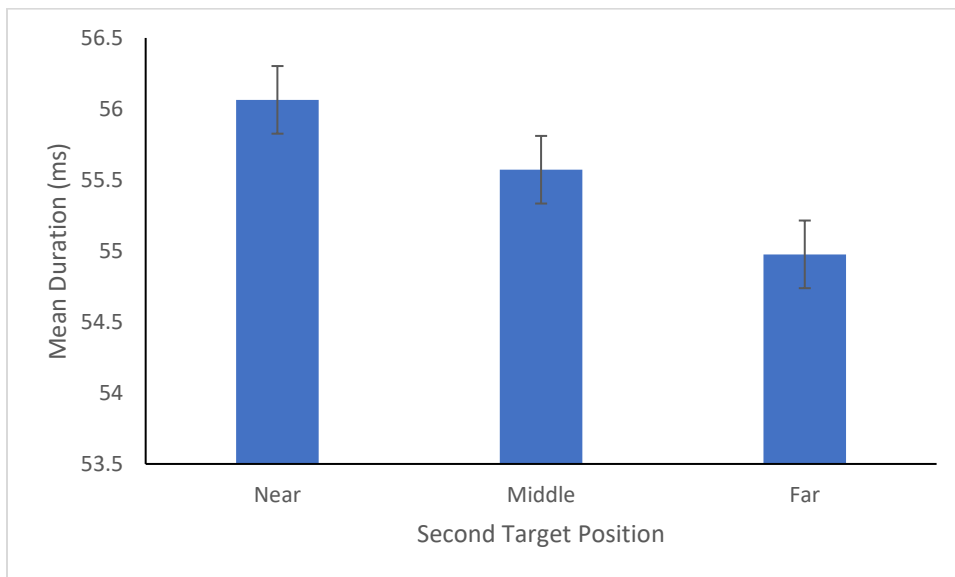


Figure 3.9. Mean duration (in milliseconds) of the first saccade, split by second target position (near, middle and far). A significant difference was found for second target position on first saccade duration. Error bars represent standard error of the mean.

3.2.1.4 Peak Velocity

The peak velocity of a saccade is the maximum velocity reached during the eye movement. Peak velocity tends to increase with saccade amplitude. There was a significant main effect found for first target location $F(2,35)=128.0$, $MSE=7042.604$, $p<0.001$. In contrast to the results from saccade amplitude, final saccade position, and duration, no significant main effect for second target location was found $F(2,39)=1.2$, $MSE=1388.856$, $p=0.321$ (Figure 3.10) although the direction of the trend is consistent

with the other effects.

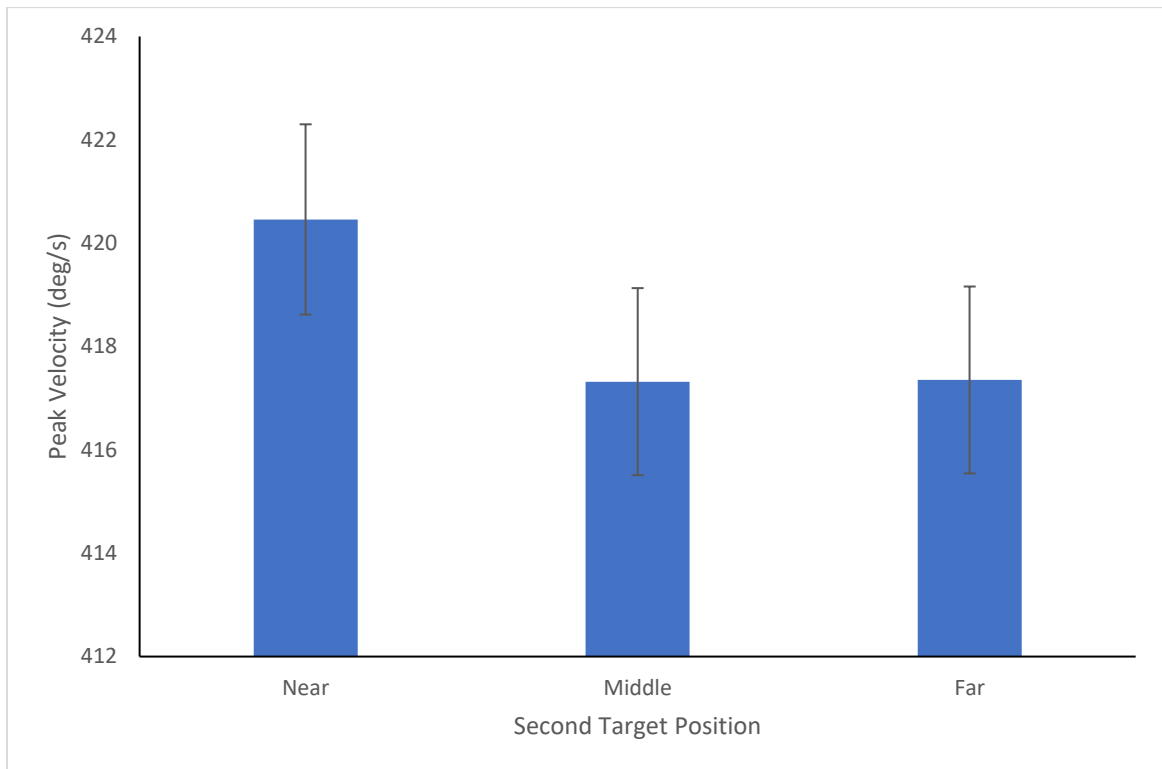


Figure 3.10. Mean peak velocity (in degrees) of the first saccade, split by second target position (near, middle and far). No significant difference was found for second target position on first saccade peak velocity. Error bars represent standard error of the mean.

3.2.2 Analysis of Single and Double Target Trials

3.2.2.1 Reaction Time

Reaction time was measured as the time between the onset of the stimuli (either one or two saccadic targets) and the initiation of the primary saccade. A significant main effect was found for first target location $F(2,35)=15.8$, $MSE=8574.887$, $p<0.001$, which indicated that as the first target was shifted further from the fixation point, reaction time increased. A significant main effect was also found for number of targets (one or

two) $F(1,17)=18.2$, $MSE=19799.836$, $p=0.001$ (Figure 3.11). In contrast to the predicted direction of the effect, reaction time was significantly *shorter* when two targets were presented, and two saccades required, compared to one target.

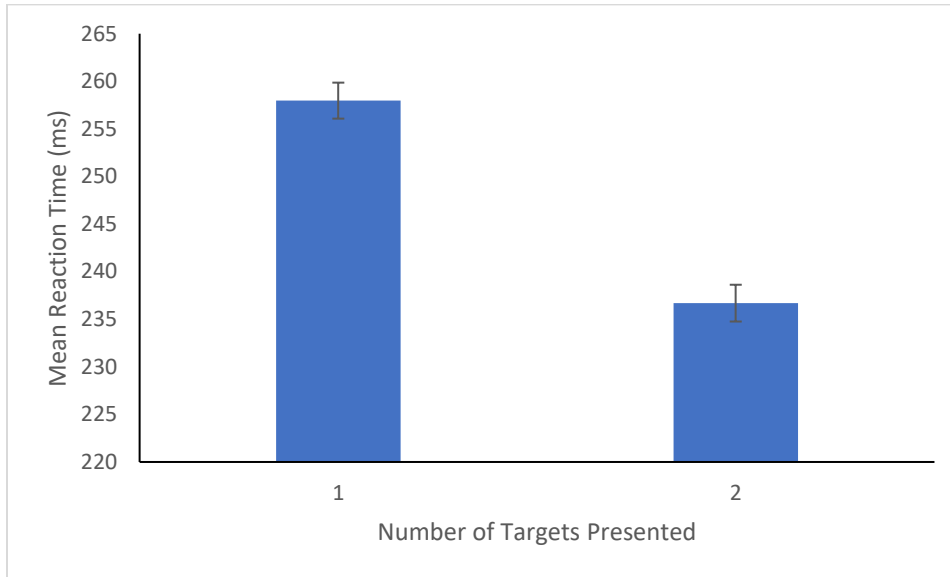


Figure 3.11. Mean reaction time (in milliseconds) of the primary saccade, split by number of targets presented (1 vs. 2). A significant difference was found between the two, with two target trials having significantly shorter reaction times than single target trials. Error bars represent standard error of the mean.

3.2.2.2 Amplitude

A significant main effect was found for first target location $F(2,34)=1146.7$, $MSE=8.817$, $p<0.01$, which indicated that as the first target was shifted further from the fixation point, the primary saccade amplitude increased. A significant main effect was also found for number of targets (one or two) $F(1,17)=6.1$, $MSE=3.361$, $p=0.024$, which indicated that primary saccade amplitude was significantly smaller when a second target was present. (Figure 3.12)

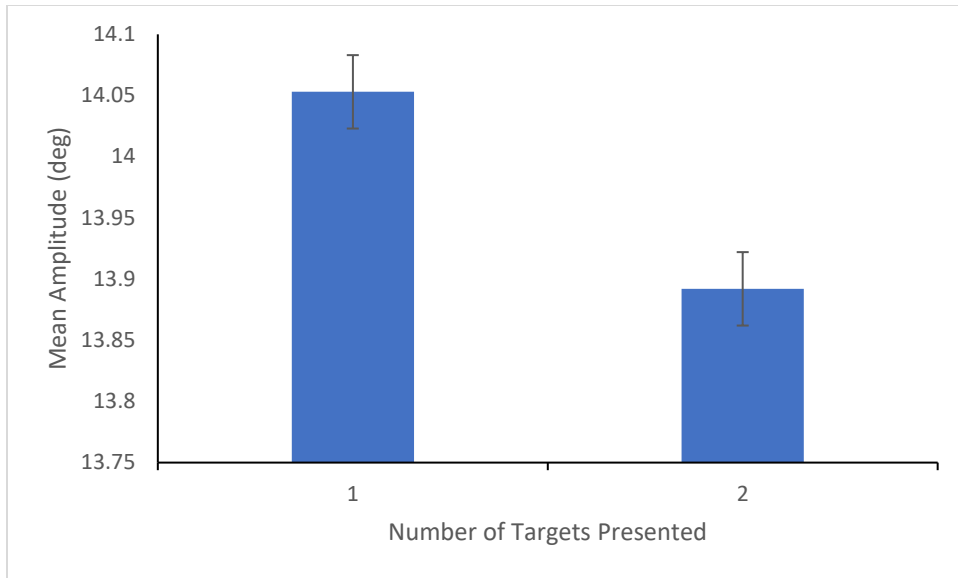


Figure 3.12. Mean amplitude (in degrees) of the primary saccade, split by number of targets presented (1 vs. 2). A significant difference was found for number of targets on primary saccade amplitude. Error bars represent standard error of the mean.

3.2.2.3 Horizontal End Position

A significant main effect was found for first target location $F(2,34)=1589.0$, $MSE=2665.416$, $p<0.001$, which indicated that as the first target location shifts further from the fixation point, so does the horizontal end position of the first saccade. A significant main effect was also found for number of targets (one or two) $F(1,17)=6.0$, $MSE=1624.150$, $p=0.025$, which indicated that when a second target was present, the endpoint of the first saccade was located closer to the fixation target (towards the left), than when a second target was not present (Figure 3.13).

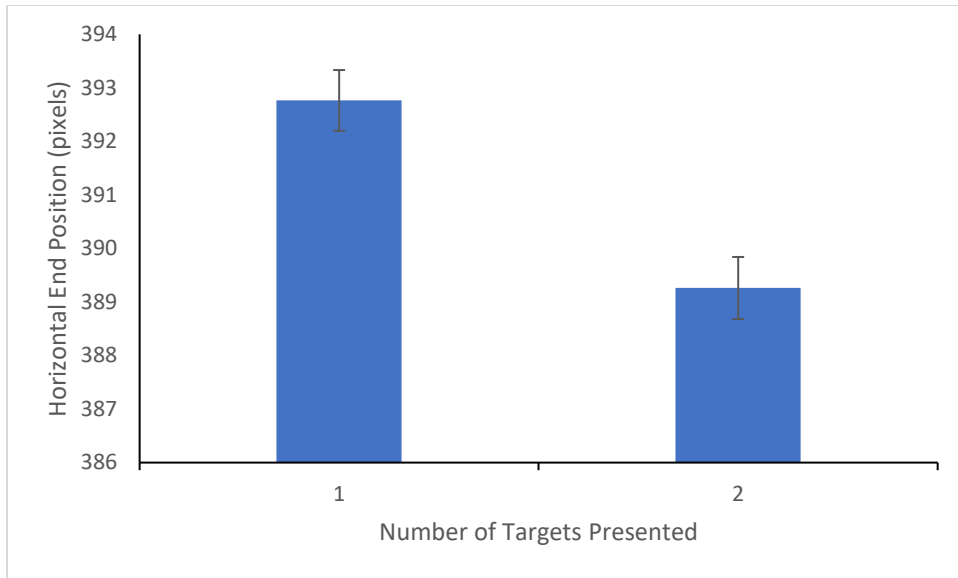


Figure 3.13. Mean horizontal end position (in pixels) of the primary saccade, split by number of targets presented (1 vs. 2). A significant difference was found for number of targets on primary saccade horizontal end position. Error bars represent standard error of the mean.

3.2.2.4 Duration

A significant main effect was found for first target location, $F(2,34)=42.9$, $MSE=849.874$, $p<0.001$, which indicated that that when the first target location was further from the fixation point, the duration of the primary saccade increased. No significant main effect was found for number of targets (one or two) $F(1,18)=0.4$, $MSE=150.103$, $p=0.532$ (Figure 3.14.)

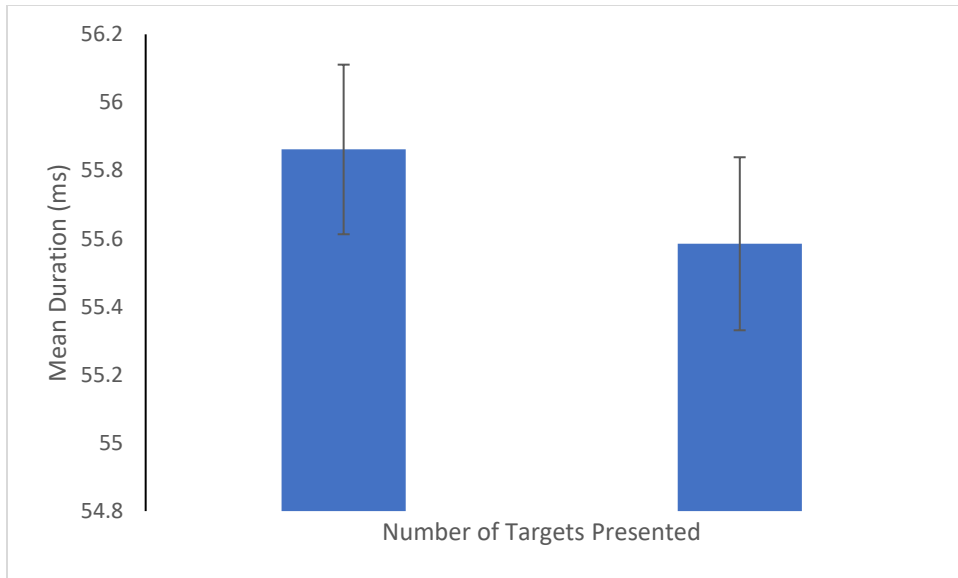


Figure 3.14. Mean duration (in milliseconds) of the primary saccade, split by number of targets presented (1 vs. 2). No significant difference was found for number of targets on primary saccade duration. Error bars represent standard error of the mean.

3.2.2.5 Peak Velocity

A significant main effect was found for first target location $F(2,34)=136.9$, $MSE=15015.199$, $p<0.001$, which indicated that when the first target location was further from the fixation point, the peak velocity was larger. No significant main effect was found for number of targets (one or two) $F(1,17)=4.1$, $MSE=5830.120$, $p=0.058$ (Figure 3.15).

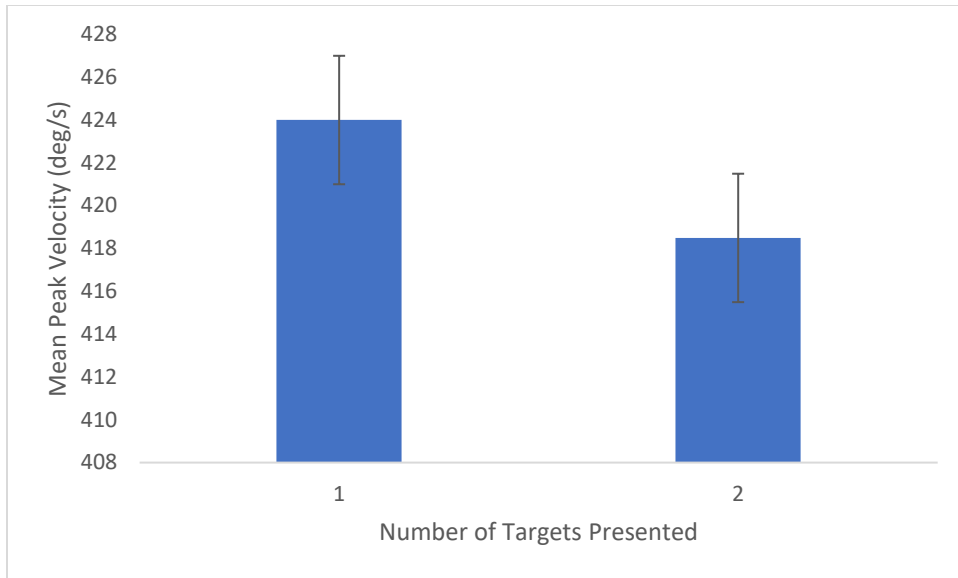


Figure 3.15. Mean peak velocity (in degrees/second) of the primary saccade, split by number of targets presented (1 vs. 2). No significant difference was found for number of targets on primary saccade peak velocity. Error bars represent standard error of the mean.

3.3 DISCUSSION

The results of Experiment 1 showed that the presence of a second target had a significant effect on saccade amplitude, horizontal end position, peak velocity and reaction time. Furthermore, second target location had a significant effect on saccade amplitude, horizontal end position, and duration. There was no significant effect of second target presence or location on peak velocity, or second target presence on duration, which would usually be expected with an effect on saccade amplitude. It is possible that this lack of an effect is the result of the fact that the effect on amplitude is very small. (The difference between mean first saccade amplitude at the near and far positions for second target location is only 0.35 degrees, and the difference between mean first saccade amplitude for single and double target trials is only 0.161 degrees).

This small, but significant change in amplitude may not be large enough to bring about a significant corresponding change in peak velocity or duration.

Contrary to the predicted direction of a second-target effect, the results indicate significantly shorter amplitude initial saccades when a second target is present, and furthermore, shorter initial saccade amplitudes when this second target is located farther away from the first target. This pattern contrasts with results from McSorley, McCloy and Williams (2016) who found that the presence of a second target had no effect on saccade amplitude (only direction, which was not examined in this study). To date, no research has been done on the effect of second target location on the primary saccade, in which a second target is clearly specified. In contrast to studies on arm movements in sequence, in which later movements in a sequence are taken into account in order to maximize comfort or efficiency in later steps in the movement sequence (Hesse and Deubel, 2010; Rosenbaum et al., 1990), this pattern seem to be somewhat counterproductive to making the second saccade, with the eye landing further from the second target when it is present.

These results also contrast with research on saccadic averaging, which has shown that in the presence of two stimuli located in close proximity, saccades will land somewhere in between the two targets (Coren & Hoenig, 1972). This phenomenon is also known as the global effect or center-of-gravity effect. Literature on saccadic averaging however, differs from this experiment in that an eye movement to the second target is not planned as a sequence. Studies are conducted in such a way that the target stimuli is not specified (Findlay, 1982), or to a specified target in the presence of non-

target stimuli (Coren & Hoenig, 1972; Van der Stigchel & Nijboer, 2013; Walker et al. 1997).

A possible explanation for the results found in this study comes from theories surrounding action-centered attention. Action-centered attention examines the mechanisms by which attention is focused on incoming perceptual information that is necessary for specific actions (Tipper et al. 1992). This idea suggests that when attention is captured by a stimulus, processes are automatically initiated to produce a response to the stimulus (Tipper et al. 1992, Welsh 2011). This has been shown to alter movement trajectories towards (Welsh et al., 1999) or away from (Howard & Tipper, 1997) the non-target stimuli in arm movements.

Similar processes have been shown to exist in eye movements, as discussed by Walker and McSorley (2008), who have found that distractor stimuli cause eye movement trajectories to deviate away from the distractor. This results from the suppression of a planned saccade towards the distractor stimuli. This result has been found in numerous studies (McSorley et al, 2004; Doyle and Walker, 2002).

Furthermore, studies such as Laidlaw et al. (2016) have found that the endpoint of saccades is also shifted away from distractor stimuli.

While the intention of the second target was not to act as a distractor stimulus, it is possible that by having a second stimulus present that was salient to the subjects and the task at hand, that action-centered attention played a role in these results. The presence of the second target may have automatically caused participants to plan a saccade directly to this second target. In order to ensure the saccade to the first target is

executed first, the saccade directly to the second target would have to be inhibited. The greater rightwards the second target, the greater the inhibition that would be required, which potentially results in the leftward shift of the primary saccade endpoint with further second target locations. As discussed by Welsh, Neyedli and Tremblay (2013), the executed movement is a result of the total sum of neuronal activity in directionally-tuned cells, including those excited by both target and non-target stimuli. Thus the results found may be the result of a summation of the inhibited plan directly to the second target, and the excitatory plan towards the first target.

The reaction time results from this study showed that when two targets were present and two saccades required, reaction times were significantly shorter than when one target was presented and one required. This result was unexpected as studies such as Inhoff (1986) and Zingale and Kowler (1987) had shown that saccadic latency increased with sequence length. In these studies, sequence length conditions were organized in blocks, such that the participant always knew how many saccades would be required in the upcoming trial. However, when Inhoff (1986) conducted a second experiment in which the number of saccades in the upcoming trial could not be predicted, this response complexity effect was found to disappear. As the single and double target trials in the present study were randomized, as opposed to blocked, these findings are somewhat consistent with Inhoff's (1986) results. What was unexpected and remains unclear however, is that unlike Inhoff's (1986) results where no significant difference was found when trials were randomized, in the present study reaction times were significantly shorter when two saccades were required compared to one. A

possible explanation for these results is that participants took longer to initiate a saccade on single target trials as a second target was not immediately visible, and participants took an extra moment to ensure, or double check possibly by using attention, that a second saccade was not required. In two saccade trials the second target would be immediately visible, and participants would not have to spend as long determining whether or not a second target was present.

To summarize, the results of Experiment 1 indicate a spatial interaction between sequential eye movements such that the metrics of the second target in a sequence affect the metrics of the first eye movement. Surprisingly, given typical findings in movement paradigms with multiple targets, the spatial effect is in an inverse direction; the farther away the second target, the shorter the distance traveled during the first movement. This effect is broadly consistent with an action-centered model in which inhibition of the second saccade translates through vector-averaging into a reduced movement amplitude.

CHAPTER 4 EXPERIMENT 2

4.1 Introduction

In Experiment 1, it was found that a second target to which an eye movement is to be made shifts the first eye movement away from the second target as the distance between the first and second target increases. An action-centered explanation was proposed in which inhibition of a automatically prepared second saccade disrupts the metrics of the primary saccade, however it is not clear from the results that it was motor-related processing of the second stimulus that produced the effect; it is possible that the effect could arise within sensory or attention rather than motor processes.

Experiment 2 sought to distinguish between motor, sensory, and attention accounts of the original effect by comparing three different conditions with different instructions with respect to the second target. Like Experiment 1, the 'look' condition required completion of a saccade to the second target. The 'attend' condition required a perceptual judgement to be made about the second target before making a saccade to the first target, and no saccade was ever made to that second target. The purpose of this condition was to encourage attention to the location of the second target without actually completing an eye movement. The 'ignore' condition required only a saccade to the first target with no task associated with the second target; consequently, any effects arising from the second target could be interpreted as arising from the mere presence of the target rather than explicit intentions on the part of the participant to make an eye movement or pay attention to it.

Drawing on the action-centered interpretation from the first experiment, it was hypothesized that only the condition in which participants are to look at the second target (the 'look' condition) will demonstrate a significant effect on the primary saccade by the second target location, which should manifest in a significant interaction between condition and target 2 location.

4.2 METHODOLOGY

Experiment 2 had similar methodology to Experiment 1. The experimental setup was identical to that of Experiment 1, with the same equipment in the same lab. The two experiments differed in that different stimuli were displayed on the participant's screen and different instructions were given to participants.

4.2.1 PARTICIPANTS

Eighteen participants (5 male, 13 female) were recruited for Experiment 2 (Table 4.1). Participants were recruited through the SONA undergraduate participant pool and received 1 credit point through SONA for participating. None of these participants had participated in Experiment 1. Ages ranged from 18 to 30, with a mean age of 21.3 (SD=3.18). Inclusion and exclusion criteria were the same as described in Experiment 1.

Participant	Biological Sex	Age
1	F	21
2	M	19
3	F	24
4	F	18
5	F	21
6	F	20
7	F	19
8	M	28
9	M	20
10	F	21

11	F	20
12	F	23
13	F	30
14	F	21
15	M	21
16	F	20
17	M	18
18	F	20

Table 4.1. Participant characteristics

4.2.2 ETHICS

Ethical approval was obtained from the Dalhousie University Research Ethics Board (Appendix B). All participants provided informed consent before participating (Appendix C).

4.2.3 PROCEDURE

Initial stages of Experiment 2 were the same as outlined in Experiment 1. Informed consent was obtained, ocular testing done, and the EYELINK II was set up, calibrated and validated as described in Experiment 1.

In Experiment 2, three blocks of trials were conducted. These included the look, attend, and ignore condition. There were six possible ways in which the blocks could be ordered, and each order was performed by 3 participants on a randomized basis, as there was a total of 18 participants. The stimuli for all 3 conditions appeared the same on the screen, with different instructions and different error detections programmed for each condition to ensure participants followed instructions.

For each trial, 2 targets appeared on screen, which will be further described below. In the “look” condition, participants were instructed to look from the fixation point to the first target (leftmost, closest to the fixation point), and then at the second target (rightmost, further from the fixation target. In the ignore condition, participants were instructed to simply look from the fixation point, to the first target, and then stop, ignoring the second target altogether. In the attend condition, participants were asked to make a judgement about the second target before beginning to move their eyes. While looking at the fixation point, they were instructed to note whether the second target that appeared in their periphery was an “x” or a “+”, then move their eyes to the first target. After completing that saccade, participants were prompted to report with the labelled keyboard which symbol they saw.

As in Experiment 1, each trial began with a drift correction procedure to adjust for head movement between trials. Participants pressed the space bar to perform the drift correct and start each trial. At the trial onset, a circular target (0.75 degrees of visual angle) with a smaller black circle in the center (0.25 degrees of visual angle) appeared to the left of the screen (5 degrees of visual angle from the left edge of the screen). This small black circle in the center served as the initial fixation point. After a period of 1000, 1250, or 1500ms, which was randomized to prevent predictability, the two targets appeared. The first target was a circle 0.5 degrees of visual angle in size, consistent with Experiment 1 and previous literature, and was located either 12, 15, or 18 degrees of visual angle from the fixation point to prevent predictability of the first target location. The second target initially appeared as a “+” or an “x” on a random basis. This target was

1 degree of visual angle in size to facilitate identification, and it was located either 12, 15, or 18 degrees of visual angle from the first target (Figures 4.1 and 4.2) Once participants moved their eyes away from the fixation point, the second target changed to a “*” so that participants could only gather information to identify that target prior to completing any eye movements (Figure 4.3). After participants looked at one or both targets (depending on the condition block), the trial ended. In the attend condition, participants were then prompted to indicate which symbol they saw. This was done on a labelled keyboard, with the up and down arrow keys being labelled with either a “+” or “x” (Figure 4.4). Whether or not the up arrow was the location of the “+” label and the down the location of the “x” label was randomized between participants; the purpose of doing this was to avoid confounding the spatial aspects of the motor response (keypress) and the identity of the stimulus. The location of both targets, and target onset time was randomized for a total of 27 possible trial combinations. Each combination was repeated 4 times for a total of 108 trials per condition block, and 324 total trial per participant overall. After completing all trials, participants were giving a debriefing form and the purpose of the experiment was explained. Participants were also given the opportunity to ask any question they may have before leaving the lab.

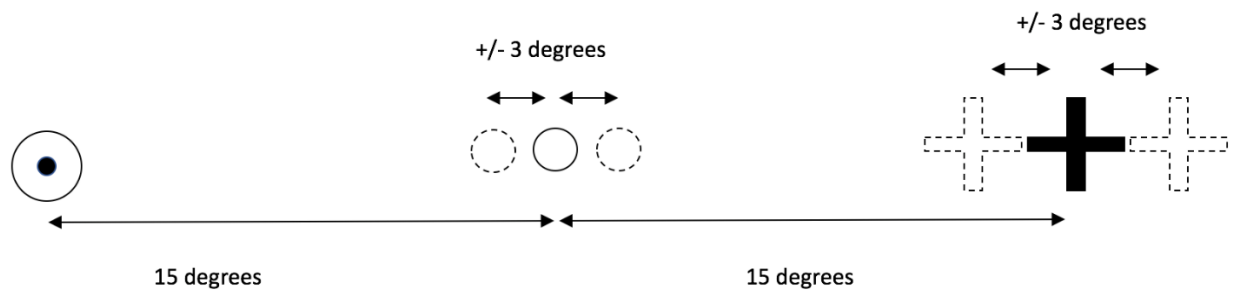


Figure 4.1 The experimental design for trials in which the second target appeared as a “+” (not shown to scale). (Note: The second target was located either 12, 15 or 18 degrees from the *first target position* for that trial (shown here in a solid outline target). Shown here are all three possible first target locations, and only possible second target locations for a first target that is located 15 degrees from fixation).

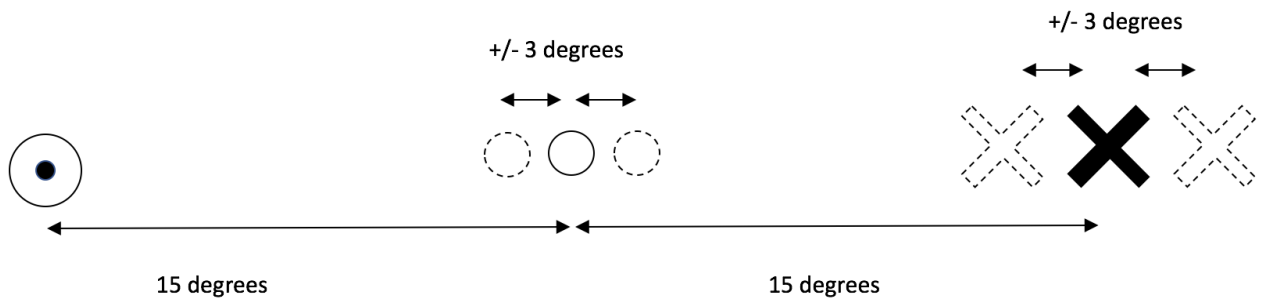


Figure 4.2. The experimental design for trials in which the second target appeared as an “x” (not shown to scale). (Note: The second target was located either 12, 15 or 18 degrees from the *first target position* for that trial (shown here in a solid outline target). Shown here are all three possible first target locations, and only possible second target locations for a first target that is located 15 degrees from fixation).

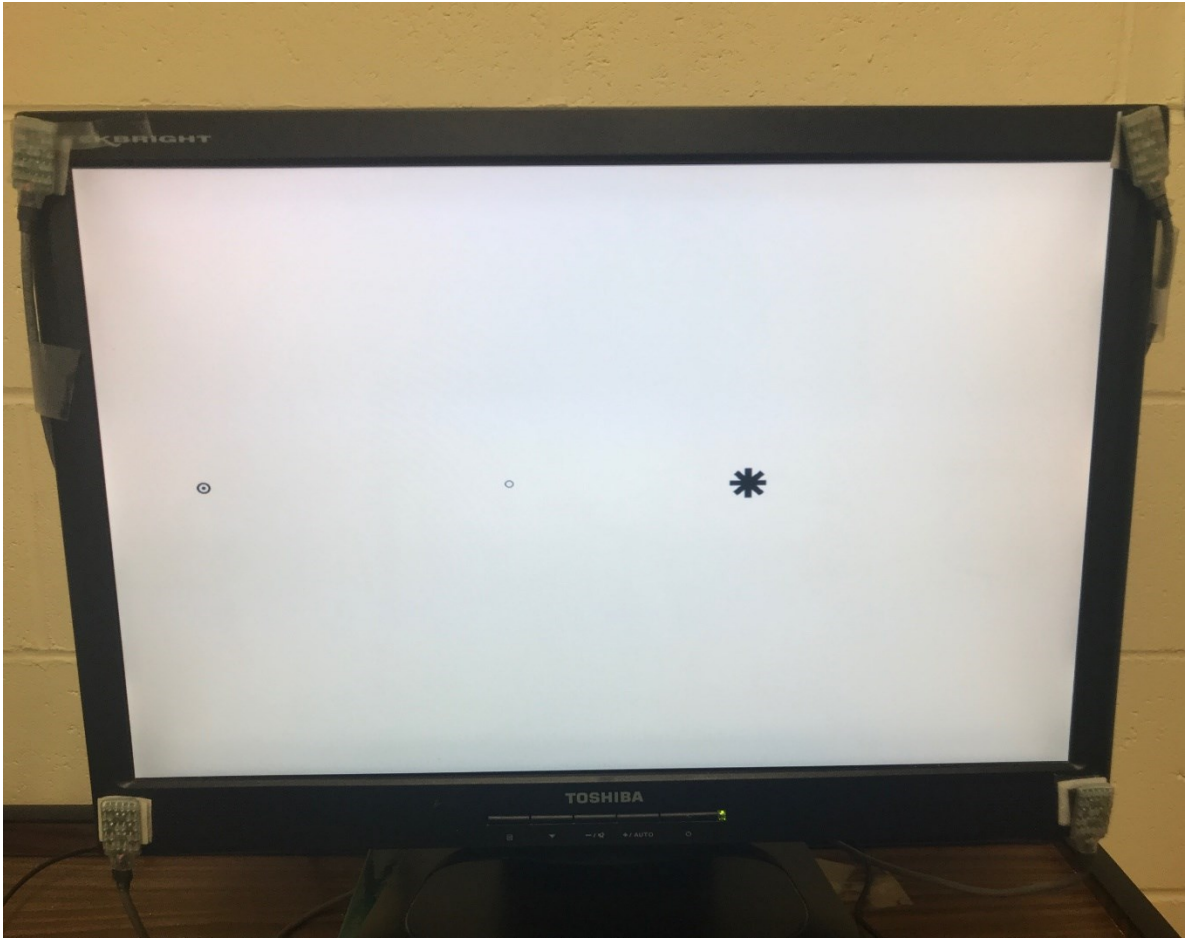


Figure 4.3. The view of the participant after the second target has changed to its masked form.

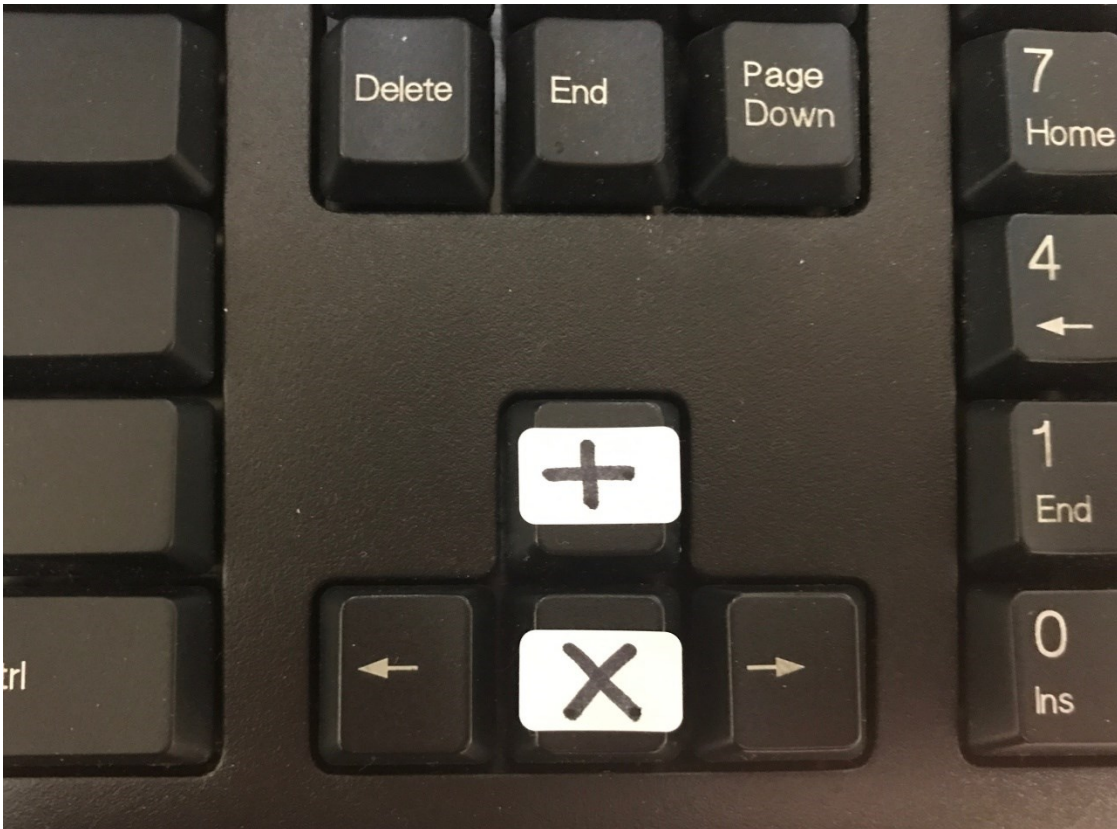


Figure 4.4. The labelled keyboard on which participants indicated their response in the “attend” condition.

4.2.4 STATISTICAL ANALYSIS

Data was analyzed using Data Viewer (SR) research to extract information about the amplitude, end horizontal position (note: end position was not redundant with amplitude because not all saccades were initiated from precisely the same initial location given the size of the fixation stimulus), duration, peak velocity and reaction time of the participant’s primary saccade in each trial. Participant responses for the attend condition were also obtained. The primary saccade was defined as the first saccade greater than 2 degrees in amplitude initiated from the fixation location after the onset of the targets. If no saccades greater than this minimum amplitude were

detected the trial was not analyzed. Error trials were then removed from analysis, which consisted of participants whose trial was aborted due to an action that was not consistent with instructions for the condition block, or whose saccade was not initiated from the fixation target. Outlier data were also removed by removing any saccade data that was more than 3 SD from the participant's own mean for each parameter analyzed; for outlier detection, trial averages were generated per target 1 location (near, middle, far) to ensure that data ranges were not affected by variation in saccade parameters naturally arising from target position.

Data analysis was done using SPSS Statistics (v24, IBM). Each dependent variable (amplitude, end horizontal position, peak velocity, duration, and reaction time) was analyzed separately using a repeated measures ANOVA. For all dependent variables except reaction time, factors included first target location (near, middle, far), second target location (near, middle, far), and condition. Reaction time was analyzed with factors first target location (near, middle, far), and condition to look for an effect of condition on reaction time. All analyses were tested for significance at an alpha level of 0.05. Variability is indicated by standard error of the mean.

4.3 RESULTS

Experiment 2 consisted of a total of 5832 trials across all participants. Of the 5832 trials, 4776 (81.9%) were used in the final analysis and 1056 (18.1%) were excluded. Reasons for exclusion were insufficient saccade size (1.4%), non-compliance with task instructions (2.6%), improper fixation at trial onset (11.6%), and z-score exclusion (2.6%)(Appendix G). No participants were found to have a number of trials

included that was greater than 3SD from the mean.

The dependent measures in this study were primary saccade amplitude, end horizontal position, peak velocity, duration, and reaction time. The measures were analyzed using repeated measures analysis of variance (ANOVA) with factors target 1 location (near, middle, far), and target 2 location (near, middle far), and condition (look, attend, ignore) for all variables except for reaction time, which did not have target 2 location as a factor.

4.3.1 Amplitude

Saccade amplitude is the size of the saccade from its starting position to its end position. As expected, there was a highly significant main effect of first target location $F(2,35)=762.7$, $MSE=11.949$, $p<0.001$. Consistent with Experiment 1, there was also a significant main effect of second target location on the primary saccade amplitude $F(2,37)=9.7$, $MSE=3.457$, $p<0.001$, once again indicating that as the second target was shifted further away from fixation (to the right), the amplitude of the primary saccade decreased. Of particular interest to the current experiment, there was no significant main effect of condition $F(2,34)=0.8$, $MSE=48.398$, $p=0.463$, and no significant interaction between second target location and condition $F(4, 74)=0.9$, $MSE=4.022$, $p=0.475$ (Figure 4.5).

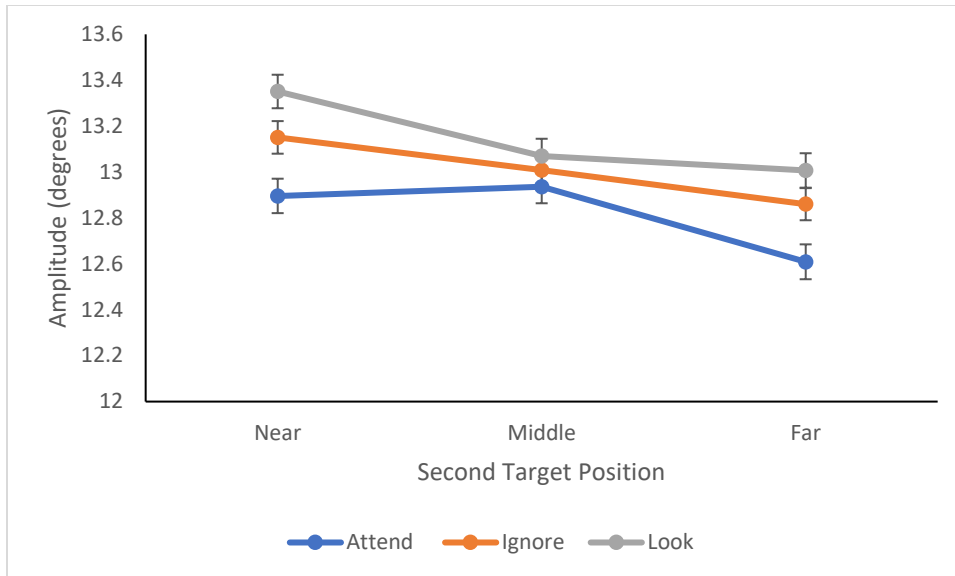


Figure 4.5. Mean amplitude (in degrees) of the primary saccade, split by second target position (near, middle and far), shown each task condition. No significant interaction was found between second target location and condition. Error bars represent standard error of the mean.

4.3.2 Horizontal End Position

The horizontal end position of the primary saccade is the location at which the primary saccade lands, in the x direction. There was a significant main effect found for first target location, as expected, $F(2,35)=897.7$, $MSE=4885.958$, $p<0.001$. There was also a significant main effect of second target position $F(2,37)=8.9$, $MSE=1708.174$, $p=0.001$. This effect, like in Experiment 1, indicated that as the second target position was shifted further to the right, the primary saccade end position was shifted closer to the left, away from the second target. There was also no significant main effect found for condition $F(2,35)=1.7$, $MSE=9285.369$, $p=0.198$, and no significant interaction between second target location and condition $F(4,74)=1.2$, $MSE=1865.519$, $p=0.308$ (Figure 4.6).

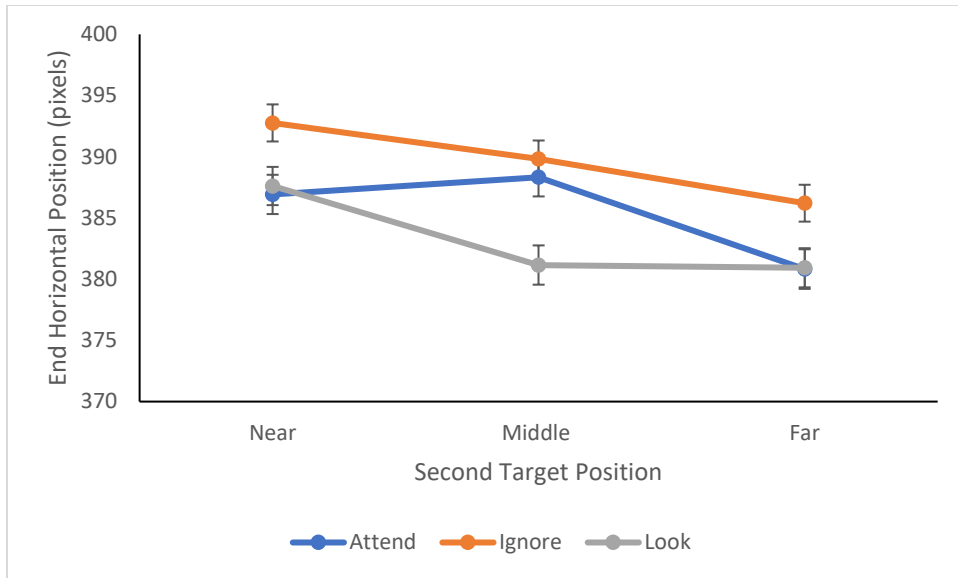


Figure 4.6. Mean end horizontal position of the primary saccade (in pixels) of the primary saccade, split by second target position (near, middle and far), shown each task condition. No significant interaction was found between second target location and condition. Error bars represent standard error of the mean.

4.3.3 Duration

Saccade duration is the length of time taken from the onset of the saccade to its end. There was a significant main effect found for first target location $F(2,35)=114.2$, $MSE=436.215$, $p<0.001$, which demonstrated that as the first target location was shifted further from the fixation point, the duration of the primary saccade increased. No significant main effect was found for second target location $F(2,35)=1.2$, $MSE=346.654$, $p=0.319$. No significant main effect was found for condition $F(2,36)=0.410$, $MSE=344.563$, $p=0.667$. There was also no significant interaction between second target location and condition $F(4,74)=0.8$, $MSE=184.418$, $p=0.501$ (Figure 4.7)

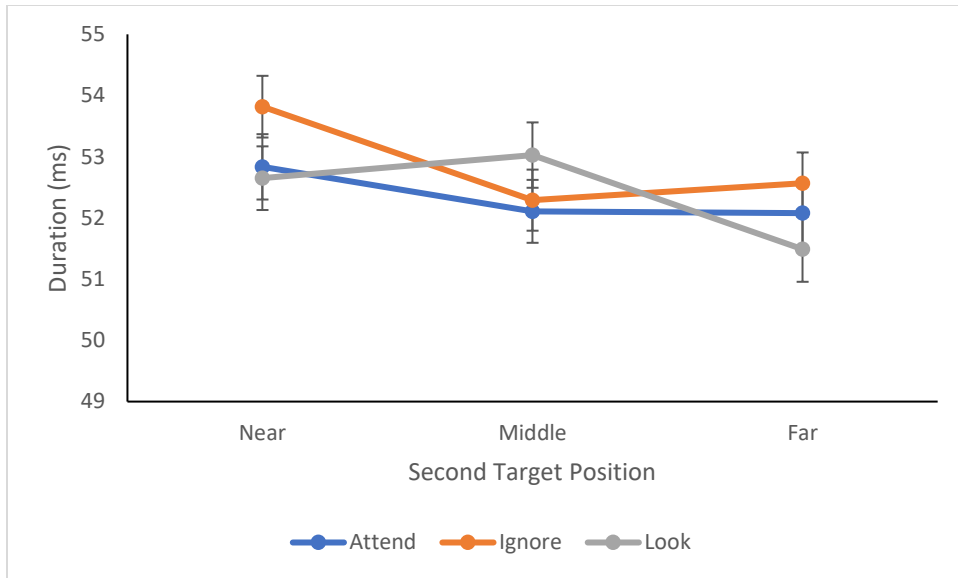


Figure 4.7. Mean duration of the primary saccade (in milliseconds) of the primary saccade, split by second target position (near, middle and far), shown each task condition. No significant interaction was found between second target location and condition. Error bars represent standard error of the mean.

4.3.4 Peak Velocity

The peak velocity of a saccade is the maximum velocity reached during the eye movement. Peak velocity tends to increase with saccade amplitude. There was a significant effect found for first target position, $F(2,35)=109.2$, $MSE=11882.966$, $p<0.001$, as well as second target position $F(2,37)=3.8$, $MSE=1889.076$, $p=0.031$. This indicated that peak velocity increased as first target position was shifted further away from the initial fixation point, and decreased as second target position was shifted further away from the initial fixation point. As with all variables previously described, there was no significant main effect found for condition $F(2,34)=1.4$, $MSE=39013.246$, $p=0.270$, and no significant interaction between second target location and condition $F(4,75)=1.7$, $MSE=1979.270$, $p=0.150$ (Figure 4.8).

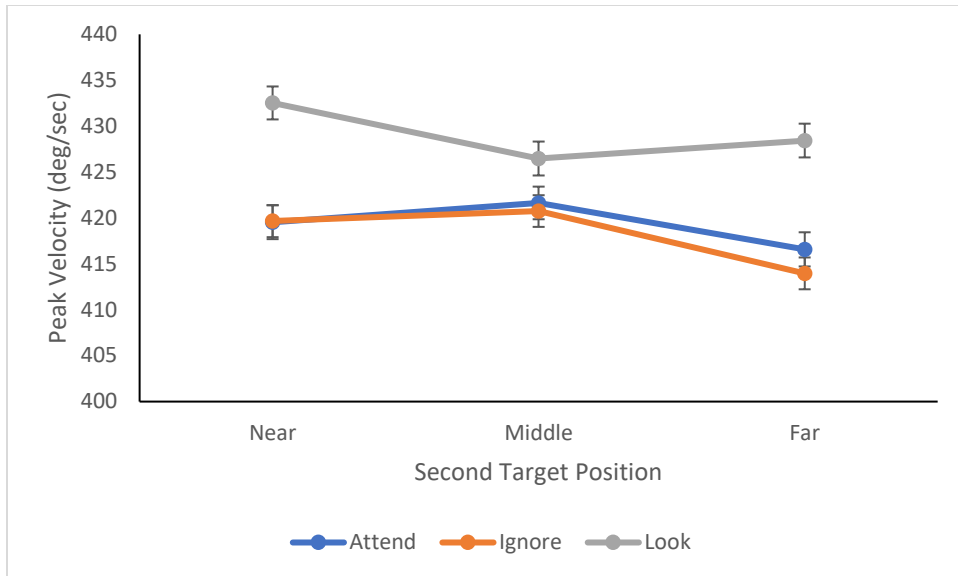


Figure 4.8. Mean peak velocity of the primary saccade (in degrees per second) of the primary saccade, split by second target position (near, middle and far), shown each task condition. No significant interaction was found between second target location and condition. Error bars represent standard error of the mean.

4.3.5 Reaction Time

Reaction time was defined as the time between the onset of the targets and the moment the eyes began their saccade. There was a significant main effect found for first target location, as expected $F(2,36)=20.9$, $MSE=8520.087$, $p<0.001$. There was also a significant main effect found for condition $F(2,34)=15.4$, $MSE=40613.974$, $p<0.001$ (Figure 4.9).

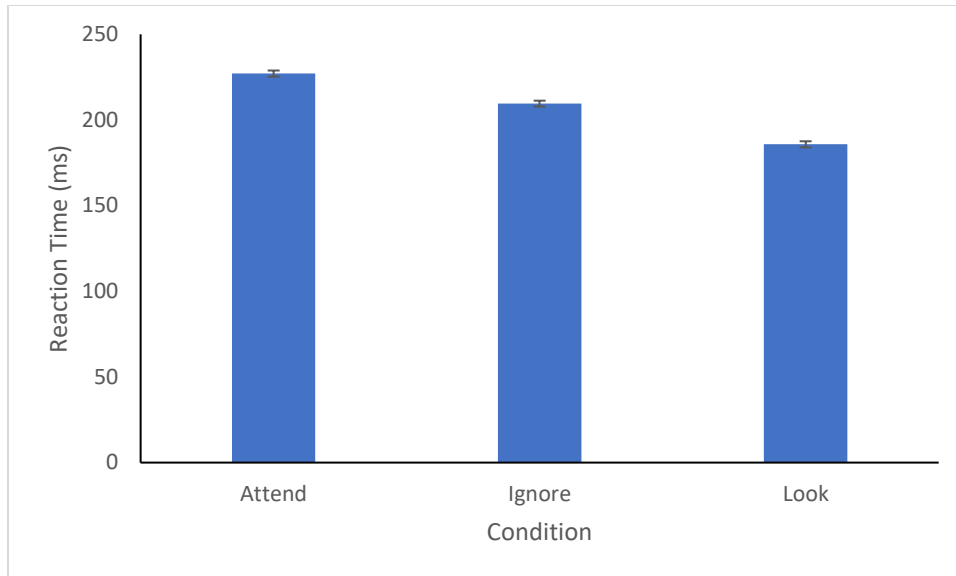


Figure 4.9. Mean reaction time of the primary saccade (in milliseconds), split by condition. A significant main effect of condition was found. Error bars represent standard error of the mean.

4.3.6 Response in Attend Condition

The percentage of correct responses (whether or not the “+” or “x” was correctly identified) for each participant for the attend condition was calculated (Table 4.1).

Correct response rates ranged from 53.0%-99.0%, with an average of 87.03% (SD=12.2).

While no participants were found to have a correct response rate that did not fall within 3 standard deviations of the mean, participants 4 and 16 did have considerably low correct responses rate, and therefore results for the attend condition were analyzed with and without these two participants. The exclusion of these two participants had no effect on results and therefore they were included in the analysis.

Participant	Percentage of Correct Responses
P1	88.1%
P2	99.0%
P3	90.5%
P4	53%
P5	96.9%
P6	84.8%
P7	84.4%
P8	86.9%
P9	86.5%
P10	85.7%
P11	95.0%
P12	91.3%
P13	94.2%
P14	83.9%
P15	94.0%
P16	59.7%
P17	98.1%
P18	94.6%

Table 4.1. Percentage of correct responses in the attend condition for each participant.

4.4 DISCUSSION

The purpose of Experiment 2 was to determine whether the effects of second target location on the endpoint and amplitude of the primary saccade found in Experiment 1 required a participant to plan to look at the second target, to pay attention to the second target without having to look at it, or simply the presence of the second target. It was hypothesized that only the condition in which the participants were instructed to look at the second target would elicit the leftward shift (away from the second target) on the primary saccade from the increasing second target distance.

This hypothesis was made as this effect was elicited in Experiment 1 by having participants look towards the second target, and it was thought that the shift in the primary saccade was brought about by participants having to inhibit a motor plan to look directly at the second target in order to stop on the first target. Thus, it was hypothesized that there would be a significant main of condition on the variables analyzed, and that there would be a significant interaction between second target location and condition.

For most variables analyzed (primary saccade amplitude, end horizontal position, duration, and peak velocity), there was no significant main effect of condition. A significant effect of condition was only found on reaction time, with the “attend” condition having the longest reaction time and the “look” condition the shortest. A possible explanation for this finding is that in the attend condition, participants required extra time to make a perceptual judgement about the second target before beginning their movement, and in the ignore condition participants may have had to suppress the automatic planning of an eye movement towards the second target before initiating their movement.

Of greatest relevance to the experimental hypothesis, there was no significant interaction between second target position and condition. Second target position was significant for most variables for which this factor was analyzed (amplitude, end horizontal position, and peak velocity, but not duration), but this effect was not found to vary between conditions, contrary to what had been predicted at the onset of this experiment.

As discussed earlier, this result is broadly inconsistent with the idea that spatial interactions observed in Experiment 1 arise from inhibition of an eye movement to the second target since participants presumably had no explicit intention to ever make an eye movement to the second target in the attend or ignore conditions of Experiment 2 yet the same effect was observed in all three conditions. There are several possible explanations for these findings. The first is that regardless of what the participants were instructed to do, the presence of the second target caused participants to unintentionally plan an eye movement directly to the second target. In order to comply with task instructions, this plan had to be inhibited, resulting in the shift further away from the second target with an increasing distance between the first and second target position, as this saccade being inhibited was larger with an increasing second target distance.

This explanation would be consistent with theories of action-centered attention described in Experiment 1, with the additional tenet that any exogenous stimulus automatically generates an eye movement plan that must be suppressed. This explanation is somewhat akin to premotor theories of attention, which posit that covert attention being directed to a location is always coupled with overt eye movement planning to that location, whether or not the movement is actually executed. Proof of covert attention and motor planning being coupled was first discussed by Rizzolatti et al. (1987), who found that oculomotor responses were faster when participants were cued to pay attention to that location, vs when a saccade was to be made to a non-cued location. The authors stated that attention is allocated to a point when an eye

movement is ready to be made to that point. In trials where subjects had to make movements to a non-cued location, the ocular motor plan to the cued target had to be cancelled, and a motor plan to the new target made. These findings have been supported by neuroimaging studies that showed brain activity in similar areas in the frontal and parietal cortex when covert attention is directed to a location, or when a saccade is made to a location (Corbetta, 1998).

However, many studies that have provided evidence for the pre-motor theory in eye movements come from studies on the global effect. These studies have found that when an eye movement is executed in the presence of a distractor target, the distractor target captures covert attention and causes eye movement planning, which ultimately results in the saccade landing between the actual target and the distractor target (Findlay & Blythe, 2009, Coren & Hoenig, 1972). Although studies have found to be conflicting in terms of whether or not the distractor needs to be on the same axis as the saccade (Findlay & Brown, 2006; Findlay & Blythe 2009), the global effect appears to be a widely accepted phenomenon that occurs when two targets are within approximately 20 degrees from each other (Walker et al, 1997). The present study's results differ from these results in that the saccade was actually shifted further away from the second target in all conditions, which we have suggested may be the result of an inhibition of this automatic movement plan. The reason for the difference in between these findings is unclear, however target selection does differ between these studies and the present study so this may have resulted in the different results. In studies in which a distractor target is present, (Walker et al., 1997, Coren & Hoenig, 1972; Findlay & Blythe, 2009),

the spatial arrangement of the target and distractors vary between trials, so that the target must be identified amongst the distractors by shape (Walker et al., 1997), by colour (Coren & Hoenig, 1972), or by a numeric label (Findlay & Blythe, 2009). If we were to compare this to the “ignore” condition in the present study, which seems superficially similar to the conditions of a typical global effect paradigm, the saccade target here is always the closest target to the fixation point so there is no need to perceptually distinguish between the two stimuli to determine which is the (initial) target. Perhaps the averaging effect seen in global effect studies arises during the target identification and/or selection process, whereas the inverse effect seen here in Experiments 1 and 2 arises more directly from the suppression of a saccade to the second stimulus.

The second possible explanation for the findings in the present study is that the results seen in the metrics of the primary saccade do not arise within motor output processes, but instead arise from a mislocalization of the target. Perhaps the presence of the second target establishes a visual frame of reference against which the first target is localized, so that participants judge the first target to be shifted away from the location of the second target. Relative effects like this are seen when larger visual frames of reference are shifted in position relative to a visual target such as in the Roelofs or induced Roelofs effect. In this effect, a target is located within a frame that has been offset from the center. The offset of the frame shifts where the observer perceives their midline to be, with their perceived midline shifted in the same direction as the frame shift. This shift in their perceived midline then causes targets within the frame to be shifted

perceptually as well, in the direction opposite the shift of the frame (Bridgeman, Peery & Anand, 1997; Bridgeman, Dasonville & Lester, 2018)(Figure 4.10).

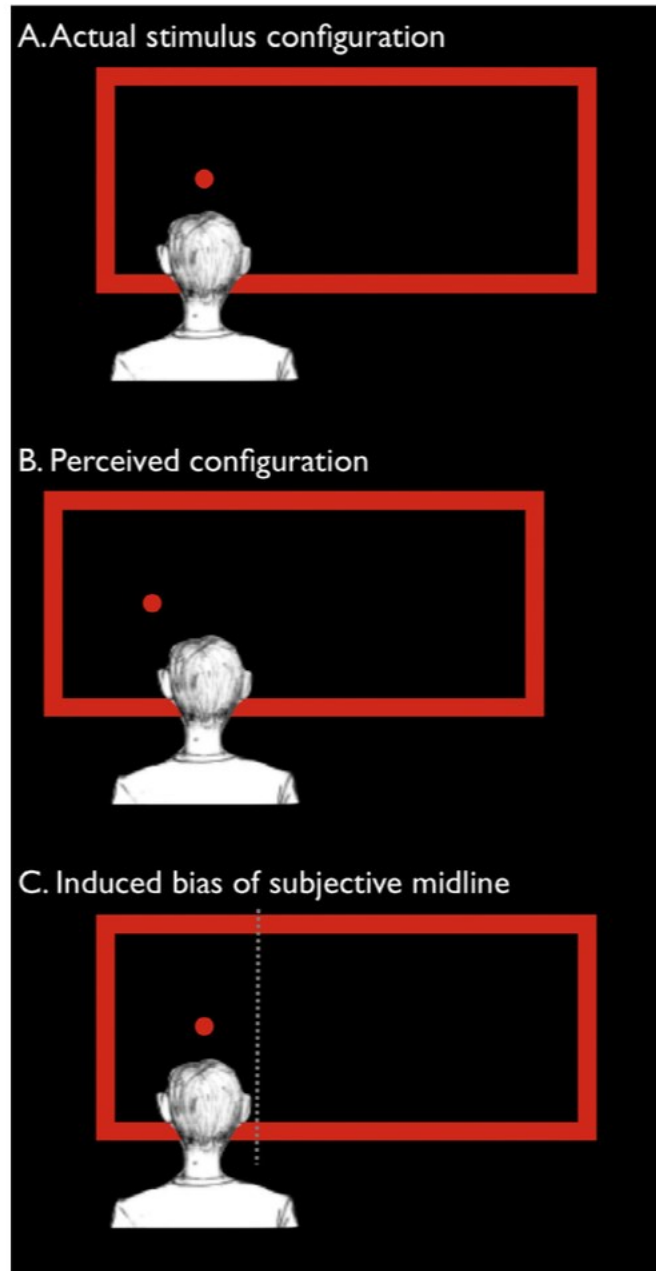


Figure 4.10 The induced Roelof's effect. The participant's subjective midline is shifted in the same direction as the frame. This shifted midline then results in targets being mislocalized, shifted in the opposite direction of the frame shift. Taken from Bridgeman, Dasonville & Lester (2018).

Expanding this theory, it is possible that the shifts in the relative position of the second target as compared to the first target, shifted the perceived location of the first target in the same manner. When the second target was shifted further to the right, perhaps the first target was visually perceived as being further to the left. In this explanation, the lack of interaction between the second target location and condition can be explained by a mislocalization of stimuli which would occur in all conditions. However, in contrast to the results of the present study, previous literature on the induced Roelofs effect has found that both manual pointing movements and saccadic eye movements are made accurately to a target despite being perceptually mislocalized (Bridgeman, Peery & Anand, 1997; Dassonville & Bala, 2004). The reasons for the second target having an impact on the motor response to the first target if the results are due to a visual processing mislocalization remains unknown.

It is worth noting that action-centered interpretations of the experimental effects observed here have focused on eye movements and their inhibition. However, it is possible that the effects might instead arise from the suppression of *head* movements rather than eye movements. Participants were given no specific instructions about moving their head, or not, and no restraints were used to limit head motion (*note: head movements are tracked and incorporated into the measurement of on-screen gaze position by the EyeLink II system). That said, however, participants may have been reluctant to move their head during the experiment due to the head-mounted nature of the EyeLink II system, because it was uncomfortable to do so or because they might have (incorrectly) assumed that they were expected to keep their head still. This might

matter in the present series of experiments given the requirement to execute two consecutive eye movements that sum to as much as 36 degrees of angle; depending upon the initial head and eye angles at fixation, this could put the eye in an extreme deviation. Under natural viewing conditions (without a head-mounted eye-tracker in play), people would probably prefer to rotate their head at least somewhat for a 36 degree gaze shift to minimize ocular discomfort, so some participants might have been inhibiting such a tendency in the experiment. Literature on head and eye movements is limited as laboratory controlled environments often involve the head being restrained. A study conducted by Stahl in 1999 looked at the amplitude of head movements with varying degrees of eye movements. In this study, a range of 35.8 ± 31.9 degrees was found in which eye-only movements occurred, and after this the head and eye both contributed to the shift in gaze. However, this value clearly varied widely by participant, the reason for which was not known. In the present experiment, it is possible that it was the suppression of head movements, rather than eye movements, that produced an inverted spatial relationship of the second target's position on the primary eye movement.

CHAPTER 5 CONCLUSION

5.1 GENERAL DISCUSSION

The purpose of the present experiments was to determine if the metrics of a primary saccade are affected by the second target in a sequence. Previous research (Zingale and Kowler, 1987) has suggested that saccades are planned as a sequence based on reaction times being longer for the first saccade as the sequence length increases, however literature on this topic is conflicting (Pratt, 2004).

In Experiment 1, participants performed randomized trials of either 1 or 2 saccades, depending on the number of targets presented. The first target position was randomized so that it was 12, 15, or 18 degrees of visual angle from the fixation point, and the second target was also randomized (if present) to be located 12, 15, or 18 degrees of visual angle from the first target. The second target was found to have a significant main effect on saccade amplitude, end horizontal position and duration. The saccade to the first target was found to be shorter (both in size and duration) as the second target was located further away. We attempted to explain these results using theories on action-centered attention. When the second target captured attention (as it was part of the movement sequence), this may have caused a motor output plan made directly from fixation to the second target. In order to follow task instructions (look at the first target, then the second one), the direct movement plan to the second target would have to be inhibited. The further the second target, the greater the inhibition required. The summation of the neuronal activity of these two motor plans, one directly to the second target, that would be inhibited, and one to the first target, may have

results in the shortening of the primary saccade.

We then conducted Experiment 2 to see if varying the task instructions (and the attention paid to the second target) would have an impact on the results on the first target demonstrated in Experiment 1. All trials were double target trials and three blocks were conducted with different instructions in regard to the second target. In the “look” condition the participants were to look at the first target, then the second. In the “attend” condition participants had to make a perceptual judgement about the second target and then look at the first target. In the “ignore” condition participants were asked to look only at the first target, and ignore the second target. Once again, the saccade to the first target was found to be shorter (in size) as well as having a reduced peak velocity, in all conditions. There was found to be no main effect of condition for any variable except reaction time, with the “attend” condition having the longest reaction time, and the “look” condition the shortest. Most importantly, there was no significant interaction between second target location and condition. We have come up with three possible explanations for these results. The first is that regardless of what you are instructed to do, the second target captures attention and a saccade is planned directly to it, and this plan must be inhibited to follow task instructions. The second is that the second target shifts the visual localization of the first target, and as the second target is shifted further to the right, the first target is perceived as being further to the right, which would occur in all conditions regardless of task instructions. The third is that participants felt as though they could not make head movements and the inhibition of this motor command influenced the target landing position, similarly to our first

explanation.

This study is one of the few to explore the effect of the second target location on the endpoint of the primary saccade in a sequence. It was also the first to look at whether or not changing task instructions, and the covert attention participants give to the second target would have an effect on the primary saccade. Several possible explanations exist in order to explain these results, and further research is needed in order to conclusively determine the cause of the results in the present study.

5.2 FUTURE DIRECTIONS

After conducting the Experiment 2, there were multiple explanations for the results found. This study is limited in that we cannot rule out the possibility that participants were planning an eye movement directly to the second target that had to be inhibited, nor can we confirm this theory. In order to test these different possibilities, future studies are required. In order to test the visual processing theory, where we have suggested that the second target may be having an illusory effect shifting the perceived location theory, a study could be conducted in which saccades are not tested, rather participants are asked to make a perceptual judgment about the location of the first target, in the presence of the second target. If the same shift where the first target is localized as further to the left as the second target is shifted further to the right is observed, this would provide evidence for the visual processing theory, and suggest that a motor plan is not required to elicit the effect.

Another possible study would be to test the motor output theory by having

subjects begin by fixating with their eyes in an eccentric gaze (abduction) such that an eye movement could be made to the first target, but not to the second. A similar paradigm has been employed by Smith et al. (2012). If participants are unable to make a saccade to the second target, this movement should in theory not be planned, and would not be inhibited, but could still be viewed. If this experimental setup did not elicit the effects on the primary saccade from the second target location found in the present study, this would provide evidence for the motor output theory.

Furthermore, as head movements were not controlled for in this study and may have played a role in the present study, this study could be redone, this time controlling for head movements in one condition, and allowing for free head movements in another, and comparing the results. This may be better executed with a non-head mounted eye tracker such as the Eyelink 1000.

5.3 LIMITATIONS

A possible limitation of this study, as suggested above, is the fact that head movements were not controlled for in this study. While the Eyelink II does incorporate head movement into the determination of the eye's on-screen gaze position, it is possible that participants may have been reluctant to make head movements due to the head-mounted nature of the Eyelink II system, which may have affected results. As head movements were not controlled in this study, this cannot be conclusively ruled out.

Another possible limitation arises from other surrounding stimuli in the room. While effort was made to not have distracting stimuli on either side of the participant, it

is possible that surrounding objects (a door, the experimental computer, etc.) may have captured participant's attention and influenced the endpoint of their eye position. However, if this was the case, as the room set up was the same across all trials in both experiments, any effect should be consistent across all trials and therefore not change the effects found by other variables, such as second target location.

A third possible limitation of this study is its real-world application. Given the nature of this study, in a laboratory setting with only two stimuli present on screen and only horizontal eye movements required, this is not truly representative of planning saccades in our day-to-day lives, as we are surrounded by an abundance of visual stimuli, of various colours, brightness, and saliency to the task at hand, and saccades are made in all directions, not exclusively horizontally as examined in the present study.

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APPENDIX A – PARTICIPANT SCREENING FORM

SCREENING FORM:

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 17?

2. 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
- Near- or far- sightedness that is corrected with glasses (not contact lenses)
- Corneal or Retinal disease
- Cataracts

3. 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
- Subjective tinnitus (ringing in ears)
- 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 – ETHICAL APPROVAL



Social Sciences & Humanities Research Board
Letter of Approval November 29, 2017
Breanne Beauchamp
Health\Clinical Vision Science

Dear Breanne,

REB #: 2017-4319 **Project Title:** Planning
sequential eye movements

Effective Date: November 28, 2017 **Expiry**
Date: November 28, 2018

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. Karen Beazley, Chair

APPENDIX C – CONSENT DOCUMENTS

Title of Study: Planning sequential eye movements

SSHREB Approval #: 2017-4319

Who is in charge of this study? Breanne Beauchamp MSc Student, Clinical Vision Science Program Email: br528160@dal.ca	Who is involved with this study? Dr. David Westwood Professor School of Health and Human Performance Dalhousie University Email: david.westwood@dal.ca Phone: 902-494-1164
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Introduction:

We invite you to take part in a research study run by Breanne Beauchamp, 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 make eye movements in response to what they see. In particular, we want to know how planning a series of eye movements affect the eye movements you make. This study will help us understand eye movement planning 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?

Individuals 17 years of age or older, who have good vision or who can see well using contact lenses. You can wear contact lenses if you need to. You cannot take part if you have had any issues with your eyes, any history of nervous system issues, or a history of movement difficulty. We have a questionnaire to help you know if you can take part.

Who is running the study?

This study is being run by Breanne Beauchamp, 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 18 people take part.

Where is the study being done?

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

What you will be asked to do:

You will be asked to volunteer in a single session study. Prior to the start of the study you will be screened for any motor, visual, or neurological problems that would prevent you from being able to complete the experiment through use of a questionnaire. After you are cleared to participate, you will be asked to wear an eye tracking system that will track where you are looking on a computer screen (the EYELINK II, eye tracking device). The system uses infrared light to measure eye movements and two headbands to fit on your head (one vertical and one horizontal). Once the EYELINK II is calibrated, you will start the experiment. You will press the space bar to begin a trial, at which point a fixation cross will appear to the right of the screen, which you will look at first. After a short period of time, two circles will appear on the screen. You will first look at the closest circle to the fixation target, and then at the further circle. On some trials, only one circle may appear on screen to look at and you will only need to make one eye movement. This process will be repeated 144 times.

Possible Benefits, Risks and Discomforts:

There are no anticipated risks to taking part in this study. There is nothing that cause you any significant discomfort. Nothing will touch your eyes. During the experiment you may experience some mild discomfort wearing the EYELINK II equipment and as such you may remove it at any time. There is no real benefit to you for taking part in this study, but you might learn a bit about eye movements. 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 one course credit 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, 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 course credits 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 Breanne Beauchamp if you have any more questions. If you know someone who might want to take part in this study, you are welcome to share Breanne Beauchamp's email address with him or her (br528160@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 eye movements.
- It is your choice to take part in this study, or not.
- The study will last 40 minutes.
- You can withdraw from the study at any time, for any reason.
- Ask as many questions as you need to.
- You will make eye movements in response to what you see on a computer screen.
- You can take breaks whenever you need to.
- An eye movement tracking system will track your eye movements.
- 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.

- **Participants Must Read And Sign This Form To Confirm That They Understand And Accept Conditions Before Experiment Can Begin**
- **Participants Must Be Given A Copy Of This Form For Their Information And Records**

Feel free to address any questions you may have about the study to the Principal Investigator / Researcher either now, or after you have participated.

Study Title Planning sequential eye movements

Name of Principal Investigator Breanne Beauchamp

Research Supervisor (if different from PI) Dr. David Westwood

Contact Person (if different from PI) Planning Sequential Eye Movements

Address

Telephone

Email Dr. David Westwood

Psychology Department Subject Pool Policy

Individuals with specific ethical concerns should contact either the Research Supervisor or a member of the Human Research Participants & Ethics Committee of the Department of Psychology & Neuroscience, Tel: 902.494.1580, email psych.ethics@dal.ca.

Please sign below to confirm that you have had your questions answered to your satisfaction, that you are aware that all records are entirely confidential and that you may discontinue participation at any point in the study.

If you anticipate receiving educational credit points for assisting in this research, you may choose to do so as either a **Research Participant** or as an **Observer**.

If you choose to be a Research Participant, the researcher will keep your data and use it in the research project.

If you choose to be an Observer, the researcher will destroy any data that you may have provided, after you complete the study.

Please check one box below to indicate whether you choose to be a Research Participant or an Observer.

Research Participant
(Use my data)

Observer
(Destroy my data)

Participant's Signature:

Date:

Researcher's Signature:

Date:

APPENDIX D – DEMOGRAPHIC FORM

Demographic Form

Assigned Participant Code Number: _____

I would like to receive group results from this study: (provide email address if YES):

Age: _____

Biological Sex: _____

Are you left-handed or right-handed? L R

DEBRIEFING FORM

Project title: Planning sequential eye movements

Principal investigator: Breanne Beauchamp, Clinical Vision Science Masters Student, Dalhousie University, (br528160@dal.ca)

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

Thank you for your participation in this research study. If you have any questions or comments about this experiment, please feel free to communicate them to us.

What is action sequencing?

You grasp a hammer, and then drive a nail. In order to reach this goal of hammering a nail, you need to interact with two different objects, one after the other. By planning this movement as a sequence, your hand may be oriented during the first movement step in a way that maximizes efficiency in the second step (reducing amount of change in hand position needed to drive the nail). Other times you may grab a pen surrounded by other objects on a messy desk. In order to make this movement as accurate as possible (not bump into other objects on the desk) you have to take other objects on the desk into account when planning your reach for the pen. These methods of optimizing movement efficiency and accuracy by taking other objects in the surrounding, that are not objects that you are immediately interacting with, are known as action sequencing. While much work has been done on this topic in arm movements, less is known about action sequencing in eye movements. By having you make two eye movements to two different targets, we can see if eye movements are planned together and if planning the second eye movement has an impact on the first eye movement you make.

Further reading:

Hesse C, Deubel H (2010) Advance planning in sequential pick– and–place tasks. *J Neurophysiol* 104:508–516. doi:10.1152/jn.00097.2010

McSorley E, McCloy R, Williams L (2016) The Concurrent Programming of Saccades. *PLoS ONE* 11(12): e0168724. doi:10.1371/journal.pone.0168724

APPENDIX F – EXPERIMENT 1 ELIMINATED TRIALS

Participant	Trials lost to insufficient saccade size	Trials lost to incorrect number of saccades made	Trials lost to improper fixation at trial onset	Outliers	Trials included in analysis	Total number of trials
P1	3	2	26	6	179	216
P2	0	1	22	11	182	216
P3	0	23	12	10	171	216
P4	0	2	3	8	203	216
P5	0	6	3	13	194	216
P6	1	7	16	8	184	216
P7	0	15	15	7	179	216
P8	1	0	14	9	192	216
P9	12	8	104	5	87	216
P10	0	9	22	13	172	216
P11	0	1	8	4	203	216
P12	0	2	3	7	204	216
P13	0	1	8	11	196	216
P14	0	0	3	8	205	216
P15	1	16	11	11	177	216
P16	3	1	7	5	200	216
P17	0	2	9	10	195	216
P18	1	1	13	6	195	216

APPENDIX G – EXPERIMENT 2 ELIMINATED TRIALS

Participant	Trials lost to insufficient saccade size	Trials lost to non-compliance with task instructions	Trials lost to improper fixation at trial onset	Outliers	Trials included in analysis	Total number of trials
P1	4	15	76	12	217	324
P2	0	5	4	7	308	324
P3	0	13	20	10	281	324
P4	51	14	120	1	138	324
P5	1	10	7	8	298	324
P6	1	3	20	11	289	324
P7	7	17	117	6	179	324
P8	7	9	81	7	220	324
P9	0	4	12	13	295	324
P10	1	10	15	10	288	324
P11	1	8	53	14	248	324
P12	2	4	10	11	297	324
P13	1	2	21	7	293	324
P14	0	2	7	6	309	324
P15	1	7	23	8	285	324
P16	2	11	55	6	250	324
P17	4	1	23	7	289	324
P18	0	15	11	6	292	324