

**The Effect of Salient and Neutral Distractors on Hand-Eye Coordination during
Goal-Directed Reaching**

by

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

OBJECTIVE: The successful perception of a target location is critical for everyday reaching behaviours. Visually-guided goal-directed action involves successful coordination of both eyes and upper limb movement execution. The purpose of the current study was to understand the impact of display characteristics, such as distractor salience, on hand-eye coupling during goal-directed reaching. It has been demonstrated that more salient distractors affect hand movement deviations less during a goal-oriented movement as compared to less salient distractors, potentially due to a suppression mechanism. Thus, the goal of this project is to further examine whether eye movements modulate the suppression effect as a function of distractor salience.

METHODS: Thirty healthy, right-hand dominant participants (15 males; mean age = 23.1 ± 2.97 years) were recruited and had no history of neurological or neuromuscular pathology. Participants executed reaching movements toward visual targets under different display conditions: target only (control), and with neutral or salient distractors. Optotrak motion tracking system was used to record right hand kinematic data and eye movements were recorded using the EyeLinkII eye tracker. Temporal coordination between hand and eye movements were examined during reach planning and execution. Movement kinematics and reach trajectories were also analyzed.

RESULTS: Chi squared frequency analyses demonstrated that primary saccades land on distractors approximately 50% of the time; however, reach initiation did not typically occur until the eyes fixated the target. One-way repeated measures analysis of variances showed that the presence and type of distractors affected the planning of primary saccades ($p < 0.0001$), reach-related saccades ($p < 0.0001$), and of the reach movement ($p < 0.0001$). Regardless of the presence of distractors, hand-eye temporal coupling was found to be consistent across display conditions, where the hand typically followed the eyes by approximately 210 ms. Finally, hand movement deviation occurred away from the target towards the upper left visual field, which was dependent specifically on target location but not influenced by distractor salience.

CONCLUSIONS: Our complex environments typically contain multiple objects that compete for attention. As a result, we are required to select relevant stimuli from the environment for further representation and processing. This work, which was a probe into complex scenarios, demonstrates that salient distractors affect both saccadic and reach motor planning. However, the presence of distractors is simply what influences reaching execution, irrespective of their salience. It was previously thought that specific cortical regions coordinate eye and limb movements, separately. However, more current literature has shown the temporal correlation of hand-eye coupling during goal-directed reaching, which demonstrates that these neural pathways are likely connected and work together to produce successful hand movements towards visual targets. We found hand-eye coupling to be moderately correlated in a more complex visually-guided reaching task. An upper leftward attentional bias may occur during visuospatial reaching tasks, and as a result, this may provide implications for future design of workspaces such that individuals can successfully function in everyday life.

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List of Abbreviations

ANOVA	Analysis of variance
AVF	Attentional visual field
CNS	Central nervous system
DLPFC	Dorsal lateral prefrontal cortex
EEG	Electroencephalography
EMG	Electromyography
ERP	Event-related potential
fMRI	Functional magnetic resonance imaging
IRED	Infrared emitting diode
LED	Light emitting diode
LIP	Lateral intraparietal
MT	Movement time
Pd	Distractor positivity
PFC	Prefrontal cortex
PMd	Dorsal premotor
PPC	Posterior parietal cortex
PRR	Parietal reach region
SC	Superior colliculus
SOA	Stimulus onset asynchrony

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Section 1.0: General Introduction

The successful perception of a target location is critical for everyday goal-directed reaching behaviours. During any given day, an average of approximately 142 objects are reached towards and handled (Zucotti, 2015). With that, accuracy, precision, and efficiency of reaching towards a specific target are important to consider when designing complex environments, such as a crowded work space. We must understand where to put the most important buttons, for example, when organizing one's workspace. Furthermore, following injury or disease due to certain neuropathologies that impact information processing, including attentional selection and inhibition, such as stroke or traumatic brain injury, it is vital to understand how environment characteristics influence behaviour for prosperous everyday functioning during recovery.

Goal-directed reaching that entails foveal vision is successfully accomplished by information processing, which requires transforming incoming sensory information into action output. When localizing a target within the environment, sensory input provides visual information about the object, such as location, colour, and size, as well as upper limb position and surrounding environment information. Sensory information is then transformed into appropriate motor responses through motor planning and movement execution. The central nervous system (CNS) acts as this information processing system through executive function, attention, and other neural processes; however, it has a limited focused attention capacity (Broadbent, 1958; Schneider & Shiffrin, 1977; Tsotsos, 1990). Everyday environments typically contain many items, but only few may be relevant to one's current behaviour. The ability to ignore irrelevant sensory input while gating in useful sensory stimuli is necessary for daily functioning (Boutros et al., 1995; Boutros & Belger, 1999). This competition between many objects is resolved via attentional selection, either bottom-up, which is an automatic deployment of attention, or top-down, which involves voluntary

control (Frith, 2001). An important goal in neuroscience research is to further understand the underlying mechanisms of selection and sensory gating, specifically during goal-oriented action.

Visually-guided goal-directed reaching involves successful coordination of both eyes and upper limb movement execution. Motor planning and execution of hand and eye movements has been extensively studied, separately, in tasks when one must reach towards or search for a specific target amongst distractors, respectively. In eye movement studies, saccadic latency is commonly used to reflect visual processing, target selection, and motor programming. It has been shown that distractors cause oculomotor capture effects, that is, the primary saccadic eye movement is typically directed towards a distractor (Gaspelin, 2017). Furthermore, it has been shown that, perceptually salient distractors capture attention (Moher, Anderson, & Song, 2015). Hand movements are often studied using 3-dimensional manual aiming tasks towards a specified target. Commonly, hand trajectories are measured to understand how distractors affect motor planning and execution. Reach studies have demonstrated that hand trajectories vary depending on the task. Stereotypically, when distractors and targets are presented together on a screen, reach trajectories deviate towards distractors (Welsh, Elliott, & Weeks, 1999; Chang & Abrams, 2004; Welsh & Elliott, 2004; Song & Nakayama, 2006), which may indicate that multiple stimuli are processed in parallel during target selection (Song & Nakayama, 2006, 2007). Thus, the study of these two motor systems, separately, has provided key concepts to understanding target selection and goal-directed reaching within current literature. However, daily activities are full of instances that require precise coordination of eye and hand movements, which demonstrate the spatial and temporal hand-eye coupling during motor tasks (Land & Hayhoe, 2001; Land 2009). Directing eyes towards a target prior to reaching facilitates hand motor programming, as it provides high-acuity visual information about the target (Bekkering & Sailer, 2002; Kato & Fukuda, 2002;

Crawford, Medendorp, & Marotta, 2004). It is evident that eye and hand motor systems are closely coupled based on studies demonstrating that people typically move their eyes to a target prior to reach initiation (Helsen, Elliott, Starkes, & Ricker, 1998; Sailer, Eggert, Ditterich, & Straube, 2002). Eye-hand research has also shown that the hand stereotypically follows the eye by approximately 40-100ms (Finbeiner, 1989; Carey, 2000; Gribble, Everling, Ford, & Mattar, 2002). Given that the exact reason as to why reach trajectories deviate towards distracting stimuli is still debated, it is clearly important for manual aiming studies to analyze both hand and eye movements together during reaching, which is currently lacking amongst neuroscientific literature.

As a probe into a complex environment, we aim to implement a visually-guided goal-directed reaching task to characterize the effect of distractors on spatial and temporal hand-eye coordination pattern. In the context of the laboratory environment, complexity is manipulated by implementing distractors in a pointing task as well as by changing specific features of the distractors, such as a shape and colour. The following literature review will comprehensively examine the current knowledge about attentional selection mechanisms that facilitate eye and hand movements, and hand-eye coordination during the planning and execution of goal-directed reaching.

Section 2.0: Literature Review

2.1 Information Processing

2.1.1 Executive Function

Effective interaction with one's environment requires successful selection of appropriate responses to incoming stimuli. The general process for everyday functioning involves information processing of incoming sensory input, which ultimately concludes with successful motor output. An important goal within neuroscience is to establish the mechanisms underlying the selection

process during perception and action. The brain is seen as an information processing system that initially transforms sensory information into perceptual depictions, next implements these to construct knowledge and make decisions, and concludes in implementing those decisions through action. It has been repeatedly shown that correlates of decision processes are distributed throughout the brain (Cisek & Kalaska, 2010). A large component of those information processing abilities is executive function. Executive function is a term used within neuropsychology that incorporates cognitive processes, such as attention, inhibition, working memory, and task switching (Grafman & Litvan, 1999; Miyake et al., 2000; Friedman et al., 2008). Specifically, one important component of executive function is one's ability to inhibit prepotent responses when necessary (i.e., inhibition) (Miyake et al., 2000). That is, purposefully stopping a response that is automatically elicited in reaction to a particular stimulus. Although one's ability to detect is relatively automatic, executive functioning has the ability to prioritize sensory input by modality or location selection, which then allows attention to be directed towards a specific task or target (Peterson & Posner, 2012). It is evident that executive functioning plays a critical role in the successful completion of everyday tasks.

The human CNS has a limited capacity when processing visual information requiring attention. As mentioned, one aspect of executive functioning is attention, which allows one to prioritize information processing. Despite only some objects being relevant to current behaviour, everyday scenes are typically full of many items. However, there is a limited capacity of one's visual system to process multiple objects at any given time (Broadbent, 1958; Schneider & Shiffrin, 1977; Tsotsos, 1990). Multiple objects visually presented at one given time will compete for neural representation due to limited processing resources (Kastner & Ungerleider, 2000). To

summarize, executive function is a limited capacity system and thus, the competition between multiple objects at a given time must be resolved.

2.1.2 Mechanisms of Attentional Selection

The competition between multiple objects is resolved by employing attentional selection (Kastner & Ungerleider, 2000). Attention is defined as the cognitive process involved in the selection of relevant sensory information while ignoring other information (Posner, 1980). An important aspect of attentional selection is that there are two ways in which it can occur: bottom-up and top-down. Automatic bottom-up selection is based primarily on the intrinsic properties of the stimuli, that is, physical salience (Desimone & Duncan, 1995; Kastner & Ungerleider, 2000; Frith, 2001). Object salience can be described as how much something stands out within its environment, where physically salient objects typically capture one's attention. More specifically, there will be an attentional bias towards a salient target grouped within other homogeneous distractors, a sudden appearance of a new object, or larger, brighter, and moving targets (Sagi & Julesz, 1984; Jonides & Yantis, 1988; Treisman & Gormican, 1988). In our environment, there is an incredible number of incoming stimuli at any given time. Thus, a competition towards the current behaviour's most relevant information is the result, which is referred to as top-down selection (Desimone & Duncan, 1995). Top-down selection is determined by significant aspects of the stimuli, typically derived based on the behavioural goal of the current task (Frith, 2001; Buschman & Miller, 2007). Often task instructions may involve direction to attend to a specific kind of stimulus, not necessarily the most salient, therefore, top-down selection will bias the choice in favour of the behaviourally relevant stimulus (Frith, 2001). To summarize, bottom-up selection involves automatic deployment of attention, whereas top-down selection involves voluntary control (Frith, 2001).

Selection for Perception

Extensive research has determined that attentional selection can occur through different mechanisms. The first means of shifting attention is through saccades, which are quick eye movements executed to peripheral targets so they can be processed by the fovea, which has the highest density of photoreceptors (Posner, 1980; Klein, Kingstone, & Pontefract, 1995). Secondly, in the absence of eye movements, attention can be directed covertly to process visual information in the periphery (Munn & Geil, 1931; Klein et al., 1995; Posner, 2012). The underlying assumption of paradigms which require searching for a target amongst distractors is that one cannot make an overt eye movement while covertly shifting attention to another location (Hoffman & Subramaniam, 1995; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999). In summary, covert shifts of attention must be inferred from task performance, while overt attention shifts can be observed from eye movements.

Two opposing theories that account for attentional capture have been proposed: stimulus driven, which primarily focuses on bottom-up selection, and goal-driven, which concentrates on top-down selection. According to the stimulus-driven theoretical accounts, salient stimuli automatically capture visuospatial attention regardless of the viewer's goals (Gaspelin et al., 2017). Studies using a visual search paradigm, where participants must find a circle target amongst diamond distractors, provide support for stimulus-driven theories (Theeuwes, 1992). Specifically, results show that the efficiency of visual search depends on distractor salience: participants are slower to respond when a salient distractor is present, which indicates that task-irrelevant distractors automatically capture attention and slow down allocation of attention towards the target (Theeuwes, 1992; Gaspelin et al., 2017). In contrast, goal-driven theories suggest that whether or not salient stimuli capture attention is determined by an individual's goals (Folk, Remington, & Johnston, 1992). That is, objects with similar features to what an observer is looking for

involuntarily capture attention (Gaspelin et al., 2017). Support for goal-driven theories is demonstrated when participants are asked to search for a specific shape and salient stimuli do not capture covert (Leber & Egeth, 2006; Cosman & Vecera, 2013) or overt attention (Theeuwes, De Vries, & Godijn, 2003; Leonard & Luck, 2011). To summarize, goal-driven and stimulus-driven theories provide complementary expectations about how attention will be captured.

In order to resolve the goal-driven vs. stimulus-driven attentional capture debate, Sawaki & Luck (2010) proposed the signal suppression hypothesis. This hypothesis proposes that salient stimuli will generate a bottom-up signal that will capture attention despite one's goals. However, top-down control processes can actively suppress this salient signal to ensure attention is not captured. Neurophysiological evidence was provided by a series of experiments, involving specified target searches, designed to examine whether salient distractors capture attention via bottom-up selection, in which the Pd (distractor positivity) was used as the electrophysiological marker of attentional suppression (Sawaki & Luck, 2010). The Pd ERP component was first identified by Hickey, Di Lollo, & McDonald (2009) in a study, which showed that this ERP component reflects direct suppression of the cortical representation of a distractor. The Pd ERP component has a latency of approximately 115 to 225 ms, with maximal amplitude at the PO7/8 electrode, which is consistent with a parietal area generator (Hickey et al., 2009). Pd amplitudes were noted to be significantly greater when salient distractors were present compared to both targets and non-salient distractors (Sawaki & Luck, 2010). Based on these findings, the researchers proposed that salient stimuli are initially automatically processed and attract attention even if they do not match one's behavioural goals. However, processing of the irrelevant salient stimuli is suppressed relatively early (i.e., ~150 ms) as evidenced by the Pd ERP component. Therefore,

electrophysiological evidence provides support for both stimulus-driven and goal-driven theories of attentional selection.

Despite behavioural (Moher & Egeth, 2012; Gaspelin, Leonard, & Luck, 2015) and electrophysiological (Sawaki & Luck, 2010; Burra & Kerzel, 2014) evidence for suppression of attention allocation to salient distractors, no studies had previously investigated the role of eye movements in the context of salient distractors. Thus, Gaspelin et al. (2017) conducted a study to investigate the signal suppression hypothesis by recording eye movements in the presence of salient distractors. Participants were asked to find a target amongst distractors, and search mode was manipulated (i.e., detecting a target by colour or shape). First, when a colour distractor was present, manual responses during the unique shape search task were significantly slower (852ms) as compared to when it was absent (801ms). There were oculomotor capture effects by task-irrelevant colour distractors present as the first saccade was more likely to be directed towards a salient distractor. Second, when instructed to search for a specified shape (for example, one green diamond target amongst two green square distractors, one green circle distractor and one red, salient circle distractor), manual responses were slightly faster when the salient colour distractor was present (840ms) than when it was absent (853ms). In this case, first saccades were more likely to be directed towards to target rather than the salient distractor. Their work suggests that salient distractors can be deprioritized during a visual search via a suppression effect. It was hypothesized that suppression can occur as a result of three different mechanisms (Gaspelin et al., 2017). First, as evidenced by electrophysiological work (i.e., Pd amplitude), salient distractors can be actively suppressed based on their unique feature, such as colour (Sawaki & Luck, 2010). Second, participants may learn to suppress a specific irrelevant feature of a salient distractor, as evidenced by participants who showed attentional capture effects towards salient colour distractors early in a

study, which disappeared later on (Moher & Egeth, 2012; Vatterott & Vecera, 2012; Gaspar & McDonald, 2014). Finally, featural upweighting, where the CNS may bias processing of features that match the target but not the salient distractor (Bichot, Rossi, & Desimone, 2005). Ultimately, further research is required to improve the understanding of attentional control of selection, and eye movements may be particularly useful in these investigations.

Selection for Action

The specific neurophysiological mechanism in which attentional selection occurs is known as sensory gating. One's ability to extract and process relevant sensory information whilst being overwhelmed by all incoming sensory stimuli is necessary for successful daily functioning. A complex neurophysiological function, sensory gating is the brain's ability to regulate incoming sensory information as it travels from the periphery to the cortex (Braff & Geyer, 1990). The idea of gating incorporates the ability to both "gate out" or ignore irrelevant sensory input, as well to "gate in" useful sensory stimuli (Boutros et al., 1995; Boutros & Belger, 1999). Evidence has been put forth in work by Grunwald et al. (2003) that the prefrontal cortex (PFC) is one of the areas involved in sensory gating, particularly during the early phase of processing information. Behavioural and electrophysiological evidence was also discussed in a review by Knight, Staines, Swick & Chao (1999), which demonstrated that patients with PFC lesions have difficulty in suppressing responses to irrelevant sensory input. Thus, the PFC likely plays an important role in sensory gating. Furthermore, both fMRI (Tregellas et al., 2007) and lesion (Knight et al., 1999) studies have provided evidence for the bilateral dorsolateral PFC (DLPFC) involvement during sensory gating.

The effect of sensory gating on perceptual processing has been studied extensively, and the effects are well established. For example, one study worked to understand how distractor stimuli

affect early somatosensory and visual processing depending on whether or not a stimulus is attended (Adams, Popovich, & Staines, 2017). The study measured electroencephalography (EEG) during a sensory selection task, which required participants to make a graded motor response to match the amplitudes of visual and tactile stimuli, when presented individually or simultaneously. This study provides a few key results. The first is that early, between 60 to 80ms, attention-based gating occurs in response to unattended somatosensory stimuli as evidenced by decreased amplitudes of N70 ERPs; however, it does not occur in response to unattended visual stimuli. Secondly, attention affects modality-specific visual potentials at a later stage compared to somatosensory potentials, which is consistent with other studies (Knight et al., 1999; Eimer, 2000). Finally, the latencies at which gating occurred were associated with a behavioural measure of distraction from stimuli. That is, when distracting tactile stimuli were gated out at an early stage, behavioural performance was preserved; however, when visual gating of stimuli occurred later, the distractor caused a decrease in accuracy of a response given that attention could not be solely directed towards the stimuli of interest (Adams et al., 2017). Ultimately, one's ability to perceptually gate distracting stimuli will determine whether or not behaviour is affected. From a behavioural perspective, visual attention is captured by both physically salient stimuli and task-irrelevant stimuli incorporating goal-related features, such as similar colour or shape (Anderson, Laurent & Yantis, 2011). Previous studies have shown that performance on perceptual tasks, as measured by reaction time, is affected differentially by distracting salient stimuli. That is, a strong salient distractor (a blue distractor amongst one red target and other red distractors) captures more attention and causes more disruption than a weak salient distractor (a pink distractor amongst one red target and other red distractors) (Theeuwes, 1992; Itti & Koch, 2001; Theeuwes, 2010). For example, Moher et al. (2015) used a keypress task in which participants were to indicate the

orientation of a line within a uniquely-shaped target, while ignoring strong and weak salient distractors. Results showed that response time was affected when salient distractors were present: interference was significantly greater when a strongly salient distractor was present as compared to when a weakly salient distractor was present, as demonstrated by response times of 963ms and 950ms, respectively (Moher et al., 2015). Similar findings were reported by Leber & Egeth (2006), Becker (2007), and Zehetleitner, Goschy, & Muller (2012), with slight adjustments to the paradigm.

The capacity to successfully inhibit irrelevant sensory information is essential to everyday life. It is clear that sensory gating, which likely involves the PFC, and its effects on perceptual processing are well established. Salient stimuli will typically capture visual attention and may potentially disrupt task performance. In contrast, action-driven selection, which could also be described as movement-related gating is not as well understood as perceptual gating. Movement-related gating has been previously documented as the neural mechanism that underlies one's ability to filter sensory stimuli specifically during movement (Brown, Ferris, Amanian, Staines, & Boyd, 2014). From a behavioural perspective, goal-directed action tasks are commonly used to understand the implication of incoming sensory stimuli on motor control during movement-related gating.

2.2 Motor Control

2.2.1 Saccadic Eye Movements

The vast majority of research surrounding attentional selection involves the study of vision, more specifically tracking of eye movements. Eye movements can be used as a proxy measure to understand how attention is deployed. Research paradigms involving eye tracking have been used to understand cognitive factors such as speed of information processing, motor planning, and

attention (Olk & Kingstone, 2003; Pierrot-Deseilligny, Milea, & Muri, 2004; Hutton, 2008; Muri & Nyffeler, 2008). More specifically, eye tracking typically assesses fixations, saccades, and smooth pursuit eye movements. First, saccades are rapid and ballistic shifts of the eyes to a new target or fixation point to ensure resolution of details (Purves et al., 2001; Gersch, Kowler, Schnitzer, & Doshier, 2008; Ciuffreda, Ludlam, & Thiagarajan, 2011). Saccadic amplitude can range from small, for example while reading, to large, such as when searching a room (Purves et al., 2001). Saccadic eye movements require activation of different brain areas, such as the frontal lobe, the parietal cortex, and many subcortical areas; and thus, saccades may be a useful indicator of an injury to one of those brain areas (Ciuffreda et al., 2011). One important aspect of saccadic eye movements is their latency. This is a useful measure of cerebral function as it represents decision-making time (Nouraei et al., 2003; Leigh & Kennard, 2004). Measuring the interval between presentation of a target and movement onset (i.e., latency) is widely applied to understand both cortical and subcortical contributions of saccade programming (Leigh & Kennard, 2004). By measuring the distribution of saccadic latency, the corresponding parameters that underlie decision making can be determined (Carpenter & Williams, 1995). With that, saccadic latency is both dependent on stimulus properties and it reflects visual processing, target selection, and motor programming (Leigh & Kennard, 2004). Additionally, the number of fixations and fixation duration indicate one's allocation of attention (Mann, Williams, Ward, & Janelle, 2007). Detailed information processing can occur as a result of fixations: more information can be extracted from a target the longer the eyes are fixated (Mann et al., 2007). To summarize, eye movement assessments, such as saccade amplitude and latency, can be used to understand key aspects of information processing and attention.

2.2.2 Upper Limb Movements

It has been established that reaching performance during goal-directed movement is altered when distractors are present compared to when distractors are absent (Welsh & Elliott, 2004). That is, when studies required participants to complete rapid manual aiming movements towards a specific target, distractors affect the trajectory of the reaching movement (Tipper, Lortie, & Baylis, 1992). In addition to trajectory deviations when distractors are present, participants have longer reaction and movement times (Tipper et al., 1992; Meegan & Tipper, 1998; Weir et al., 2003). However, these studies do not agree on the directionality of the reach deviation (Song & Nakayama, 2009). Specifically, it has been shown that movement trajectories shift away from (Howard & Tipper, 1997; Tipper, Howard, & Jackson, 1997; Tresilian, 1998), as well as towards (Welsh et al., 1999; Chang & Abrams, 2004; Welsh & Elliott, 2004; Song & Nakayama, 2006) a distracting stimulus. For example, Tipper et al. (1992) examined a reaching task in which participants had to reach to press keys with distractors present. In this case, distractors that were closer to the hand interfered with the task more compared to distractors that were further from the hand, causing an increase in total response time. Subsequent work by Tipper et al. (1997) specifically analyzed the reach kinematics instead of simple key-press responses. Participants were instructed to reach to the wooden cube that was the same colour as the previous cue given. The main finding of this work was that the hand deviated away from the distractors, even when the distractors were not physical obstacles to the reach. Given the distractors' similarities to the target, the deviation was interpreted as the inhibition that was associated with the interfering distractor object (Tipper et al., 1997). In similar work, Howard & Tipper (1997) found that adjusting the location of the cue (an LED light) was associated with different effects on trajectory deviations. Specifically, when the cue is close to the reaching hand, the hand deviates away from the distractor compared to when the cue is further from the hand. Tresilian (1998) found likewise results of hand

movement deviation away from the distractor, specifically when the distractor was an obstacle to be avoided. Opposingly, Welsh et al. (1999) presented a study by instructing subjects to move the cursor to the red disk (target) while ignoring the yellow disk (distractor). Results showed that when distracting stimuli were present, the movement path deviated towards the yellow distractor. Further work by Welsh & Elliott (2004), involving slight adjustments to the paradigm in which the potential targets were lined up vertically with respect to the subject, replicated the results previously discussed by Welsh et al. (1999). In addition, this work added stimulus-onset asynchronies (SOAs), where the distractor was cued either before the target, after the target or in sync with the target. Results showed that when participants were given enough time to inhibit the competing response (i.e., the distractor was presented 750ms prior to the target), the trajectory deviated away from the distractor. However, when there was not enough time to inhibit the distractor (i.e., the distractor was presented less than 250ms prior to the target), the trajectory deviated towards the distractor (Welsh & Elliott, 2004). Chang & Abrams (2004) did a series of experiments involving reaching to targets amongst distractors that were either adjacent to the target or located along the reach path. In both tasks, the reach movements deviated toward the distractors when the distractor was a potential target as well as when it was never a potential target. In studies involving a colour-odddity task, where participants reach towards an odd-coloured target amongst distractors, reach trajectories deviate towards a distractor (Song & Nakayama, 2006). This deviation is particularly evident in tasks with competition between the target and the distractors, that is, when the colours of each are randomly interchanged (Song & Nakayama, 2009). A number of hypotheses have been set out to account for these differences in directionality of trajectory deviations (Moehler & Fiehler, 2017). For example, trajectory deviations curving away from distractors may occur specifically when the distractors are presented long before the target,

allowing ample time to appropriately inhibit the distractor (Welsh & Elliott, 2004). Additionally, deviations curving away from the distractor may be a result of studies where the distractor provided movement information (i.e., an LED cue) but it was never a potential target location (Welsh et al., 1999). Results from studies demonstrating reaches curving towards the distractors are thought to occur because the distractors are action-relevant or because pre-cueing may facilitate the distractor's location (Welsh et al., 1999, Welsh & Elliott, 2004; Moehler & Fiehler, 2017). Additionally, trajectory deviation towards distractors may indicate that multiple, competing stimuli are processed in parallel during target selection, which will be discussed later on (Song & Nakayama, 2006, 2007).

In addition to distractors simply being present, it is also important to understand how the properties of those distracting stimuli may affect the planning and execution of a reaching task. The first behavioural study on this topic was conducted by Moher et al. (2015). In this experiment, participants reached to a shape-defined target (for example, one diamond amongst three circles), while trying to ignore either a strong or weak salient distractor. In opposition to previous results with perceptual tasks, it was found that the more physically salient distractor causes less hand movement deviation from the target than the less physically salient distractor. Such results were determined by computing a distractor attraction score, a measure of how far hand movements deviated toward the salient distractor and by measuring the initial trajectory angle of the movement. In this experiment, the distractor attraction scores from when the weak salient distractor was present were greater from 10 to 78% of the movement trajectory compared to when the strong salient distractor was present. Additionally, the initial trajectory angle was greater when the weak salient distractor was present as compared to when the strong salient distractor was present (i.e., 21.0° vs 19.3°), which indicates more deviation from the direct path towards the

target. This was the first study to show that a strongly salient distractor triggers a stronger suppression mechanism and thus, a weakly salient distractor becomes more distracting during action execution (Moher et al., 2015). Hand movement trajectories may potentially provide insights into the nature of selection for action, as revealed by the continuous nature of the reach trajectory (Moher & Song, 2013).

Action-based theories of selective attention (Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Tipper et al., 1992; Tipper, Howard, & Houghton, 1998) provide some evidence as to why trajectory deviations occur in the presence of distractors, given that distractors clearly interfere with movement planning as demonstrated by deviation described previously (Howard & Tipper, 1997; Tipper et al., 1997, Welsh et al., 1999; Welsh & Elliott, 2004). Due to capacity limitations of human perception and motor planning, it is essential for the relevant to be distinguished from the irrelevant during selection when several different objects are competing for attention and action. Aside from the selection of the correct target, an appropriate motor plan needs to be deployed based on the visuospatial information of the target (Neumann, 1987). Deviation of movement trajectory has been used as a sensitive measure to reflect how the competition is resolved when reaching towards a target amongst distractors (Tipper et al., 2000; McSorley et al., 2004). Specifically in visual search paradigms where information from distractors is essential for target selection and target features vary unpredictably, it has been proposed that the target and distractors are processed in parallel and evoke competing responses (Tipper et al., 1997; Song & Nakayama, 2009). In order to resolve this competition, multiple movement plans are setup in parallel (Tipper et al., 2000; McSorley et al., 2004). When two potential targets were presented for selective reaching, Cisek and Kalaska (2002, 2005) showed that two simultaneous signals corresponding to each target were generated; suggesting that, prior to making a cognitive decision

about the target, pre-motor areas within the brain can represent multiple action plans simultaneously. Depending on the state of the competition between parallel movement plans, trajectories curving away from or towards distractors have been related to inhibitory or facilitatory processes, respectively (Tipper et al., 2000; McSorley et al., 2004). More specifically, two parallel movement plans will remain active when the competition is not resolved resulting in a trajectory deviation towards the distractor. Whereas, a trajectory will deviate away from the distractor when the distractor-specific movement plan has been inhibited (Moehler & Fiehler, 2017). It is perhaps this parallel response planning followed by inhibition that causes people to react and move slower when distracting stimuli are present compared to when a single target is the only choice (Meegan & Tipper, 1998; Welsh & Elliott, 2004).

2.2.3 Hand-Eye Coupling

One major limitation of these reaching trajectory studies is that eye movements were not recorded. For example, work by Moher et al. (2015) demonstrated greater trajectory deviation towards a weak salient distractor due to a suppression of strong salient distractors. However, without incorporating eye movements, it is not clear as to how exactly this suppression mechanism is triggered as a result of salience. The analysis of eye movements, such as saccades, could provide a better understanding as to how this mechanism is occurring, by specifically investigating overt shifts of attention toward or away from a salient distractor, and the effects of these eye movements on the trajectory deviation. This is particularly key because work has shown that goal-directed arm movements, such as reaching towards a visual target, are stereotypically accompanied by an eye movement (Gribble et al., 2002). Reaching precision and accuracy has been shown to depend on one's ability to effectively extract environmental information in order to successfully organize appropriate saccadic and motor responses. This hand-eye coordination involves the interactive

function of sensorimotor systems, such as proprioception and the visual system, in addition to aspects of cognition, such as attention and memory (Crawford et al., 2004). Vercher, Magenes, Prablanc, and Gauthier (1994) suggested that successful reaching to a target occurs as a result of three fundamental events: (1) coding of target position with respect to the body and the eye; (2) proprioceptive knowledge of hand position; and (3) eye and arm movement coordination causing eye and hand movement towards the target. Initially, Woodworth (1899) suggested that fast and accurate manual reaching requires visual information. In reference to this classical work, many investigators have since established that visual information availability during goal-directed movements contributes to endpoint accuracy (Carlton, 1981; Desmurget & Grafton, 2000). Furthermore, it has been demonstrated that the ability to generate an eye movement, rather than fixation, allows for improved quality of information to guide the hand. That is, participants tend to reach less accurately towards a target during fixation compared to when an eye movement has been made, supporting the need for additional information provided by foveal vision (Fisk & Goodale, 1985; Desmurget & Grafton, 2000). It is clearly necessary for motor information to be coupled with visual information to successfully complete a visually guided goal-directed action. Reaching motor programming is facilitated by directing the eyes to a target prior to hand movement initiation, which provides high-acuity visual information of the target details in order to enhance precision of the hand movement (Bekkering & Sailer, 2002; Kato & Fukuda, 2002; Crawford et al., 2004). Based on extensive study in visually-normal individuals who typically move their eyes to a target prior to reach initiation, it is evident that eye and hand motor systems are closely coupled given the reliance on visual information when reaching (Helsen et al., 1998; Sailer et al., 2002). Previously, this oculomotor/limb motor systems coupling has been shown by assessing the onset time of eye and hand movements, where saccades were found to typically occur

approximate 40-100ms prior to hand movements (Finbeiner, 1989; Carey, 2000; Gribble et al., 2002). Additionally, Goodale, Pellision, and Prablanc (1986) demonstrated that a saccade arrives at a target at approximately the same time that a hand movement to the target is initiated. Gribble et al. (2002) investigated the coupling nature of eye and hand movements using electromyography (EMG) recordings of arm muscles with eye position during manual pointing tasks to visual targets. Their work demonstrates a tight trial-to-trial coupling between saccade latencies and EMG arm muscle activity, suggesting a common source for neural control of eye and hand movement initiation (Fisk & Goodale 1985; Gribble et al., 2002). Other recent studies have shown a similar eye-hand coupling in which the saccade reached the target as the hand was approaching peak velocity (Binsted, Chua, Helson, & Elliott, 2001; Wilmut, Wann, & Brown, 2006a). There is also some additional evidence to suggest that the relative timing of this hand-eye coupling may vary based on the spatial accuracy of a task (Gribble et al., 2002). For example, hand-eye coordination differed by several hundred milliseconds in a task requiring grasping and manipulation of small objects (Johansson, Westling, Backstrom, & Flanagan, 2001). The temporal coupling of eye-hand motor systems has been thoroughly investigated in tasks involving a single target; however, less is known in regard to the coupling of eye and hand end-point correlations (i.e., spatial coupling) particularly during tasks with targets and distractors simultaneously. While some have suggested that end-point correlations were low between the eye and the hand (Sailer, Eggert, Ditterich, & Straube, 2000; Lee, Poizner, Corcos, & Henriques, 2014), others have argued that spatial end-point representations of eye and hand movements are related (Tipper, Howard, & Paul, 2001; Horstmann & Hoffmann, 2005), which indicates that spatial coupling may be a result of a common target selection process for the eyes and hand. Stritzke & Trommershauser (2007) demonstrated that eye movements were in fact driven by low level target features, such as luminance, while others have

suggested that hand trajectories are related to saccadic eye movement locations (Reina & Schwartz, 2003). Thus, the target selection process for eye and hand movements are still debated and need to be further investigated.

The purpose of the hand-eye coupling is relatively clear: use vision to guide hand movements (Crawford et al., 2004); however, the interaction between the perceptual and motor processes of the eyes and hands is very extensive (Vercher et al., 1994). Typically, hand movement trajectory deviations are analyzed in a lab setting separately from the temporal and spatial components of eye movements, such as saccades. However, in natural tasks, eye and hand movements are commonly coordinated for successful completion of a goal. Thus, in a task involving perceptual selection for action output, clearly understanding the temporal as well as spatial eye and hand movement coupling during reaching is very important.

Section 3.0: Proposed Study

3.1 Rationale

The visual system is critical in guiding actions in order to interact with the external world. It has been demonstrated that movement kinematics and trajectories are affected by the presence of distractors, compared to when only a single target is present. However, this effect is shown to be controversial depending on the task characteristics. Movement trajectories tend to deviate away from distractors in certain scenarios (Howard & Tipper, 1997; Tipper et al., 1997; Tresilian, 1998), as well as towards distractors in other tasks (Welsh et al., 1999; Chang & Abrams, 2004; Welsh & Elliott, 2004; Song & Nakayama, 2006). The display characteristics of a scene have also been shown to affect movement trajectory differentially during perceptual and action tasks (Moher et al., 2015). Given the inconsistency amongst trajectory deviations, further understanding the impact

of eye movements on reach trajectory may prove important in comprehending the planning and execution of goal-directed reaching.

The purpose of the current study was to understand the impact of display characteristics, such as distractor salience, on hand-eye coupling during visually-guided goal-directed reaching. It has been demonstrated that more salient distractors affect hand movement deviations less during a goal-oriented movement as compared to less salient distractors, potentially due a suppression mechanism (Moher et al., 2015). Thus, the goal of this project is to further examine whether eye movements modulate the suppression effect as a function of distractor salience. The current study used a similar task paradigm to Moher et al. (2015) to achieve the objectives outlined in the next section.

3.2 Objective, Research Questions & Hypotheses

The objective of this work was to characterize the effect of distractors on spatial and temporal hand-eye coordination pattern during goal-directed reaching.

Research Question #1: Does the presence and nature of distractors affect the temporal hand-eye coordination pattern during goal-directed reaching?

Hypothesis #1a: In the presence of distractors, the eyes will initially be more likely to be directed towards distractors, which will be further modulated by salience.

Hypothesis #1b: Distracting stimuli will capture attention (Sawaki & Luck, 2010); however, goal-directed reaching is typically accompanied by a saccade to a visual target (Gribble et al., 2002); therefore, reaching will be initiated once a saccade has been made to the target. Consequently, the reach latency will be longer in the presence of distractors.

Hypothesis #1c: Studies have demonstrated that the eye and hand latencies are tightly coupled during manual pointing tasks (Carey, 2000; Gribble et al., 2002). Thus, it is hypothesized that the stereotypical temporal hand-eye coupling will be preserved in the presence of distractors.

Research Question #2: Does eye fixation modulate hand movement deviation in the presence of distractors?

Hypothesis #2a: Similar to previous literature, there will be greater deviation in hand movement trajectory away from the target when distractors are present, importantly, this effect will be further modulated by eye fixation. As a result, there will be greater hand movement deviation when the eyes fixate the distractor during reaching.

Hypothesis #2b: It is hypothesized that there will be greater deviation in hand movement trajectory away from the target during neutral trials (where one red target is embedded amongst three red distractors) compared to during salient trials (where one red target is embedded amongst one blue and two red distractors). This is similar to the effects found by Moher et al. (2015), where the neutral distractors could be considered weakly salient.

3.3 Methods

3.3.1 Participants

Thirty individuals from the University of Waterloo and the surrounding community were recruited to participate in the study (15 males; mean age = 23.1 ± 2.97 years). Participants were healthy, right-hand dominant and had no history of neurological or neuromuscular pathology. All subjects had normal or corrected-to-normal vision acuity of at least 20/25 binocularly and in each eye, stereoacuity better than 50 sec of arc, and normal colour vision.

3.3.2 Equipment

The visual stimulus was displayed on a 19-inch LED monitor with 1920x1080 resolution. Participants were seated in an adjustable seat to ensure the LED monitor is centered and positioned perpendicular to their line of vision. A chin rest was positioned at 60 cm from the monitor to restrict head movements throughout the experiment.

The Optotrak motion tracking system (Northern Digital Inc., Waterloo, ON, Canada) and NDI First Principles Motion Capture Software was used to record hand kinematic data as participants performed a goal-directed pointing task at a sampling frequency of 250 Hz. One infrared emitting diode (IRED) was taped to the right index metacarpophalangeal joint and another one to the medial right wrist, just above the radial styloid process. The Optotrak system was calibrated using a three-marker digitizing probe. The Cartesian coordinate system for Optotrak was defined by an origin located at the bottom left corner of the workspace. The three-dimensional system was defined with respect to the participant: x-axis is the horizontal plane (azimuth); y-axis is the vertical plane (elevation); and z-axis is the median plane (depth). Participants rested their hand on top of a mouse that was 42cm away from the monitor to ensure the same start position for each trial.

Eye movements were recorded using a head-mounted, video-based binocular eye tracking system (EyeLinkII, SR Research Ltd., Mississauga, ON, Canada). The eye tracker was calibrated using a 9-point calibration grid presented on the LED monitor, and a validation was performed to ensure that both eyes are recorded with less than one degree of error. Eye position data was recorded at a sampling frequency of 250 Hz, using pupil recording mode. The recordings from Optotrak and EyeLinkII were temporally synchronized using VIEWPixx software (VPixx Technologies, Saint-Bruno-de-Montarville, QC, Canada).

3.3.3 Protocol

Prior to experimental testing, participants completed several screening tests. First, the Waterloo Handedness Questionnaire was used to determine hand dominance. To ensure normal colour vision, participants completed the Colbinder colour arrangement test. To ensure normal visual acuity, participants completed visual acuity and stereoacuity tests. The acuity test was conducted with participants standing six meters away from a Bailey Lovie #5 eye chart (Multimedia Center, Berkeley, CA, USA). Participants were encouraged to read the smallest visible line to determine visual acuity. The test was performed binocularly, followed by the right and left eye separately. The stereoacuity test was conducted with participants seated while wearing polarized 3-D viewing glasses. The experimenter held the Randot Stereotest book at 40cm away from the participant's eyes. To determine participant's stereoacuity threshold, subjects were asked to state which images appear in front of the display level. Finally, participants completed the eye dominance test to determine which eye is dominant. Eye dominance was determined by instructing participants to form a triangle with their index finger and thumb of both hands. Participants were encouraged to look at an object within the triangle. While looking at the target, participants separately closed each eye and whichever eye maintained target alignment as the other eye closed was determined to be the dominant eye.

For the experimental protocol, participants were seated in front of a computer monitor, with the center of the monitor in line with the participant's line of vision. Participants rested their right hand on top of a mouse. The eye tracker was placed on the participant's head, and the head was stabilized using a chin rest. After calibration, the following experimental sequence appeared on a white screen: a black fixation cross, followed by four shapes appearing in each of the corners of the screen (visual angle of viewing distance is approximately 11 degrees), followed by a blank screen (see Figure 3.1). The participant was instructed to point to the unique shape by reaching to

full extension, while no instruction was given for the eye movements. Each trial followed the same sequence. A unique shape was randomly selected for each trial.

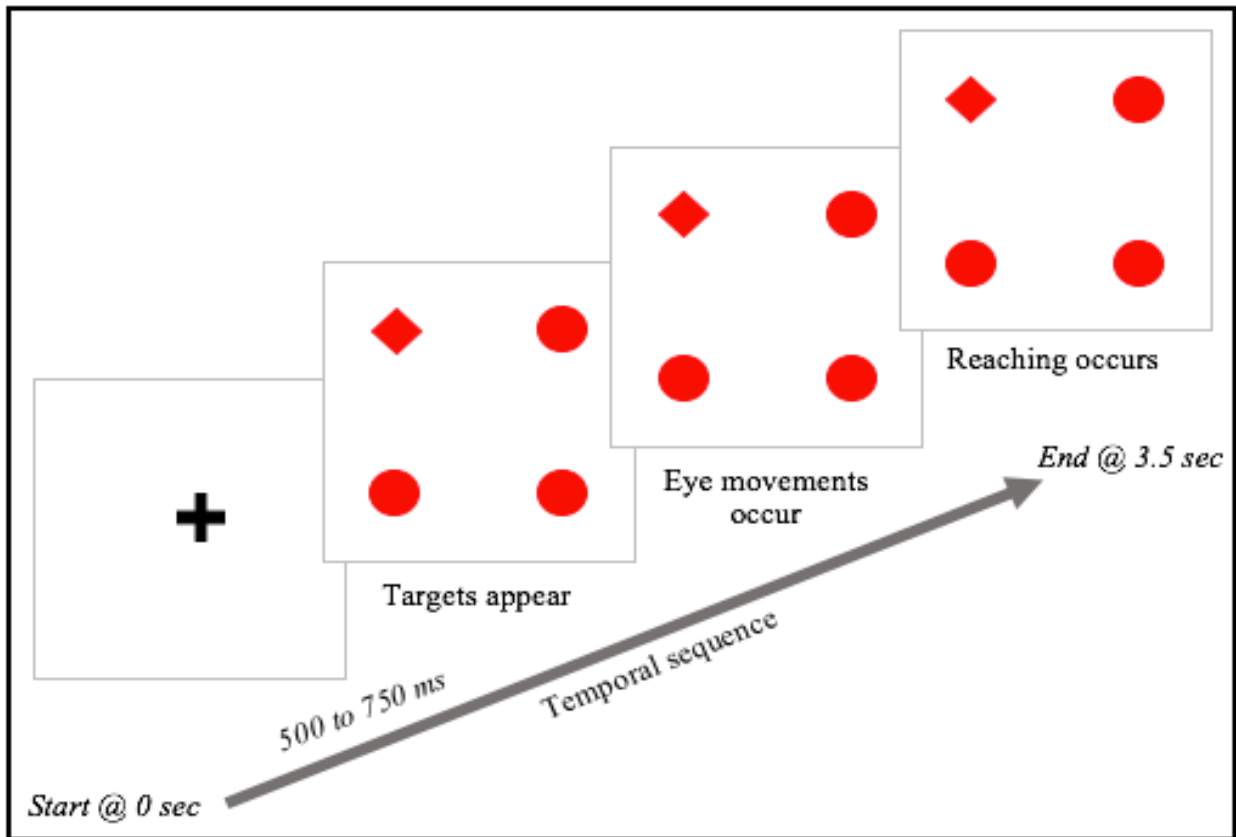


Figure 3.1. Illustration of the experimental paradigm. Each trial sequence was as follows: a fixation cross appeared with a delay ranging from 500-750ms until the targets appeared. Once the targets appeared, the participants typically made an eye movement and then reached to full extension towards the target.

Randomized throughout the experiment, 12% of the trials were the control display condition in which only one red target appeared in one of the four locations (RGB = 255, 0, 0). Within the trials, the shape was always a circle and the purpose of these trials was to provide a measure of the trajectory that would be the most direct to the target (i.e., 4 locations x 5 trials each to calculate an average trajectory). For 24% of the trials, all distractor and target shapes were red, which is considered the neutral display condition (see Figure 3.2), where the target could appear in all four locations. This condition is repeated five times with a diamond as the distinct shape and

five times with a circle as the distinct shape. For the remaining 61% of trials, a salient distractor was presented among two neutral distractors and one distinctly-shaped target. Sixty trials contained a salient blue distractor (RGB = 0, 0, 255) embedded amongst one red target and two other red distractors, which was the salient condition. To reduce the total number of trials, this condition only contained a target in either location #2 or location #4, with five repetitions using a diamond as the target and five repetitions using a square as a target, with a distractor in each of the three possible locations. The additional 40 trials were the reverse salient display condition; in which there was a salient red distractor amongst one blue target and two other blue distractors (see Figure 3.2). These trials contained a target in all of the four possible locations, with the distractor diagonal to the target. They were implemented in the task to provide some uncertainty and to prevent participants from discovering the pattern of the experimental display conditions. The remaining 3% of trials were “catch” trials to prevent participants from anticipatorily preparing a movement to an intermediate position between the four possible locations, where the movement might have been initiated before the target was identified. The experiment was comprised of a total of 165 trials.

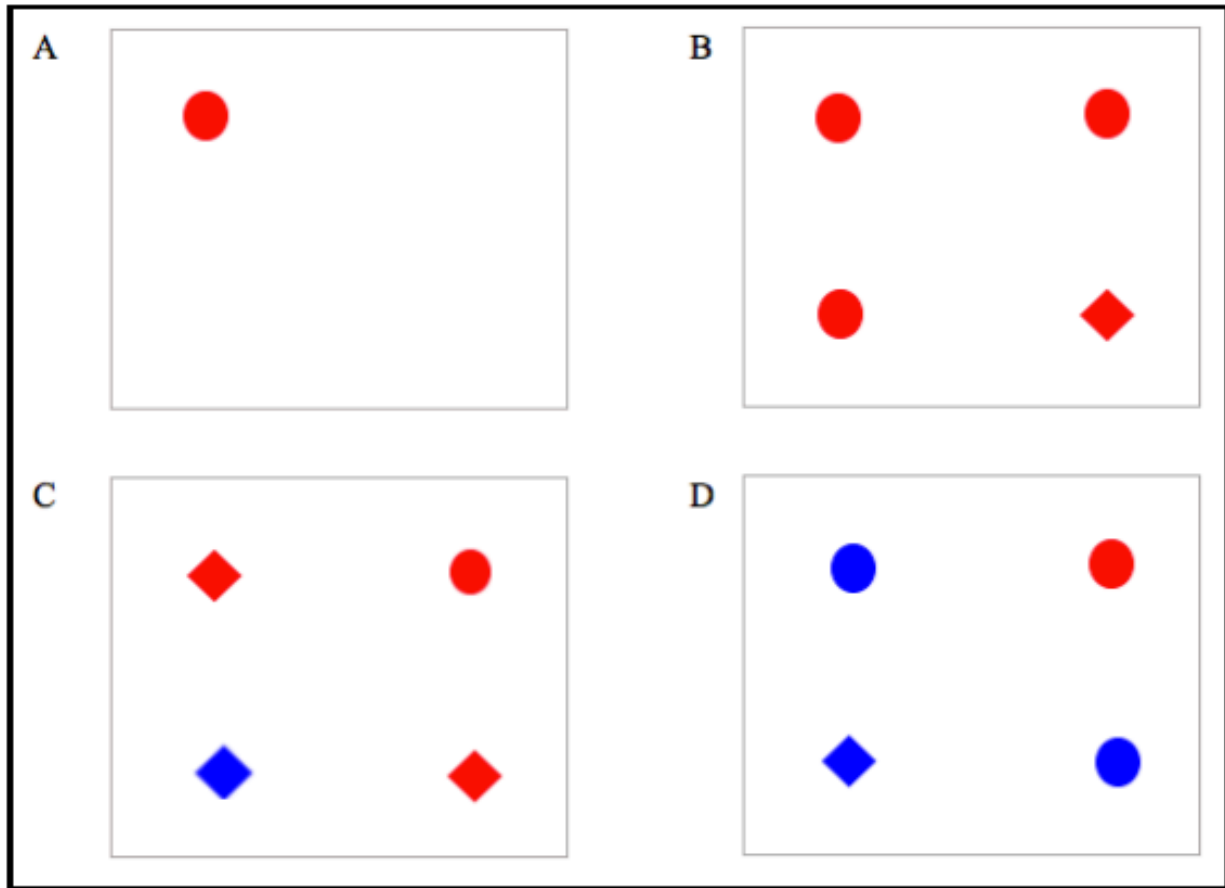


Figure 3.2. Four different displays that were randomized throughout the experiment. (A) Control display condition, where only one red circle target was presented. (B) Neutral display condition, in which either one red diamond was amongst three red circles or one red circle was amongst three red diamonds. (C) Salient display condition contained either one red diamond amongst two red circles and one blue circle or one red circle amongst two red diamonds and one blue diamond. (D) Reverse salient display condition contained either one blue diamond amongst two blue circles and one red circle or one blue circle amongst two blue diamonds and one red diamond.

3.3.4 Data Analysis & Reduction

Eye Movement Data

Approximately 1% of trials (see appendix A1) were excluded from analysis due to EyeLink collection error or VPixx trigger error. Eye movement data were analyzed using DataViewer (SR Research Ltd., Mississauga, ON, Canada). In DataViewer, a standard algorithm is used to identify a saccade based on eye velocity and acceleration, specifically a saccade is detected when eye velocity exceeds 30deg/s. Eye movement data were analyzed to determine the

direction and latency of primary saccades (i.e., the first saccade following display onset) and of reach-related saccades (i.e., the saccade immediately prior to reach initiation). Saccade latency was defined as the time from target appearance to eye movement onset.

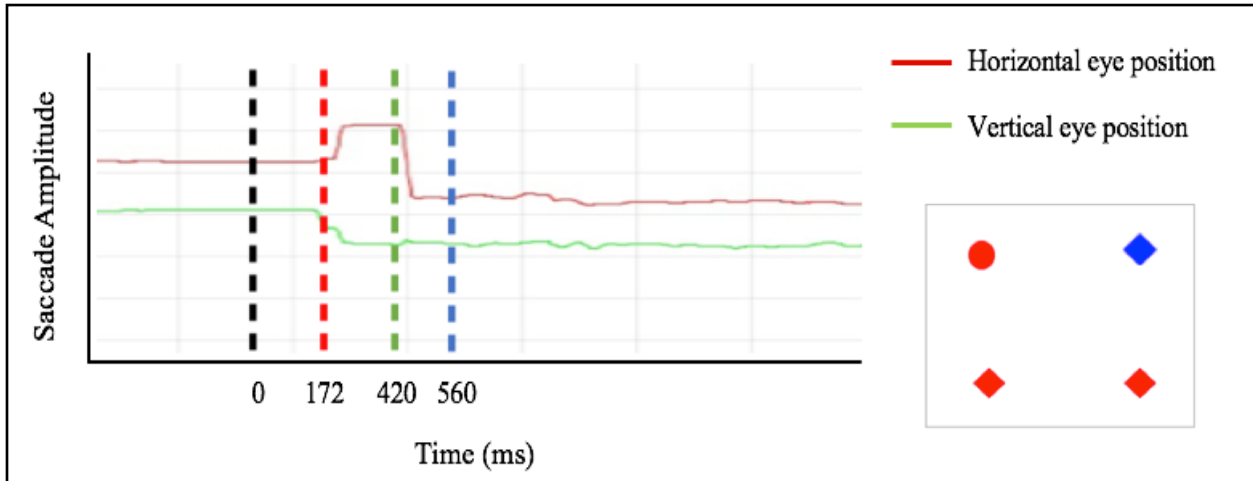


Figure 3.3. Typical eye movement data from one trial. This figure represents one trial with a salient distractor present (one red target amongst one blue and two red distractors), where the target was located in location #1. The black line represents when the target appeared on the screen, the red line represents the primary saccade to the salient distractor in location #2, the green line represents reach-related saccade to the correct target, and the blue line is reach initiation (reach kinematics not plotted).

Hand Kinematic Data

Five percent of trials (see appendix A1) were excluded from the analysis due to Optotrak collection error (i.e., loss of tracking: 2.4%). An additional 2.6% of trials were excluded due to incorrect reach location. Kinematic outliers were removed based on movement latency $<200\text{ms}$ (anticipatory movement), $>1100\text{ms}$, and >3 standard deviations outside of the subject mean; less than 3% of trials were removed based on these criteria (Miller, 1991). Hand kinematic data were analyzed using a custom MatLab R13 script (MathWorks, Natick, MA, USA). All raw data were filtered using a dual-pass Butterworth filter with a low cut-off frequency of 10 Hz. The position data were differentiated to obtain velocity using a 2-point differentiation method. The start and end of the movement was defined based on velocity criteria. Specifically, movement onset was

detected when velocity reached at least 20 mm/s for 20 milliseconds, with the end of the movement detected when velocity fell under 100 mm/s for 20 milliseconds after peak velocity. Such values are consistent with previous literature (Elliott, Hansen, & Grierson, 2009; Grierson & Elliott, 2009; Gnanaseelan, Gonzalez & Niechwiej-Szwedo, 2014). Kinematic measures extracted include movement latency (i.e., the time from target appearance to hand movement onset), movement time (MT), which is the time from movement onset to end of the movement, peak velocity (PV), which is the maximum value along the depth direction of the movement, the mean hand position at PV, and the duration of the acceleration interval, which was the interval from movement onset to the time that PV was reached. The outcome measure used to assess trajectory deviation is hand position at PV, analyzed along the azimuth (x) and elevation (y) direction separately.

3.3.5 Statistical Analysis

Eye Movement Data

Initially, all data were analyzed to determine the frequency of primary saccades (i.e., the first saccade initiated after the onset of the display) that were initiated towards the distractors and towards the target. Because primary saccades often landed on a distractor, a secondary saccade was executed, which landed on the target. These secondary saccades will be referred to as reach-related saccades; therefore, a reach-related saccade could be either a primary or a secondary saccade (i.e., it is the saccade that lands on the target). All eye movement data were then analyzed using a univariate analysis to assess the distribution of primary saccade latency, and reach-related saccade latency. Chi-square tests were used to analyze the frequency of trials in each of the possible primary saccade locations and reach-related saccade locations, separately. A one-way repeated measures ANOVA with 3 levels of display condition (control, neutral, and salient) was used to determine the effect of display condition on primary saccade latency. A post hoc Tukey

test was used to determine which conditions differed from the other. In regard to the reach-related saccade latency, a one-way repeated measures ANOVA was also completed with 3 levels of display condition (control, neutral, and salient). A post hoc Tukey test was similarly used to determine which display condition differed from each other. All outcome measures are reported using means and standard deviations.

Hand Kinematic Data

All hand movement data were analyzed using a univariate analysis to assess the distribution of each outcome measure: movement latency, MT, PV, and acceleration interval duration. All MT, PV, and acceleration interval data were approximately normally distributed, which was examined using a visual approach, (i.e., quantile-quantile plots and boxplots), and the Shapiro-Wilks test ($p > 0.05$). Four one-way repeated measures ANOVA was used to test whether the presence of distractors affects reaching kinematics (i.e., latency, MT, PV, and acceleration duration interval), with 3 levels of display condition (control, neutral, and salient). Post hoc Tukey tests were used to determine which conditions differed from each other. Mean reach latency was then further examined using a two-way repeated measures ANOVA with within-subject factors of display condition (neutral and salient) and primary saccade location (target or distractor). A post hoc Tukey test was similarly used to determine where significance lies between the means. All outcome measures are reported using means and standard deviations.

Deviations in hand movement trajectory were assessed using hand position at PV. Four one-way repeated measures ANOVAs were completed to analyze hand position at PV for two target locations (i.e., location 2 or 4, Figure 3.4) and movement direction (i.e., azimuth or elevation), separately. Each ANOVA tested differences across display conditions (3 levels: control, neutral, and salient) on hand position at PV. A post hoc Tukey test was used to determine

which display conditions differed from each other. All deviation measures are reported as mean deviation away from the target and corresponding standard deviation.

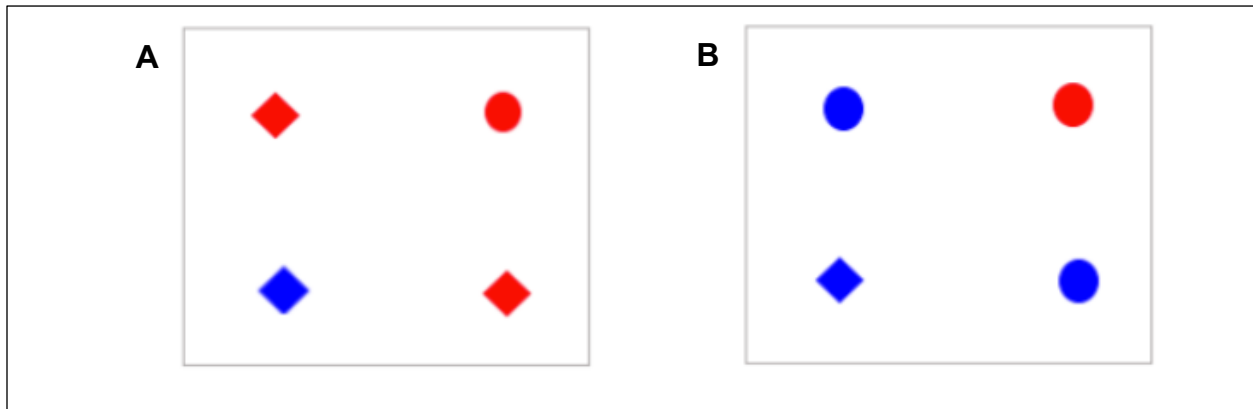


Figure 3.4. Sample displays for hand movement trajectory analysis. (A) Unique target is located in position #2, upper, right corner. (B) Unique target is located in position #4, bottom, left corner.

Hand-Eye Coupling Data

To assess the temporal coordination of eye and hand movements, the coupling was calculated as the reach-related saccade initiation time subtracted from the reach initiation time, where a negative value indicated that the reach was initiated prior to the eye movement. Initially, all hand-eye coupling data were analyzed using a univariate analysis to assess the normality. All data were approximately normally distributed, which was examined using a visual approach (i.e., quantile-quantile plots and boxplots), and the Shapiro-Wilks test ($p > 0.05$). A one-way repeated measures ANOVA was conducted to assess differences across display conditions (3 levels: control, neutral, and salient) for the hand-eye coupling. A post hoc Tukey test was used to determine which conditions differed from each other. A Pearson correlation was also used to assess the within-subjects correlation of the relationship between reach-related saccade latency and reach latency during hand-eye coupling. All outcome measures are reported using means and standard deviations.

3.4 Results

3.4.1 Characterization of Hand-Eye Coordination

With respect to the objective of this study: characterizing the effect of distractors on spatial and temporal hand-eye coordination pattern during reaching, the frequency of primary and reach-related saccades was assessed first to establish a pattern of behaviour during this task. To assess this, the location where the primary saccade landed is summarized in Table 3.1 below. In addition to the primary saccade to the target or a distractor, there were a few trials where participants did not move their eyes prior to or after reaching. These trials are referred to as fixation trials. Chi-square tests were used to analyze the number of trials in each of the possible primary saccade locations. Specifically, there was a significant effect found for primary saccade location in the control display condition (χ^2 (df = 1) = 3.84, $p < 0.0001$), in the neutral display condition (χ^2 (df = 2) = 5.99, $p < 0.0001$) and in the salient display condition (χ^2 (df = 3) = 7.82, $p < 0.0001$). Results in Table 3.1 reveal that neutral and salient distractors have a significant influence on the direction of eye movements.

Table 3.1
Summary of Primary Saccade Location per Display Condition

	Control Trials		Neutral Trials			Salient Trials			
<i>Primary Saccade</i>	Target	Fixation	Target	Neutral Distractor	Fixation	Target	Salient Distractor	Neutral Distractor	Fixation
<i># of Trials</i>	269	9	325	213	18	726	344	444	82
<i>Percentage</i>	97%	3%	58%	39%	3%	46%	28%	21%	5%

Next, a summary was created to determine where the eyes were fixating prior to reach initiation (i.e., reach-related saccade direction). Chi-square tests were used to analyze the frequency of trials for reach-related saccade locations. Specifically, in the neutral display condition, there was a significant effect found for reach-related saccade location (χ^2 (df = 2) =

5.99, $p < 0.0001$). There was also a significant effect found for reach-related saccade location in the salient distractor condition (χ^2 (df = 3) = 7.82, $p < 0.0001$). As displayed in Table 3.2, it is evident that participants most commonly (approximately 85% of trials) initiated the reaching movement when they were fixating the target. Therefore, the analysis of eye and hand kinematics presented below will focus on these trials. The remaining trials where the eyes fixated the distractor when the reach was initiated will be also presented in the latter part of the results section.

Table 3.2
Summary of Reach-Related Saccade Location per Display Condition

	Control Trials		Neutral Trials			Salient Trials			
<i>Reach-Related Saccade</i>	Target	Fixation	Target	Neutral Distractor	Fixation	Target	Salient Distractor	Neutral Distractor	Fixation
<i># of Trials</i>	269	9	473	65	18	1276	114	123	82
<i>Percentage</i>	97%	3%	85%	12%	3%	80%	7%	8%	5%

Eye Movements

A one-way repeated measures ANOVA determined an effect of display condition on primary saccade latency (F (2,58) = 15.07, $p < 0.001$). Post hoc testing demonstrated a significant difference in primary saccade latency, where control display condition ($m = 264.5 \pm 139$ ms) was significantly faster compared to the neutral (321.7 ± 136 ms) and salient (322.4 ± 137 ms) display conditions, which were not different from each other. Primary saccade latency can be further separated by considering whether the saccade landed on the target or distractor, which is summarized in Table 3.3 for each display condition.

Table 3.3

Summary of Primary Saccade Latency (ms) per Display Condition

	Control Trials	Neutral Trials		Salient Trials		
<i>Reach Saccade</i>	Target	Target	Neutral Distractor	Target	Salient Distractor	Neutral Distractor
<i>Mean (ms)</i>	264.5	356.8	244.5	374.9	255.0	251.5
<i>Standard Deviation</i>	139	141	79	147	69	93

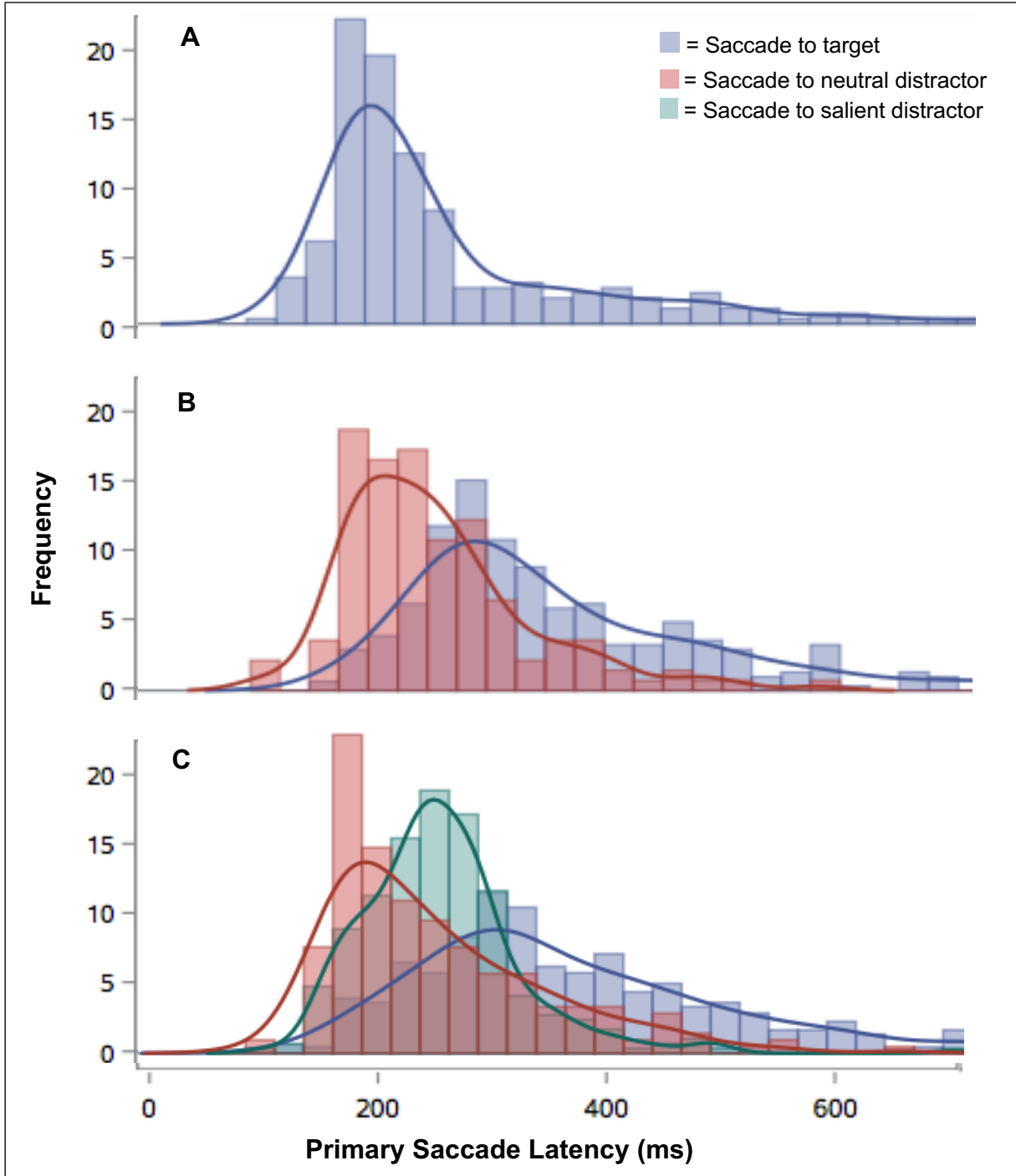


Figure 3.5. Distributions of primary saccade latency by location for the 3 display conditions. (A) Distributions of primary saccade latency for control condition. In this condition, the primary saccade lands on the target as no distractors are present. (B) In the neutral display condition, the primary saccade either occurs to the target (blue bars) or to a neutral distractor (red bars) for this condition. (C) In the salient display condition, the primary saccade lands on the target (blue bars), a neutral distractor (red bars) or the salient distractor (green bars).

Results additionally confirmed a significant effect for reach-related saccade latency ($F(2,58) = 64.60, p < 0.0001$). Post hoc testing showed a significant difference in reach-related saccade latency across all three display conditions. Reach-related saccade latency was significantly faster during control condition ($m = 263 \pm 138\text{ms}$) compared to neutral ($m = 381 \pm 139\text{ms}$) and salient ($m = 408 \pm 144\text{ms}$) conditions, as well as during neutral compared to salient condition ($p < 0.05$).

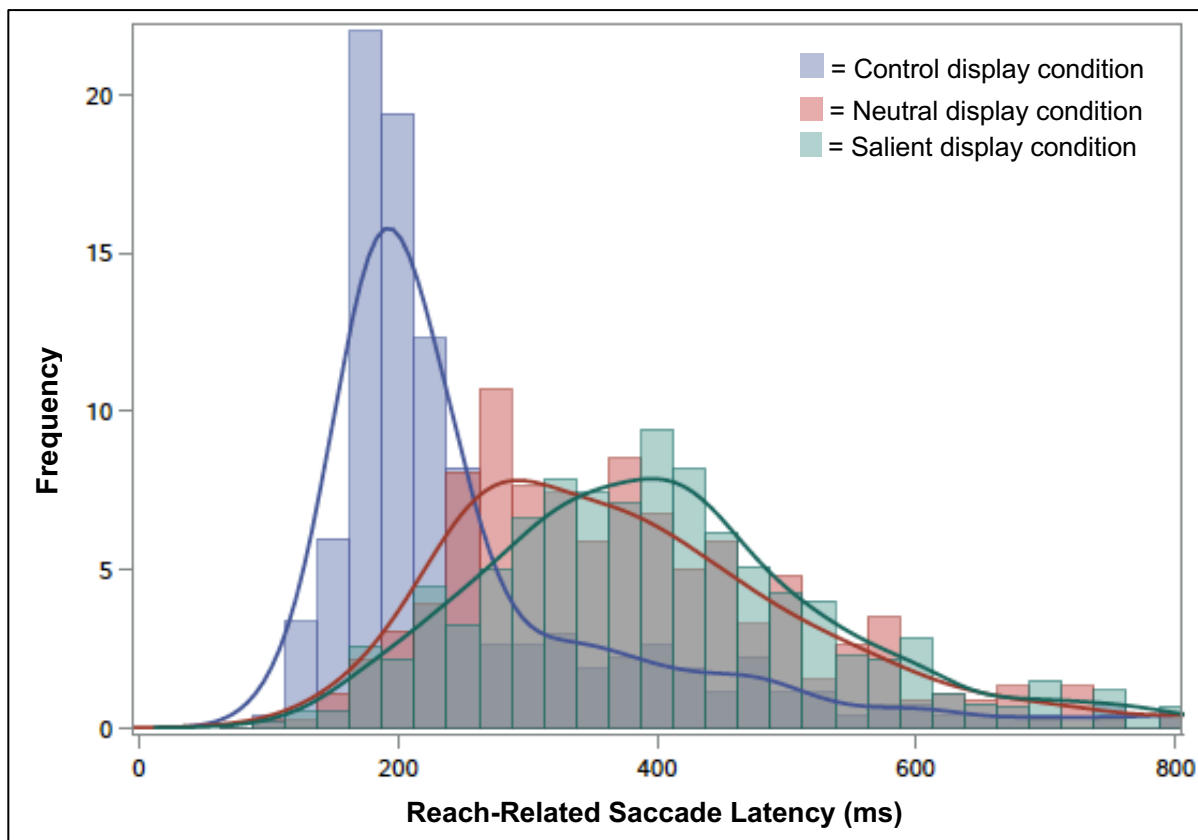


Figure 3.6. Distributions of the reach-related saccade latency for display conditions.

Hand Movements

For hand movement kinematic data, results from the statistical analysis confirmed an effect of display condition on reach latency ($F(2,58) = 72.39, p < 0.0001$). Post hoc testing showed a significant difference in reach latency across all three display conditions. Movement latency was

significantly faster during control ($m=463 \pm 110\text{ms}$) compared to neutral ($m=566 \pm 142\text{ms}$) and salient ($m=594 \pm 154\text{ms}$) conditions, as well as neutral compared to salient condition ($p<0.05$).

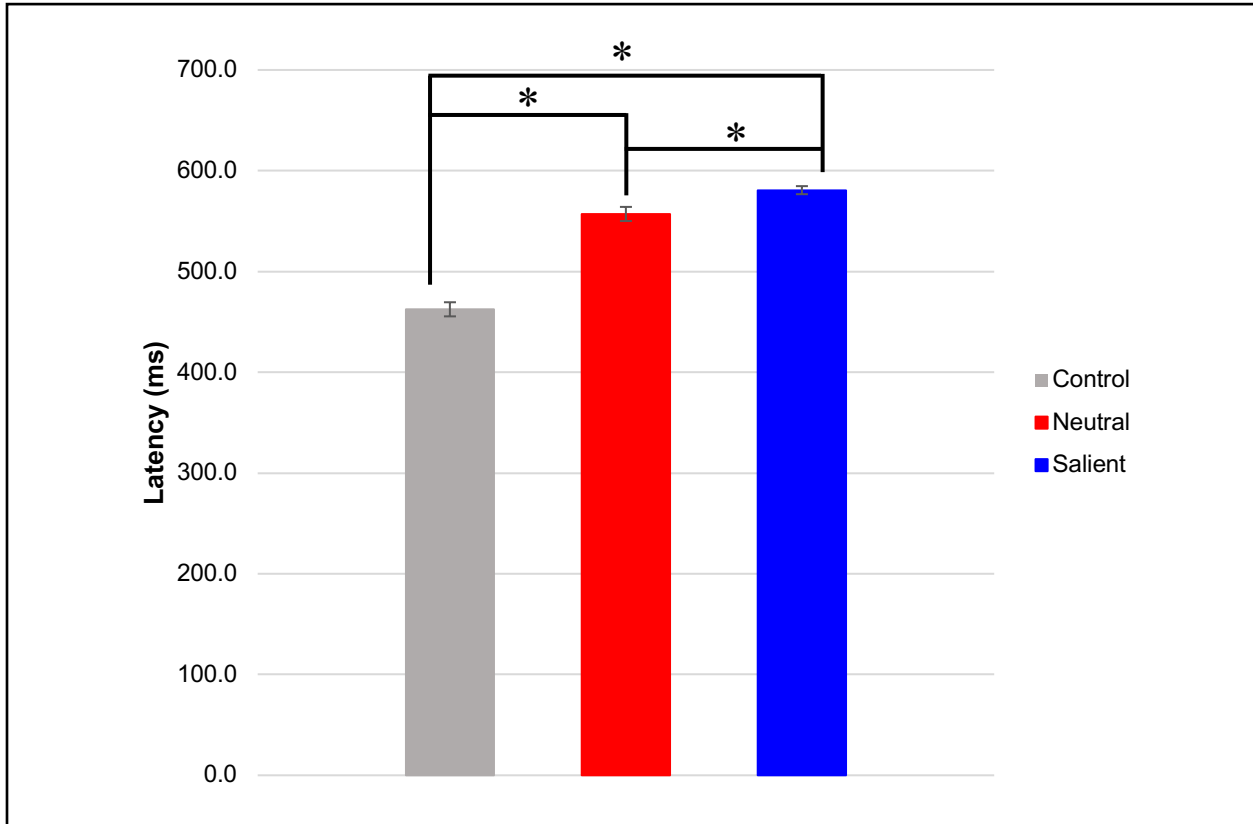


Figure 3.7. Mean reach latency time across display conditions with standard error.

A repeated measures two-way ANOVA was then used to determine if there was an effect on reach latency when participants initially foveated on a distractor, but still ultimately initiated the reach once the eyes foveated the target. In addition to a main effect for display condition (neutral vs. salient), statistical results showed a main effect for primary saccade location ($F(1,56) = 29.15, p<0.0001$), which confirmed that reach latency was longer when the eyes fixated a distractor ($m=643.0 \pm 153\text{ms}$) as compared to target fixation ($m=548.3 \pm 138\text{ms}$). The interaction between display condition and initial eye movement location was not significant ($F(1,50) = 2.45, p=0.130$).

There was no significant effect of display conditions on hand movement time ($F(2,58) = 1.10, p=0.338$; control = $520 \pm 101\text{ms}$; neutral = $511 \pm 98\text{ms}$, salient = $518 \pm 99\text{ms}$). There was also no significant effect of display condition on PV ($F(2,58) = 0.02, p=0.980$; control = $1.01 \pm 0.29\text{m/s}$, neutral = $1.01 \pm 0.29\text{m/s}$, salient = $1.02 \pm 0.29\text{m/s}$). There was no statistically significant effect of display for acceleration interval duration ($F(2,58) = 4.90, p=0.011$; control = $242 \pm 61\text{ms}$, neutral = $244 \pm 62\text{ms}$, salient = $250 \pm 67\text{ms}$).

Hand-Eye Coupling

To assess the temporal coupling between saccade initiation and reaching, we examined the distributions of the hand-eye coupling for each display condition. A one-way repeated measures ANOVA was conducted with display condition (control, neutral, and salient) as the independent variable and hand-eye temporal delay as the dependent variable. Results confirmed there was no significant effect of hand-eye temporal coupling between display conditions ($F(2,58) = 1.19, p=0.313$; control = $221.0 \pm 177\text{ms}$, neutral = $207.7 \pm 192\text{ms}$, salient = $205.9 \pm 219\text{ms}$). A Pearson correlation was also completed to assess the correlation of hand-eye temporal coupling. A significant relationship between reach-related saccade latency and reach latency was found ($r = 0.57, p<0.001$), which suggests moderate positive correlation of hand-eye coupling. Correlation coefficient results for each subject are included in Table 3.4 below.

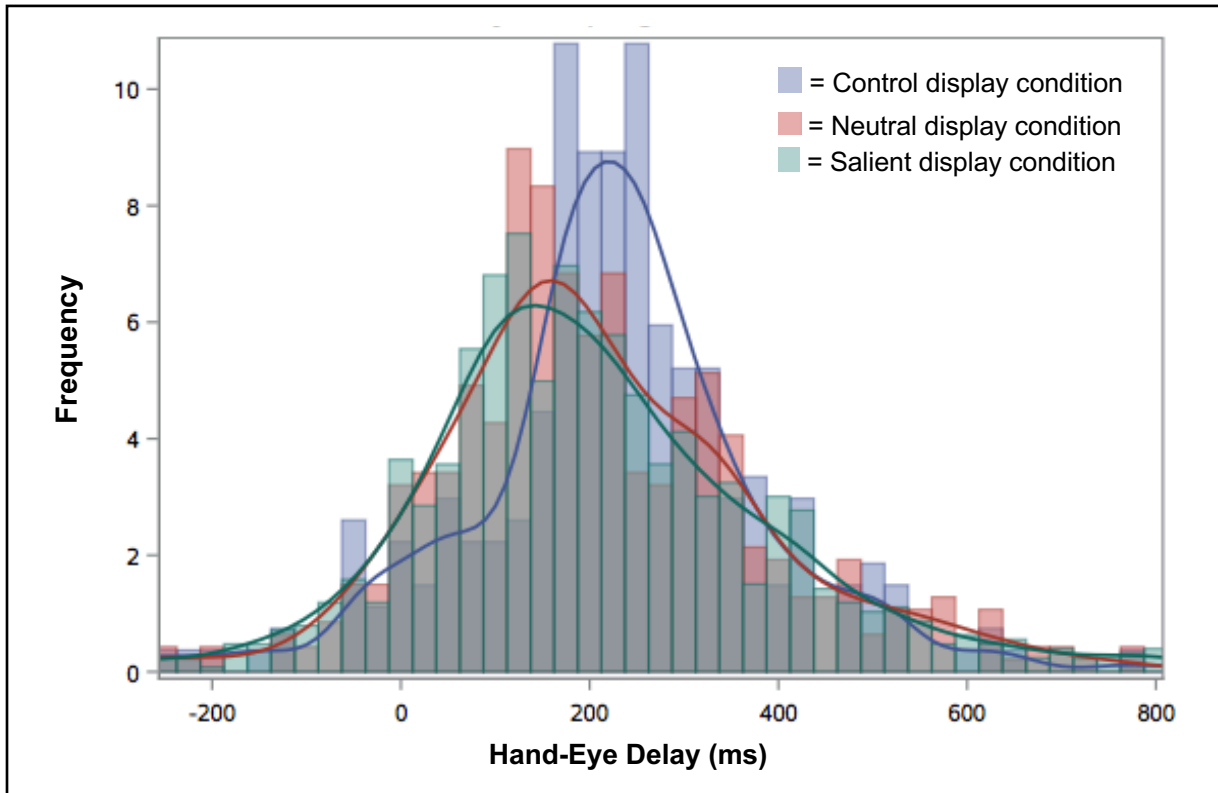


Figure 3.8. Distribution of the hand-eye temporal coupling for display conditions.

Table 3.4

Correlation Coefficients per Participant for Hand-Eye Temporal Coupling

Participants	Correlation Coefficient	Prob > r
1	0.34	0.007
2	0.69	<0.0001
3	0.42	0.008
4	0.95	<0.0001
5	0.75	<0.0001
6	0.70	<0.0001
7	0.56	<0.0001
8	0.34	0.013
9	0.92	<0.0001
10	0.58	<0.0001
11	0.37	0.006
12	0.61	<0.0001
13	0.60	<0.0001
14	0.29	0.012
15	0.86	<0.0001
16	0.32	0.012
17	0.60	<0.0001
18	0.57	<0.0001
19	0.65	<0.0001
20	0.79	<0.0001
21	0.48	<0.0001
22	0.14	0.242
23	0.50	<0.0001
24	0.54	<0.0001
25	0.45	<0.0001
26	0.54	<0.0001
27	0.57	<0.0001
28	0.72	<0.0001
29	0.56	<0.0001
30	0.65	<0.0001
<i>Mean</i>	0.57	

Distractor Fixation when Reaching

Although reaching was initiated when the eyes fixated the target in approximately 85% of the trials, it is important to examine if fixating on the distractor when reaching is initiated affects reach kinematics. In other words, is there a cost on reach execution, which would be demonstrated by a longer MT, when the reach-related saccade lands on a distractor as compared to the target. Given the unbalanced design (i.e., only 15% of trials with reach-related saccade to the distractor

vs. 85% of trials with reach-related saccade to the target), a paired statistical t-test was performed to compare the means. Results confirmed a significant effect of reach-related saccade on MT ($t(29) = -4.48, p < 0.0001$), where MT for reach-related saccades directed to the target ($m = 521.1 \pm 104\text{ms}$) was significantly faster than MT for reach-related saccades directed to a distractor ($m = 552.7 \pm 109\text{ms}$).

3.4.2 Reach Trajectory

A secondary objective of this thesis was to examine if eye fixation modulates hand movement deviation in the presence of distractors. Following the frequency analysis of reach-related saccade location which demonstrated that the reach-related saccade occurs to the target for approximately 85% of trials, this question has been rephrased: When the reach-related saccade occurs to the target, is hand movement deviation modulated by the presence of distractors? Hand movement trajectory deviations were analyzed using separate one-way repeated measures ANOVAs. When the target was in location #2, results confirmed there was a statistically significant effect for display condition on hand position at PV ($F(2,58) = 9.16, p = 0.003$) along the azimuth. Post hoc testing demonstrated a significant difference between the control and neutral conditions ($m = 3.8\text{mm}$ away from target $\pm 10.0\text{mm}$) as well as a significant difference between control and salient conditions ($m = 5.2\text{mm}$ away from target $\pm 9.4\text{mm}$).

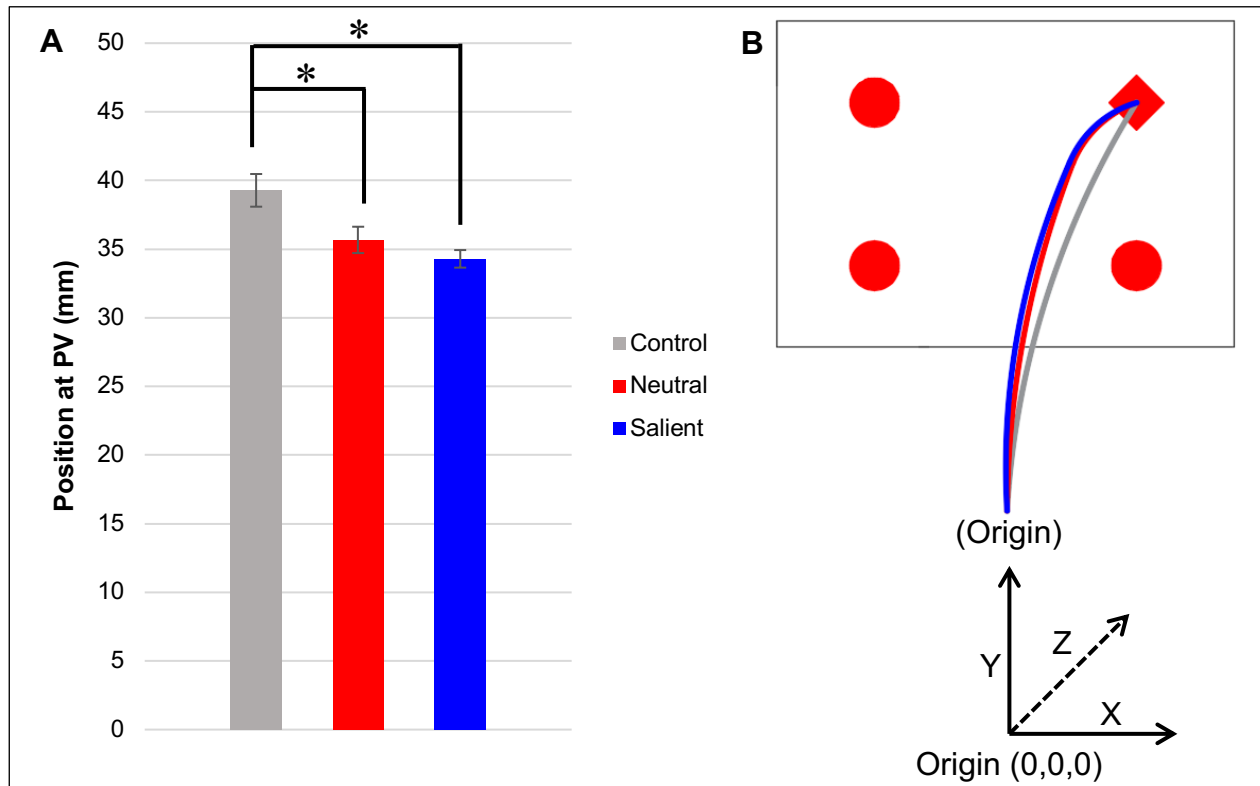


Figure 3.9. Mean hand position at PV in azimuth with target in location #2. (A) Mean hand position at PV with standard error, where control display condition is the most direct path to the target, and more negative values indicate deviation away from the target. (B) Schematic illustration of reach trajectory to provide a visual display of average deviations away from target.

Statistical testing also confirmed a significant effect of display condition on hand position at PV ($F(2,58) = 4.63, p=0.014$) along the elevation when the target was in location #4. Post hoc testing demonstrated a significant difference between control and neutral conditions ($m = 7.6\text{mm}$ away from target $\pm 22.7\text{mm}$) as well as a significant difference between control and salient conditions ($m = 5.4\text{mm}$ away from target $\pm 18.2\text{mm}$). No other effects reached significance.

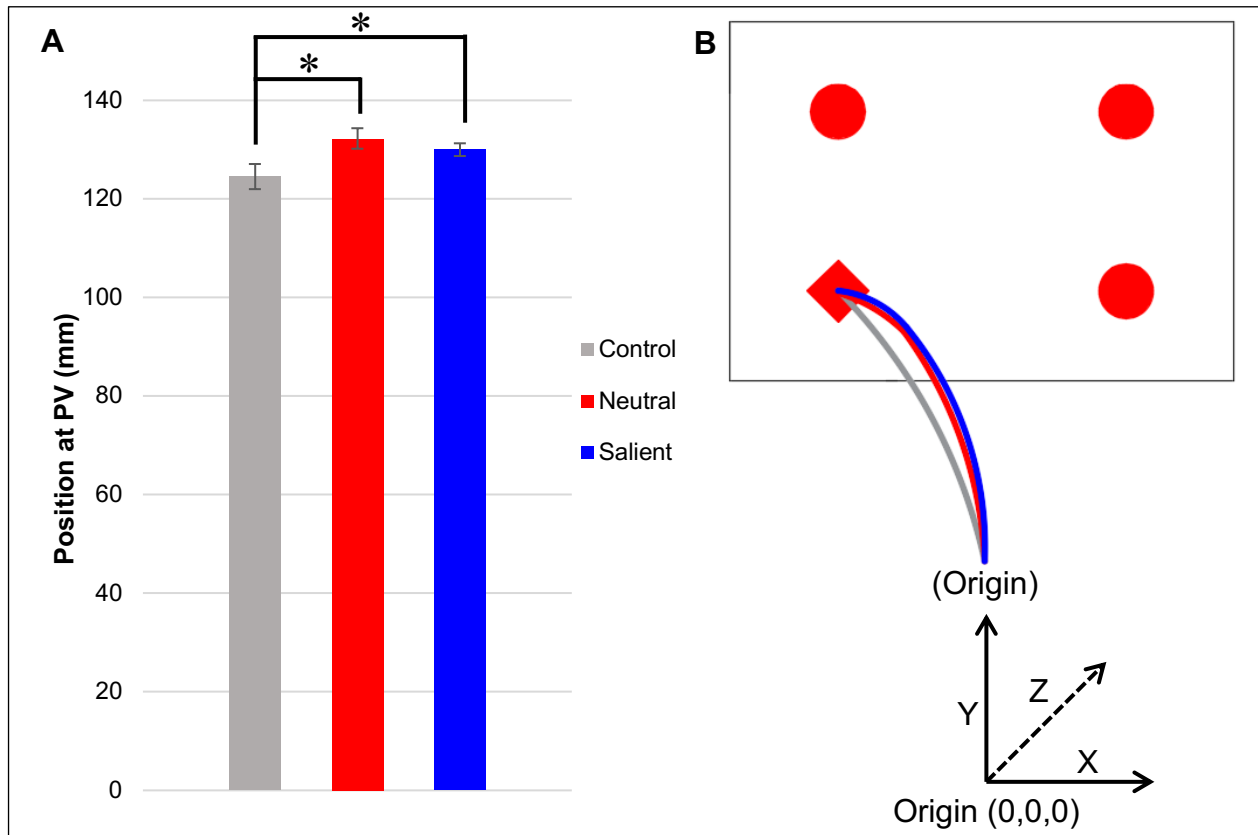


Figure 3.10. Mean hand position at PV in elevation with target in location #4. (A) Mean hand position at PV with standard error, where control display condition is the most direct path to the target, and more negative values indicate deviation away from the target. (B) Schematic illustration of reach trajectory to provide a visual display of average deviations away from target.

Given the unbalanced design based on natural task behaviour, a summary was created below to demonstrate hand movement deviations when the reach-related saccade occurs to the target compared to when the reach-related saccade occurs to the distractor. This is included to assess whether the eye movements are a further determinant of hand deviation when reaching specifically towards targets embedded among neutral and salient distractors. Results in Table 3.5 below demonstrated a few key exploratory outcomes. First, when the target is in location #2, there is a deviation in the azimuth depending on the reach-related saccade location. That is, when the reach-related saccade occurs to the neutral distractor, there is 7.6mm of trajectory deviation away from the target. When the reach-related saccade occurs to the salient distractor, there is 11.8mm of trajectory deviation away from the target. Secondly, when the target is in location #4, there is

deviation in the elevation direction depending on the reach-related saccade location. That is, when the reach-related saccade occurs to the neutral distractor, there is 6mm of trajectory deviation away from the target. When the reach-related saccade occurs to the salient distractor, there is 5.4mm of trajectory deviation away from the target. However, no other deviation was found in elevation for location #2 or azimuth for location #4.

Table 3.5
Summary of Hand Position at PV (mm) per Reach-Related Saccade

	Position at PV for Location #2 (Azimuth)			Position at PV for Location #4 (Elevation)		
	Target	Neutral Distractor	Salient Distractor	Target	Neutral Distractor	Salient Distractor
<i>Reach Saccade</i>						
<i>Mean (mm)</i>	39.5	31.9	27.7	-124.3	-130.3	-129.7
<i>Standard Deviation</i>	14.1	20.3	26.5	28.8	40.7	34.7

Section 4.0: General Discussion

4.1 Discussion

The aim of this work was to characterize the effect of distractors on spatial and temporal hand-eye coordination pattern during goal-directed reaching. Previous studies have shown that hand movements deviate away from or toward distractors depending on task environments. It is also understood that oculomotor and limb motor systems are typically coupled during manual tasks requiring foveal vision, where the hand follows the eyes by approximately 40-100ms. Using a display containing multiple distractors during a visually-guided goal-directed reaching task as a probe into a more complex environment than has been studied previously, we assessed eye and hand kinematics to further understand the effect of distractors on hand-eye coupling pattern. The overall major findings of this work are: (1) primary saccades land on distractors approximately 50% of the time; (2) the presence and type of distractors affect the planning of primary saccades,

reach-related saccades, and of the reach movement; (3) reach initiation does not typically occur until the eyes fixate the target; (4) hand-eye temporal coupling is consistent across display conditions, where the hand follows the eye by approximately 200ms, regardless of the presence of distractors; and (5) reach trajectory deviation depends on target location, but is not influenced by distractor salience.

Effects of salience on primary & reach-related saccades

The mechanism underlying attentional selection of behaviorally relevant sensory inputs is a key topic in neuroscience research. Given the limited capacity of the brain to selectively attend to visual inputs simultaneously, it is important to understand how the characteristics of the sensory stimulus, for example salience, capture attention. In this reaching study, we initially assessed the direction of primary saccades to establish the pattern of where the eye foveates first in order to understand how salience affects visual attention during goal-directed action. Previous research has shown that attention initially shifts towards the most salient stimulus within the visual field, that is, an overt attentional shift demonstrated by an eye movement (Theeuwes, 1992, 2004; Hickey, McDonald, & Theeuwes, 2006). As such, it was hypothesized that in the presence of distractors, the primary saccade will be more likely directed towards distractors, which will be further modulated by salience. Our results are consistent with this hypothesis and show that primary saccade direction is modulated by the type of distractors present. Specifically, we found that when neutral distractors are present, these distractors are less likely to capture selective attention as the primary saccade is more likely (58%) to be directed to the target. In contrast, saccades are directed to the target on only 46% of trials in the presence of a salient distractor.

Our environment contains multiple stimuli that compete for attention. As such, we are forced to select one or more relevant object(s) from the environment for further representation and

processing. A biased competition model has been derived by Desimone and Duncan (1995) based on our limited attentional resources. This framework primarily assumes that a competition towards the current behaviour's most relevant stimuli is how selection of one specific stimulus over another occurs, where the selected stimulus receives further processing. As discussed in the introduction, a distinction has been made between the two ways in which this selection can occur. Bottom-up, stimulus-driven, attentional selection is determined by salient stimuli, which capture overt attention regardless of an individual's goals; the most salient stimulus wins the competition. Whereas, top-down, goal-driven attentional selection is based on task instructions to attend to a specific kind of stimulus, such that the competition is biased in favour of that pre-specified object (Frith, 2001). During bottom-up attentional selection, a conceptual framework known as the salience map has been proposed (Koch & Ullman, 1985; Itti & Koch, 2001). The salience map is thought to consist of a topographical map of space, where all objects within a visual scene compete for cortical representation. The most distinctive, salient stimulus is thought to be selected first, given that it is the object which possesses the greatest sum of activity within the map (Itti & Koch, 2001; Fecteau & Munoz, 2006). However, the salience map does not refer specifically to the relevance of stimuli or the observer's goals. It has been suggested that the relevance of a stimulus, or top-down control, influences later processing more in oculomotor structures elsewhere (Desimone & Duncan, 1995; Colby & Goldberg, 1999; Reynolds & Chelazzi, 2004). Consequently, bottom-up and top-down sources of input converge to produce the prioritized representation (Wolfe, 1994; Serences & Yantis, 2006).

In our reaching task, neutral distractors were less likely to capture bottom-up attention, and thus, it is likely that top-down influences ensured that distractors were suppressed resulting in a greater probability of an overt attentional shift towards the target. However, when neutral and

salient distractors were present simultaneously, the primary saccade was more likely to be directed towards a salient stimulus (28%) compared to other neutral distractors (21%). Thus, the task-irrelevant salient distractors won the competition over other irrelevant, neutral distractors, as demonstrated by overt oculomotor capture effects. Essentially, a neutral, non-salient distracting stimulus is less likely to win the selection competition when competing for attentional resources in comparison to the more salient, bottom-up input.

Our results are consistent with previous studies. For example, Gaspelin et al. (2017) demonstrated that primary saccades are twice as likely to be directed towards a salient distractor (16%) compared to a non-salient stimulus (9%). It has been shown that salient distractors win the competition for attentional selection via bottom-up input and are then processed further (Constantinidis & Steinmetz, 2005). In the salience map, salient distractors are the most distinctive stimuli and thus, possess the largest activity sum resulting in initial selection for cortical representation (Itti & Koch, 2001). Our results provide support for this bottom-up, automatic attentional selection of salient distractors. Specifically, we found that primary saccade latency was comparable, approximately 260ms, when directed towards a single target (i.e., no distractors were present – control condition) or to a salient distractor. In both cases, there was a bottom-up capture effect, either by a single target or by a salient distractor. Either the sole target or salient distractor produced the greatest activity within the salience map, resulting in attentional selection. In contrast, when the primary saccade was directed to the target during distractor-present trials, its latency was approximately 100ms longer, which provides evidence for top-down control. Covert attention is used to locate the target, as top-down control suppresses an oculomotor shift to distractors, which is why a delay in reaction time is seen. Additional insight into the bottom-up or top-down attentional selection during this visually-driven task could be provided by a

neurophysiological EEG study. Specifically, the Pd ERP component has been used as an electrophysiological marker that reflects attentional suppression of the distractor representation within the parietal cortex (Hickey et al., 2009; Sawaki & Luck, 2010). Therefore, it would be expected that Pd amplitudes would be significantly greater during trials where the primary saccade does not occur to the salient distractor, which indicate that salient stimuli are suppressed and do not attract attention.

Effects of salience on spatio-temporal hand-eye coupling

It has been suggested that goal-directed reaching is typically accompanied by a saccade to a visual target as it allows for a clear target image, which is associated with more precise and accurate hand movements (Bekkering & Sailer, 2002; Kato & Fukuda, 2002; Crawford et al., 2004). When several visual targets are presented simultaneously, Gielen, Van den Heuvel, & Van Gisbergen (1984) found that typically eye and hand movements move to the same target. Accurate hand movements require the use of foveal vision prior to reaching in order to better localize a target (Bekkering & Sailer, 2002; Crawford et al., 2004). Furthermore, foveal visual feedback of the target during reaching can improve the accuracy and precision of trajectory control as it can be used to update the initial motor plan (Elliott, Helsen, & Chua, 2001). Based on previous literature, we hypothesized that reaching will be initiated once a saccade has been made to the target. In support of this hypothesis, our results showed that reaching was initiated following a saccade to the target on approximately 85% of the trials, regardless of distractor presence. However, reach latency was approximately 120ms slower when a target was presented amongst distractors, which was further modulated by the salience of the distractor: latency was approximately 30ms slower when a salient distractor was present compared to only neutral distractors. These results were expected because it takes time, first, for the eyes to locate the target, and second, for the reach to

be initiated. Other experiments that do not specifically instruct participants to move their eyes, as is the case for our study, showed that people typically foveate the target prior to hand movement initiation (Abrams, Meyer, & Kornblum, 1990; Helsen et al., 1998). Visually foveating the target allows for accurate representation of the target's location to produce the correct reaching movement. In the present study, given that the eye foveates the target on majority of the trials, it is likely that subjects use visual information about the target to correctly form initial motor plans as well as to adjust the limb in the final reaching phase (Prablanc, Pelisson, & Goodale, 1986).

Reach and saccadic latencies are commonly studied, but this work often discusses these two systems separately. Building on previous research, our study assessed if primary saccade location is a potential factor influencing reach latency delays. We found that when the primary saccade occurs to a distractor, the reach is initiated approximately 100ms slower than when the primary saccade occurs to the target. This delay is likely because the oculomotor system must make another saccade, which would be to the target, prior to initiating the reaching movement. Thus, we have found that if one fails to suppress an overt attentional shift, as demonstrated by a reflexive saccade to a distractor, there is a reach latency cost. Overt attention is captured by the distractor, which then causes a delay in the reach initiation because overt attention must then be shifted to the target.

Previous research has shown that the eyes typically proceed the hand by 40-100ms during a variety of manual tasks (Angel, Alston, & Garland, 1970; Prablanc, Echallier, Komilis, & Jeannerod, 1979; Biguer, Jeannerod, & Prablanc, 1982; Niechwiej-Szwedo, Goltz, Chandrakumar, Hirji, & Wong, 2014). For example, when participants were instructed to follow the target using a cursor controlled by a metal rod in a pursuit tracking task, Angel et al. (1970) found that the eyes were initiated between 45ms to 162ms prior to hand movement initiation. Another study found

that the hand typically follows the eyes by 100ms during an optimal (i.e., requiring speed and accuracy) hand pointing task to a peripheral target, which jumped from an initial starting position (Prablanc et al., 1979). Biguer et al. (1982) required subjects to track appearing targets with their eyes, head, and hand using EMG. Their study demonstrated that eye movement latencies are moderately correlated with arm EMG latencies (Biguer et al., 1982). Furthermore, when participants were required to touch targets within a horizontal plane, where target vision was removed after hand movement onset during half the trials, healthy, control subjects showed a stereotypical pattern of hand-eye delay of approximately 110ms (Niechwiej-Szwedo et al., 2014). Based on this literature, it was hypothesized that the stereotypical temporal hand-eye coupling will be preserved in the presence of distractors. The temporal delay in initiation of hand movements following a saccade could be due to several reasons. First, it takes longer to initiate reaching due to neuromuscular delay as a result of a higher limb inertia relative to that of the eye (Gribble et al., 2002). Second, retinal and extraretinal feedback after the saccade lands on the target could be used to fine tune the reaching plan and reach trajectory. Our moderately correlated hand-eye delay results support the hypothesis, but the average hand-eye delay was approximately 210ms. Why, then, does our study demonstrate such a large timing difference in hand-eye delay (approximately 210ms) compared to previous studies (approximately 40-100ms)? It has been suggested that the relative timing of hand-eye coupling could be different when a high degree of spatial accuracy is crucial to the manual task (Johansson et al., 2001; Gribble et al., 2002). For example, Johansson et al. (2001) found that eye movements occurred several hundred milliseconds in advance of reaching when participants were required to grasp and manipulate small objects. Eye and hand movement timing can vary in a task-dependent manner, such that one can optimize the useful flow of incoming visual information (Crawford et al., 2004). Previously discussed studies most

commonly presented one sole visual target, where participants were required to track and/or reach towards. Our task complexity varies from one target as we incorporated distractors, and also vary target features across trials. Thus, it is quite likely that the varied control set of this study, where shape, colour, and location can all vary on a trial-to-trial basis, influences the speed of perceptual and motor processing (Gribble et al., 2002). Ultimately, in our study, the sufficient time between saccadic eye movements and limb movement initiation allowed participants to successfully reach to the target, as it allowed for hand trajectory adjustments based on visual feedback.

Specific cortical regions that have been implicated in the coordination of eye and limb movements during visually-guided reaching tasks. Specifically, it was initially thought that regions of the posterior parietal cortex (PPC) have been shown to coordinate eye and limb movements independently. It was hypothesized that two areas within the PPC, the lateral intraparietal area (LIP) and parietal reach region (PRR), primarily code eye movements and reaching movements, respectively (Shipp, Blanton, & Zeki, 1998; Galetti, Fattori, Kutz, & Gamberini, 1999; Gribble et al., 2002). However, work by Andersen et al. (1998) has since suggested that the PPC combines sensory signals from different modalities to coordinate movement of both the eyes and limbs simultaneously. Indeed, Batista, Buneo, Snyder, and Andersen (1999) have found responses of cells within the PRR were modulated by initial eye position prior to limb movement onset. There is further evidence that the PPC also works to facilitate current arm movements by incorporating visual feedback (Desmurget et al., 1999; Pisella et al., 2000). The superior colliculus (SC), a brainstem structure, has been shown to be involved in orienting movements of the eyes (Sparks & Hartwich-Young, 1989). While similarly thought to function independent of reaching movements, evidence has also been reported that the SC is involved in the production of visually-guided limb movements (Sparks & Hartwich-Young, 1989). Neurons within the SC have been shown to

discharge prior to, with limb onset, or during movement, as well as in the absence of eye movements, which have been classified as SC “reach neurons” (Werner, Danneberg, & Hoffmann, 1997; Werner, Hoffman, & Danneberg, 1997). Furthermore, it has been suggested that primary and premotor cortices work to integrate visuomotor information with limb neural commands (Mushiake, Tanatsugu, & Tanji, 1997; Boussaoud & Bremmer, 1999; Jouffrais & Boussaoud, 1999). During EMG studies, tight trial-to-trial coupling between saccade and arm movement reaction times provide support that there is a link between neural control signals for eye and arm movement initiation (Gribble et al., 2002). Our results, where hand-eye coupling is consistent during goal-directed reaching, provide additional support that there is a likely connection between neural pathways during eye and hand movements. Visually-guided reaching is initially coded in a gaze-centered frame, but in order to formulate a reaching motor program, this must then be transformed into a hand-centered frame for appropriate muscular contraction to bring the hand to the target (Crawford et al., 2004). Following target detection and localization within the periphery, eye and hand system commands seem to be organized in parallel (Prablanc et al., 1979; Munoz, Dorris, Pare, & Everling, 2000). Thus, it is evident that neural commands for the two separate motor systems do, in fact, function in a parallel rather than a serial organization to produce successful visually-guided reaching movements.

Effects of distractors and distractor salience on reach trajectory

Manual aiming studies have previously demonstrated that distractors affect the trajectory of reaching movements (Tipper et al., 1992). However, when reaching towards a target amongst distractors, the directionality of the movement deviation has been disputed (Song & Nakayama, 2009). For example, studies have shown that reaches deviate away from irrelevant distractors, specifically when distractors are obstacles to be avoided or are presented prior to the target

(Howard & Tipper, 1997; Tipper et al., 1997; Tresilian, 1998). Similar studies have demonstrated that reaches deviate towards distractors, particularly when they are task-relevant (i.e., a potential target) or when priming facilitates the distractor's location (Welsh et al., 1999; Chang & Abrams, 2004; Welsh & Elliott, 2004; Song & Nakayama, 2006). Based on previous work and the characteristics of our task design, we hypothesized that there will be greater deviation in hand movement trajectory away from the target when distractors are present. Our results provide further support that reach trajectories do in fact deviate away from the target when distractors are present.

Furthermore, Moher et al. (2015) found that the nature of distractors additionally influences reach deviation, such that weakly salient distractors cause greater interference than strongly salient distractors, as demonstrated by larger trajectory deviations. As such, we hypothesized that there will be greater deviation in hand movement trajectory away from the target specifically during neutral trials, which could be considered weakly salient compared to during salient trials, which are equivalent to strongly salient conditions used by Moher et al. (2015). Our results demonstrate that salience does not further influence hand deviation, simply the presence of distractors causes deviation in reaching trajectory. We were unable to replicate results from previous work, which is likely because our task set differed slightly from their study. Moher et al. (2015) implemented weak salient distractors, which were pink; however, our “weakly salient” display condition was in fact our neutral display condition, where distractors were all red. Further, their study used a control condition as a baseline trajectory measure that was similar to our neutral display condition. Our study does not support the idea that weakly salient objects cause greater deviation, but this could potentially be a result of differing task sets between the experiments. Ultimately, more research is required to understand specifically how ranges of salience influence reach deviation differentially.

Nevertheless, the present results provide clear evidence that distractors cause interference during goal-directed reaching. Action-based theories of selective attention (Rizzolatti et al. 1987; Tipper et al. 1992, 1998) suggest that interference effects on movement kinematics demonstrate that distracting stimuli interfere with motor planning (Howard & Tipper 1997; Welsh & Elliott 2004). As such, movement deviations during reaching are an effective behavioural measure to reflect potential competition between multiple motor plans organized in parallel (Tipper, Howard, & Houghton, 2000; McSorley et al. 2004). When trajectories deviate away from a distractor, it is suggested that the distractor-specific motor plan has been inhibited (Moehler & Fiehler, 2017). However, movement trajectories are thought to be directed towards distractors when the two competing motor plans are not resolved due to a lack of inhibition, and both remain active in parallel (Moehler & Fiehler, 2017). Specifically, when distractors are present but also potential targets in previous and subsequent trials, it has been suggested that both the target and distractors automatically initiate independent motor response processes (Tipper et al., 1992; McGarry & Franks, 1997; Welsh et al., 1999; Welsh & Elliott, 2004). As a result of shared neuron pools within overlapping areas of the motor cortex, it is likely that independent responses are represented and programmed for both the target and distractor stimuli, which compete for activation (Welsh & Elliott, 2004). More specifically, one possible neural structure for this simultaneous processing of multiple reach plans is the dorsal premotor area (PMd). An area primarily involved with limb motor initiation and execution, the PMd has been shown to represent multiple potential motor plans in parallel prior to a cognitive decision about the correct target (Cisek & Kalaska, 2002, 2005; Song & Nakayama, 2006). This parallel activation likely results in target and distractor components present in initial descending motor commands, which affects the reach trajectory (Goodale et al., 1986; Flanagan et al., 1993). Successful completion of a visually-guided reaching

task to a target then depends on selection of the correct target, which diminishes activity for the distractors, and ultimately on rapid online adjustments using visual feedback (Welsh et al., 2004; Cisek & Kalaska, 2010). Our work provides further evidence that there is a lack of inhibition during motor planning when distractors are present, which results in reach deviations directed away from the target rather than towards it.

Our work, however, specifically emphasizes deviation away from the target towards the upper left visual field. That is, in the presence of distractors when the target is located in the upper right visual field, we found significant deviation to the left. Further, when the target is located in the lower right visual field, we found significant deviation upwards. Attentional differences between visual fields have been previously demonstrated during a large variety of perceptual and cognitive tasks (Feng & Spence, 2014; Thomas, Castine, Loetscher, & Nicholls, 2015). The visual area from which information can be obtained within the periphery is the attentional visual field (AVF) (Hassan et al., 2008). AVF is a useful measure of spatial attentional processing, especially during tasks demanding selective attention, such as detecting, discriminating, and localizing a target amongst distractors (Chan & So, 2007; Feng & Spence, 2014). In comparison to the lower visual field, it has been shown that better performance in the upper visual field occurs during visual searches and other discrimination tasks (Previc, 1990; Goldstein & Babkoff, 2001). Specifically, stimuli within the upper visual field, particularly distracting salient objects, capture more attention (Jeerakathil & Kirk, 1994). Based on previous attentional field biases noted, a group of researchers used functional magnetic resonance imaging (fMRI) to assess differential activation of areas during a target detection task along both vertical and horizontal axes (Mao, Zhou, Zhou, & Han, 2007). Mao et al. (2007) found additional right hemispheric activation for targets located in the upper visual field compared to the lower visual field, which implied a visuospatial attention bias.

Furthermore, Feng and Spence (2014) investigated vertical asymmetries in the AVF when localizing a target amongst distractors. Results determined an upper visual field bias during early attentional processing, which is similar to previous tasks when a target was searched for amongst distractors (Previc, 1996). It was suggested that the spatial attentional processing bias likely contributes to behavioural biases in perceptual and cognitive task performance (Feng & Spence, 2014). This attentional difference likely results from differential involvement of two visual streams, where the lower visual field is associated with peri-personal space and the upper visual field is part of extra-personal space (Previc 1990, 1996).

Further to an upper visual field attentional bias for perceptual tasks, it has been demonstrated that healthy individuals over-attend to objects on the left side for the visual field (Bowers & Heilman, 1980; Jewell & McCourt, 2000). Nicholls et al. (2012) found a strong leftward bias when distractors were present in the upper visual field, which suggests a connection between horizontal and vertical space for visuospatial attention. Thus, a combination of right hemisphere activation during visuospatial tasks and additional right hemisphere activation due to stimuli within the upper visual field can, ultimately, accentuate leftward attentional biases. Replicating previous work, Thomas et al. (2015) found a stronger leftward attentional bias during a line bisection task when distractors were presented within the upper visual field. It has been suggested that attentional biases to the left visual field occur as a result of contralateral innervation, in which the right hemisphere primarily regulates visuospatial attention (Kinsbourne, 1970). More specifically, stimuli within the left visual field activate right hemisphere attentional networks, causing attention to be more strongly guided towards the left (Siman-Tov et al., 2007; Thomas et al., 2015).

On the contrary, research involving visually-guided manual pointing movements has suggested an over-representation of the lower visual field, where anatomical asymmetry may cause a functional bias during action (Danckert & Goodale, 2001; Binsted & Heath, 2005). As such, Danckert and Goodale (2001) examined movement time when reaching to different sized targets and found that visual feedback processing was more effective in the lower visual field. Their work also demonstrated an accuracy advantage for movements within the lower visual field (Danckert & Goodale, 2001). Similarly, additional work reported that reaching within the lower visual field reduced spatial variations in the later phase of trajectories and improved endpoint accuracy, which resulted from improved feedback processing (Khan & Lawrence, 2005). Furthermore, Krigolson and Heath (2006) had participants perform reaching movements to different targets amongst both lower and upper visual space. Their work demonstrated larger endpoint spatial distribution variance when targets were located in the upper visual field, suggesting that a lower visual field advantage which may be preferential during later reaching stages (Binsted & Heath, 2005; Krigolson & Heath, 2006). Thus, attentional biases may depend on the stage of processing, where perceptual decision tasks may demonstrate an upper visual field advantage, but limb trajectory adjustments may be more effective within the lower visual field.

Attentional bias within the upper visual field provides a potential explanation as to why our study demonstrates upper left visual field deviations, specifically. However, it's important to note that support for upper attentional biases comes from perceptual experimental paradigms, such as line bisection and landmark tasks (McCourt & Jewell, 1999; Dufour, Touzalin, & Candas, 2007; Thomas et al., 2015). Whereas, support for lower attentional biases comes from work focusing on online control throughout different stages on movement, specifically during deceleration phases of reaching (Danckert & Goodale, 2001; Binsted & Heath, 2005; Krigolson & Heath, 2005).

Although, visuospatial attentional tasks may suggest potential implications for our results, it is evident that further study is required to understand how attentional biases specifically influence goal-directed reaching in a complex visual display. Ultimately, our study notes an upper left visual field trajectory deviation during visually-guided reaching, which may be a result of upper left visuospatial attentional bias.

Effects of foveating distractors when reaching

As is now quite evident, people's natural behaviour is to initiate arm movements towards a visual target once they have already foveated that target during goal-directed reaching. As an exploratory method, we investigated the remaining 15% of trials where participants reached while foveating a distractor. This behaviour occurred on a minimal number of trials as we did not instruct participants on where to direct their eyes during this task. First, movement time was examined to determine if there is a cost on reach execution when the eyes foveated a distractor as compared to the target. Our study found that movement time was significantly slower, by approximately 30ms, when the reach-related saccade occurred to a distractor as compared to the target. Previous reaching studies have demonstrated that distractor interference causes longer reaction and movement time (Tipper et al., 1992; Pratt & Abrams, 1994). For example, Tipper et al. (1992) found one's response time to be longer when an irrelevant distractor was present compared to a target presented alone, suggesting that the distractor is processed and competes for representation for action output. Furthermore, Pratt and Adams (1994) confirmed a movement time cost for trials with distractors in a close proximity to the hand, when participants were required to move a cursor towards a target. Woodworth (1899) proposed a two-component upper limb control model for visually-guided movements. The initial movement phase involves a typical acceleration and deceleration that moves the limb within the general area of the target, which is followed by second

closed-loop phase that requires vision. Visual feedback about the limb position relative to the target is used to correct errors within the initial movement trajectory during the second phase, such that the target is successfully reached (Woodworth, 1899; Beggs & Howarth, 1972; Carlton, 1981; Ricker et al., 1996). In the case of our results, it is evident that movement time is slower because the movement trajectory needs to be corrected and adjusted along the way, which is due to participants formulating an initial motor plan when looking at the wrong location.

As an additional exploratory analysis, we investigated trajectory deviation in the 15% of trials where participants initiated reaching while fixating a distractor. We found that reach-related saccade location was a further determinant of reaching deviation, specifically when targets were embedded amongst distractors. Our results demonstrate that there is greater hand movement deviation away from the target when eyes are foveating a distractor compared to when eyes are foveating a target. As previously discussed, it is likely that two competing motor plans were not resolved because of a failure to inhibit the distractor, and as such, perhaps both motor plans remain active in parallel resulting in reach deviation. These results demonstrate a similar emphasis on deviation away from the target towards the upper left visual field, as we noted with previous results. It is likely that there is an increase in right hemispheric activation, and as a result attention is more strongly directed to the left and to the upper visual field. Distracting stimuli may cause an attentional bias, which results in trajectory deviations towards upper left space during reaching.

4.2 Future Directions & Limitations

Work from this research provides implications for future studies. First, our results indicate that reaching almost always occurs once the eyes foveated the target. Our study focused on participants' natural behaviour, as we did not explicitly provide instructions relevant to the eyes during this task. As a result, a major limiting factor to our analysis was approximately 2000 trials

where the eyes were foveating the target compared to approximately 300 trials where the eyes were foveating a distractor when reaching was initiated. As a result, statistical analyses comparing these groups of trials were unbalanced. Future research could explicitly instruct participants on where to foveate prior to reaching to allow for a valid comparison of how saccade location affect reaching kinematics. Secondly, future research involving a similar paradigm could implement neurophysiological EEG measures. Using this instrumentation could help to further understand cortical regions involved in hand-eye coordination during goal-directed reaching tasks requiring foveal vision, as well as provide insight into suppression of distracting stimuli. As previously discussed, the Pd ERP component is an electrophysiological marker reflecting attentional suppression, where the greater the response amplitude, the greater the suppression of distractor representation within the parietal cortex. This ERP component, for example, could be used to understand how salient stimuli that attract attention are suppressed during goal-directed reaching. Finally, we have demonstrated that reaching is typically initiated following a saccade to a visual target in healthy systems to facilitate successful reaching. A pattern of reaching when foveating a distractor is something that might be seen with children or with certain neuropathologies, such as Parkinson's or acquired brain injury (Romero, Van Gemmert, Adler, Bekkering, & Stelmach, 2003; Wilmut, Wann, & Brown, 2006b). A future direction of this work could be to examine and understand how neurological impairments influence reaching to a visual target in the presence of distractors. More broadly, this work could then provide a better understanding of how to design complex every day or work environments, such that recovering individuals can successfully reach towards visual targets in order to care for themselves.

There are some limitations of this research study that should be addressed in future research. First, our target locations may limit the understanding of trajectory deviations. Targets

were only located in either the upper right or bottom left corners of the display as opposed to all four corners. This was implemented to limit our study length; however, it should be addressed in future work to better understand how reaching deviates in all directions. Further to this, our analysis included an oversimplification of trajectory deviation. Due to analysis time constraints, we were unable to investigate specifically which distractor locations caused greater deviation over others. Future research could execute more in-depth analyses to understand which distractor the trajectory precisely deviated towards.

Our second major limitation was only examining a young, healthy population. Participants included only healthy individuals from the University of Waterloo with no history of neurological or neuromuscular pathology, with an average age of 23 years. As a result, this study is not generalizable to older or younger populations, as well as individuals with neurological impairments. As previously mentioned, future study should investigate hand-eye coordination during goal-directed reaching in other populations.

4.3 Final Conclusion

Our complex environments typically contain multiple objects that compete for attention. As a result, we are required to select relevant stimuli from the environment for further representation and processing. This work, which was a probe into complex scenarios, demonstrates that salient distractors affect both saccadic and reach motor planning. However, the presence of distractors is simply what influences reaching execution, irrespective of their salience. It was previously thought that specific cortical regions coordinate eye and limb movements, separately. However, more current literature has shown the temporal correlation of hand-eye coupling during goal-directed reaching, which demonstrates that these neural pathways are likely connected and work together to produce successful hand movements towards visual targets. We found hand-eye

coupling to be moderately correlated in a more complex visually-guided reaching task. An upper leftward attentional bias may occur during visuospatial reaching tasks, and as a result, this may provide implications for future design of workspaces such that individuals can successfully function in everyday life.

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Appendices

Appendix A: Waterloo Handedness Questionnaire

Each of the questions below offers five possible responses: RA (right always), RU (right usually), EQ (equal), LU (left usually), and LA (left always).

1. Which hand would you use to spin a top?				
LA	LU	EQ	RU	RA
2. With which hand would you hold a paintbrush to paint a wall?				
LA	LU	EQ	RU	RA
3. Which hand would you use to pick up a book?				
LA	LU	EQ	RU	RA
4. With which hand would you use a spoon to eat soup?				
LA	LU	EQ	RU	RA
5. Which hand would you use to flip pancakes?				
LA	LU	EQ	RU	RA
6. Which hand would you use to pick up a piece of paper?				
LA	LU	EQ	RU	RA
7. Which hand would you use to draw a picture?				
LA	LU	EQ	RU	RA
8. Which hand would you use to insert and turn a key in a lock?				
LA	LU	EQ	RU	RA
9. Which hand would you use to insert a plug into an electrical outlet?				
LA	LU	EQ	RU	RA
10. Which hand would you use to throw a ball?				
LA	LU	EQ	RU	RA
11. In which hand would you hold a needle while sewing?				
LA	LU	EQ	RU	RA
12. Which hand would you use to turn on a light switch?				
LA	LU	EQ	RU	RA

13. With which hand would you use the eraser at the end of a pencil?				
LA	LU	EQ	RU	RA

14. Which hand would you use to saw a piece of wood with a hand saw?				
LA	LU	EQ	RU	RA

15. Which hand would you use to open a drawer?				
LA	LU	EQ	RU	RA

16. Which hand would you turn a doorknob with?				
LA	LU	EQ	RU	RA

17. Which hand would you use to hammer a nail?				
LA	LU	EQ	RU	RA

18. With which hand would you use a pair of tweezers?				
LA	LU	EQ	RU	RA

19. Which hand do you use for writing?				
LA	LU	EQ	RU	RA

20. Which hand would you turn the dial of a combination lock with?				
LA	LU	EQ	RU	RA

<p>21. Is there any reason (e.g. injury) why you have changed your hand preference for any of the above activities? YES NO (circle one) Explain.</p> <p>22. Have you ever been given special training or encouragement to use a particular hand for certain activities? YES NO (circle one) Explain.</p>				
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Appendix B

Table B1.

Percentages of Trials Excluded for Eye & Hand Data Analysis

Participant	# of Optotrak Collection Error	# of EyeLink Collection Error	# of Incorrect Trials	# of Kinematic Outliers	Total Number of Trials Excluded	% of Trials Excluded
1	8	2	10	3	23	14.4%
2	12	4	9	13	38	23.8%
3	9	5	1	3	18	11.3%
4	0	3	0	6	9	5.6%
5	5	3	5	2	15	9.4%
6	7	3	0	4	14	8.8%
7	4	13	8	4	29	18.1%
8	6	6	4	2	18	11.3%
9	4	2	7	5	18	11.3%
10	11	0	2	2	15	9.4%
11	0	4	2	4	10	6.3%
12	1	6	4	3	14	8.8%
13	1	4	4	6	15	9.4%
14	3	0	5	9	17	10.6%
15	1	4	6	6	17	10.6%
16	0	5	5	8	18	11.3%
17	1	1	7	7	16	10.0%
18	0	2	3	6	11	6.9%
19	1	1	1	3	6	3.8%
20	2	0	2	3	7	4.4%
21	4	6	2	4	16	10.0%
22	6	0	1	2	9	5.6%
23	5	0	3	1	9	5.6%
24	1	0	4	5	10	6.3%
25	1	5	3	6	15	9.4%
26	4	0	2	3	9	5.6%
27	6	2	6	6	20	12.5%
28	3	0	14	4	21	13.1%
29	0	0	0	4	4	2.5%
30	8	1	1	6	16	10.0%
Total	114	82	121	140	457	9.5%
Percentage	2.4%	1.7%	2.5%	2.9%		

Table B2.
Number of Trials for each Primary Saccade Location

Participant	Control Display Condition		Neutral Display Condition			Salient Display Condition			
	Target	Fixation	Target	Neutral Distractor	Fixation	Target	Salient Distractor	Neutral Distractor	Fixation
1	10	0	15	3	0	27	10	8	0
2	6	0	2	12	0	14	18	18	0
3	7	2	14	1	3	31	6	7	11
4	9	0	20	0	0	41	5	4	3
5	9	0	15	4	0	25	13	9	3
6	9	0	20	0	0	23	30	1	0
7	10	0	8	10	1	29	9	6	3
8	9	0	10	9	0	30	11	12	0
9	10	0	6	12	0	9	17	26	0
10	10	0	8	11	0	25	21	10	0
11	6	4	10	6	2	19	12	9	15
12	8	1	8	4	7	25	3	3	20
13	9	0	6	12	0	17	18	17	0
14	9	0	13	4	0	18	25	11	0
15	8	2	14	3	1	23	8	10	10
16	9	0	14	3	1	31	5	7	7
17	9	0	9	9	1	31	10	10	3
18	10	0	10	6	0	25	18	14	0
19	10	0	12	7	0	31	10	17	1
20	9	0	10	10	0	24	25	8	0
21	10	0	11	7	0	31	15	5	0
22	10	0	11	8	0	13	22	20	0
23	10	0	10	8	2	20	24	12	2
24	9	0	9	10	0	16	27	15	0
25	10	0	14	6	0	28	7	14	0
26	9	0	17	2	0	50	3	5	0
27	8	0	7	12	0	15	19	18	0
28	10	0	12	6	0	23	16	7	4
29	10	0	1	19	0	11	18	30	0
30	7	0	9	9	0	21	19	13	0

Table B3.

Mean Eye Movement Data with Standard Deviations & Interquartile Ranges

Dependent Variable	Control Display Condition			Neutral Display Condition			Salient Display Condition		
	Mean	SD	IQR	Mean	SD	IQR	Mean	SD	IQR
<i>Primary Saccade Latency (ms)</i>	266.7	144	180 to 300	322.4	136	236 to 376	322.8	137	232 to 384
<i>Reach-Related Saccade Latency (ms)</i>	266.7	144	180 to 300	381.1	139	272 to 456	407.6	144	312 to 480

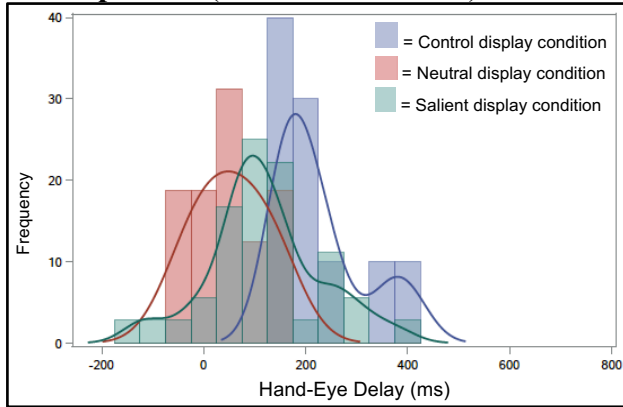
Table B4.

Mean Hand Kinematic Data with Standard Deviations & Interquartile Ranges

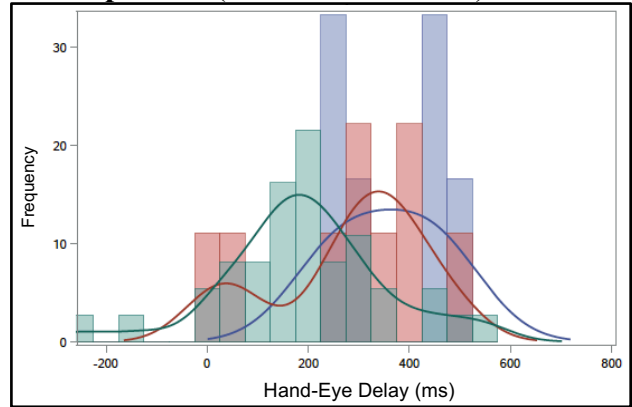
Dependent Variable	Control Display Condition			Neutral Display Condition			Salient Display Condition		
	Mean	SD	IQR	Mean	SD	IQR	Mean	SD	IQR
<i>Movement Latency (ms)</i>	463.7	110	392 to 516	566.2	142	464 to 632	594.3	154	488 to 664
<i>Movement Time (ms)</i>	520	101	456 to 592	510.6	98	444 to 572	517.6	99	448 to 584
<i>PV (m/s)</i>	1.01	0.29	0.84 to 1.14	1.01	0.29	0.82 to 1.15	1.02	0.29	0.82 to 1.17
<i>Acceleration Interval Duration (ms)</i>	241.8	61	202 to 280	243.7	62	204 to 276	249.7	67	204 to 292

Appendix C: Hand-Eye Temporal Coupling for Each Participant (with means and SDs)

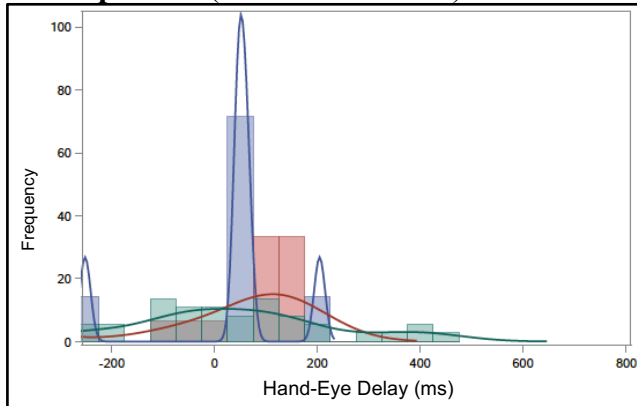
Participant #1 ($m = 119.4 \pm 110\text{ms}$)



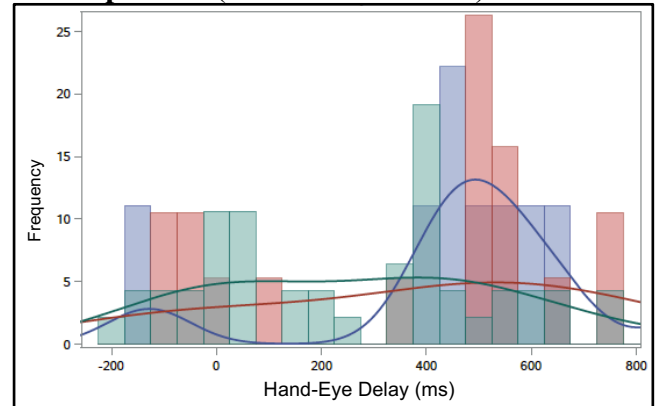
Participant #2 ($m = 226.6 \pm 162\text{ms}$)



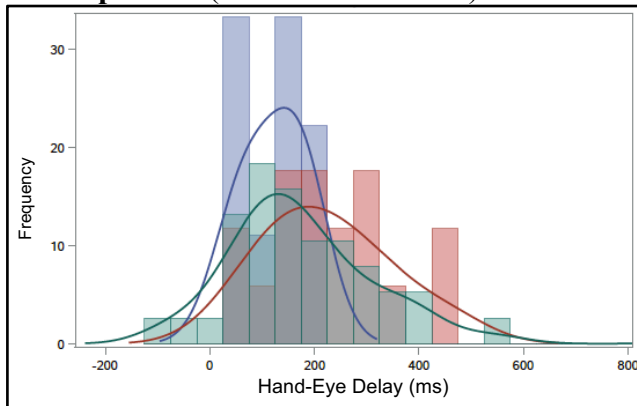
Participant #3 ($m = 23.3 \pm 198\text{ms}$)



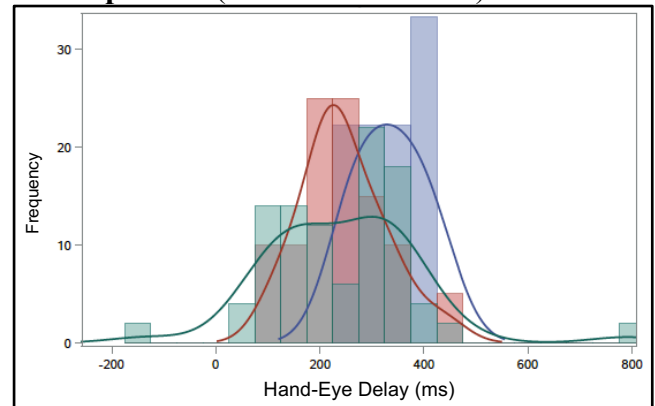
Participant #4 ($m = 341.9 \pm 314\text{ms}$)



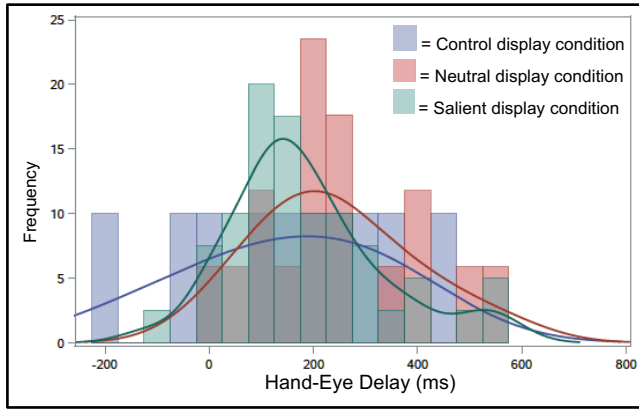
Participant #5 ($m = 192.1 \pm 158\text{ms}$)



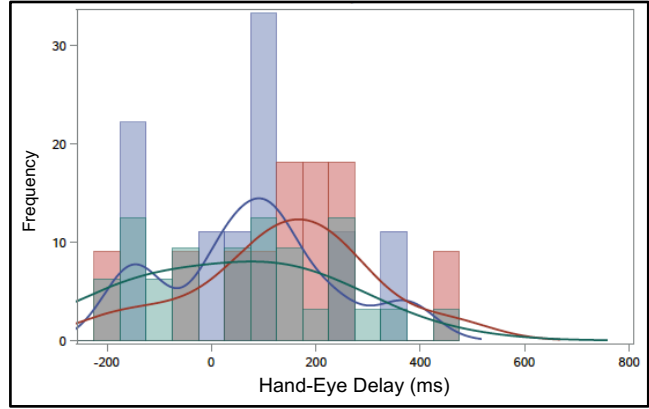
Participant #6 ($m = 254.3 \pm 126\text{ms}$)



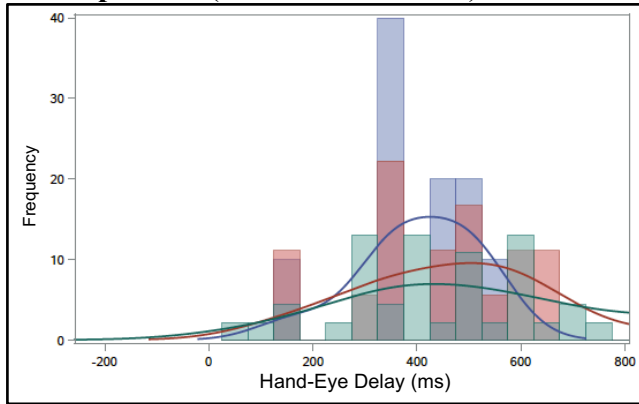
Participant #7 ($m = 194.9 \pm 156\text{ms}$)



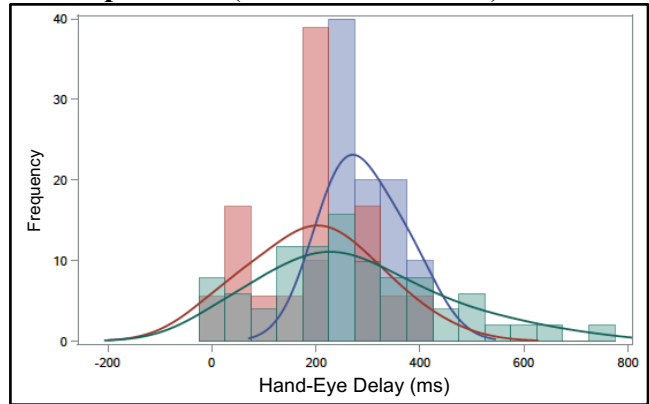
Participant #8 ($m = 54.8 \pm 208\text{ms}$)



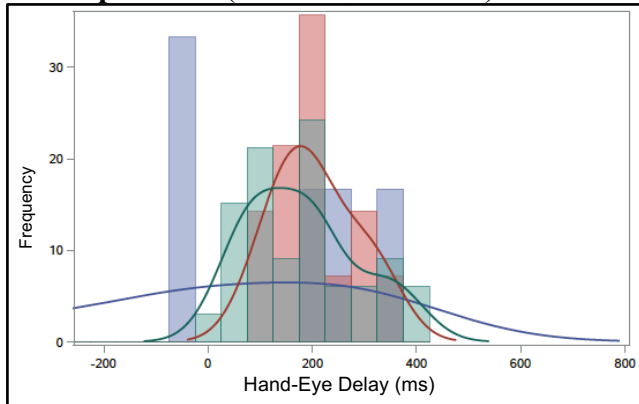
Participant #9 ($m = 512.4 \pm 245\text{ms}$)



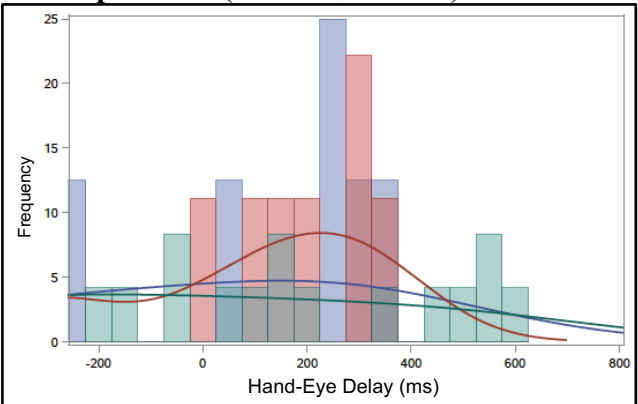
Participant #10 ($m = 257.5 \pm 154\text{ms}$)



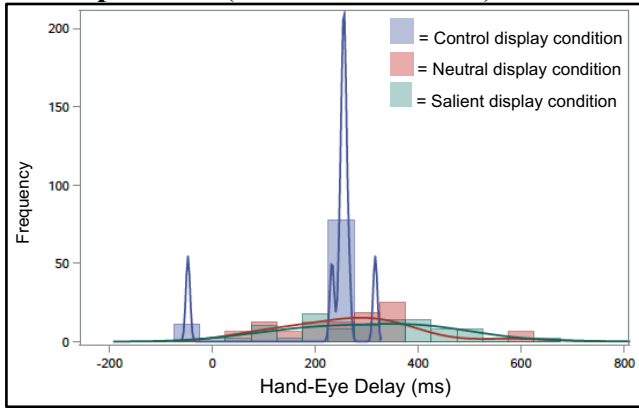
Participant #11 ($m = 173.7 \pm 127\text{ms}$)



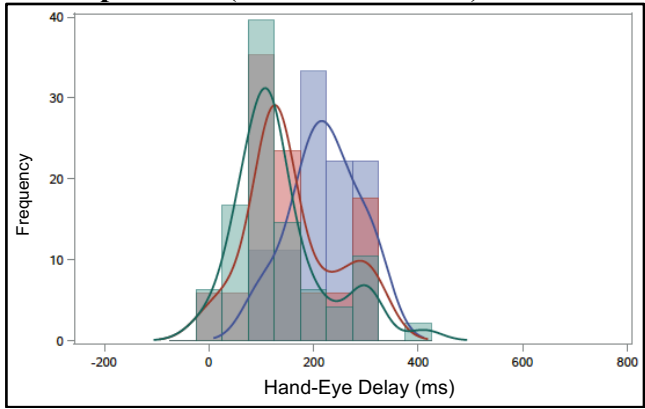
Participant #12 ($m = 2.7 \pm 354\text{ms}$)



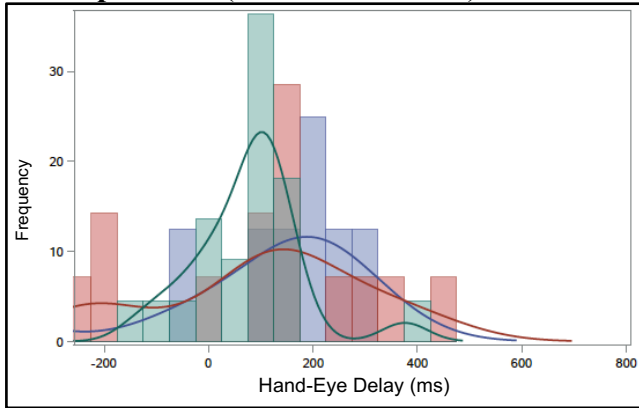
Participant #13 ($m = 288.7 \pm 138\text{ms}$)



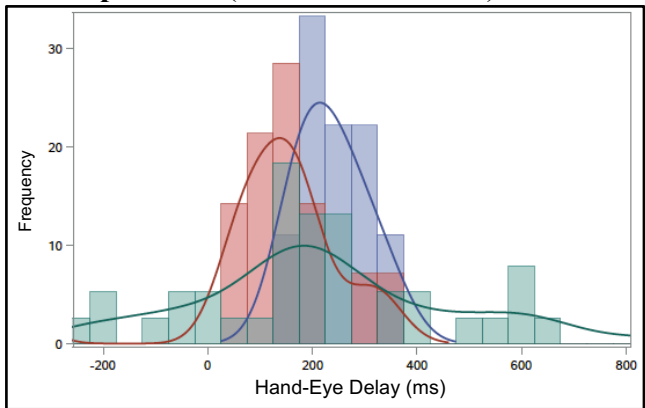
Participant #14 ($m = 150.8 \pm 90\text{ms}$)



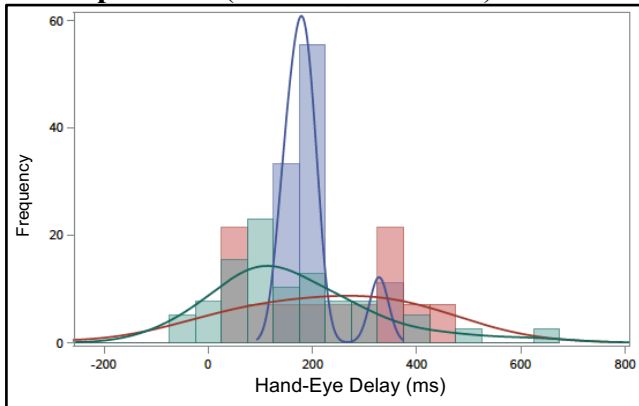
Participant #15 ($m = 72.9 \pm 186\text{ms}$)



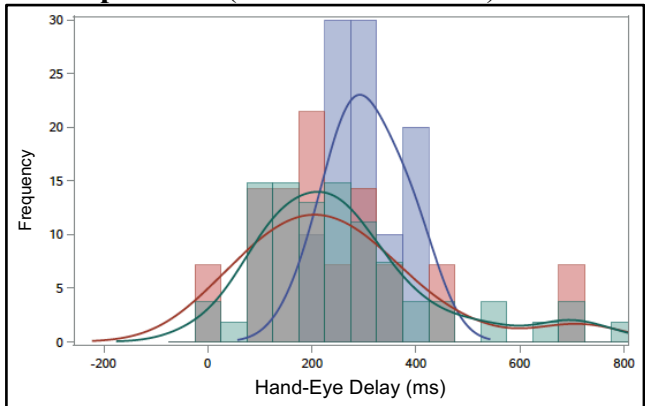
Participant #16 ($m = 201.4 \pm 216\text{ms}$)



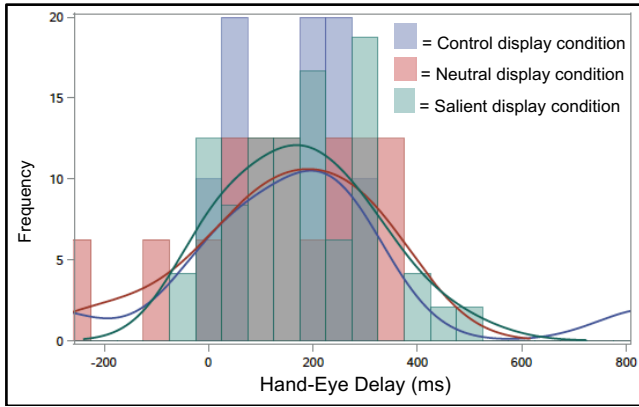
Participant #17 ($m = 170.8 \pm 166\text{ms}$)



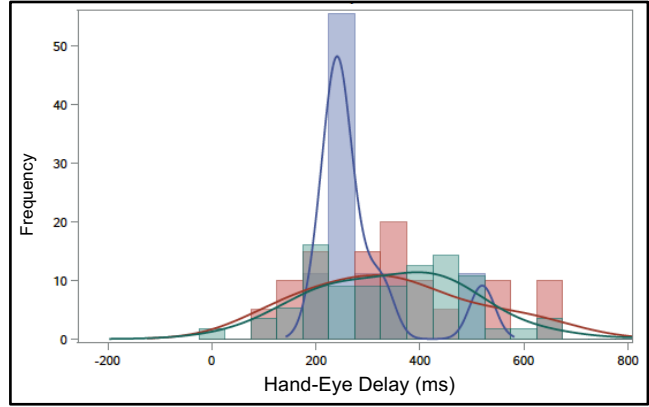
Participant #18 ($m = 267.5 \pm 165\text{ms}$)



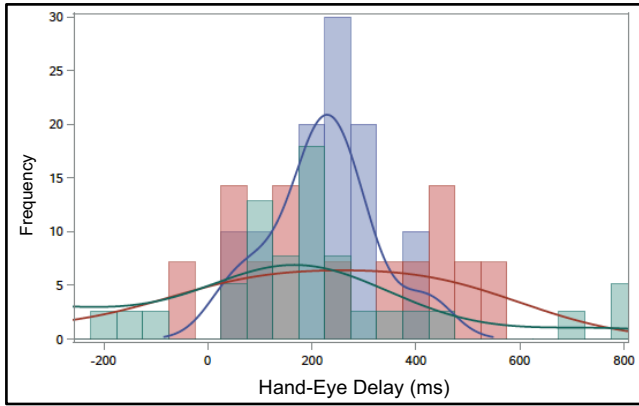
Participant #19 ($m = 169.3 \pm 170\text{ms}$)



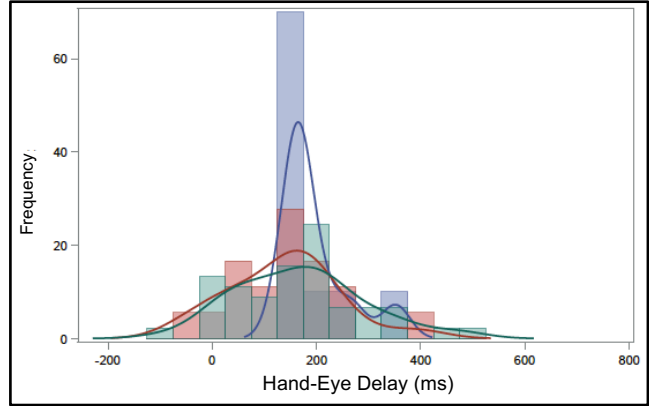
Participant #20 ($m = 343.9 \pm 154\text{ms}$)



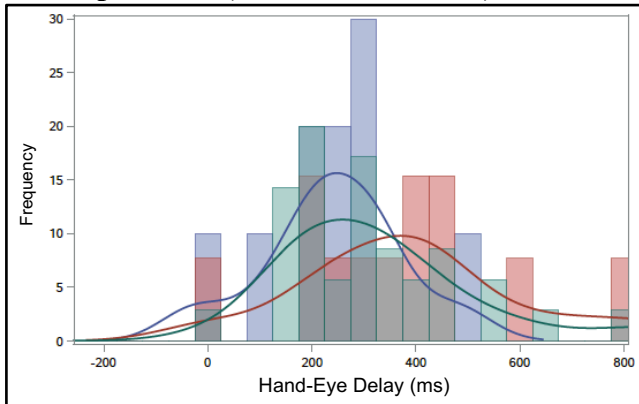
Participant #21 ($m = 126.9 \pm 295\text{ms}$)



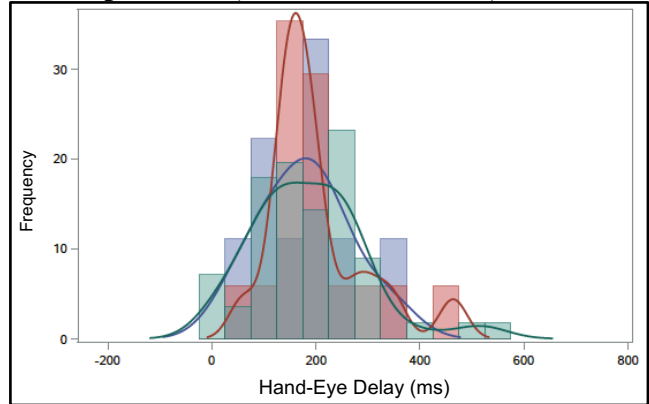
Participant #22 ($m = 164.3 \pm 112\text{ms}$)



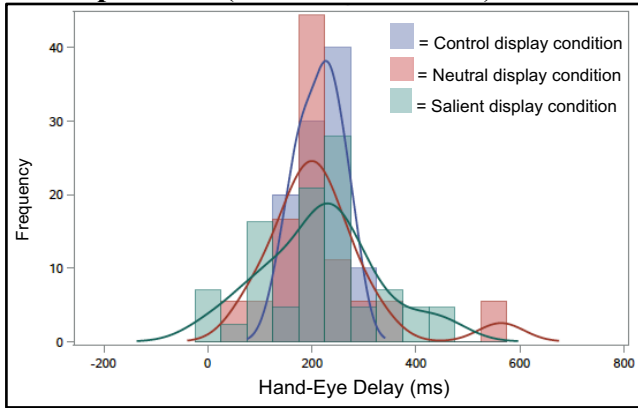
Participant #23 ($m = 316.9 \pm 232\text{ms}$)



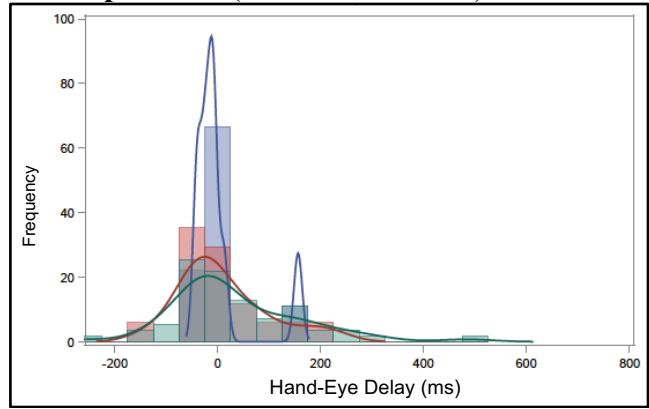
Participant #24 ($m = 188.6 \pm 102\text{ms}$)



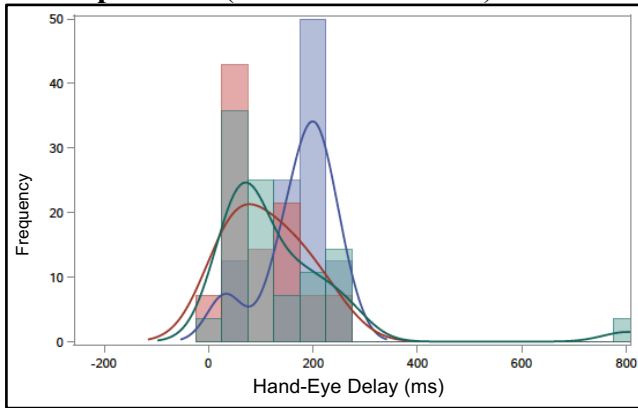
Participant #25 ($m = 216.6 \pm 102\text{ms}$)



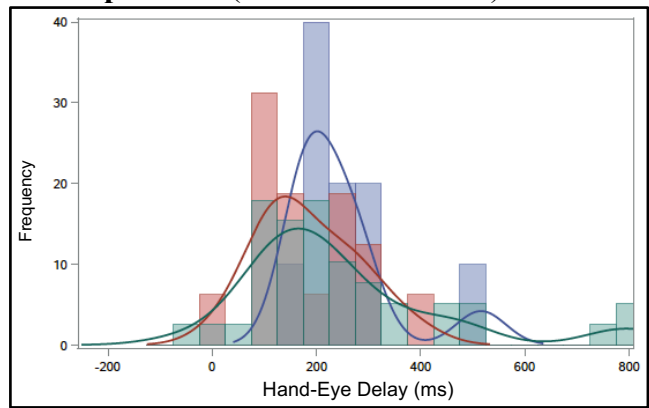
Participant #26 ($m = 24.9 \pm 114\text{ms}$)



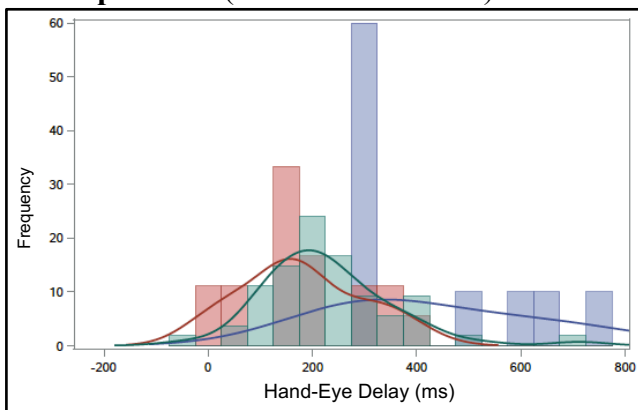
Participant #27 ($m = 137.1 \pm 122\text{ms}$)



Participant #28 ($m = 233.4 \pm 168\text{ms}$)



Participant #29 ($m = 242.7 \pm 149\text{ms}$)



Participant #30 ($m = 306.9 \pm 220\text{ms}$)

