

COGNITIVE MECHANISMS OF TRANSSACCADIC PERCEPTION

A Thesis Submitted to the
College of Graduate and Postdoctoral Studies
In Partial Fulfillment of the Requirements
For the Degree of Master of Arts
In the Department of Psychology
University of Saskatchewan
Saskatoon

By

AMANDA SINCLAIR

PERMISSION TO USE

In presenting this thesis/dissertation in partial fulfillment of the requirements for a Postgraduate degree from the University of Saskatchewan, I agree that the Libraries of this University may make it freely available for inspection. I further agree that permission for copying of this thesis/dissertation in any manner, in whole or in part, for scholarly purposes may be granted by the professor or professors who supervised my thesis/dissertation work or, in their absence, by the Head of the Department or the Dean of the College in which my thesis work was done. It is understood that any copying or publication or use of this thesis/dissertation or parts thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of Saskatchewan in any scholarly use which may be made of any material in my thesis/dissertation.

DISCLAIMER

Reference in this thesis/dissertation to any specific commercial products, process, or service by trade name, trademark, manufacturer, or otherwise, does not constitute or imply its endorsement, recommendation, or favoring by the University of Saskatchewan. The views and opinions of the author expressed herein do not state or reflect those of the University of Saskatchewan, and shall not be used for advertising or product endorsement purposes.

Requests for permission to copy or to make other uses of materials in this thesis/dissertation in whole or part should be addressed to:

Head of the Psychology Department
154 Arts, 9 Campus Drive
University of Saskatchewan
Saskatoon, Saskatchewan, S7N 5A5 Canada

OR

Dean
College of Graduate and Postdoctoral Studies
University of Saskatchewan
116 Thorvaldson Building, 110 Science Place
Saskatoon, Saskatchewan, S7N 5C9 Canada

ABSTRACT

Transsaccadic perception is characterised as the ability to perceive our visual world as stable and unmoving, despite the retinal image of our visual world changing each time we make rapid eye movements (called saccades). Currently the underlying mechanisms of transsaccadic perception, specifically the mechanisms that maintain an updated internal spatial map of objects in our environment during saccades, remain unclear. Although considerable progress has been made toward a better understanding of the basic mechanisms of transsaccadic perception with stationary objects in our environment, little is known about how our brain keeps track of moving objects during a saccade, which is a real-world task we do everyday (e.g. when driving or playing sports). In this thesis I describe two studies where I investigated transsaccadic perception of moving objects. The first examines how well we can track moving objects across saccades when the saccade amplitude and eccentricity of the target vary in a purely egocentric task. The second assess the extent to which we rely on visual cues in our environment (i.e. allocentric information) during transsaccadic motion tracking. My research is among the first to explore how our brain processes and integrates moving stimuli during saccades. Additionally, it sheds further light on the cognitive mechanisms of transsaccadic perception and offers insights into our everyday visual conscious experience.

Keywords: Motion perception, Eye tracking, Saccades, Transsaccadic perception, Visual perception, Spatial updating

ACKNOWLEDGEMENTS

Foremost, I would like to express my very great appreciation to my supervisor, Dr. Steven Prime. His patient guidance, thoughtful critiques, and enthusiastic encouragement have allowed me to grow as a researcher and scholar in my academic career. I could not have imagined having a better suited advisor and mentor for this project.

I would also like to offer a special thank you to my committee members, Dr. Jamie Campbell and Dr. Janeen Loehr, for their advice, wealth of knowledge, and assistance in keeping this project on schedule.

A sincere thank you also goes to the University of Saskatchewan Psychology department and the Social Sciences Research Laboratories (SSRL) for offering me the resources to run this project. Support provided by the research assistants and honours students who worked in the Psychophysics and Neurocognition lab during this project is also greatly appreciated.

Finally, I would like to thank my parents, Barb and Lyle Sinclair, for their support and encouragement throughout my studies. As well as my husband, Jared McRorie, for whom the completion of this project would not have been possible.

TABLE OF CONTENTS

PERMISSION TO USE	i
DISCLAIMER	i
ABSTRACT	ii
ACKNOWLEDGEMENTS	iii
TABLE OF CONTENTS	iv
LIST OF TABLES	vi
LIST OF FIGURES	vii
CHAPTER ONE	1
Introduction	2
Anatomy of the Visual System	4
The Stable World Problem	15
Theories of Transsaccadic Perception	20
Transsaccadic Integration	27
Cortical Areas Governing Eye Movements and Spatial Remapping	31
Transsaccadic Motion Perception	42
The Present Study	45
CHAPTER TWO	47
Effects of Saccade Size and Target Position in Transsaccadic Perception	48
<i>Method</i>	50
<i>Data Analysis</i>	56
<i>Results</i>	58
<i>Discussion</i>	69

CHAPTER THREE	73
Effects of Allocentric Cues in Transsaccadic Motion Perception	74
<i>Methods</i>	77
<i>Data Analysis</i>	84
<i>Results</i>	8
<i>Discussion</i>	97
CHAPTER FOUR.....	103
General Discussion	104
<i>Target Displacement</i>	107
<i>Saccade Amplitude and Retinal Eccentricity</i>	108
<i>Allocentric Information</i>	112
Limitations and Future Directions	115
Conclusion	118
REFERENCES	120

LIST OF TABLES

Table 2.1. Saccade-target combination with saccade size and target eccentricities in Exp. 1..... 51

Table 2.2. Mean accuracy in saccade-target combination by target displacement and saccade
direction 68

Table 3.1. Saccade-target combination with saccade size and target eccentricities in Exp. 2..... 79

Table 3.2. Target-bar combinations with target direction and background direction in Exp. 2... 81

Table 3.3. Mean accuracy in saccade-target combination by target displacement and target-bar
combination..... 95

LIST OF FIGURES

Figure 1.1. Anatomy of the eye	5
Figure 1.2. Cortical pathways of the visual system.	7
Figure 1.3. Divisions of the visual cortex.	11
Figure 1.4. The ventral and dorsal visual streams.	13
Figure 1.5. Retinal shifts during saccades.	17
Figure 1.6. Retinal shifts during fixation.	19
Figure 1.7. Theoretic depiction of how the visual system combines saccadic snapshots.....	21
Figure 1.8. Example of an early visual memory task.	22
Figure 1.9. Example of transsaccadic integration of stationary object.	28
Figure 1.10. Diagram of the extraocular muscles.	32
Figure 1.11. Diagram of saccade latency.....	34
Figure 1.12. Example of spatial remapping.	37
Figure 2.1. Depiction of the different saccade-target combinations in Experiment 1.	51
Figure 2.2 General experimental paradigm of Experiment 1.	53
Figure 2.3. Example of custom MATLAB output when analyzing gaze direction and amplitude.	57
Figure 2.4. Displacement detection in displacement and no-displacement trials, collapsing across all other factors.....	60
Figure 2.5. Displacement detection in the No-Displacement trials by saccade-target combination and saccade direction.	61
Figure 2.6. Displacement detection by displacement direction in all five saccade-target combinations for both saccade directions.	63

Figure 2.7. Displacement detection by saccade-target combination and saccade direction, collapsed across all other factors.	65
Figure 3.1. Depiction of the different saccade-target combinations in Experiment 2.	79
Figure 3.2. Different target-bar combinations of Experiment 2.	82
Figure 3.3. General experimental paradigm of Experiment 2.	83
Figure 3.4. Displacement detection by saccade-target combination (panel A) or target displacement (panel B).....	87
Figure 3.5. Displacement detection in the target-bar combinations, collapsed across target displacement and saccade-target combination.	88
Figure 3.6. Displacement detection in the different target-bar combinations and saccade-target combinations as a function of target displacement.	90
Figure 3.7. Displacement detection by target displacement and target-bar combination in each Saccade-Target Combination.	92
Figure 3.8. Example of boundary crossing when dot is moving downward and three stable allocentric cues are presented	98
Figure 4.1 Example of transsaccadic integration in different saccade conditions	111

CHAPTER ONE

Introduction

Eye movements are fundamental to visually processing the world around us. Our visual acuity (the capacity to see fine details) is not homogenous across the visual field. High visual acuity is limited to a small region of the retina (the inside surface of the eye), called the fovea. Rapid eye movements, called saccades, rotate the eye to direct our fovea to different parts of a visual scene allowing us to process these parts in greater detail. On average we make 2-3 saccades per second (Henderson, 2003) and these eye movements result in two fundamental problems. First, during a saccade our visual processing is suppressed until our eyes land on their target and fixation occurs. Yet our brain creates such a seamless percept of our world that when told little information is being processed during a saccade, many people do not believe it until presented with a mirror, since when looking in a mirror you are unable to see your own eyes move. Second, after each saccade the image of the visual world shifts across the retina, yet we still perceive the world as being visually stable. If we did, the experience of our world would be much like a badly filmed movie where the camera rapidly moves around causing a sense of nausea or unease. Thus, a fundamental problem in cognitive neuroscience is how does the brain produce and maintain a stable, seamless, and predictable percept of the world across eye movements? This area of study is known as transsaccadic research.

To better understand this problem, most transsaccadic research has studied how well subjects detect small spatial displacements of otherwise stationary stimuli (Bays & Husain, 2007; Bedell & Lott, 1996; Byrne & Crawford, 2010; Collins, Rolfs, Beubel, & Cavanagh, 2009; Deubel, 1995; Deubel, Bridgeman, & Schneider, 1998; Deubel, Schneider, & Bridgeman, 1996; Higgins & Rayner, 2015; Li & Matin, 1990; Niemeier, Crawford, & Tweed, 2003; Thier & Erickson, 1992; Ostendorf, Kiliyas, & Ploner, 2012; van Donkelaar & Müri, 2002; Verfaillie,

1997). To date there is very little research examining this question using dynamic stimuli that are more akin to real world motion stimuli. The purpose of this project is to address this major gap in the literature and investigated how well participants can transsaccadically track the location of smoothly translating stimuli in several different experimental conditions.

In this introductory chapter, I review the anatomy and neural pathways of the visual system, discuss some of the complications our visual system must overcome in order to view a scene or tracking moving objects, discuss the cortical areas involved in spatially mapping our visual world, analyze past research on transsaccadic perception as well as outline the major theories thereof, and finally, outline the objectives of the current study. Chapter Two is a detailed description of Experiment 1 where participants were asked to detect whether a target, moving across a blank screen, was displaced along its trajectory. Participants were tested under various experimental conditions that examined how saccade amplitude (size) and eccentricity of targets (location of object relative to central fixation) influence our ability to track moving objects while only egocentric information (encoding the location of another object relative to one's own body) is available. Chapter Three describes Experiment 2 where participants performed a similar transsaccadic task as in Experiment 1, but this time the target moved on top of a background which consisted of alternating black and grey bars of varying number. These background cues could either be motionless, move with target motion, or move against the target. The purpose of this experiment was to determine the extent to which allocentric information (encoding the location of objects relative to one another) enhances transsaccadic tracking of motion stimuli. Each experiment chapter will conclude with a discussion of their respective results. The final chapter will include a summary of both experiments, review of the main findings, and discussion

of how this research integrates with past transsaccadic perception theories. The chapter will conclude with a discussion of the limitations of the study and directions for future research.

Anatomy of the Visual System

The eye is composed of several structures which all work together to achieve our visual representation of the world. Figure 1.1 shows a diagram depicting the overall structure and major parts of the eye. Light entering the eye through the pupil is refracted by the lens so that the light is focused on the fovea centralis, a small area at the back of the retina. As a consequence of this refraction, visual images are inverted when projected onto our retina. This causes retinal images to be ambiguous and in turn requires the brain to invert the images again in order for us to perceive the world in its true orientation (Meister & Tessier-Lavigne, 2013).

The surface of the retina is comprised of several specialized receptor cells, more commonly known as photoreceptors, which are involved in transducing light energy into neural signals to be transmitted to the brain. In humans there are two types of photoreceptors, rods and cones, which differ in several ways, namely their sensitivity to light, colour processing capabilities, acuity, and distribution. Rods are highly sensitive to light, as they are able to signal the absorption of a single photon and are responsible for vision during dim light, such as moonlight (Meister & Tessier-Lavigne, 2013). Cones, on the other hand, are less sensitive to light and make little contribution to our vision during night but are mainly responsible for vision in daylight (Meister & Tessier-Lavigne, 2013). Cones also process colour due to three types of cone photoreceptors that respond to long, short, and medium wave lengths (Meister & Tessier-Lavigne, 2013). In addition to these differences, rods and cones have different distributions across the retina. The fovea is densely packed with cone photoreceptors, approximately 125,000-180,000 cones/mm² (Jonas, Schneider, & Naumann, 1992). This area is only about 1.5mm wide

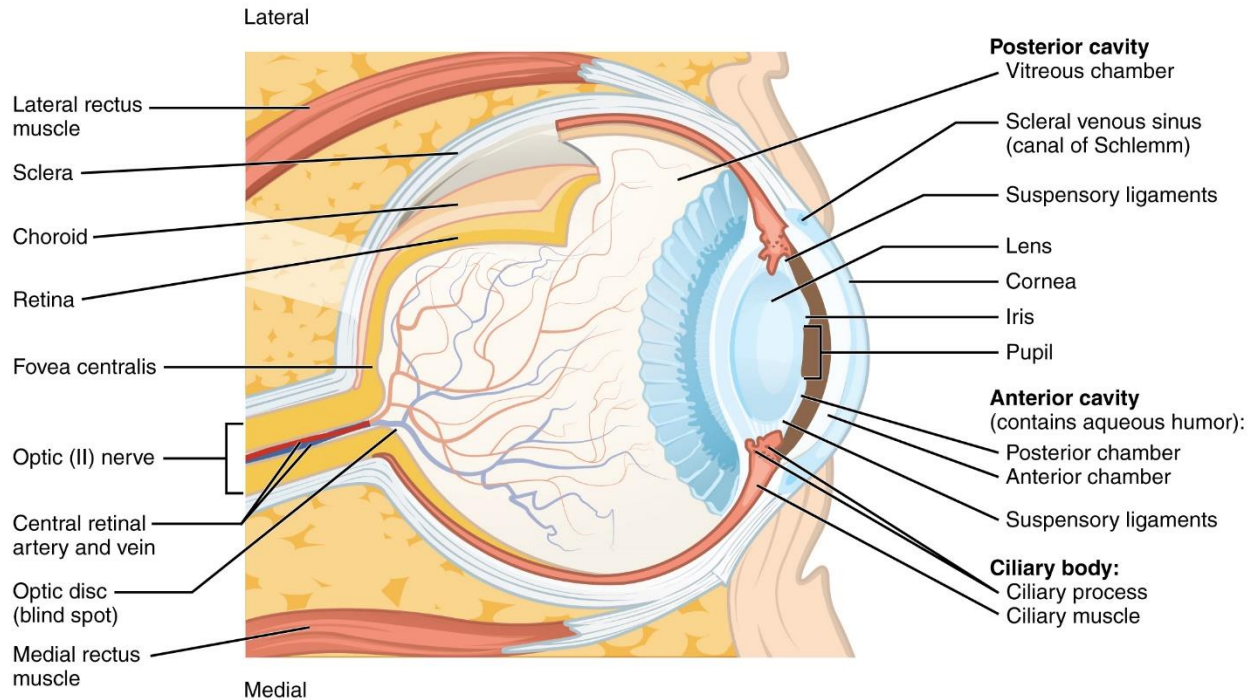


Figure 1.1. Anatomy of the eye. Light enters the eye through the pupil and is magnified by the lens to focus the light onto the back of the retina on a region called the fovea centralis. The fovea is a small area on the retina and is densely packed with cone photoreceptors, which provide high visual acuity and colour information. The densities of cones and rods rapidly decreases and increases, respectively, as distance from fovea increases into the peripheral region of the retina. Photoreceptors within the retina process raw spatiotemporal information and project the signals along the optic nerve which exits at the back of the eye. Reprinted from *Anatomy and Physiology* (p 617) by J.G. Betts et al., 2017, Texas: OpenStax.

and accounts for only 1% of our retina (Jerath, Crawford, & Barnes, 2015). Due to this high density of photoreceptors in the area it results in very detailed and fine resolution of images (i.e. high acuity). Surrounding the fovea is the macula, a 4mm area around the fovea of densely packed rods, 75,000-150,000 rods/mm², which is responsible for the majority of our vision at night when light levels are low (Jerath, Crawford, & Barnes, 2015). The macula accounts for approximately another 2.6% of our retina (Jonas et al., 1992; Peyman, Meffert, Chou, & Conway, 2001; Yanoff & Sassani, 2009). Moving further into the peripheral regions of the retina the density of cones continues to decline, ~6,000 cones/mm², and is populated with a sparse distribution of rods, 40,000 rods/mm², thus providing poor visual acuity in our peripheral visual field (Jonas et al., 1992). This overall retinal circuitry of rods and cones extracts the raw spatial and temporal information from the projected images.

Photoreceptors transmit their neural signals to retinal ganglion cells, which make up the optic nerve that leaves the eye and project to subcortical structures. Connections here are more complicated than some other sensory areas, this is due to the way in which contralateral processing occurs in the visual system (Betts et al., 2017). As Figure 1.2 illustrates, the visual field is divided in half, with each eye viewing a certain proportion of the visual field and with some overlap between each eye. The retina of each eye is also divided into two halves (also known as hemiretina; Betts et al., 2017). The left side of the visual field is projected onto the right sides of both eyes (the right temporal hemiretina and the left nasal hemiretina), whereas the right side of the visual field is projected on left sides of both eyes (left temporal hemiretina and right nasal hemiretina). Within these hemiretina, the retinal ganglion cells travel down different pathways towards the brain. The retinal ganglion cells from the medial side of each retina (i.e. the two nasal hemiretina) are directed toward the contralateral side of the brain, while retinal

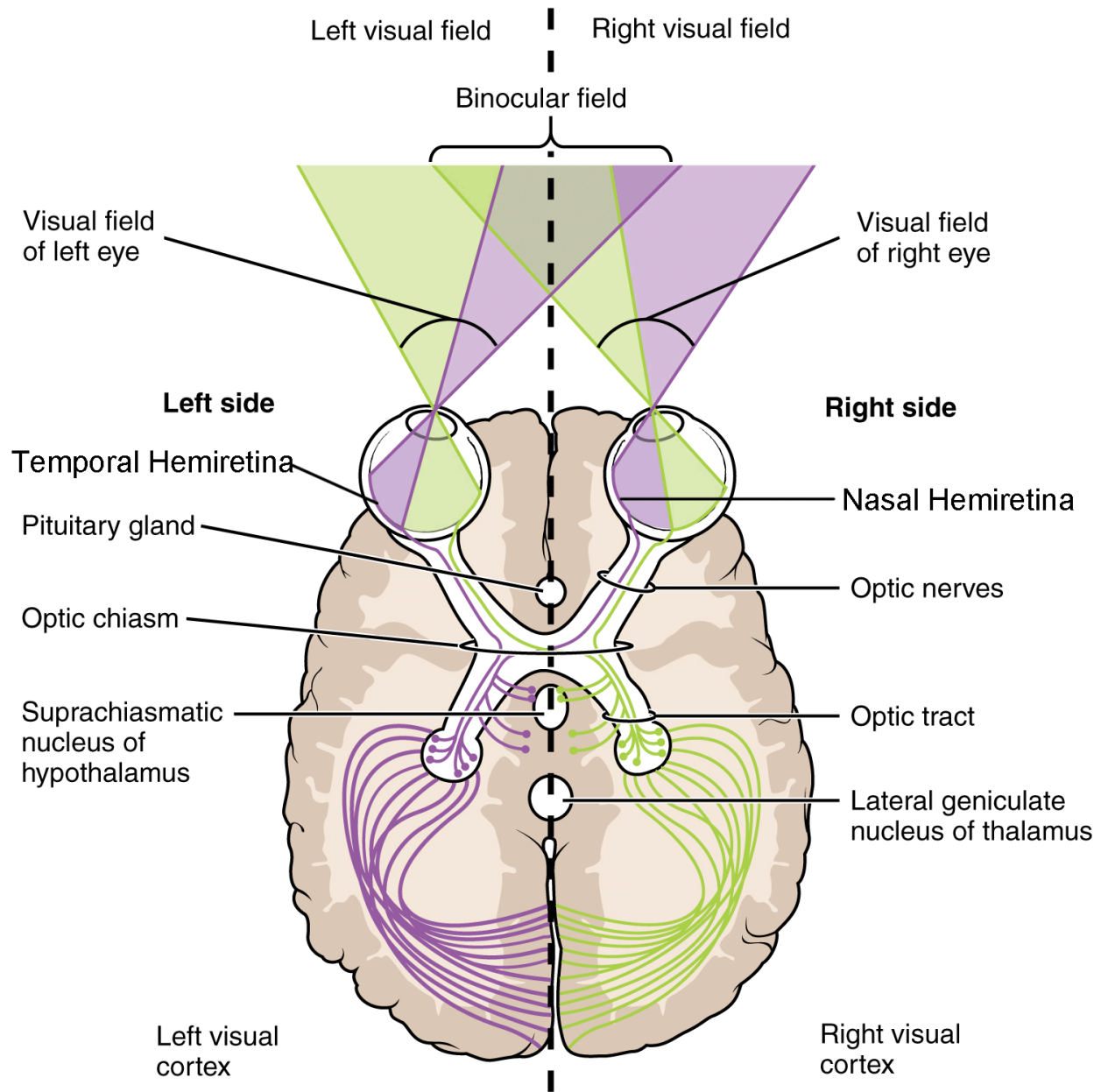


Figure 1.2. Cortical pathways of the visual system. Signals project from the optic nerve into the optic chiasm through lateralized pathways which correspond to the medial and lateral sides of each retina. Continuing from the optic chiasm retinal signals project along the optic track into the lateral geniculate nucleus, suprachiasmatic nucleus, pretectum, and the superior colliculus. Signals from the lateral geniculate nucleus and superior colliculus are finally projected to several other areas involved in sensory processing, the majority of which terminate at the primary visual cortex. Modified from Anatomy and Physiology (p 627) by J.G. Betts et al., 2017, Texas: OpenStax.

ganglion cells from the lateral side of each retina (i.e. the two temporal hemiretina) project to the ipsilateral side of the brain. This arrangement means that visual information from the left visual field is processed by the right subcortical structures and right early visual areas in the neocortex (green pathway in Figure 1.2). Visual information from the right visual field is processed by left subcortical structures and then the left early visual areas (purple pathway in Figure 1.2). The optic nerve of each eye projects signals to the optic chiasm where the ipsilateral visual field information decussates (Betts et al., 2017).

Continuing from the optic chiasm, retinal ganglion axons project along the optic tract and terminates at four major areas. The majority of retinal ganglion inputs (85-95%) go to the lateral geniculate nucleus (LGN; Kerschensteiner & Guido, 2017). The remaining inputs send retinal signals to the suprachiasmatic nucleus (SCN) of the hypothalamus, pretectum of the midbrain, and the superior colliculus (SC). Of these areas, only the signals continuing from the LGN and SC play a role in visual processing (Colby & Goldberg, 1999). Signals sent to the pretectum help control the pupillary light reflex (Gilbert, 2013). Both the SC and LGN are layered structures with several levels that are dedicated to different kinds of visual processing. The LGN is composed of six primary layers, four upper parvocellular layers and two deep magnocellular layers. Smaller layers of extremely small koniocellular cells separate these primary layers. A detailed account of the various kinds of visual processing by parvo, magno, and konio cells is beyond the scope of this literature review. Briefly, parvo cells receive the majority of their inputs from cones and have been shown to transmit information about visual details and colour to the primary visual cortex (Yantis, 2014). Magno cells receive information from the rods and, although they do carry information about visual details or colour, magno cells are specialized in transmitting information about brightness and motion (Yantis, 2014). Konio cells are still a

relatively recently discovered group of cells and not much is known of their function. Research so far indicates Konio cells transmit colour information (Yantis, 2014). Each layer of the LGN receives input from one eye, therefore LGN neurons are monocular (Anderson, Dakin, & Tees, 2009; Jones, 1985; Shatz, 1996). Moreover, each LGN cell on a specific layer responds to information from specific photoreceptors in the retina, a phenomenon known as retinotopic organization. That is to say, if the visual world was mapped via the location of photoreceptor cells within the retina, that same retinal map would correspond to cells within the LGN. Therefore, retinotopic organization can be seen as a brain area being organized as a map of our visual world.

Like the LGN, the SC can also be grouped into broad layers, the superficial layers and the deeper layers. These superficial layers of the SC are also retinotopically organized and are exclusively involved in visual processing. The deeper layers respond to not only visual information but also processing other sensory stimuli (Calvert, Hansen, Iversen, & Brammer, 2001; Leo, Bertini, de Pellegrino, & Làdavias, 2008; Meredith & Stein, 1986; Wallace, Meredith, & Stein, 1998). Additionally, these deep layers contain motor-related neurons which have been found to be involved in activation of eye movements (Gandhi & Katnani, 2011). In order to control eye movements, so-called burst neurons fire at high frequencies just before and during a saccade. The frequency of the bursts determines the speed of the saccade, whereas the duration of the burst determines the duration of the saccade (Goldberg & Walker, 2013). It is generally thought that the SC receives signals from higher oculomotor areas, specifically the frontal eye fields (FEF) and parietal eye fields (PEF), as motor commands for moving the eyes (Goldberg & Walker, 2013). In addition to these motor commands the SC also receives other visual information relayed through the pretectum, primary visual cortex, and secondary visual cortex (Goldberg & Walker, 2013). Outgoing signals from the SC extend to several areas which are

involved in sensory processing, motor control, and generating eye movements (Goldberg & Walker, 2013).

Continuing from the LGN, signals project to the visual cortex located in the occipital lobe. The visual cortex is sectioned into several areas based on the level and type of processing that occurs, with many of the early processing areas displaying retinotopic organization. Up until this point much of the visual network has been primarily feed-forward. However, within the visual cortex and associated areas, the anatomical connections begin to show a substantial increase in feedback circuitry (Yantis, 2014). As signals move through the visual cortex each area increases in the complexity of processing, with initial areas processing simple stimuli characteristics and the higher order areas processing more complex information as well as integrating simple characteristics into a greater whole (Melcher & Colby, 2008; Yantis, 2014). Within the visual cortex, information is first processed at the primary visual cortex (a.k.a. V1 or the striate cortex) which is located at the posterior pole (i.e. tip) of the occipital lobe (see Figure 1.3).

V1 is retinotopically organized, with information from the fovea being processed at the occipital pole and peripheral retinal processing occurring towards the anterior edges of the cortex (Betts et al., 2017). Additionally, the foveal-processing area of V1 is proportionally larger than the peripheral processing regions due to the number of photoreceptors located in the fovea compared to surrounding retinal cells (a phenomenon known as cortical magnification; Yantis, 2014). The earliest visual processing in the neocortex begins in V1, and some have found this processing to be crucial for deciphering both local and global analysis of form (Anzai, Peng, & Van Essen, 2007; von der Heydt, Zhou, & Friedman, 2000). Neurons within V1 respond selectively to specific properties of a stimulus, such as orientation, stereoscopic depth, and

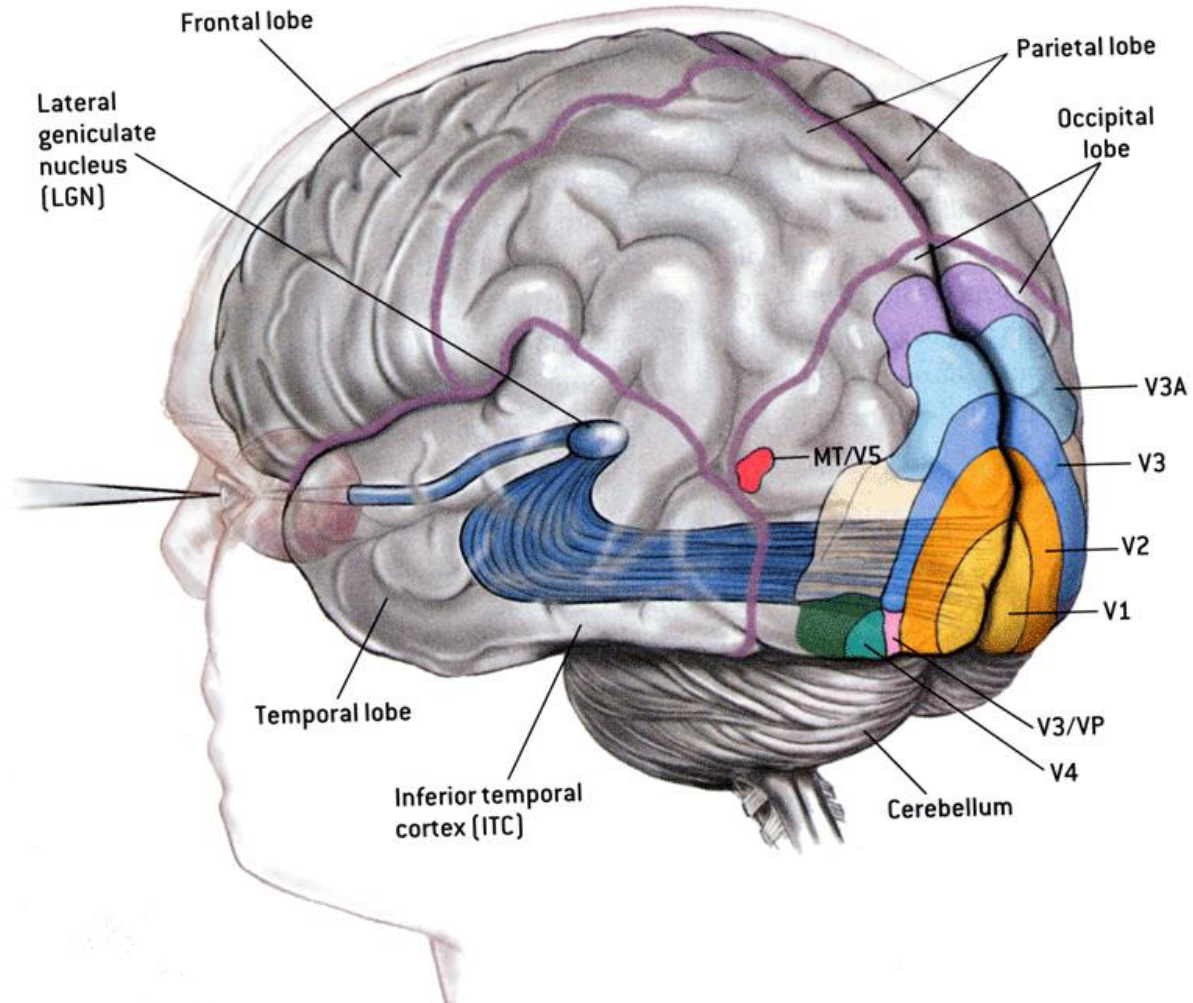


Figure 1.3. Divisions of the visual cortex. Stimuli processing occurs by both serial and parallel networks beginning with the primary visual cortex (V1). V1 is retinotopically organized and is involved in processing information regarding orientation, stereoscopic depth, and direction of movement. V2 is also retinotopically organized and processes orientation, colour, and spatial frequency information. V3 is involved in temporal and colour processing and, in this depiction, is further divided into V3A (which extends into the parietal cortex) and V3/VP (which descends into the temporal cortex). V4 plays a role in colour perception and encoding of complex shapes while V5/MT is a main center for motion processing. Adapted from McGill University (<http://thebrain.mcgill.ca/>).

direction of movement (Gilbert, 2013; Qiu & von der Heydt, 2005). Surrounding V1 are extrastriate visual areas, including V2, V3, V4, and V5/MT+. V2 receives strong feed-forward signals from V1 and projects strong connections to V3, V4, and V5/MT+, as well as sending feedback connections to V1 (Gattas, Sousa, Mishkin, & Ungerleider, 1997). Like V1, V2 is retinotopically organized and is involved in processing simple properties of visual stimuli, such as orientation, colour, and spatial frequency (Yantis, 2014). V2 is the first region within the visual association area, and therefore, is also involved in more complex processing of images, such as illusory contours, binocular fusion for seeing depth, and distinguishing figures from the ground (Anzai, Peng, & Van Essen, 2007; Maruko et al., 2008; Qiu & von der Heydt, 2005; von der Heydt, Peterhans, & Baumgartner, 1984; von der Heydt, Zhou, & Friedman, 2000). V3 is located adjacent to V2, and while there is still some controversy regarding how far V3 extends into the surrounding cortex and its full function, it has been found to be involved in temporal and colour processing (Gegenfurtner, Kiper, & Levitt, 1997). From here the neural projections carrying visual information for more elaborate processing are broadly segregated into two visual streams originating around area V3. One pathway projects from V3A to the parietal cortex and is known as the dorsal stream, while the other projects from V3/VP (ventral posterior area) to the inferior temporal cortex and is known as the ventral stream (Gilbert, 2013; Rizzolatti & Strick). These two visual processing streams are depicted in Figure 1.4.

One of the first structures along the dorsal stream, in the middle temporal region, is V5/MT+ which is a crucial area for visual motion processing (see Figure 1.3; Yantis, 2014). V5/MT+ is composed of cells that are selectively responsive to motion direction and speed (Beckers & Zeki, 1995; Gysen, Varfaillie, & De Graef, 2002; Yamasaki, Muranaka, Kaseda, Mimori, & Tobimatsu, 2012). Also included in this dorsal stream of visual processing is V6

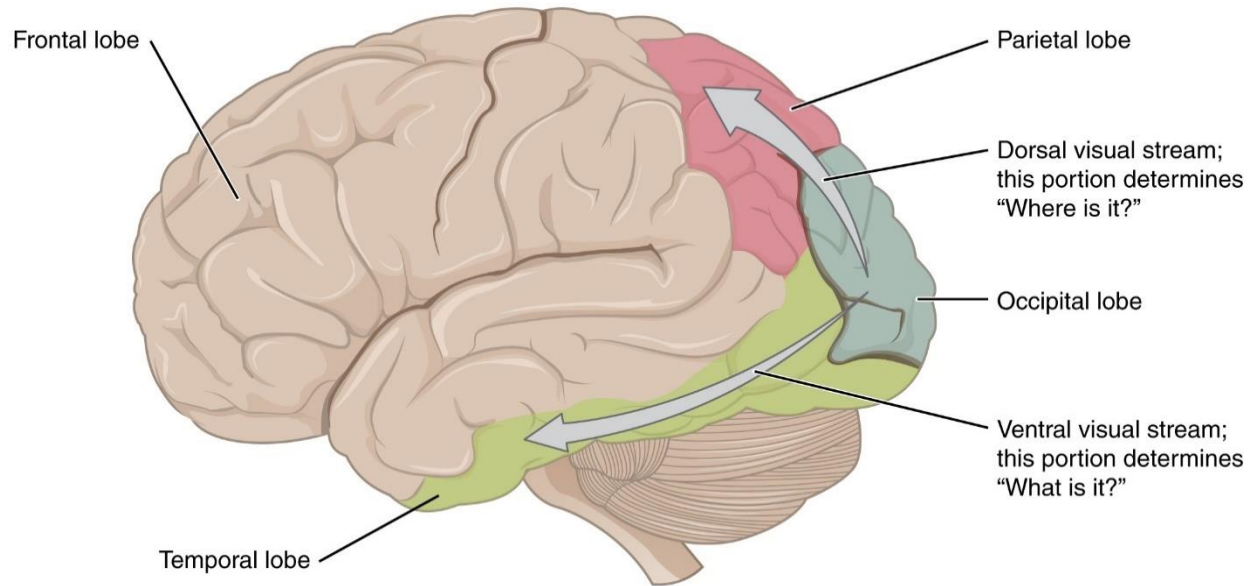


Figure 1.4. The ventral and dorsal visual streams. There are two main divisions of visual processing both of which begin at V1. The dorsal stream stretched forward into the parietal lobe and is known for guided actions and processing object location. The ventral stream connects into the medial temporal lobe and is involved in object recognition. Reprinted from *Anatomy and Physiology* (p 634) by J.G. Betts et al., 2017, Texas: OpenStax.

(located in the parieto-occipital sulcus and along the medial longitudinal fissure). V6 also has cells that respond selectively to visual motion direction (Pitzalis, Fattori, & Galletti, 2012). Recent evidence in human and macaque studies have shown both V5/MT+ and V6 to be retinotopically organized and the receptive field cells to be much larger than the cells in V1 (Yamasaki et al., 2012). The dorsal stream terminates in the posterior parietal lobule, which consists of various structures that play roles in visual spatial and motion processing (Livingstone & Hubel, 1988; Tobimatsu & Celesia, 2006). These projections from V5 /MT+ into neighboring parietal areas, such as the lateral intraparietal area (LIP; Andersen, 1989; Ruff, 2008; Ungerleider & Desimone, 1986), precuneus, and the superior parietal lobule (Andersen, 1989; Andersen, 1987), are thought to be used in predicting the spatial location of tracked targets and therefore coordinating eye movements in order to saccade to the predicted location (Andersen, 1989; Jovicich et al., 2001; Yantis, 2014). Due to its specialized role in the spatial processing of visual stimuli, the dorsal stream has become more commonly known as the “where” pathway (Yantis, 2014).

The ventral stream projects through area V4, which has been shown to play a role in colour perception and encoding more complex visual shapes (Gilbert, 2013; Yamasaki et al., 2012). Information from V4 is projected to the inferior temporal lobe. These temporal cells selectively respond to specific visual stimuli and show evidence of high-level visual processing as they are responsive to whole and complex shapes, such as a hand or house, rather than simple features like the cells in V1 that are sensitive to only simple line orientations (Albright, 2013; Chelazzi, Miller, Duncan, & Desimone, 1993; Gilbert, 2013). Moreover, inferior temporal cells have relatively large receptive fields that extend beyond the fovea into the peripheral visual field (Chelazzi et al., 1993; Rolls, Aggelopoulos, & Zheng, 2003). Due to this they respond to the

presence of specific visual objects regardless of where that object is located on the retina (that is to say, inferior cells are location independent; Fournier, Müller, Schneider, & Laurent, 2018). Therefore, this stream is crucial for object recognition and has fittingly been named the “what” pathway (Albright, 2013; Gilbert, 2013). Both dorsal and ventral streams send signals back down to lower visual areas via re-entrant pathways.

The Stable World Problem

As just discussed, due to the small retinal region that processes information in high resolution (i.e. macula and fovea), humans must make multiple eye movements in order to focus their center of sight and clearly view stimuli in their environment. If humans were incapable of moving their eyes our vision would be much like an owl’s, whose eyes are fixed into sclerotic tubes and are unable to move their eyes. In order for an owl to foveate on an object it must twist and turn its head and body. This results in a very inefficient way of scanning the surroundings, since it takes more energy and much longer time to turn one’s head than make a saccade. However, humans do not have this problem since we are able to move our eyes within our eye sockets, looking around our environment relatively independently of our head’s position. While scanning our world we make approximately 2-3 saccades per second (Henderson, 2003) with a single saccade usually lasting less than 40ms (Henderson & Hollingworth, 1999; Prime, Niemeier, & Crawford, 2006). Typically, saccades reflect the attentional shifts and cognitive processes of the individual. Yarbus (1967) seminal work on eye tracking showed how people make strategic and stereotypical scan paths when visually inspecting a scene or object. He found that individuals tended to fixate on areas of interest, like people’s faces, and ignored background objects. This shifting of attention, and therefore fixation, allows us to accurately determine events occurring in our environment and plan actions in accordance with those. Yet due to their

fast paced and abrupt nature, saccades create a unique challenge in understanding how the visual system is able to create a stable and consistent perception of our environment.

During saccadic eye movements the visual world dramatically and rapidly shifts across the retina. This rapid shift of information results in a so-called ‘retinal smear’ of the visual world (Bedell & Lott, 1996; Festinger & Holtzman, 1978; Monty & Senders, 1976). For example, imagine you are taking a photo. Moving the camera during the photo results in a blurred photograph. A similar principle happens during a saccade, since the image of the world is “smeared” across the retina as the eyes move. Retinal smearing during saccades typically goes unnoticed due to a decrease in, or suppression of, visual processing during a saccade, a phenomenon known as saccadic suppression (Matin, 1974). In one of the first studies on saccadic suppression, Jeannerod and Chouvet (1973) found that rapid shifts in the visual field resulted in reduced activity in the optic tract, LGN, and visual cortex. Additionally, Latour (1962) found that this suppression began before saccade movement onset. Some have theorized that this suppression is a mechanism the visual system utilizes in order to avoid any adverse effects of retinal smear (Campbell & Wurtz, 1978). In order to experience, and become more aware of this saccadic suppression, all you need is a mirror. If you look into a mirror and glance from one eye to the other, you are unable to see your own eyes move. However, if you watch someone else do this task you can see their eye movements. The inability to see your own eyes move is due to saccadic suppression.

While saccadic suppression may aid the visual system in avoiding disorientation, due to retinal smear, it also temporally separates the images we see as we move our eyes to view our world. Additionally, these images are projected to different retinal locations after each successive saccade. For example, imagine you are sitting at your desk, working on a paper and enjoying a

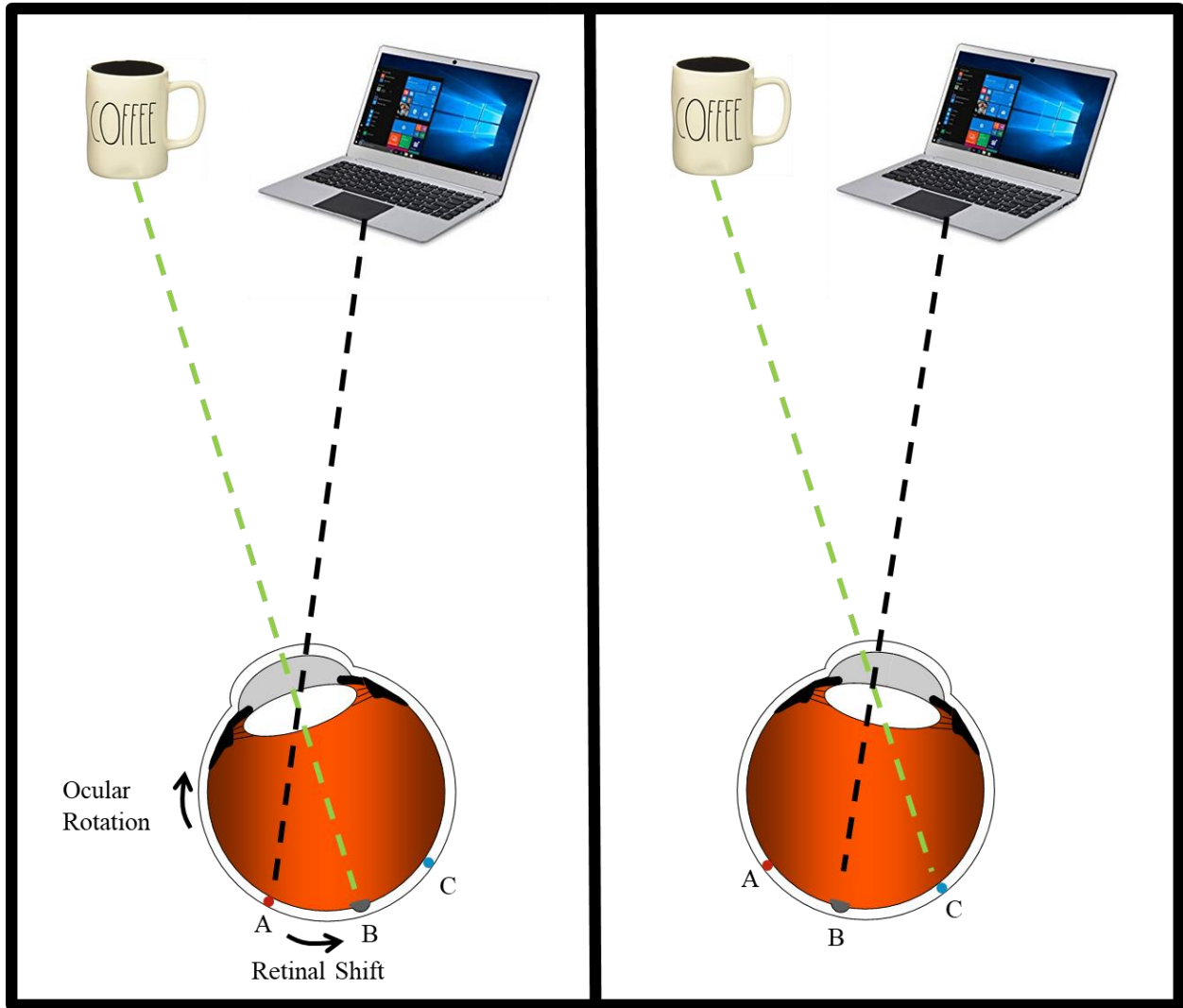


Figure 1.5. Retinal shifts during saccades. While fixating on the coffee mug the image of the computer is projected onto retinal cells “A”. Once a saccade is initiated, the image of the computer is shifted across the retinal cells between point A and B, from the lateral side to central fixation. After a saccade is made to the computer is now projected onto retinal cells “B”. However, even though these retinal coordinates changed the coffee mug and computer did not appear to “move” in the real world since the visual system knows the retinal shift was due to the eye movement.

cup of coffee. First, you look down at your coffee mug and fixate on it (Figure 1.5 left panel). The image of your coffee mug is currently being projected onto your fovea (retinal cells 'B') with the computer in your peripheral vision (falling onto retinal cells 'A'). Now you decide to look from your coffee to your computer. So, you make a saccade toward your computer, which results in the image of your computer shifting across the retina from point 'A' to 'B' while the image of the coffee mug shifts from retinal cells 'B' to 'C' (Figure 1.5 right panel). Due to saccadic suppression you do not consciously perceive the image shift across your retinal cells (a process known as retinal shift). However, both objects are projected onto different retinal locations as a consequence of the saccade. Therefore, the visual system would need some type of mechanism to account for these retinal shifts and integrate the information.

Complicating this process is the fact that the same retinal shift can occur when an object moves in our visual field. Imagine again you are sitting at your computer, looking appreciatively at your coffee (see Figure 1.6). As you gaze at your coffee mug a fly lands on your computer (Figure 1.6 right panel). Again, the coffee mug is projected onto the foveal cells 'B' while the fly (and computer) is projected onto peripheral cells 'A'. The fly then takes off, moving toward your coffee mug, while you keep staring at your coffee. Here the fly's image shifts across your retinal cells from point 'A' to point 'B'. Yet this time we do perceive that retinal shift even though it is the exact same shift ('A' to 'B') that occurred when we made a saccade (compare Figure 1.5 and Figure 1.6). The only difference being that in this context there was no eye movement, therefore, our visual system perceived the retinal shift to be movement of an object (the fly), rather than side-effects of the saccade. The fact that these changes in retinal locations are not confused with movement of the stimulus in the world suggests the visual system anticipates the retinal shift when it is caused by a saccade versus a moving target. In later sections of this chapter I will

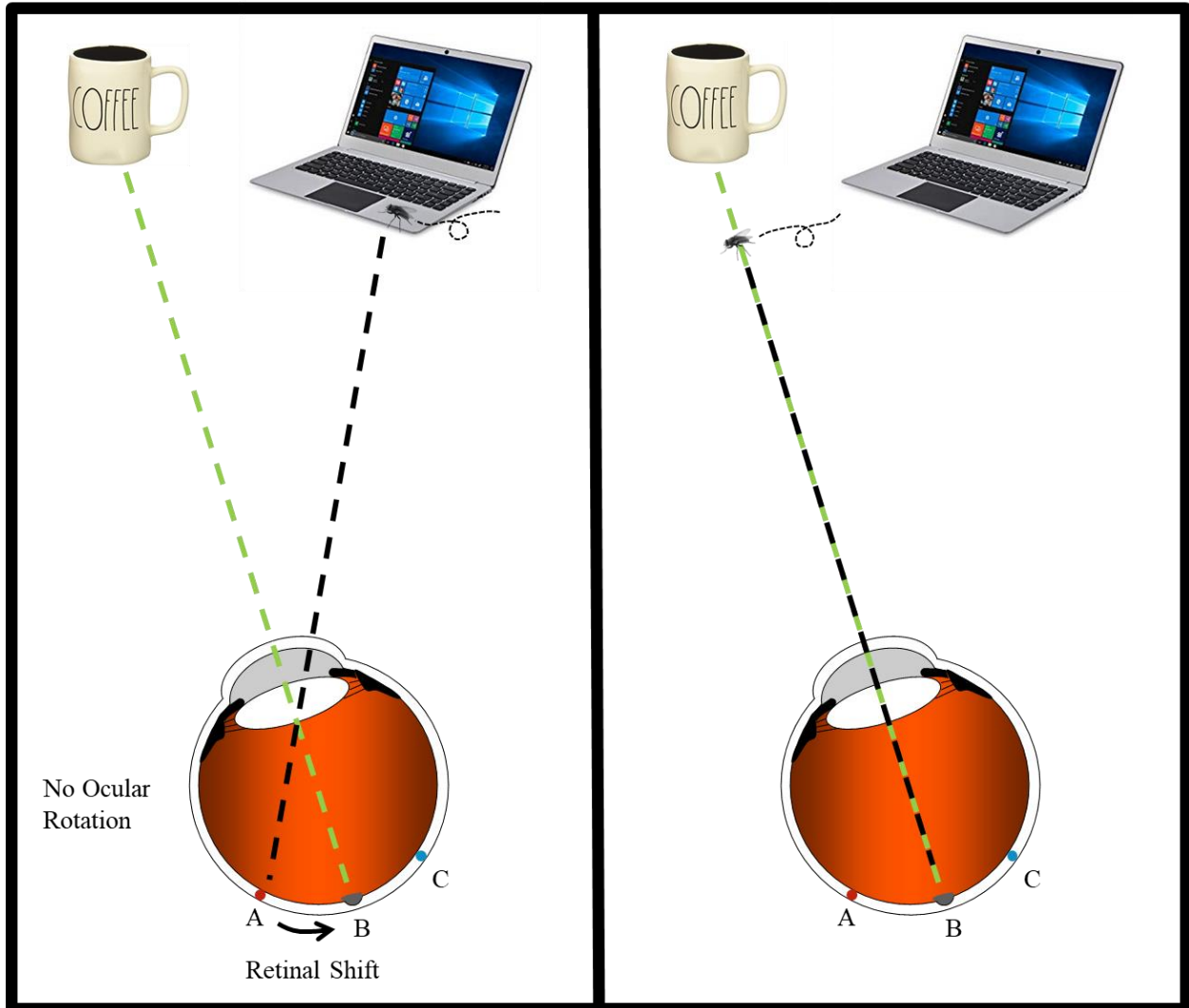


Figure 1.6. Retinal shifts during fixation. While fixated on the coffee mug the image of the fly is projected onto retinal cells “A”. While the fly moves across the environment the image also shifts across the retinal cells between point A and B, from the lateral side to central fixation. At the end of the scene the image of the fly is now projected onto retinal cells “B”. In this case we do perceive the fly to have moved across our environment, yet in Figure 1.5 the environment remained stable even though the exact same retinal shift process occurred.

further expand on the concept of how the brain accounts for retinal shifts during saccades versus fixation.

As demonstrated, these predictions and calculations performed by the visual system are quite complicated. Exactly how our visual system deciphers when retinal shifts are important and when they are not is still quite unclear. The system cannot simply ignore retinal shift, since that information is valuable when tracking moving objects during smooth pursuit or when fixated. So, not only must our visual system anticipate saccades in order to ignore the resultant blur through saccadic suppression, but it also must predict where on the retina images in our world will be projected after the saccade is completed. Furthermore, if there are moving objects in the world it must predict how fast and in what direction those objects are moving in order to determine their future retinal coordinates. This requires the visual system to calculate both the velocity of the object and the eye. Then compute how those velocities will interact in order to accurately view our world. These transsaccadic perception processes are important in understand the stable world problem, or how do we perceive our world as stable despite these complications?

Theories of Transsaccadic Perception

Early findings appeared to suggest that the brain creates multiple clear and accurate representations of the visual world across several fixations via a highly detailed and accurate spatial buffer, and our perception of the world was the summed representation of those “snapshots” (for an example of this “snapshot” integration see Figure 1.7; Goldberg & Wurtz, 2013). This information then would allow for detailed knowledge about changes in our visual world, with little chance of error (Jonides et al., 1982; McConkie & Rayner, 1976). An example of a typical transsaccadic perception test is shown in Figure 1.8. In these early tasks, participants



Figure 1.7. Theoretic depiction of how the visual system combines saccadic snapshots. Early theories of transsaccadic perception proposed we perceived our world by piecing together visual “snapshots”, that is visual images of the world occurring during fixation which are cut off during a saccade. Further evidence found that this theory does not account for the complexity of vision processes. Used with the permission of the author, retrieved from https://commons.wikimedia.org/wiki/File:Installation_1_to_2001_collage.jpg

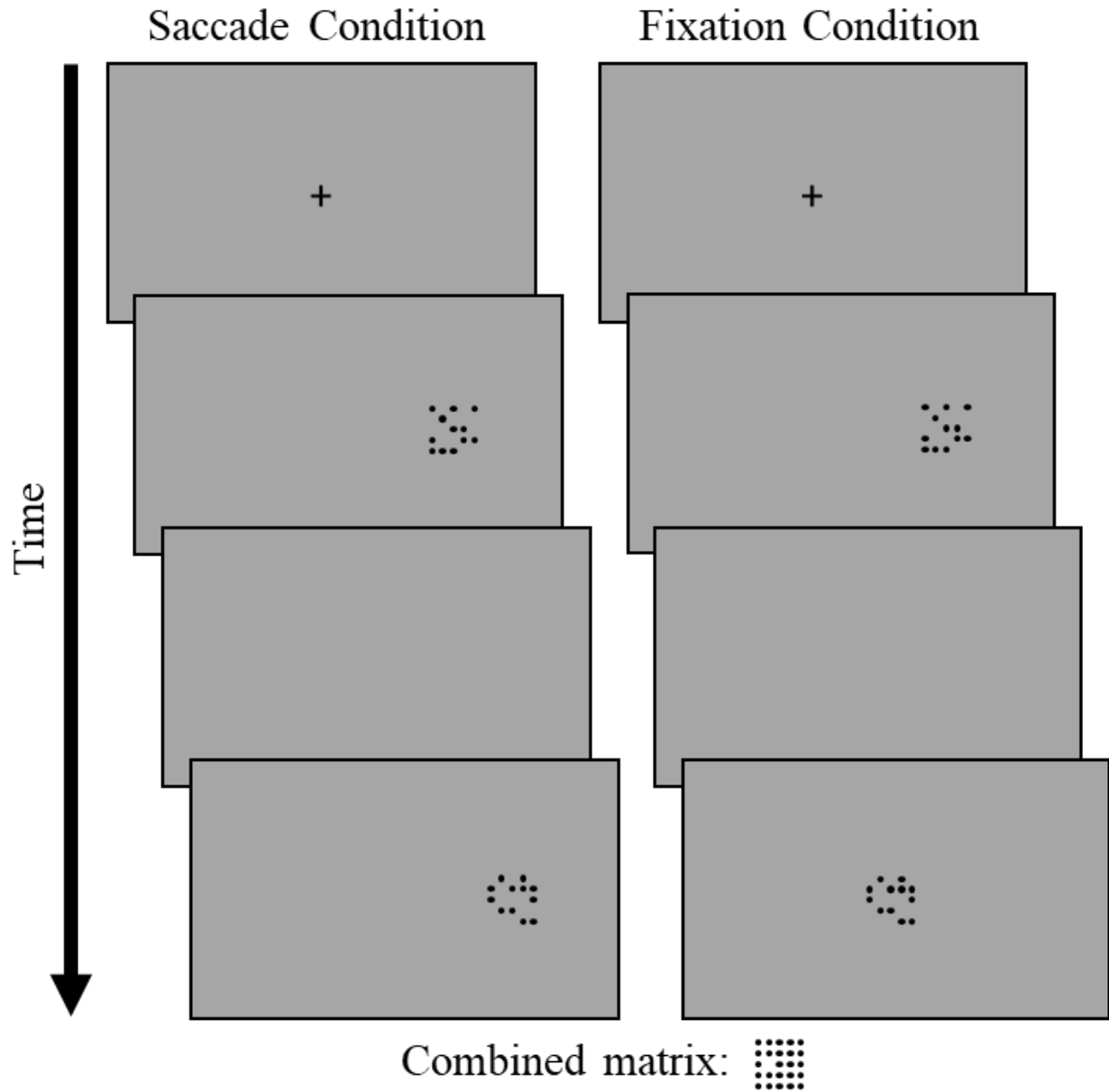


Figure 1.8. Example of an early transsaccadic memory task. A 24-dot matrix with one dot missing would be presented to participants in two parts. First, a fixation-cross appeared to indicate central fixation. Then the first 12 dots were presented followed by a blank interval where participants were instructed to either saccade to the location of the matrix (saccade condition) or maintain fixation (fixation condition). Finally, the remaining 12 dots were presented. If memory of the initial partial matrix was intact participants would perceive the full dot matrix (shown below as the combined matrix) and indicate which dot was missing.

would be asked to identify the location of a missing dot from a dot matrix (Di Lollo, 1977; Di Lollo, 1980; Jonides et al., 1982). The example shown in Figure 1.8 shows this task occurring in two different contexts, one where participants were asked to make a saccade (left panel) and the other where they maintained fixation (right panel). In both tasks one half of the matrix was shown followed by the second half after a saccade or a blanking screen. In the saccade task, participants were instructed to saccade to the second half of the matrix as soon as it appeared (i.e. after the blank screen shown in Figure 1.8). In the example this saccade results in the image shifting from peripheral retinal cells to central, foveal, cells. In the fixation task participants continued to stare at the center of the screen throughout the trial. After the first matrix is presented the screen is blanked to simulate a saccade and then the second half of the matrix is presented at fixation. In this condition the image also shifts from peripheral to foveal cells. In both tasks participants had high accuracies for detecting which dot was missing (Di Lollo, 1980). Due to the complicated nature of this task it was thought that it would be practically impossible to accomplish unless there was some type of visual buffer to bridge the blanking or saccadic gap (Di Lollo, 1980). Despite these early results indicating high accuracy within the visual system, it was later discovered that there were methodological flaws that allowed participants to cheat at the tasks.

Specifically, when a stimulus was presented on a screen and then blanked or displaced, the original location of the stimulus was still visible in the form of a persistent afterimage on the screen (i.e. some lingering phosphor persistence on the display) allowing participants to cheat on the task by comparing the new image with the old dimming image. Once advances were made in technology, researchers had access to better visual displays that eliminated visual persistence and reduced pixel burn in. After these advances researchers began to find that little information was

retained across saccades (Bridgeman, Hendry, & Stark, 1975; Irwin, Brown, & Sun, 1988; Irwin, Yantis, & Jonides, 1983; McConkie & Zola, 1979; O'Regan & Levy-Schoen, 1983; Rayner, McConkie, & Zola, 1980; Rayner & Pollatsek, 1983).

When examining change blindness (detecting whether an object has suddenly disappeared from a scene or not) during a saccade tasks, researchers found that even large scene changes went unnoticed (Grimes, 1996; O'Regan, Deubel, Clark, & Rensink, 2000; Simons, 1996). This occurred even when participants were instructed to watch for changes in the scene (Goldberg & Wurtz, 2013). Evidence that participants failed to notice changes, or retain information across saccades, led to the proposal of the blank slate hypothesis, which stated that no memory is retained across eye movements. In this hypothesis it was thought that our ability to track and monitor stimuli in our environment is due to repeated “sampling” of the external world through eye movements (Bridgeman, Van der Heijden, & Velichkovsky, 1994; O'Regan, 1992; Tatler, 2001). MacKay (1967) proposed that not only is it inefficient to hold an internal representation of the outside world, but that we are simply unable to do so. Therefore, instead of creating an internal memory store, our visual system utilizes the environment as an “external memory store” which it samples from upon each successive saccade. Constructing the environment at each fixation and wiping that image from “memory” during eye movements (MacKay, 1967; O'Regan, 1992). While this theory did account for some failures and illusions in visual processing, there are several problems with the blank slate hypothesis.

For one thing, if there is no internal memory storage we would be unlikely remember what, or at least where, objects are after looking away from them. Human vision would be constantly plagued by the inability to understand object permanence. Also, humans are clearly able to interact with objects outside of our visual field. If you turn your head and look away from

your computer, you are still able to reach behind yourself and touch your computer screen. The ability to do this implies that there is some enduring internal spatial memory of the environment around you. Furthermore, the blank slate hypothesis suggests that observers would visually process the world anew each time we shifted our gaze or even blink. This implies greater processing demands on the visual system since a new representation of our environment would be created 2-5 times per second (Henderson, 2003; Rayner, 1998) and would also require the subsequent processing of information each time.

More recent studies have clearly shown that information can be remembered and integrated across saccades (Bosco, Lappe, & Fattori, 2015; Fracasso, Caramazza, & Melcher, 2010; Herwig, 2015; Ibbotson & Krekelberg, 2011; Melcher & Colby, 2008; Prime et al., 2006; Prime, Tsotsos, Keith, & Crawford, 2007; Verfaillie, 1997; Wolf & Schütz, 2015), suggesting at least some visual information is stored in visual memory across saccades and combined with the visual contents from other fixations (Prime et al., 2007). Prime and colleagues (2007) showed that the amount of information retained across a single saccade is similar to visual working memory, approximately 3-4 items. They postulated that the same memory system mediating visual working memory might also be utilized in transsaccadic memory. Other studies have found that attention seems to also play a role in transsaccadic perception, since if attention is directed towards an object, or a stimulus is altered enough to capture attention, then changes in that stimulus can be detected more reliably (Cavanagh, Hunt, Afraz, & Rolf, 2010; Fracasso et al., 2010; Higgins & Rayner, 2015). Currently, there seems to be a consensus in the literature that attention facilitates transsaccadic memory and salient stimuli are more reliably tracked across saccades (Gottlieb, Kusunoki, & Goldberg, 1998; Melcher & Colby, 2008).

This leaves the question of what happens to the rest of the visual information in our environment (e.g. the background) that is not attended to? Ernst Gombrich (1979) applied a popular art theory, called the ‘etcetera principle’, to describe why background information may or may not be integrated across saccades. In art there is a point at which the background detail is ignored and simply becomes the scene (forest, beach, etc.) on which more interesting stimuli are displayed. When viewing art, we assume the background on which stimuli are displayed will be more or less consistent and provide only basic information to aid us in analyzing the main focus of the art (Gombrich, 1979). A similar principle in psychology exists called ‘gist’, wherein our visual system interprets the meaning of a scene based on the information that can be collected in a single glance. The gist of a scene is abstract and not always detailed depending on how far it is in the distance or our periphery. Therefore, the visual system may not prioritize integrating gist compared to other, more salient, visual stimuli between saccades.

Studies examining change blindness have found that we only become sensitive to changes in a scene’s background when it violates the general layout of the scene (i.e. the gist; O’Regan & Noe, 2001; Simons & Rensink, 2005). The change goes unnoticed when the items are non-salient or do not affect the overall scene. It is thought that the benefit of integrating the entire scene across saccades is greatly outweighed by the lack of valuable information that would be gained and the high processing costs that information would come at (Melcher & Colby, 2008). Additionally, the chances of background information drastically changing during a saccade is highly unlikely in a natural setting. It is uncommon for trees to suddenly fall or buildings to disappear. Thus, the background information may only be processed superficially, with enough detail to retain the gist of the scene. This allows our visual system to instead focus

on displaying a rich and accurate visual percept of salient objects on an environment full of ‘etcetera’.

In summary, current research shows that at least some visual information is retained across saccades. Exactly what information is retained is still being examined, with several theories proposing that the visual system is limited in capacity and that the visual system attends more often to salient stimuli compared to background or task-irrelevant information (Gottlieb, Kusunoki, & Goldberg, 1998; Melcher & Colby, 2008; O’Regan & Noe, 2001; Prime et al., 2007; Richard et al., 2002; Simons & Rensink, 2005). Therefore, it appears that the visual system is strategic in what information is attended to and integrated across saccades. With this understanding researchers have begun to turn their attention to examining exactly how the visual system integrates information before and after a saccade, a process known as transsaccadic integration.

Transsaccadic Integration

The mechanisms of transsaccadic integration can first be explained by examining what occurs when we foveate on an object. If something in our periphery grabs our attention the following saccade results in the image moving from peripheral rod photoreceptors into central vision, where the fovea (cone photoreceptors) can provide greater detailed visual information. Due to the increased acuity of foveal cells and cortical magnification of V1, the image movement from peripheral cells to foveal cells results in a magnification of the image (an example of this magnification can be seen in Panel A of Figure 1.9). Therefore, our visual system would likely have a mechanism to determine whether the resulting magnification of the object is due to retinal changes or the stimuli moving closer to the eye. For example, imagine you are looking at ants on the ground with a magnifying glass. Before you move the magnifying glass overtop of the ant,

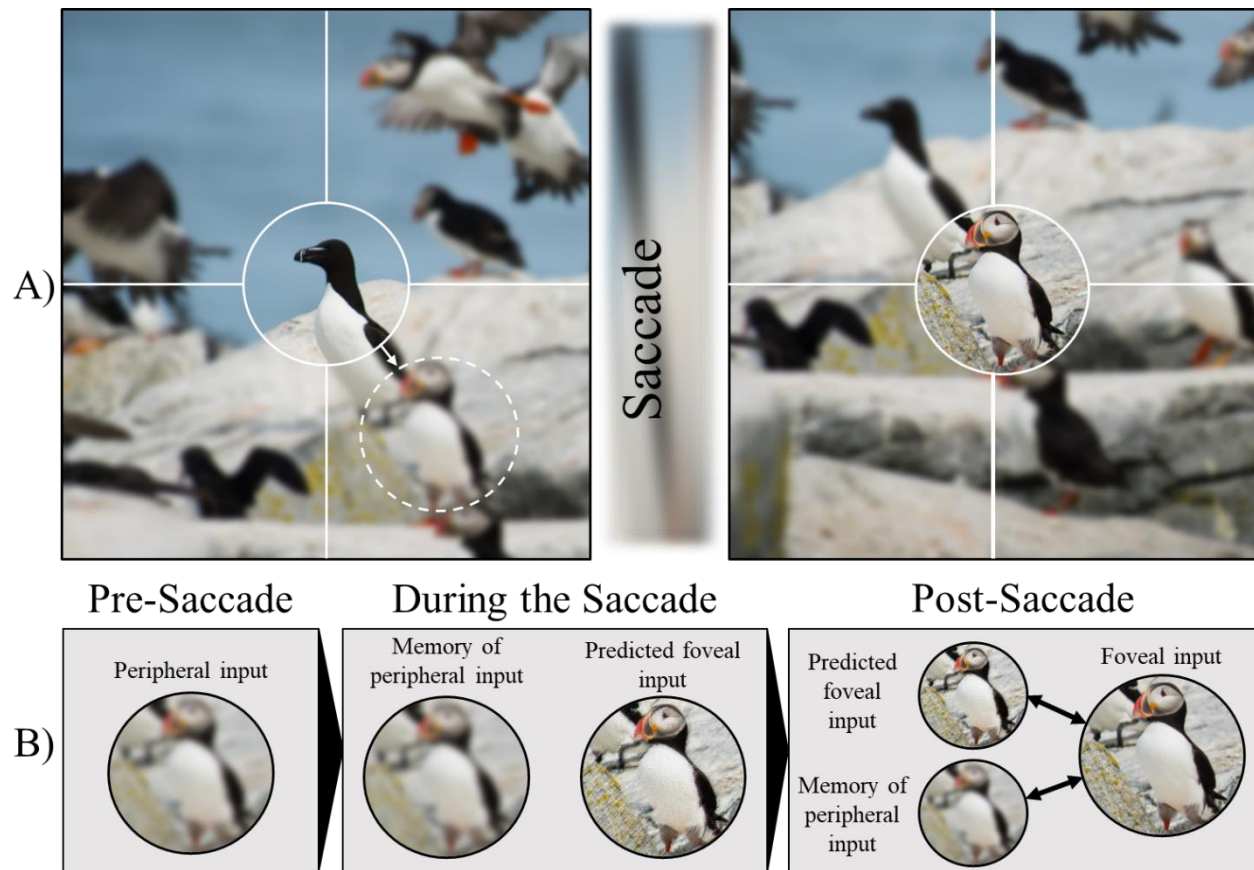


Figure 1.9. Example of transsaccadic integration of stationary object. Panel A shows an example of change in resolution and magnification due to foveation as perceived by V1. The white circle and cross hairs indicate the location of central (foveal) vision while the dotted circle shows the target to which a saccade will be made. When the image of the puffin moves from peripheral vision into central focus it results in a magnification and increase in resolution. This is due to the high acuity of foveal photoreceptors and the cortical magnification of V1. Panel B shows a theoretical depiction of the transsaccadic integration occurring in Panel A. The first step in Panel B shows the peripheral input the visual field is receiving while fixating on the razorbill. Once a saccade is about to be initiated, the peripheral input is stored in a visual memory buffer and the visual system predicts the to-be foveated contents *after* the saccade is completed (i.e. predicts the contents that will be brought into fixation). These processes are shown in the second, during the saccade, step. Once the saccade is completed, the predicted input and peripheral memory is compared to the image of the post-saccade foveal input, as depicted in the post-saccade step. If the post-saccade foveal input is sufficiently similar to the memory and predicted comparisons visual stability is maintained. Photo by Ray Hennessy (2017).

Note: The predicted foveal input in panel B is depicted as slightly pixelized to indicated that it is a prediction made by the visual system and is therefore may not be completely accurate.

you would likely predict that the lens will amplify the ant so you may see it in more detail.

Therefore, when you do view the ants through the magnifying glass, versus your naked eye, you are aware that the ant is being enlarged due to the lens of the glass and do not assume the ant has suddenly grown in size. These predictions, and ability to understand what caused the changes in how you view the object are akin to how the visual system integrates information from one fixation to another.

When we view an object, the visual system integrates and compares pre- and post-saccadic retinal images by taking into account the saccade metrics (e.g. size and direction) and predicted information about our environment. This process is depicted in Figure 1.9. Before a saccade is made the visual system attends to the location the saccade will be made to (indicated by the dotted circle in panel A). Before a saccade is made, a visual image of the scene is retained in some visual memory buffer. Then, the system predicts what the retina image of the scene would be after the saccade is completed, accounting for saccade size and direction. Once the saccade is finished the visual system compares the resulting image (post-saccade foveal input image in Figure 1.9) to the predicted mental representation of the image and the memory of the peripheral input. If the post-saccade image is sufficiently similar to what was predicted and remembered, then visual stability is maintained. This image integration occurs on a point-by-point system, with detailed information being collected at each retinal receptive field prior to the saccade and again after the saccade. The information is then integrated together according to the coordinates of where the images were taken. If the comparisons are not similar, then our visual system may be cued to a change in our environment and we may feel like something is amiss or be more likely to notice what once was a non-attended object.

While the example of transsaccadic integration depicted in Figure 1.9 shows this process for stable stimuli, two birds standing on a rock, objects in our environment are rarely stable and move in several trajectories at different speeds. This complicates the integration processes for the visual system, since tracking moving objects would require the system to not only do all the same calculations involved with stable stimuli but also anticipate the direction and distance travelled during the saccade as well. Prime et al. (2006) postulated several different mechanisms that might underlie perceptual stability across saccades and the calculations the visual system undergoes to maintain that. A simplified version of these calculations can be thought of as the visual system subtracting the saccade amplitude from the tracked object's retinal coordinates to determine whether a change in the stimulus occurred or if it was stationary. For example, if a 5° visual angle¹ saccade was made and the object's retinal coordinates shifted by 5° in the opposite direction, then the system would determine that the stimuli remained stationary and the shift was due to eye movement ($5^\circ_{\text{retinal shift}} - 5^\circ_{\text{saccade size}} = 0^\circ_{\text{change}}$, as shown in Figure 1.5). If instead the object's coordinates shifted by 5° and no saccade was made the visual system would determine that shift was due to the object moving ($5^\circ_{\text{retinal shift}} - 0^\circ_{\text{saccade size}} = 5^\circ_{\text{change}}$, as shown in Figure 1.6). Finally, if there was no retinal shift after a 5° saccade the visual system may determine that the object moved in the same direction and amplitude as the saccade ($0^\circ_{\text{retinal shift}} - 5^\circ_{\text{saccade size}} = -5^\circ_{\text{change}}$, i.e., the same retinal location before saccade). In this case we could conclude the object is moving with our eye movements, for instance when we are tracking moving objects with our eyes.

¹ Hence forth all degree measurements will indicate degree visual angle, unless otherwise indicated. The visual angle of an object is a measurement of the size of the object's image on the retina.

These calculations are a very simple model used to understand how the brain might interpret and analyze object changes during saccades. Currently, the exact mechanisms of transsaccadic perception are quite unclear. Since other variables that can influence transsaccadic perception are not included in this simple model, such as allocentric cues, visual memory, spatial awareness, or vector calculations for moving stimuli. One of the ways we are trying to understand how the complicated mechanisms of transsaccadic integration is by examining the cortical areas that control eye movements, visual memory, and attention.

Cortical Areas Governing Eye Movements and Spatial Remapping

To understand how the visual system might track the location of objects across saccades, we must first discuss the cortical mechanism responsible for controlling eye movements, the characteristics of saccadic eye movements, and a process known as spatial remapping. As shown in Figure 1.10, eye movements are controlled by six extraocular muscles within the eye socket (orbit) organized as 3 antagonist pairs (Goldberg & Walker, 2013). The superior and inferior rectus muscles allow for rotating the eyes up and down, respectively. The medial and lateral rectus muscles allow for rotating the eyes side to side, either toward the side of the head or the nose, respectively. The superior and inferior obliques allow for torsional rotations, which are most common when looking either up or down and right to left at the same time. This torsional rotation compensates for the fact that the eye is not perfectly aligned on the sagittal plane, and therefore, a slight torsional rotation must be made in order to compensate for the rectus muscles pulling at a slight angle (Betts et al., 2017; Goldberg & Walker, 2013). The muscles are innervated by three cranial nerves, the abducens nerve, which stimulates the lateral rectus; trochlear nerve, which controls the superior oblique; and the oculomotor nerve, which stimulates

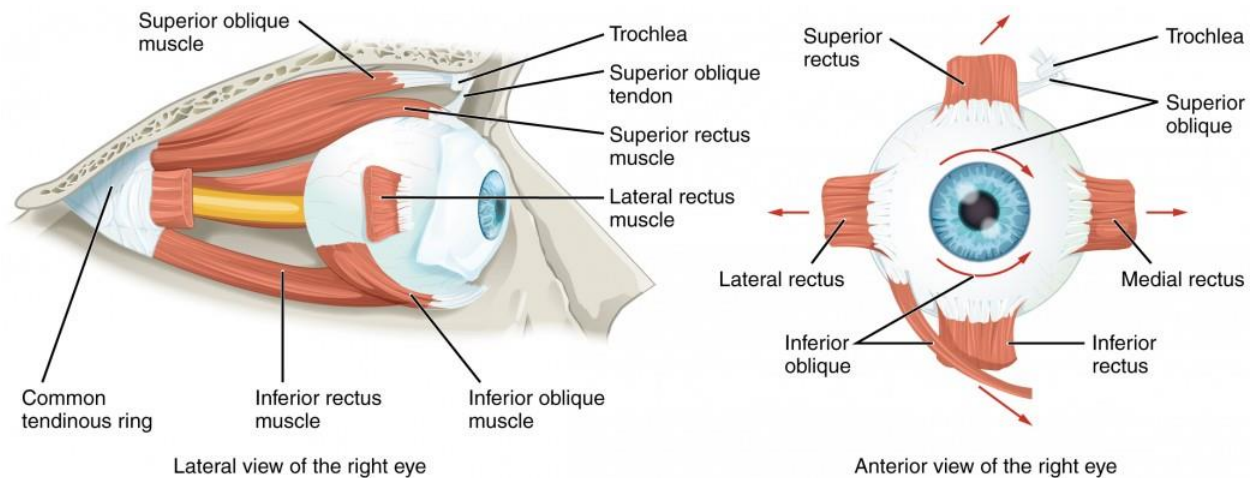


Figure 1.10. Diagram of the extraocular muscles. The six extraocular muscles are responsible for moving the eye within the orbit. The superior rectus, medial rectus, inferior rectus, and lateral rectus, control eye movement within the four cardinal directions. Contractions of these muscles cause the eye to move toward the contraction. The superior oblique muscle allows for medial rotations of the eye, due to the angle of the tendon through the trochlea. Conversely, the inferior oblique allows for lateral rotations of the eye. These muscles receive signals from three nerves (abducens, trochlear, & oculomotor nerve) which project to the brain stem. Reprinted from *Anatomy and Physiology* (p 616) by J.G. Betts et al., 2017, Texas: OpenStax.

all the other ocular muscles (Goldberg & Walker, 2013). These cranial nerves connect to the brain stem, which acts as a hub for all ocular motor control signals.

When making an eye movement information regarding the current position and velocity of the saccade are conveyed to the eye muscles via ocular motor neurons in the brain stem. Regardless of the type of eye movement (smooth pursuit vs. saccade), all ocular motor neurons participate equally in initiating and maintaining the movement and are recruited in a fixed sequence dependent upon the desired size and direction of the saccade (Goldberg & Walker, 2013). Ocular motor neurons receive motor commands from a heavily interconnected network spanning fronto-parietal areas, between the FEF, PEF, and SC in the brainstem. The extent to which these oculomotor centers contribute to eye movements depend on the type of eye movement. Volitional saccades (i.e. goal-driven, voluntary saccades) appear to be initiated by the FEF, which sends signals to the PEF and the SC directly (Goldberg & Walker, 2013). Reflexive saccades (i.e. stimulus-driven, involuntary saccades) have been found to be driven initially by the SC and the PEF, with a later contribution from the FEF (Goldberg & Walker, 2013).

The programming of a saccadic eye movement takes approximately 200ms (a depiction of this timing is shown in Figure 1.11; Purves et al., 2004; Yang, Bucci, & Kapoula, 2002). This interval between the decision to make a saccade and the actual onset of the saccade is commonly referred to as saccade latency. It is thought that during this saccade latency the visual system computes the position of the saccade target with respect to the fovea in order to calculate the saccade velocity. Once the movement is initiated, saccades are ballistic in that their trajectory, distance, and speed cannot be altered or corrected in response to changes to the target's location (Purves et al., 2004). If the target moves during the course of the saccade, the saccade will still go to the target's initial location and a second corrective saccade must be made to move the eyes

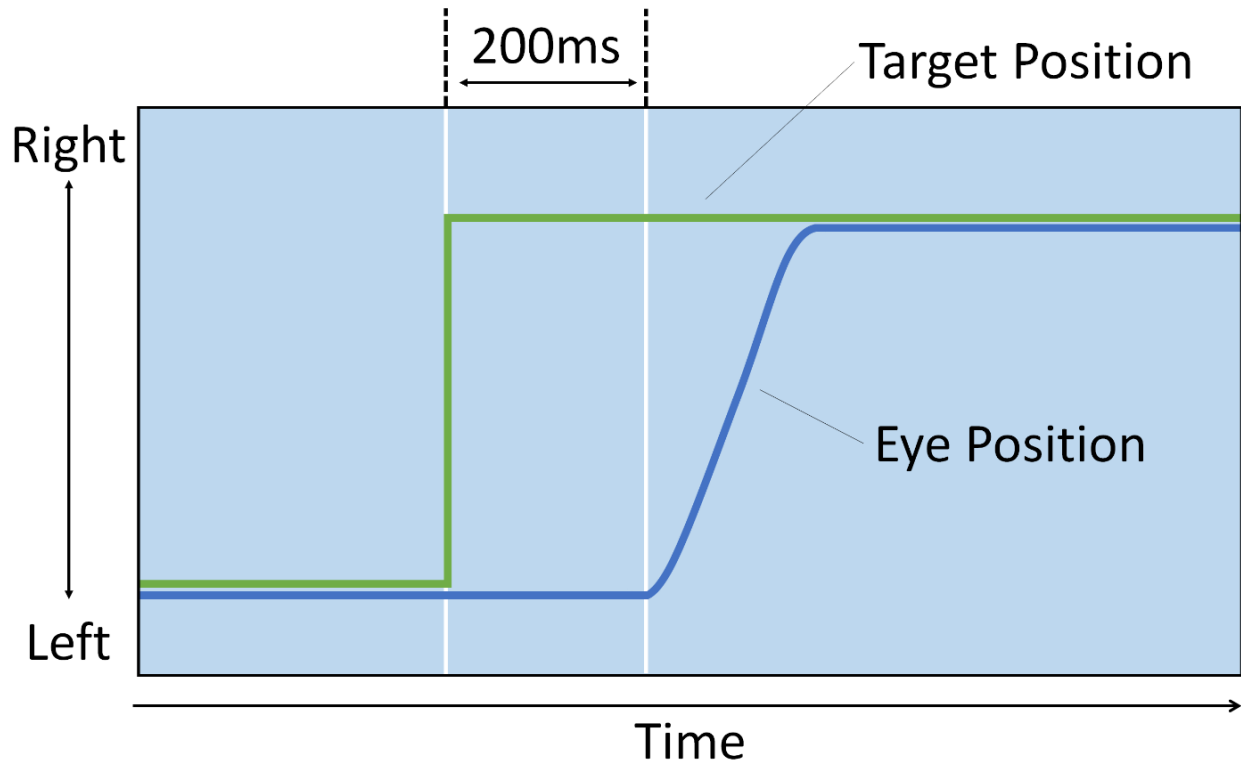


Figure 1.11. Diagram of saccade latency. The green line indicates fixational target, while the blue line indicates foveal position. After target movement the eye takes approximately 200ms before saccade onset (Yang et al., 2002).

to the target's new location. During flight, the duration of a saccade depends on the amplitude (i.e. size) of the saccade. Carpenter (1988) developed a formula that calculates this duration while the eyes are in flight: $T = 2.2A + 21$ (where T is time in milliseconds and A is saccade amplitude). Since the average saccade amplitude in everyday tasks is 18° - 20° (Land, Mennie, & Rusted, 1999), the average flight duration is approximately 60-65ms. As mentioned earlier, Latour (1962) found that saccadic suppression begins before the onset of a saccade. Therefore, the amount of time we are unaware of our environment extends beyond simply the time of the eye movement itself. Studies have found that this suppression can occur 100ms before the eye's flight and continues shortly after fixation (Diamons, Ross, & Morrone, 2000; Matin, 1974; Remington, 1980; Richards, 1969).

As mentioned earlier, the SC, FEF, and PEF are crucial for governing eye movements by representing the visual field as a retinotopic map and using the coordinates of this map to compute the saccade metrics to move the eye to a specific location. (Colby, Duhamel, & Goldberg, 1995; Goldberg & Bruce, 1990; Higgins & Rayner, 2015; Goldberg & Wurtz, 2013; Melcher & Morrone, 2003; Meredith & Stein, 1986; Quail, Optican, & Goldberg, 1998; Wallace, Meredith, & Stein, 1998). How these areas monitor objects that are not currently being projected onto the retina is a hotly debated topic, with some proposing that our spatial world is represented in the brain as an explicit spatiotopic map of the scene that is independent from our eyes, head, and body (Breitmeyer, Kropfl, & Julesz, 1982; Cavanagh et al., 2010; Duhamel, Bremmer, BenHamed, & Graf, 1997; Galletti, Battaglini, & Fattori, 1993; Melcher, 2005; Melcher & Colby, 2003). While other still proposed that spatiotopic organization in the visual system is unnecessary and unsupported within the literature (Andersen, 1989; Colby & Goldberg, 1999; Galletti & Battaglini, 1989; Irwin, 1996; O'Regan & Noe, 2001; Wurtz, 2008).

However, these challenges to spatiotopic organization have lost much of their ground due to the discovery of remapping occurring in human and monkey cortices.

Saccadic remapping is the process by which cortical areas encode the future retinal locations stimuli *will have*, after a saccade is completed. It is in saccadic remapping research where we begin to see neural evidence for the subtraction model and the theories behind transsaccadic integration mentioned earlier. One of the first studies that showed evidence of saccadic remapping was Duhamel, Colby, and Goldberg (1992). While recording neurons from monkey LIP, they found that the retinotopically organized parietal neurons were activated in preparation for a stimulus to come into their receptive field, even if the stimulus is far outside the visual field. That is, before a saccade was initiated the visual receptive fields of some LIP cells appeared to shift, from their current receptive field (RF) to the location of a future receptive field (FF) that would appear *after* the saccade was made (Duhamel et al., 1992). The steps to this process are shown in Figure 1.12.

In the first panel of Figure 1.12, the pre-saccade receptive field (RF) cortical cells are processing very little information, as there is no stimuli presented in that receptive field and it is not currently being attended to. Therefore, the LIP neurons that respond to RF would have very low activation at this point. When a saccade is prepared, but immediately before it is executed (second Panel of Figure 1.12) the cortical cells responsible for processing RF suddenly begin to fire, even before the saccade is made. This firing has been attributed to the visual system preparing for the information that will come into view after the saccade is made and spatially remapping the FF's information onto the RF (Prime, Vesia, & Crawford, 2011; Duhamel et al., 1992). It is during this spatial remapping that the visual system is thought to predicted the information that will come into view (i.e. the strawberry), as mentioned in earlier sections (see

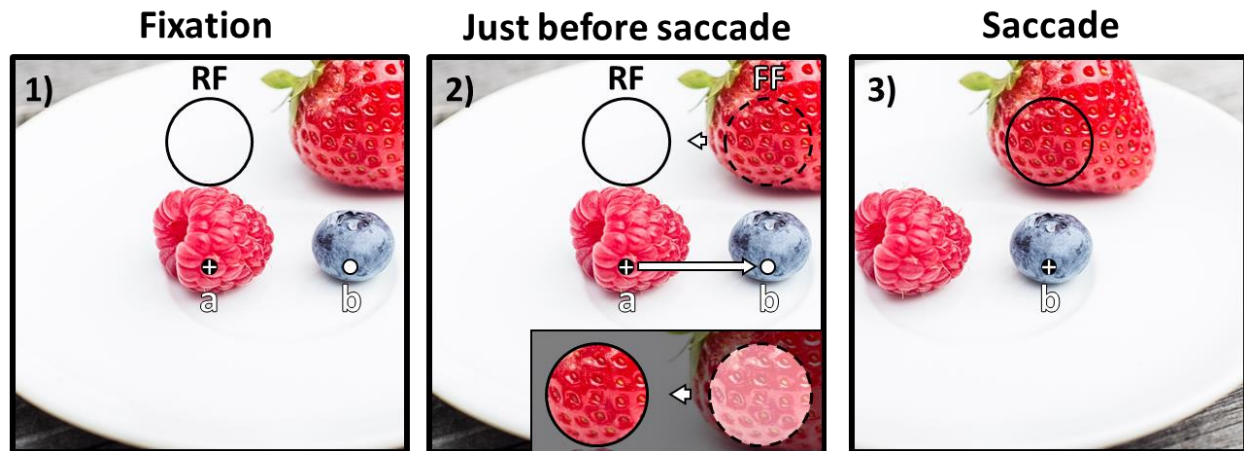


Figure 1.12. Example of spatial remapping. 1) Point ‘a’ represents initial fixation with pre-saccadic receptive field (RF) indicated above fixation. Point ‘b’ indicates the target to which a saccade will be made. 2) Immediately before the saccade is initiated, indicated by the arrow from point ‘a’ to ‘b’, the brain predicts what will come into the RF after the saccade is completed. This future receptive field (FF) is indicated by the dashed circle above point ‘b’. The neurons in RF begin to fire even before the beginning of the saccade, anticipating the information that will be brought into their receptive field. The remapping of the future field to the current receptive field is depicted in the bottom of panel 2. 3) After the saccade is made, fixation has now shifted the view of the world to the right. The remapped RF now corresponds to the expected FF location and the visual system compares the predicted image with the current view of the objects. Finally, FF becomes the current RF processing information and the process can start over. Photo by Markus Spiske (2017).

Figure 1.9 for a review of pre-saccade predictions).

The final step in the saccade remapping process is shown in panel 3 of Figure 1.12, when the saccade is completed. At this point, the FF information is now projected onto the RF and is processed consciously. The comparisons mentioned earlier between pre-saccade and post-saccade information are completed, the FF now becomes the RF, and the entire spatial remapping processes can start anew. During the remapping process the RF becomes temporarily untied from its typical retinotopic co-ordinates and is remapped to the FF (as depicted in the bottom of panel 2 Figure 1.12; Duhamel et al., 1992). The preparatory firing of RF only occurs if a stimulus is presented in the expected FF location (Duhamel et al., 1992) and if the stimulus disappears during the saccade RF firing dramatically reduces upon saccade completion (Duhamel et al., 1992). Finally, in some cases neural firing in both the pre-saccadic and post-saccadic receptive fields has been found (Kusunoki & Goldberg, 2003), thereby increasing the effective receptive field size (Higgins & Rayner, 2015).

Overall, spatial remapping allows the visual system to predict what the world *should* look like once the saccade is finished with true spatial information such as depth (Mlecher & Colby, 2008). This process is particularly remarkable since the pre-saccadic neurons remapping the image are responding to stimuli that is not being presented to them at the moment, rather they are engaging in a preparatory action for what they predict *will be* presented once the saccade is finished. Additionally, these processes are likely how retinal shifts are ignored during a saccade (as shown in Figure 1.5) yet processed during fixation (as shown in Figure 1.6) as mentioned earlier.

This spatiotopic organization and resultant spatial remapping are thought to be candidates of how we maintain visual stability across saccades. Several studies have now found there to be a

distributed saccade network that supports the spatial updating of target locations in both monkeys (Walker, Fitzgibbon, & Goldberg, 1995; Umeno & Goldberg, 1997; Duhamel, Colby, & Goldberg, 1992) and humans (Medendorp, Goltz, Vilis, & Crawford, 2003; Merriam, Genovese, & Colby, 2003; Morris, Chambers, & Mattingley, 2007; Ostendorf, Kiliyas, & Ploner, 2011; Prime et al., 2011; van Donkelaar & Müri, 2002). Besides the SC, FEF, and PEF (Sommer & Wurtz, 2006; Umeno & Goldberg, 1997; Umeno & Goldberg, 2001; Walker et al., 1995), this network also includes the posterior parietal cortex, striate cortex, extrastriate cortex, and areas of the visual cortex such as V1 and V5/MT+ (Duhamel et al., 1992; Goldberg, Colby, & Duhamel, 1990; Melcher & Morrone, 2003; Merriam, Genovese, & Colby, 2003; Moore, Tolias, & Schiller, 1998; Nakamura & Colby, 2000; Nakamura & Colby, 2002; Tolias et al., 2001). However, in humans remapping in early visual areas appears to be less common compared to monkeys (Merriam et al., 2007). Nevertheless, this evidence suggests that saccadic remapping is multiplexed across several visual and oculomotor areas.

In order to remap a stimulus, the spatiotopic maps require internal signals of saccade metrics. Since several of the areas involved in saccadic remapping are also involved in ocular motor control, it is likely the visual system is using outgoing signals (i.e. internal motor signals) during spatial remapping (Cavanaugh, Berman, Joiner, & Wurtz, 2016). This copied signal is known as a motor efference copy and has been found to occur in several areas of the motor system (Goldberg & Walker, 2013). When combined with internal computations of visual processing an efference copy could allow the brain to predict the impending effects and by-products of a saccade. Thereby selecting the appropriate retinal and spatial remappings across cortical cells on the basis of saccade vectors (Sommer & Wurtz, 2006, 2008).

Currently the exact mechanisms of efference copy in the visual system are unclear since both the FEF and PEF/LIP are involved in commanding voluntary eye movements and spatial remapping. Therefore, the source in which efference copy signals arise is controversial. It is possible that signals originate in both the FEF and PEF to solely be used within those structures as they remap our world (Brotchie, Andersen, Snyder, & Goodman, 1995; Pouget, Sejnowski, & Hughes, 1999; Thier & Erickson, 1992). Alternatively, some studies have found evidence to support the idea that the SC is the central hub of remapping since it is heavily involved in ocular motor processing and shows spatiotopic organization. First, projections from the SC to oculomotor nuclei specify the target of impending saccades (Goldberg & Walker, 2013). Second, recent studies have found that these signals are also projected in the opposite direction, sending motor commands to the FEF and PEF through the mediodorsal nucleus of the thalamus (MD; Sommer & Wurtz, 2002, 2004). These MD projections allow the FEF and PEF to utilize the efference copy for remapping. If this path is disrupted through unilateral inactivation of the MD, remapping in the FEF is impaired (Sommer & Wurtz, 2006). Thus, this pathway may underlie the basic cortical circuitry of saccadic remapping.

While there is still ongoing debate about these efference copy pathways, what is known is that when an ocular motor command is generated a copy of that signal is used to spatially remap the locations of objects in our world as well as determine whether the saccadic by-products should be ignored or processed. With this current understanding of efference copy signals the research has turned back to past questions of what information is remapped and what influences the remapping of stimuli across saccades. Mirpour & Bisley (2012) found that saccadic remapping occurs for all content within the visual field, which is inconsistent with the gist theory. However, studies like this have been criticized for using distractors that are relatively

salient (e.g. bright lights or unstable stimuli) and therefore grab attention. Joiner, Cavanaugh, & Wurtz (2011) found that salient stimuli have a greater chance of being remapped compared to less salient stimuli. Supporting this idea, Gottlieb, Kusunoki, and Goldberg (1998) found that when a stable stimulus was task-relevant or appeared abruptly, saccadic remapping occurred versus if it was just part of the background. Several other studies have supported this finding that saccadic remapping occurs more efficiently and accurately for salient, attention capturing, or task-relevant stimuli (Kusunoki, Gottlieb, & Goldberg, 2000; Melcher & Colby, 2008; Rosenholtz, 1999; Wurtz, 2008).

Studies examining transsaccadic perception have found that the remapping process is not without error, even when stimuli are attended to (Higgins & Rayner, 2015; Prime et al., 2007; Prime et al., 2006). In a seminal paper Niemeier and colleagues (2003) aimed to examine what influences our ability to accurately remap stimuli across saccades. During the experiment participants fixated at center screen and were instructed to saccade to a static target (0.8° round dot) as soon as it appeared in their periphery. During the saccade the computer displaced the target by $0-6^\circ$. Therefore, participants needed to track the targets position across saccades (i.e. transsaccadically). 200ms after the saccade was finished participants were asked whether or not the target had moved. Throughout the experiment Niemeier and colleagues systematically manipulated the size of the saccade participants made, as well as the size of the target's displacement. Through these manipulations they found two main results: as saccade size increased participants' ability to accurately detect target displacement decrease, and as target displacement increased so did participants' accuracy for displacement detection. These results were modeled by examining how large a displacement must be for participants to reliably (>75% of the time) detect a displacement in relation to the saccade size. When fixated (i.e. no saccade

made), participants were able to correctly detect a 0.2° change 75% of the time (Niemeier et al., 2003). However, when a 7.5° saccade was made the target needed to be displaced by 1.1° in order to reliably detect the displacement and the largest saccades (15°) required a 2° displacement.

Overall these results show that remapping errors increase as saccade size increases. One can think of this as if small saccades require less computational processes therefore leading to less calculation errors. While large saccades would result in more calculation errors and thus the system would find it more difficult to predict the location of post-saccade stimuli. These errors have also been found to be disproportional dependant upon the direction of the saccade and displacement of the tracked object, with displacements orthogonal to the saccade vector incurring less error, and therefore resulting in better participant performance, than parallel displacements (Bray, Bansal, & Joiner, 2016).

Transsaccadic Motion Perception

Currently, the vast majority of transsaccadic perception and spatial remapping research has focused on studying how we track the location of static stimuli that may be spatially displaced during a saccade. Since the real-world rarely involves only stable objects, it is unclear how our visual system predicts or tracks the locations of an object traversing across space as our eyes move. Ostensibly, tracking moving objects would seem to involve more complicated calculations due to the movement of the object. For static stimuli, remapping is relatively straightforward: the neural activity encoding a stimulus' location shifts from one region of the neural map to another, according to the direction and size of the saccade. For moving stimuli on the other hand, the visual system must also account for the stimulus' current direction and speed,

and possible changes in direction or speed in order to predict where the stimulus will move after each saccade. One thing aiding the visual system in these calculations is that fact that, in our environment, dynamic stimuli tend to smoothly translate across our field of vision, rather than moving in random, unpredictable, directions with sudden changes in trajectory. However, the transsaccadic experiments that have examined dynamic objects have used types of stimuli that only occur occasionally in the real world, such as random dot stimuli or objects that rotate in space (Fabius, Fracasso, & Van der Stigchel, 2016; Fracasso et al., 2010; Kuroki, Watanabe, Mabuchi, Tachi, & Nishida, 2012; Melcher, 2008; Melcher & Morrone, 2003; Ong, Hooshvar, Zhang, & Bisley, 2009).

In one of the few experiments that has used naturally translating stimuli, Gysen, De Graef, and Verfaillie (2002) examined whether detecting intrasaccadic displacements of targets is better when viewing smoothly moving objects or static objects. Participants were presented with a moving object and a stationary object simultaneously. Dependent on the trial they were instructed to make an 8° saccade to either the moving or stationary target at the sound of a tone. During the saccade, the saccade target (either moving or stationary) was displaced by 0.5° or 1°. For the moving stimulus, displacements meant that it either jumped ahead along its path or double back on itself, and then continued its initial trajectory. As with Niemeier et al. (2003), participants were then asked to report whether they noticed a displacement of the target object after they completed the saccade. Gysen, De Graef, and Verfaillie found that participants were better able to detect large target displacements (1°) compared to small displacements (0.5°) for both stimuli (moving and stationary). Contrary to what would be expected, participants performed better at detecting displacements when the object was moving compared to if it was stationary. Note that, unlike Niemeier et al., Gysen, De Graef, and Verfaillie did not manipulate

saccade size, and therefore it is unknown whether saccade amplitude influences displacement detection of translating objects in the same manner as it does changes in stationary stimuli.

In a follow up study, Gysen, Verfaillie, & De Graef (2002) examined whether the presence of a stationary landmark aided performance when detecting displacements in a translating object. Using a similar transsaccadic paradigm as in their previous study, Gysen, Verfaillie, and De Graef presented participants with two translating objects in the left and right visual field which moved in opposite directions. A stationary object was positioned in the path of one of the moving objects such that one object would move toward the stationary landmark, while the other would be moving in “isolation” in the opposite visual field. Gysen, Verfaillie, and De Graef found no difference in performance between the isolation and landmark conditions. However, it is possible that this lack of difference between conditions was due to the “isolated” target not truly existing in isolation. During the task all three objects were presented simultaneously on the screen, with two objects (a stable landmark and moving object) being presented to one hemifield, and the other, isolated, object being presented to the other hemifield. This would have allowed the visual system to use the additional non-target objects as landmarks, even if one or both of them were in the opposite hemifield as the targeted object. Several studies have shown that when allocentric information is present participants will encode target positions relative to the spatial position of other stimuli (Germeys et al., 2004; Hollingworth, 2007; Verfaillie, 1997; Verfaillie & De Graef, 2000). Verfaillie (1997) found the more information was presented, the more accurate participants were at detecting target displacements. Gysen, Verfaillie, and De Graef argued that since the post-saccadic eccentricities of the non-target objects were ‘fairly large’, participants would not use the available allocentric information that occurred in the opposite hemifield. However, they did not include manipulations which would

test this theory and the influence of post-saccadic target eccentricities on use of allocentric cues during transsaccadic perception is currently not known. To explain their results, Gysen, Verfaillie, De Graef stated that the eccentricity of the landmark from the target may have been too large to allow for allocentric encoding between target and cue in their landmark condition. However, rather than participants' not using the allocentric information at all, it is just as possible that all presented allocentric information was used throughout both landmark and isolation tasks. Therefore, there was no true "isolation" condition.

The Present Study

As discussed, humans make several saccades in order to view their environment. During these eye movements the image of the world is suppressed and shifts across our retina, yet we typically have little trouble keeping track of objects in our surroundings. Several studies have examined this transsaccadic perception using stable stimuli and found that the visual system does not perfectly track objects across saccades, with attention, saccade size, amount of object change, presence of allocentric cues, and several other factors affecting the tracking process.

Currently, it is unclear how these factors influence the tracking of moving objects during a saccade. The fact that displacement detection is increasingly difficult with larger saccades as Niemeier and colleagues (2003) found with static stimuli has yet to be examined with motion stimuli. Additionally, there has yet to be a study examining how the eccentricity of a target, that is how far a target is in the periphery, influences our ability to detect changes in dynamic stimuli during a saccade. Finally, it is unclear how both egocentric (location and awareness of one's own body in relation to other objects) and allocentric (location of other objects in relation to each other) information influence transsaccadic memory of dynamic stimuli since past studies have either examined transsaccadic perception of translating stimuli in isolation (i.e. only egocentric

cues were available) or with additional stimuli presented (allocentric cues available). Therefore, the presented study involved two experiments the first of which examined how saccade amplitude and eccentricity of targets influence transsaccadic perception of translating stimuli in an egocentric task. While the second examined whether allocentric information is used to aid in change detection of translating stimuli.

CHAPTER TWO

Effects of Saccade Size and Target Position in Transsaccadic Motion Perception

The aim of Experiment 1 was to examine whether saccade size and target displacement influence our ability to detect changes in moving stimuli during a saccade when only egocentric information is available. During an egocentric task, we have limited information available to us with which to judge whether objects in our visual field have changed between saccades. Therefore, we must rely on own sense of body position in relation to other objects. During egocentric tasks we rely on three main sources of information, all of which are imperfect (Niemeier et al., 2003). First is the location of images on the retina, which has high acuity at central fixation but this acuity declines with eccentricity. Second is the neural signals processing the speed and direction of the tracked object, which are reliable during fixation but unavailable during a saccade due to saccadic suppression. The final source of information is our sense of eye positions, acquired from motor commands to the ocular muscles. All of these signals have been found to be flawed, particularly during a saccade (Dassonville, Schlag, & Schlag-Rey, 1992; Honda, 1997).

Using a purely egocentric task Niemeier et al. (2003) showed that intrasaccadic spatial displacements of otherwise static stimuli are more likely to be noticed with small saccades or large displacements. Currently, it has yet to be examined whether these findings also hold true for transsaccadic perception of motion stimuli. Gysen, De Graef, and Verfaillie's (2002) found subjects were more sensitive to intrasaccadic displacements of moving objects than static objects. However, Gysen, De Graef, and Verfaillie only varied displacement size, not saccade size, and did not vary the target position relative to pre- and post-saccadic central vision. Additionally, they did not use a truly egocentric task, where the screen is impoverished of all

other information, thereby providing participants with additional information that may have aided in their displacement detection.

Experiment 1 will examine how the spatial position of the target, relative to fixation, influences our ability to detect changes in moving stimuli during a saccade. During the experiment the target was presented in isolation. Thus requiring participants to utilize egocentric information in order to judge the target's position and displacement. By using this impoverished condition, we can be confident that egocentric information is all participants will have, thereby forcing them to rely on their internal saccade metrics to remap the stimuli. Using a classic transsaccadic perception task, participants will monitor a moving stimulus in their periphery. While monitoring the stimulus participants will be cued to make a saccade, at which point the target may be displaced. After the saccade is finished participants will be asked whether or not the target was displaced. In order to examine whether the same saccade metric influence transsaccadic perception of motion stimuli as Niemeier et al. (2003) found for static stimuli, I will be manipulating the direction of participant's saccade (toward or away from the target) as well as the size of the saccade (e.g. 4° vs. 12°). Considering Niemeier et al.'s findings, it is predicted that larger saccades will impair participants ability to detect target displacements. Additionally, saccades made away from the target will likely result in a lower performance on the task compared to if participants saccade toward the target. This is due to the increase in target eccentricity that results from looking away, thus a smaller proportion of photoreceptors are processing the target. Building on Niemeier et al.'s work I will also be examining how the distance from central fixation (i.e. eccentricity of the target) influences how we track stimuli. In order to do so the target will be placed at different distances from central fixation. It is predicted that the further an object is in the periphery the more difficult it will be to accurately detect

displacements. Following Niemeier et al., I will also be manipulating the displacement size of the target (e.g. 1° vs. 2°). It is predicted that larger displacements will be easier to detect than smaller displacements, however, this will likely be influenced by the size of the saccade and eccentricity of the target.

Method

Participants. Forty-one 18-30 year-old University of Saskatchewan students and members of the public (21.2 mean age, 20 female, 34 right-handed) participated for course credit. All participants reported normal or corrected-to-normal vision and hearing.

Apparatus & stimuli. Presentation and collection of data was done using a PC computer (Intel(R) Core™ i5-4460 CPU @ 3.20GHz, 3201 Mhz, 4 cores, 8.00GB RAM) with a Benq LED monitor (1080p resolution, 144Hz frame rate) and specialized PsychoPy software (Peirce, 2007). Eye tracking was done using an SMI iView Red-m (120Hz sample rate). This was done to ensure participants-maintained fixation on the fixation-cross during the task and did not foveate on the target. In order to reliably record eye movements, participants heads were kept in place using a chin and forehead rest. Participants' chairs were adjusted so that they were kept tight to the headrest with their back straight to avoid discomfort and aid in reliable eye tracking.

All fixation-crosses were a 2° black Ariel font cross. The initial fixation-cross was presented in the center of the screen. The second fixation was presented either 4° , 8° , or 12° left or right of the first fixation-cross, thus creating saccades of different directions and sizes. Figure 2.1 shows the position of the first fixation-cross (black cross) and the different potential positions of the second fixation-cross (white cross) with the different saccade sizes labels. Henceforth, unless otherwise specifically mentioned, 4° saccades are referred to as small saccades, 8° saccades as medium saccades, and 12° saccades as large saccades. The moving target was a

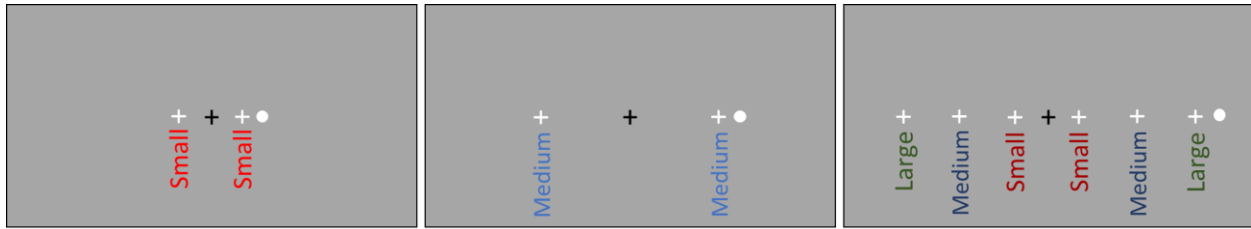


Figure 2.1. Depiction of the different saccade-target combinations in Experiment 1. Target position was measured in degree visual angle relative to initial fixation. Initial fixation was at center screen, white crosses indicate approximate distance the cross moved horizontally in order to prompt a saccade. Note, the white fixation-crosses is only drawn white to indicate potential fixation-cross positions after the first fixation-cross disappeared prompting a saccade. The target (white dot) translated vertically either upward or downward in the right visual field. Target displacement occurred during a saccade and when the target was vertically aligned with the fixation-cross.

Table 2.1

Saccade-target combinations with saccade size and target eccentricities in Exp. 1

Saccade Size	Pre-saccadic Target Eccentricity	Rightward Post-saccade Target Eccentricity	Leftward Post-saccade Target Eccentricity	Saccade-Target Combination
4	6	2	10	Small S-Close T
4	14	10	18	Small S-Far T
8	10	2	18	Medium S-Medium T
8	14	6	22	Medium S-Far T
12	14	2	26	Large S- Far T

Note. The table defines the different saccade-target combinations, which were derived from the different saccade sizes and pre-saccade target positions (values are in visual angle). Thus, a 4° saccade with a pre-saccade target positioned 6° from the fixation-cross will be henceforth referred to as Small S-Close T to denote small saccade and close pre-saccade target position in the present study.

white dot ($0.5^\circ \times 0.5^\circ$) smoothly traversing on the computer screen (either upward or downward) at a constant speed of $2.7^\circ/\text{s}$. The target was always on the right side of the screen, but its exact distance relative to the first fixation-cross on the horizontal plane was systematically varied depending on the second fixation-cross position.

Table 2.1 shows the different target distances from the first fixation-cross (6° , 10° , and 14°) and the possible saccade sizes (i.e. the distance of the second fixation-cross relative to the first fixation-cross). The combination of different saccade sizes and target distances led to five different saccade-target combinations, not taking into account saccade direction. These saccade-target combinations, were as follows with ‘S’ representing Saccade and ‘T’ representing Target: 1) a small 4° saccade with a close 6° target (Small S-Close T); 2) a small 4° saccade with a far 14° target (Small S-Far T); 3) a medium 8° saccade with a medium 10° target (Medium S-Medium T); 4) a medium 8° saccade with a far 14° target (Medium S-Far T); and, 5) and a large 12° saccade with a far 14° target (Large S-Far T). These target positions and saccade distances were chosen based on Niemeier et al.’s (2003) systematic variation of saccade size and target displacement. Note that target eccentricities are based on the *pre-saccadic position* of the target in relation to central fixation. Due to the natural viewing conditions of the experiment, the post-saccade target eccentricities differed dependent upon the direction of the saccade (toward vs. away from the target) and the saccade size. These differences are listed in Table 2.1.

Procedure. Every experimental session began with participants completing a demographics questionnaire to record their age, sex, and handedness as well as completing a consent form. Figure 2.2 shows the general experimental paradigm. Participants were instructed to detect when a moving target in their periphery made a jump forward or backward along its

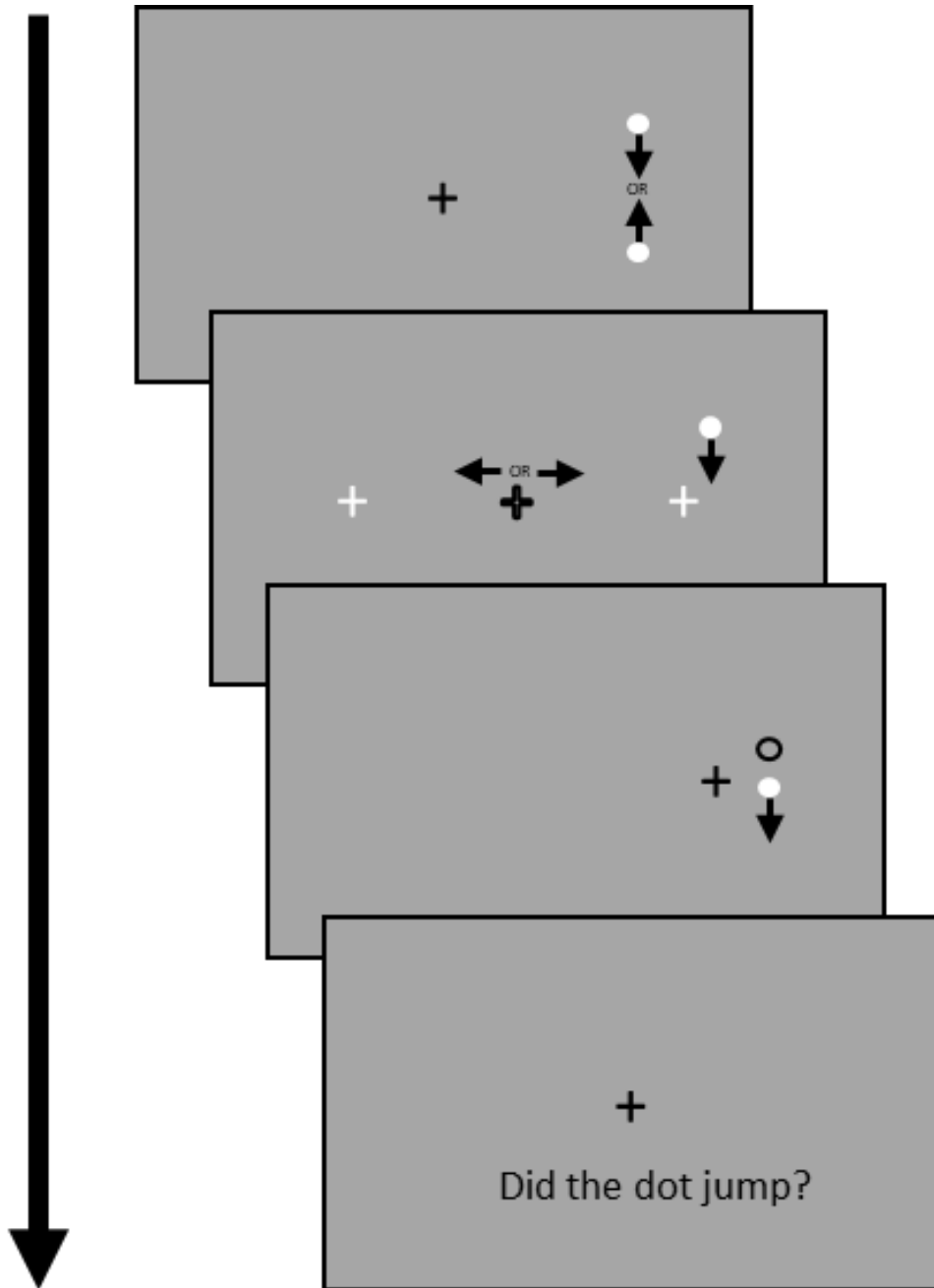


Figure 2.2. General experimental paradigm of Experiment 1. Trials began with a fixation-cross presented in the center of the screen and a target (white dot) presented to the right of fixation. The target immediately began its movement, either upward or downward. The initial fixation-cross then disappeared and a new fixation-cross appeared either to the left or the right. Participants were instructed follow the fixation-cross with their eyes as soon as it moved, thus prompting a saccade. During the saccade the target could either be displaced, i.e., jump, or it could continue its smooth movement (a displacement is depicted in the third screen). Finally, participants were prompted to answer whether the dot “jumped” with a yes or no response.

motion path which might occur during their saccadic eye movements. Each trial began with presentation of the first fixation-cross, in the center of the screen, and the target, on the right side of the screen, on a light grey background (RGB colour space: 0.506, 0.506, 0.506; 55cd/m²). The target began its movement immediately, either upward or downward, and continued its movement until the trial ended. The target's starting position on the vertical plane depended on whether it was moving upward or downward (i.e. target direction). Starting positions were either 2° above or below the horizontal midline of the screen for downward and upward target directions, respectively. Participants were instructed to maintain fixation on the fixation-cross but pay attention to the moving target in their periphery, without looking at it. After either 500ms or 800ms, randomly determined, the first fixation-cross disappeared and a second fixation-cross was presented at one of the different locations specified in the Apparatus & Stimuli section (see Figure 2.1 and Table 2.1). Participants were instructed to make a saccade to the second fixation-cross as soon as it appeared. The purpose of varying the onset of the second fixation-cross was to prevent participants getting used to the timing of the second fixation's onset and anticipating when the fixation-cross would disappear and saccading too early. The different saccade-target combinations determined the position of the target and second fixation-cross. Saccade-target combination and saccade direction (toward or away from the target) were randomly interleaved across trials.

After presentation of the second fixation-cross the target could either maintain its smooth movement as it traversed across the screen or be abruptly displaced by jumping either forward or backward along its motion-path. The size of the target displacements (i.e. how big the jump was) were the same as used in Niemeier et al. (2003), either 0.5°, 1°, or 2°. Because participants were asked to detect whether the target jumped during its motion, the uninterrupted continuous

movement trials, where no target displacement occurred, acted as a control condition. Altogether, there were a total of seven target displacement conditions: 1) No-displacement, 2) 2° backward displacement, 3) 1° backward displacement, 4) 0.5° backward displacement, 5) 2° forward displacement, 6) 1° forward displacement, and 7) 0.5° forward displacement. Target displacement occurred 174ms after the presentation of the second fixation-cross. This was done to ensure displacement took place during the typical period where saccadic suppression of visual processing occurs. Additionally, the displacement was timed so that the target was approximately vertically aligned on the x-axis with the fixation-cross during displacement. Upon presentation of the second fixation-cross the target's motion continued for 500ms. Afterward, the target disappeared and the fixation-cross returned to its central position. Just below this central fixation appeared text which read "Did the dot jump?". This fixation-cross was presented so that participants could orient and prepare themselves for the start of the next trial. Participants responded via a 2-alternative forced choice (2AFC) response as either yes or no on a keypad. Responses were not timed.

Since this is somewhat of a challenging task, before running in the experimental trials, participants were shown examples of the dot's movement and displacement so that they could be acquainted with: the overall layout of the experimental trials, what constituted a smooth movement of the target, and what the different displacement sizes looked like. Participants performed practice trials that were identical to the experimental trials until they felt comfortable with the task and the researcher confirmed they were following the fixation-cross with their eyes and not looking directly at the dot. Each participant completed a total of 1400 trials where saccade-target combination, saccade direction, target direction, and target displacement were randomly interleaved. The experimental session was broken up over three blocks. Block 1

consisted of 560 trials while blocks 2 and 3 had 420 trials. Within each block participants were given short breaks every 140 trials where they were told to rest their eyes but keep their head in the chinrest. Between blocks participants were given long breaks where they were given the opportunity to get up from the desk, stretch, and rest their eyes for several minutes before continuing the experiment. Eye-tracker calibration-validation sequences were done at the beginning of the experiment as well as after each long break in order to maintain accurate eye coordinates. The entire experiment lasted 90 minutes including breaks and instructions.

Data Analysis

Before conducting the main data analysis, eye data of every trial was analyzed to ensure participants followed the task as instructed (i.e. maintaining fixation on the fixation-crosses and making the saccade to the second fixation-cross as soon as it appears). Eye data was analyzed using a custom-made program on MatLab R2018a (MathWorks Inc., Massachusetts, 2018) which allowed me to examine the saccade amplitude, direction, and acceleration. Figure 2.3 shows a screenshot of the output graph generated by this custom analysis program. The criteria for acceptable trials were: 1) if participants maintained fixation within a 2° window centered on the fixation-cross; 2) if participants made saccades in the correct direction within 250ms after the onset of the second fixation-cross, and; 3) if participants' saccade endpoints (i.e. where their eyes landed after the saccade) were within 2° of the second fixation-cross. Trials where eye data failed to meet these criteria were excluded from analysis. Participants who had more than 20% (a conventional threshold in eye tracking literature) of their trials excluded were removed completely from data analysis. This resulted in a total of 27 participants lost prior to data analysis, leaving 14 participants in the data analysis (mean age 20.93, 7 female, 13 right-handed)

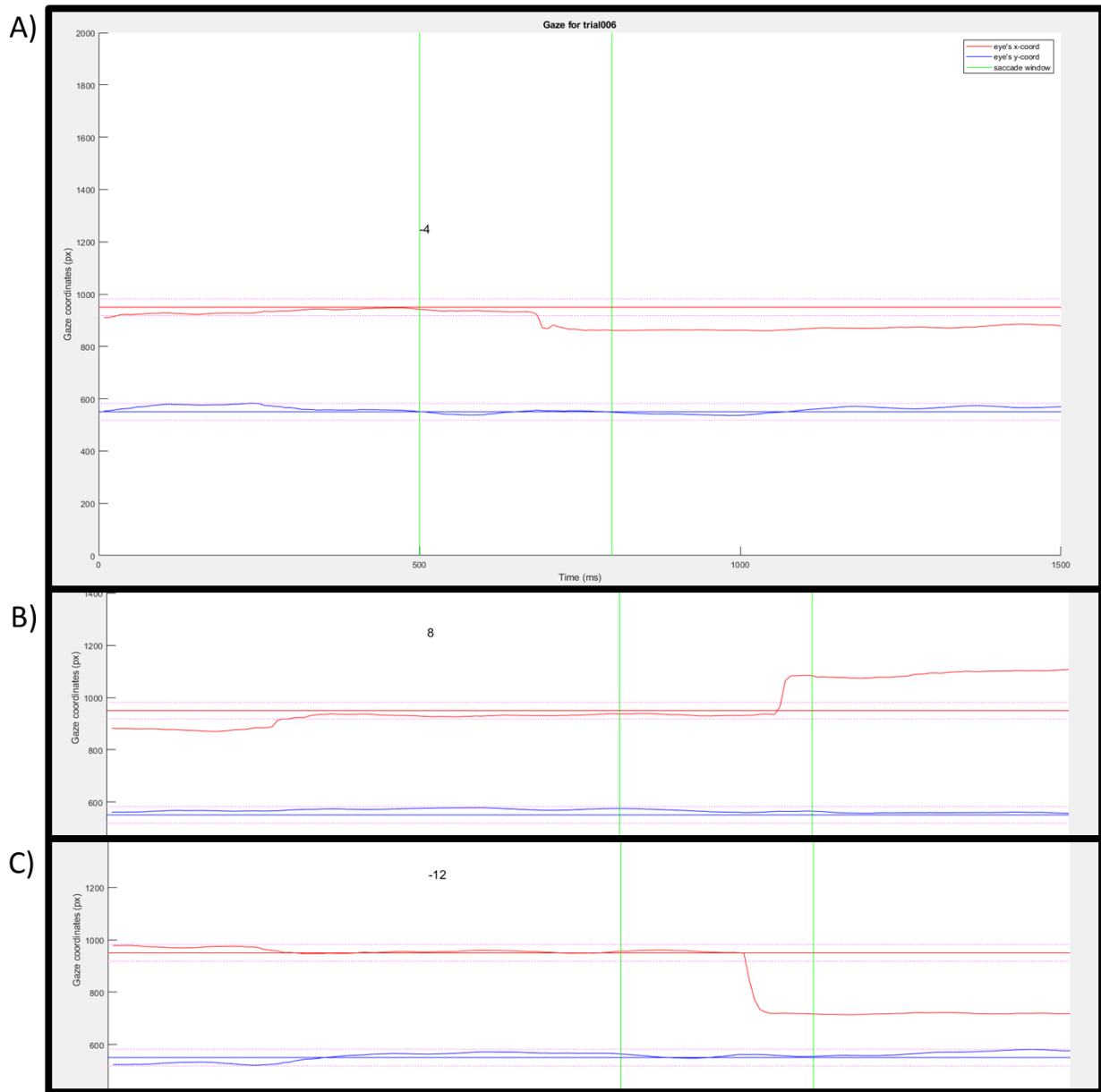


Figure 2.3. Example of custom MATLAB output when analyzing gaze direction and amplitude. Straight horizontal red and blue lines indicate the x and y coordinates of the initial fixation-cross. The dashed lines surrounding these coordinates is the permitted error within fixation. The non-linear red and blue lines are the x and y coordinates of a participant's eye. The vertical green lines indicate the window of time participants needed to make their saccade, with the first green line indicating the moment at which the initial fixation-cross moved. Panel A is an example a leftward 4° saccade. Panel B shows a rightward 8° saccade and panel C shows a 12° leftward saccade.

Data analysis was conducted using JAMOVI statistical analysis software (The jamovi project, 2019). Therein, calculations for the descriptive statistics and factorial analysis were conducted using *afex* and *emmeans* R-packages for data analysis (Lenth, 2018; R Core Team, 2018; Singmann, 2018). The variables used in the analysis were labeled as follows: saccade direction (away & toward target), target direction (up & down), target displacement (No-displacement, 2° backward, 1° backward, 0.5° backward, 2° forward, 1° forward, & 0.5° forward), and saccade-target combination (Small S-Close T, Small S-Far T, Medium S-Medium T, Medium S-Far T, & Large S-Far T). Responses were analyzed according to proportion of ‘yes’ responses (i.e. indication that there was a displacement). In trials where a displacement occurred this would be equivalent to proportion of correct responses, whereas in trials where there was no displacement a positive response would be an incorrect response. Repeated measures analyses of variance (ANOVA) were used to analyze main effects and interactions. Tukey post-hoc tests were conducted to further examine the variables.

Results

Overall analysis. Since the experimental design of the present study included several different independent variables, I first conducted an overall analysis to identify variables that yielded no significant effects which then can be collapsed in order to conduct more simplified analyses. This overall ANOVA was conducted on the displacement detection rates (i.e. proportion of yes responses) with the factors as saccade direction, target direction, target displacement, and saccade-target combination. This analysis showed no significant main effect of target direction ($F(1,13)=2.419, p=.144$), nor were there any significant interactions target direction and any of the other factors. Thus, the following analyses were conducted after collapsing across target direction.

I then examined the effects of target displacement to determine whether participants were truly monitoring the target for displacements and completing the task as directed. A significant main effect of target displacement ($F(6,78)=161.164, p<0.001$; Figure 2.4) was found in the overall analysis, with participants reporting a displacement occurred more often in the displacement (experimental) trials compared to the No-displacement (control) trials. Post-hoc comparisons revealed that all displacement sizes were significantly different from the No-displacement condition (all comparisons $p<0.001$), thus confirming that participants were in fact monitoring the target for displacements (since they were more likely to correctly respond ‘no’ when there was no displacement).

Analysis of control trials. After this confirmation, the No-displacement trials were then removed from the analysis and a separate repeated measures ANOVA was conducted on only the No-displacement trials with saccade direction and saccade-target combination as factors. This separate analysis was conducted due to a fundamental difference in expected responses between the No-displacement and displacement trials (that is when asked “did the dot jump” a response of “no” was expected in these trials, rather than “yes” in all other trial types). Therefore, continuing to analyze the No-displacement trials with the displacement trials may skew the results. The No-displacement analysis showed a significant main effect of saccade-target combination ($F(4,52)=5.086, p<0.002$; see panel A in Figure 2.5). Post hoc tests showed fewer errors (i.e. lower proportion of yes responses) in the Small S-Close T condition compared to both Large S-Far T and Medium S-Far T (both comparisons $p<0.002$). Saccades directed away from the target do show a higher proportion of yes responses, however, this was not significant ($p=0.394$; see panel B in Figure 2.5).

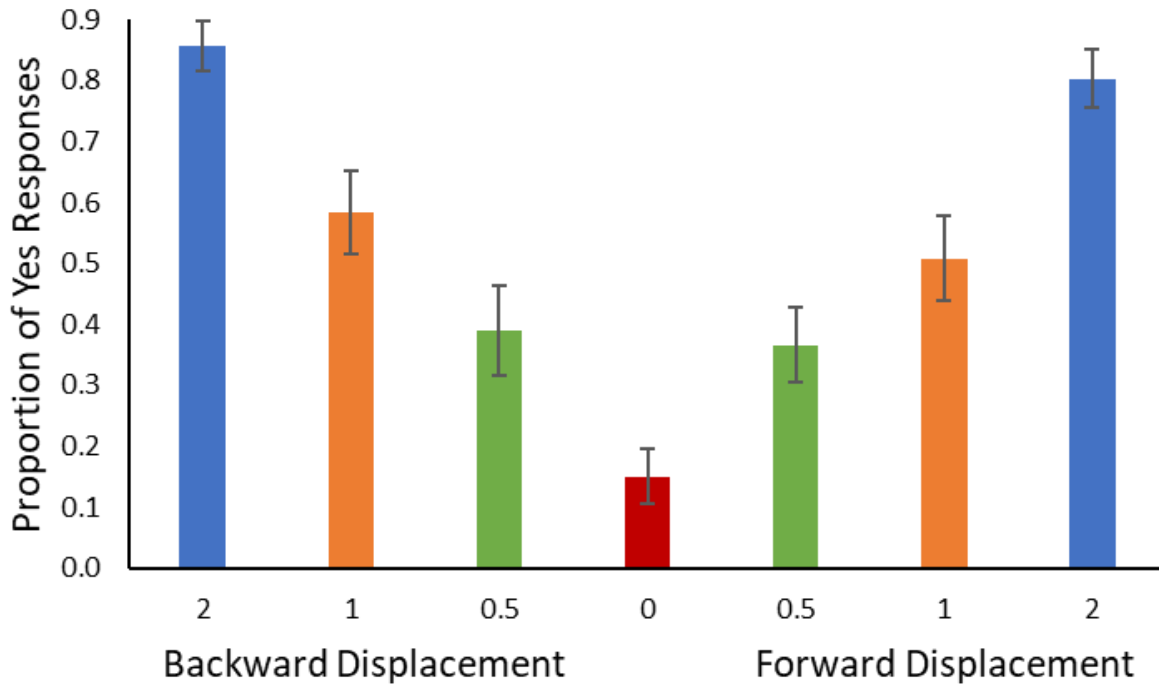


Figure 2.4. Displacement detection in displacement and no-displacement trials, collapsing across all other factors. Participants reported a displacement occurred significantly more often in trials where the target was displaced (0.5°-2° displacement) compared to trials where the target maintained a smooth movement (0° displacement).

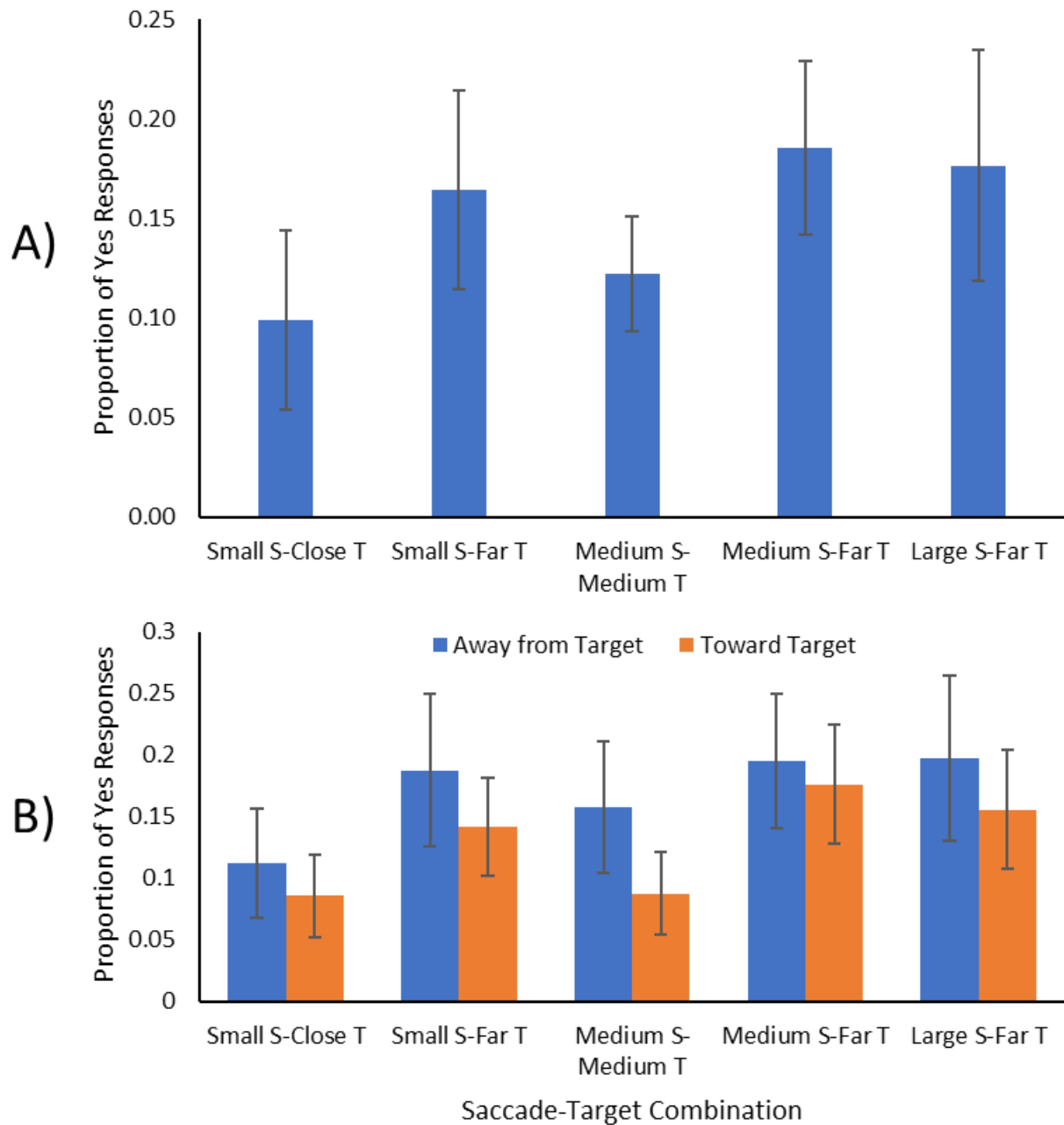


Figure 2.5. Displacement detection in the No-Displacement trials by saccade-target combination and saccade direction. Panel A shows the main effect of saccade-target combination in the No-displacement condition. Panel B shows the influence of saccade direction (away vs. toward the target) which did not reach significance. Correct response in the control trials would be ‘no’, a ‘yes’ response indicates a false-positive. Therefore, the lower the proportion of yes responses in this graph the more accurate the participants were in detecting smooth movement of the target.

Analysis of experimental trials. After removing the No-displacement trials and collapsing across target direction, a final repeated measures ANOVA was conducted with saccade direction, target displacement (excluding the no-displacement conditions), and saccade-target combination as factors.² Figure 2.6 shows an overall depiction of participants performance in the different saccade-target combinations and target displacements when saccades were made away from the target or towards, after collapsing across target direction. This figure is presented to give the reader an overall view of all the data that can be referred to throughout the remaining results. Note that zero on the x-axis indicates the No-displacement condition (i.e. 0° displacement). The left columns show the results when saccades were made away from the target (i.e. leftward saccades), while the right columns show the results when saccades were made toward the target (rightward). The panels in Figure 2.6 show participants performance when comparing difference aspects of saccade amplitude, pre-saccade retinal eccentricity of target, and post-saccade retinal eccentricity of target.

The top panel A of Figure 2.6 shows participants' performance when both the saccade size (small, medium, & large) and pre-saccadic target eccentricity (6°, 10°, & 14°) differ. Note that when saccades were made toward the target all post-saccade eccentricities were the same (2°), however, when saccades were made away from the target these eccentricities differed (see Table 2.1). The center panel B also shows displacement detections when saccade sizes differ, but the pre-saccadic retinal eccentricity is maintained, regardless of saccade direction (i.e. target was always 14° from initial fixation). Finally, panel C compares how changes in post-saccadic retinal eccentricity of a target influence performance while the saccade size remains the same

² All of these factors in the first overall analysis yielded similar significant or non-significant main effects and interactions between each other as reported in this simplified ANOVA.

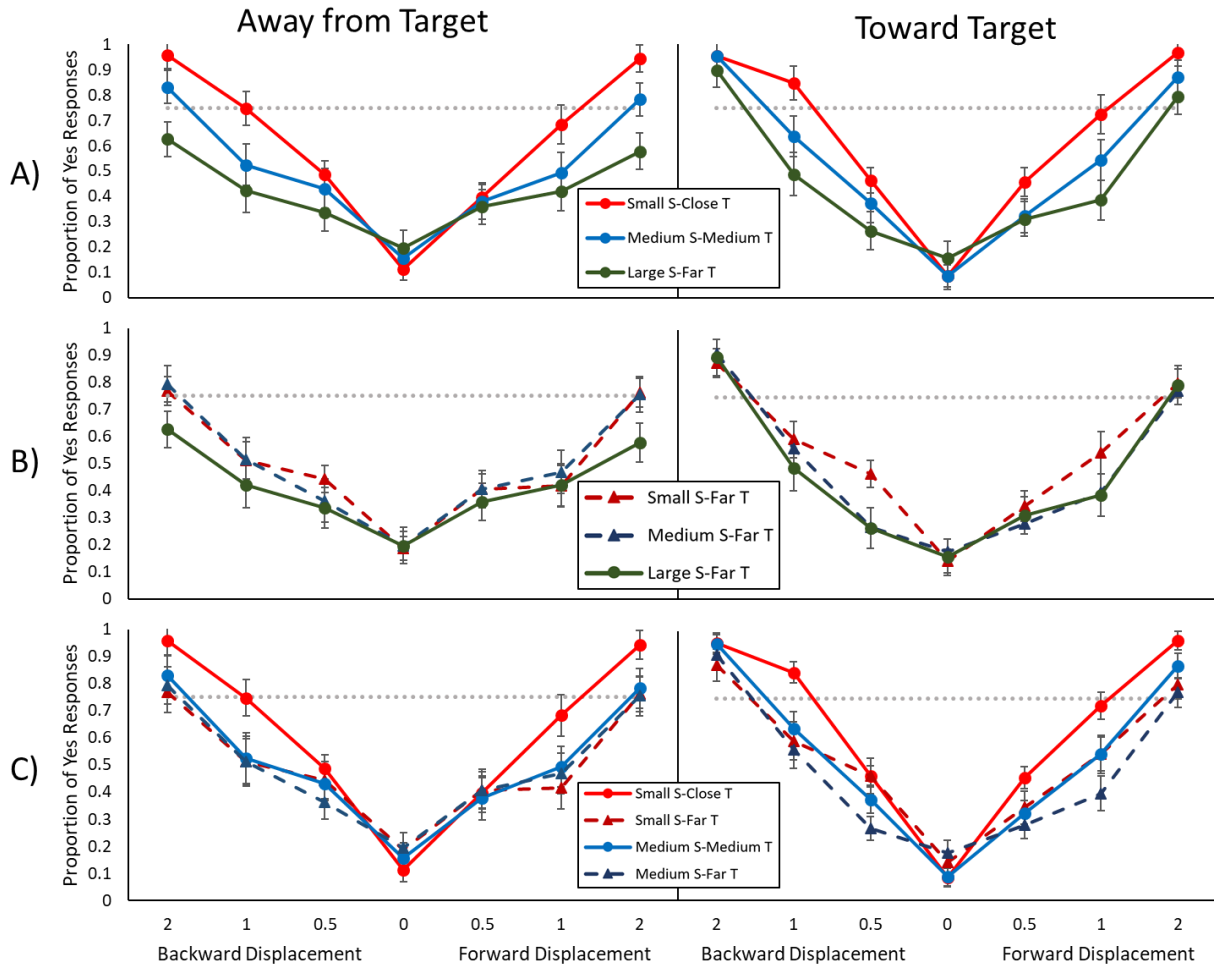


Figure 2.6. Displacement detection by displacement direction in all five saccade-target combinations for both saccade directions. The left columns show performance when saccades were made away from the target while the right columns show performance when saccades were made towards the target. The light grey dotted line indicates Niemeier et al.'s (2003) 75% perceptual threshold. The panels show participants performance when comparing: A) different saccade sizes with the same post-saccadic retinal eccentricity of the target when saccades are made toward the target, and different post-saccadic eccentricity when saccades are made away; B) different saccades sizes with the same pre-saccadic retinal eccentricity of the target; and C) same saccade size with different post-saccadic retinal eccentricity of the target.

(comparing small saccades to small saccades and medium to medium). For example, when small saccades were made toward the target, a close 6° target would result in a 2° post-saccade eccentricity while a far 14° target would result in a 10° post-saccade eccentricity. On the other hand, when small saccades were made away from the target a close 6° target would result in a 10° post-saccade eccentricity while a far 14° target would result in a 18° eccentricity. In toward target Medium S-Medium T and Medium S-Far T trials the post-saccade eccentricity would be 2° and 8°, respectively, while the away from target would result in a 18° and 26° post-saccade eccentricity.

Effect of target displacement. After removing the No-displacement trials a significant main effect of target displacement was still found ($F(5,65)=135.991, p<.001$). This effect is visible in Figure 2.4, showing that 2° displacements yielded the highest detection rates, followed by 1° displacements, and finally 0.5° displacements had the lowest detection rates (all comparisons $p<.001$). The direction of these displacements had no effect on participants' performance (all comparisons $p<0.121$). For example, if the target was traveling upward and made a 1° backward displacement (doubled back on itself), participants were just as accurate in detecting that displacement than had it made a 1° forward displacement (moved further along its path). This effect can also be seen throughout each panel of Figure 2.6, with participants' accuracy improving as target displacement increases (0.5°-2°).

Effect of saccade-target combination. A significant main effect for saccade-target combination ($F(4,52)=34.297, p<.001$) was found. Post hoc comparisons reveal that overall the highest detection rates were found in the Small S-Close T trials, regardless of saccade direction (all comparisons $p<0.001$; see Figure 2.7). Conversely, the lowest detection rates were found in Large S-Far T regardless of saccade direction (all comparisons $p<.010$). No significant

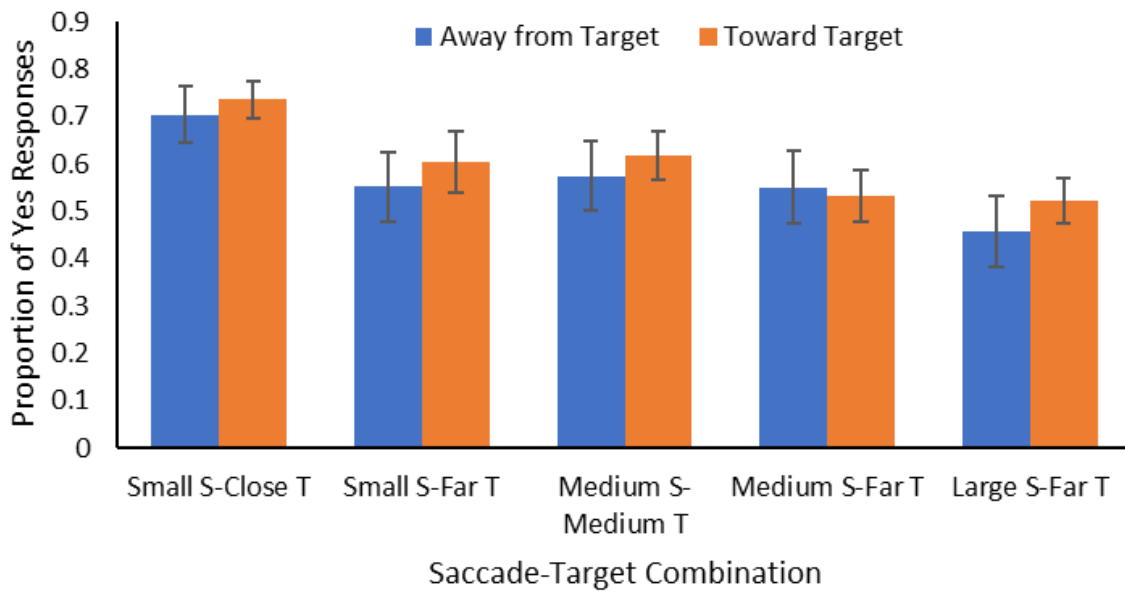


Figure 2.7. Displacement detection by saccade-target combination and saccade direction, collapsed across all other factors. Correct response in the experimental trials would be “yes”, therefore, the higher the proportion of yes responses the more accurate participants were at detecting target displacements. Small S-Close T showed the highest accuracy while Large S-Far T showed the lowest accuracy. There was no difference between conditions if saccades were made away or toward the target.

differences were found when comparing among Medium S-Medium T, Medium S-Far T, and Small S-Far T (all comparisons $p > .880$). These results indicate that participants were more likely to correctly detect a displacement when the target was close to the initial fixation and saccades were small. Alternatively, participants were least likely to answer correctly when the target was far and saccades were large. Significant interactions were also found for saccade-target combination*target displacement ($F(20,260)=2.775, p < .001$). In each panel of Figure 2.6, the overall effect of saccade-target combination can also be seen.

Effect of saccade direction. As found in the No-displacement analysis, there was no significant main effect of saccade direction ($F(1,13)=0.814, p=.383$), indicating that saccading away from the target did not significantly influence performance on the task. However, a significant interaction between saccade direction*target displacement ($F(5,65)=10.386, p < .001$) and saccade direction*saccade-target combination*target displacement ($F(20,260)=2.883, p < .001$) was found. A visual inspection of Figure 2.6 shows a subtle effect of saccade direction when comparing between the panels and saccades away from the target vs. towards. Overall it can be seen that when saccades were made toward the target ceiling effects were more likely and overall performance was slightly increased.

Effect of saccade size versus target eccentricity. In Figure 2.6 panel A, the effect of saccade size and target position on participants' performance can be seen. With small saccades and close targets resulting in higher performance (>50%), regardless of saccade direction. However, when saccades are made towards the target, thus resulting in smaller post-saccade eccentricities (all saccades landing 2° from the target), performance seems to increase. This is particularly evident with large target displacements.

In Panel B, the pre-saccadic eccentricity was the same regardless of saccade direction (the target was 14° from fixation in these conditions), while the saccade size, and therefore post-saccade eccentricity, differed. A visual inspection of the graph shows that the Small S-Far T has better overall performance than the other two conditions. This comparison shows the importance of saccade size, since small saccades allowed participants to more accurately detect small displacements compared to other saccade conditions. This is true even when these larger saccades ended up bringing the target closer to fixation, such as in the toward target condition.

Finally, panel C shows how the retinal eccentricity influences performance when saccade size is maintained yet the post-saccade retinal eccentricity changes. When comparing the Small S-Close T and Small S-Far T conditions, performance is overall better when the target was close. In this case both the pre- and post- retinal eccentricity changes, with a small saccade toward a close target resulting in a 6° pre- and 2° post-retinal eccentricity. While a small saccade toward a far target would result in a 14° pre- and 10° post-retinal eccentricity. With this analysis it is unclear which matters more, the pre- or post- eccentricity, however, it does indicate that retinal eccentricity plays a role in transsaccadic perception of dynamic stimuli.

A final examination of the data was conducted using Niemeier et al.'s (2003) perceptual threshold, which they set at 75%. This perception threshold represents the level of stimulus intensity necessary for a participant to become consciously aware of the target displacement. That is to say, if participants' displacement detection meets or exceeds 75% accuracy it can be confidently said that they are detecting the target displacements and not guessing. Table 2.2 depicts the results of this analysis. Additionally, this threshold is displayed in Figure 2.6 as a grey dotted line. The results are similar to Niemeier et al., showing that a small 4° saccade requires a minimum displacement of 1° in order to reliably detect the displacement. For all other

Table 2.2.

Mean accuracy in saccade-target combination by target displacement and saccade direction.

		Backward Displacement				Forward Displacement		
		2	1	0.5	0	0.5	1	2
Away from Target	Small S-Close T	0.96	0.75	0.49	0.89	0.40	0.68	0.94
	Small S-Far T	0.77	0.51	0.44	0.81	0.41	0.42	0.76
	Medium S-Medium T	0.83	0.52	0.43	0.84	0.38	0.49	0.78
	Medium S-Far T	0.79	0.51	0.36	0.80	0.41	0.47	0.76
	Large S-Far T	0.63	0.42	0.34	0.80	0.36	0.42	0.58
Toward Target	Small S-Close T	0.95	0.85	0.46	0.91	0.46	0.72	0.97
	Small S-Far T	0.88	0.59	0.46	0.86	0.35	0.54	0.80
	Medium S-Medium T	0.95	0.64	0.37	0.91	0.32	0.54	0.87
	Medium S-Far T	0.91	0.56	0.27	0.82	0.28	0.40	0.77
	Large S-Far T	0.90	0.49	0.26	0.84	0.31	0.38	0.79

Note. Items bolded and shaded in gray exceed Niemeier et al.'s (2003) 75% displacement detection threshold, indicating target displacements were reliably detected. The "0" column shows accuracy of reporting no displacement occurred and was not analyzed with Niemeier et al.'s perception threshold.

conditions (i.e. when the saccade size was larger than 4° or the target was further in the periphery) a 2° displacement was necessary for reliable detection. The exception to this is when saccades were made away from the target in Large S-Far T trials. Here, when large saccades were made away from the target participants' overall performance did not reach the reliability threshold with any of that target displacements. However, when the large saccade were made toward the target a 2° displacement could be reliably detected. This finding supports the idea that saccading away from a target decreases performance, even though the overall main effect of saccade direction was found to be non-significant.

Discussion

The results from Experiment 1 show three main influences on detection rates of intrasaccadic displacement of moving objects: 1) size of the displacement, 2) size of the saccade (i.e. saccade amplitude), and 3) the position of the target relative to central vision (i.e. retinal eccentricity). Consistent with Niemeier et al.'s (2003) results using static stimuli, it was found that as target displacement increased so did participants' accuracy in detecting those displacements. This was found regardless of saccade size, direction, or target eccentricity, indicating that larger displacements are overall more noticeable. This effect was most evident with the 2° displacements, where detection rates reached ceiling levels. It is possible that the larger displacements were more likely to capture attention, since past studies on scene detection have found that large changes in the scene are more likely to be detected while small changes tend to go unnoticed (Cavanagh, Hunt, Afraz, & Rolf, 2010; Fracasso et al., 2010; Higgins & Rayner, 2015).

Niemeier et al.'s (2003) saccade size results were also replicated in the present study, since participants' detection rates were lower when saccade size increased. This finding is most

evident when examining saccade size (small, medium, & large) when the target was at 14° from initial fixation. Here participants were overall better able to detect displacements when they made small (4°) saccades compared to both medium (8°) or large (12°). Building on this we also found that detection rates were influenced by target eccentricity, in that the further the pre- or post-saccade eccentricity was the worse participants' performance. When participants made a small saccade, their performance was better if the target was closer (6° from initial fixation) compared to further away (14°). This result was also apparent in the medium saccade conditions although it was not statistically significant. Finally, it was also found that the retinal eccentricity of the target and saccade size interact to improve, or hinder, participants' performance. This is evidenced by the best performance overall occurring when small saccades and close targets were paired together (i.e. Small S-Close T).

If our visual system does allow for some computational errors during spatial remapping then it is possible that saccade amplitude and target eccentricity could act as moderators to this spatial remapping error value, with large saccades and target eccentricity increasing the amount of error we allow for. Referring back to the subtraction model, if a 5° saccade is made and retinal shift was 5° the visual system will assume the retinal shift was entirely due to the saccadic eye movement.³ However, if the saccade is still relatively small but retinal shift is 8° then that 3° difference may be noticed and attributed to a change in the stimulus.⁴ Now, suppose we keep the same large target displacement (3°) but pair it with a large 15° saccade, thus resulting in a 18° retinal shift. The same 3° change⁵ may now be attributed to error in the system and ignored due to the large saccade size. If this is true then larger saccades and target eccentricities will increase

³ 5° retinal shift - 5° saccade size = 0° change

⁴ 8° retinal shift - 5° saccade size = 3° change

⁵ 18° retinal shift - 15° saccade size = 3° change

the difficulty of a task, since the internal mechanisms with which we rely on for transsaccadic perception are not as reliable in these cases. The results from Experiment 1 and Niemeier et al. (2003) seem to support this theory. When no saccade is made participants are fairly accurate in reporting whether or not displacements occurred (Niemeier et al., 2003), and as saccade size or eccentricity of the target increases this detection reliability decreases.

When examining the results using Niemeier et al.'s (2003) perception threshold, participants' performance appeared to have a small benefit from saccading toward the target. When large saccades were made away from the target participants' performance did not exceed this threshold for any of the displacements (<63% accuracy), however, when saccades were made toward the target 2° displacements could be reliably detected (>79% accuracy). Additionally, when comparing between saccade directions for each saccade-target combination in Table 2.2, we can see a general overall benefit in performance when saccades are made toward the target. For example, a Small S-Close T saccade away from target with 1° backward displacement has a 75% detection accuracy while the same condition made toward the target has an 85% accuracy. This supports Niemeier et al. (2003), who found that a large saccade made away from the target was associated with lower detection rates. This also supports the hypothesis that increased target eccentricity also increases the amount of error the visual system allows for. Since target eccentricities increase the further we saccade away from a target, and post-saccadic eccentricities are smaller when saccades are made toward the target.

Considering these findings together it may be the case that we compare saccade vectors (size, direction, speed) to some average displacement across the retina in order to gauge stability, allowing for some error within these calculations. However, it is clear that not all of the variables (saccade size, target eccentricity, & target displacement) are weighted equally when making the

calculations. For example, while target eccentricities mattered (things further away had lower correct responses), the saccade size appeared to matter more, since saccading away from the target, and increasing the eccentricity by several degrees, didn't influence performance as much as large saccades did in general. Additionally, throughout all the conditions, the target displacement appeared to modify participants' response the strongest. Therefore, it is possible that we compare saccade vectors with retinal (i.e. target) shifts, but that the target displacements are given more weight than other internal mechanisms such as the motor efference copy. I will expand on the further theoretical implications of these results in the general discussion.

CHAPTER THREE

Effects of Allocentric Cues in Transsaccadic Motion Perception

Experiment 1 examined participants' transsaccadic perception of dynamic stimuli when only egocentric information was at their disposal. In this impoverished conditions participants had to rely on the retinal location of images, signals from visual motion detectors, and the internal efference copy of the saccade in order to determine whether or not changes in the scene occurred. The results from Experiment 1 showed three main variables that influenced displacement detections, 1) the size of the displacement, 2) the size of the saccade, and 3) the pre- and post-saccade retinal eccentricity of the target. While these findings are valuable in the understanding of transsaccadic perception, natural scenes are usually rich with other information, such as other objects, which provide allocentric information the visual system might be able to use in spatial updating. In a natural environment, not only will you be able to rely on the internal processes mentioned above, but you can also encode the position of targets in relation to one another to aid in tracking objects and viewing the scene.

Currently it is unclear whether we efficiently utilize allocentric information during transsaccadic perception or how that use influences our ability to track translating stimuli. While several studies have shown that allocentric information is used to aid in tracking stationary targets (Germeys et al., 2004; Hollingworth, 2007; Verfaillie, 1997; Verfaillie & De Graef, 2000), Gysen, Verfaillie, and De Graef (2002) found that allocentric cues do not aid in the tracking of moving targets. However, Gysen, Verfaillie, and De Graef's control condition may not have truly had a target moving in "isolation" as indicated. During Gysen, Verfaillie, and De Graef's task, three stimuli were presented on the screen simultaneously, with two objects presented in one visual field and a single object in the opposite visual field. Gysen, Verfaillie, and De Graef argued that the single object was presented in isolation, since it was presented to

one hemifield. Thus, they did not control for whether the participants utilized the allocentric information that was presented in the opposite hemifield during “isolation” trials, instead they seemed to be assuming that allocentric information is not integrated across visual fields. Consequently, participants may have utilized all the allocentric information presented throughout both the landmark and isolation trials to aid in their performance.

Therefore, it is still unclear how or whether allocentric information influences transsaccadic perception of translating stimuli. Experiment 2 aims to fill this gap in the literature and examine whether participants utilize allocentric information to aid in tracking moving targets during a saccade. Prime et al. (2011) argued that an optimal visual system would utilize as much information during spatial updating as possible, which includes allocentric cues based on their availability. Some studies have found that our sensitivity to stimulus shifts is not homogeneous across the visual field (Higgins & Rayner, 2015). The visual system is more likely to notice shifts of a static target on a stable background, than shifts of the background behind a stationary target, as the principle of gist suggests (Higgins & Rayner, 2015). In a recent study, Byrne and Crawford (2010) found that when judging displacements of a static target’s position, participants relied more heavily on their egocentric sense of target location compared to allocentric cues. This reliance on sense of self was found to be especially true when the allocentric cues were moving themselves (Byrne & Crawford, 2010), suggesting the visual system regarded moving allocentric cues as unreliable for use in spatial updating. However, other studies have found that when allocentric cues are presented they will be used (Germeys et al., 2004; Hollingworth, 2007; Verfaillie, 1997; Verfaillie & De Graef, 2000). Therefore, it is possible that the visual system strategically utilizes allocentric cues. Relying on them more often when egocentric information

isn't as reliable or visual processing introduces a large amount of error into the spatial remapping calculations, such as when saccades are large, or target eccentricity is far.

Overall, in these allocentric transsaccadic studies, the target used was always stationary or static, therefore, it is unknown whether these principles hold true for translating objects. Additionally, it is unclear whether the disregard for the allocentric cues found in some studies is due to the difference in stability (i.e. stable target vs. moving background) or relative motion between the objects. It is possible that if both target and background were moving in the same direction, as in the case of runners in a marathon, the allocentric cues may be considered more reliable and therefore used to aid in transsaccadic perception. Thus, it remains unclear what influences our reliance on allocentric cues: the number of cues available, their stability, or their reliability. For example, imagine you are sitting in a park watching two children catch a ball next to a large oak tree and some bushes, while several other children run around. Both the trees and bushes are stable cues for our vision, since they are non-moving, while the children would be dynamic stimuli. Additionally, the oak tree may be considered more reliable, since it is larger than both the bushes and the children. If you are shifting your gaze from one child to the other, would our visual system rely mostly on egocentric information? Thereby depending more on our internal metrics than allocentric cues provided by the background bushes and oak tree, as suggested by Byrne and Crawford (2010)? Or, would background allocentric cues be utilized and to what extent? Further imagine that it is a windy day and the bushes and branches of the oak tree are swaying, and therefore, the background allocentric cues are constantly shifting; to what extent are these unstable allocentric cues utilized? Moreover, to what extent might the stability and amount of allocentric cues interact to modulate spatial updating performance?

In the following experiment I test how the amount of and stability of allocentric cue influence target displacement detection in the same transsaccadic paradigm used in Experiment 1. During the experiment, targets were presented in both isolation, thus requiring participants to use egocentric information, as well as with allocentric cues, therefore providing participants additional information on top of their own sense of self. Using a similar task as in Experiment 1, participants monitored a moving stimulus in their periphery and the saccade size, eccentricity of target, and target displacement was systematically manipulated. The number (1 vs 3) and stability (moving vs. stable) of allocentric cues available was also manipulated in order to examine whether moving cues would be considered more reliable than stable cues as hypothesized above. As found in the first experiment, it is predicted that large displacements will be easier to detect than smaller displacements, regardless of allocentric information provided. Additionally, small saccades and close target eccentricities should result in increased performance compared to large saccades or far target eccentricities.

Methods

Participants. Forty-one 18-44 year old University of Saskatchewan students and members of the public (22.3 mean age, 30 female, 36 right-handed) participated for course credit. All participants reported normal or corrected-to-normal vision and hearing. Due to equipment limitations, data from participants with corrected-to-normal vision through glasses was not collected.

Apparatus & Stimuli. The same equipment was used as in Experiment 1. The stimulus details of the fixation-cross and moving target were identical as in Experiment 1, with the following exceptions: medium saccade-target position combinations (Medium S-Close T & Medium S-Far T) were removed from Experiment 2; subjects made only rightward saccades

toward the target; and consequently, the second fixation-cross was only presented to the right at either 4° or 12° from the first fixation-cross and the target was presented on the right side of the screen at either 6° or 14° from initial fixation (See Figure 3.1). Following the labelling convention used in Experiment 1, these saccade-target combinations used in Experiment 2 were labeled as follows: 1) Small S-Close T, 2) Small S-Far T, and 3) Large S-Far T (see Table 3.1). The target's speed and direction (up or down) was the same as in Experiment 1. The 2° displacement size was removed due to ceiling effects found in Experiment 1. Therefore, in Experiment 2 there were a total of five target displacements: 1) No-displacement, 2) 1° backward displacement, 3) 0.5° backward displacement, 4) 1° forward displacement, and 5) 0.5° forward displacement.

Allocentric cues were provided by solid dark grey bars (RGB colour space: -0.506, -0.506, -0.506; 10cd/m²) presented against the same light grey background used in Experiment 1. The amount of allocentric cues available was manipulated by varying the number of dark bars between one and three. These bars stretched across the length of the screen (340mm) and were 300mm wide when a single bar was presented or 120mm when three bars were present. Reliability of the allocentric cues was manipulated by the bars being either stable or slowly moving upward at the speed of 2.7°/s. In trials when the bars moved, the target would travel either in the same (both upward) or opposite (bars upward and target downward) direction relative to the bars, which offered an opportunity to explore potential differences in task performance based on relative motion. A control condition was also included where no allocentric cues were presented and looked identical to the display in Experiment 1. This also

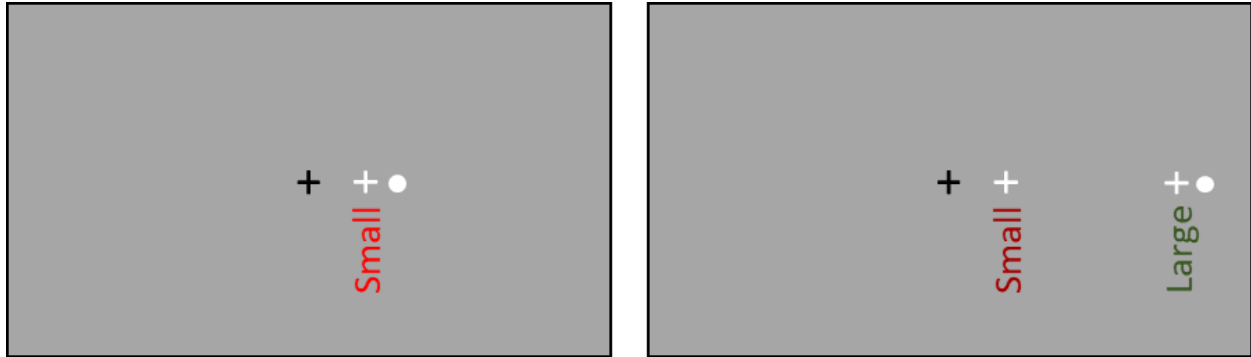


Figure 3.1. Depiction of the different saccade-target combinations in Experiment 2. Target position was measured in degree visual angle relative to initial fixation. Initial fixation was at center screen, white crosses indicate approximate distance the cross moved horizontally in order to prompt a saccade. Note the white fixation-crosses is only drawn white to indicate potential fixation-cross positions after the first fixation-cross disappeared prompting a saccade. The target (white dot) translated vertically either upward or downward in the right visual field. Target displacement occurred during a saccade and when the target was vertically aligned with the fixation-cross.

Table 3.1

Saccade-target combination with saccade size and target eccentricities in Exp. 2

Saccade Size	Pre-saccade Target Eccentricity	Rightward post-saccade target eccentricity	Saccade-Target Combination
4	6	2	Small S-Close T
4	14	10	Small S-Far T
12	14	2	Large S- Far T

Note. The table defines the different saccade-target combinations, which were derived from the different saccade sizes and pre-saccade target positions (values are in visual angle). Thus, a 4° saccade with a target positioned 6° from the fixation-cross before the saccade is referred to as Small S-Close T to denote small saccade and close target position in the present study.

offered an opportunity to replicate the results of Experiment 1. Table 3.2 defines and provides the abbreviations for all the different possible conditions according to target direction (upward or downward), number of allocentric cues (one or three bars), and stability of allocentric cues (static or moving). As shown in Table 3.2, these different factors resulted in seven different target-bar combinations: Solid grey background with no bars (NB), one stable bar (1-Stable), three stable bars (3-Stable), one bar moving with the target (1-With), three bars moving the target (3-With), one bar moving in the opposite direction as target (1-Against), and three bars moving in the opposite directions as target (3-Against). Note that target direction was randomly interleaved upward or downward in NB, 1-Stable, and 3-Stable trials, whereas target direction was always upward in 1-With and 3-With and downward in 1-Against and 3-Against trials. These different conditions are depicted in Figure 3.2.

Procedure. Participant instructions followed the same procedure as in Experiment 1 with the exception of participants being informed to ignore all background information during the trial and that the fixation-cross and target were the only important information presented. Figure 3.3 shows the general experimental paradigm. Each trial began with presentation of the first fixation-cross in the center of the screen. Background bars were presented at the beginning of each trial with the exception of NB trials. In trials with moving bars (1-With, 3-With, 1-Against, & 3-Against), the target and bars began their movement simultaneously and continued their motion until the end of the trial. The target-bar combinations were blocked. Block A contained trials with stable bars (1-Stable & 3-Stable) and half of the NB trials. Block B contained trials with moving bars (1-With, 3-With, 1-Against, & 3-Against) and the second half the of NB trials. The saccade-target combinations and target displacements were randomly interleaved within blocks. This resulted in a total of 750 trials per block (1400 trials total). All participants completed both

Table 3.2

Target-bar combinations with target direction and background direction in Exp. 2

Target Direction	Background Type	Target-bar Combination
Up or Down	Solid Grey (control)	NB
Up or Down	One Stable Bar	1-Stable
Up or Down	Three Stable Bars	3-Stable
Up	One Bar Moving Up	1-With
Up	Three Bars Moving Up	3-With
Down	One Bar Moving Up	1-Against
Down	Three Bars Moving Up	3-Against

Note. There was no significant effect of target direction in NB, 1-Stable, and 3-Stable. Therefore, these conditions were collapsed across target direction. However, for conditions where the bar moved, target direction created an important factor for analysis – whether congruent motion, between targets and cues, influences utilization of allocentric cues.

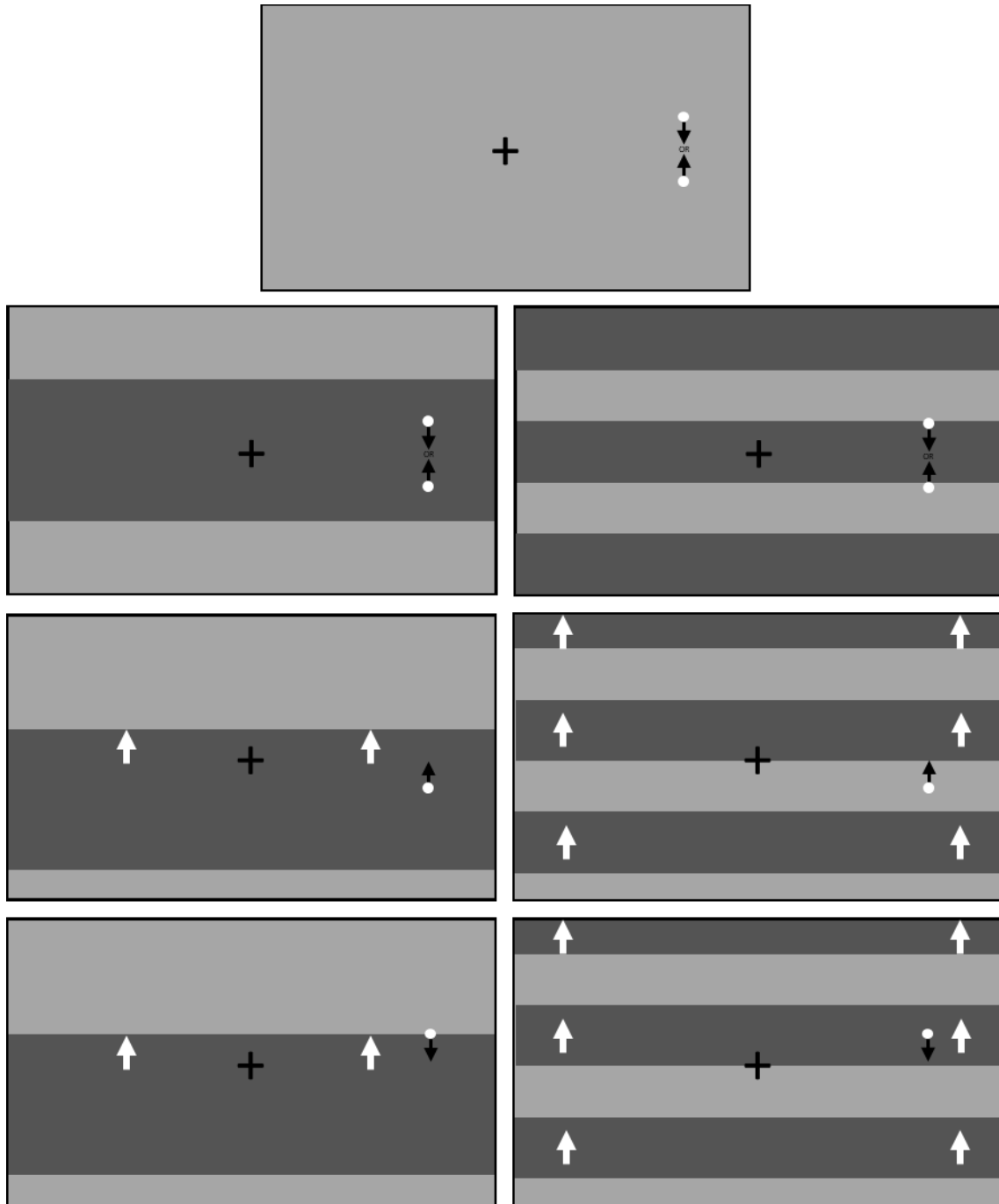


Figure 3.2. Different target-bar combinations of Experiment 2. The white arrows depict the direction of bar motion while the black arrows show the direction of target motion. From top down, left to right: solid grey back with no bars (NB), one stable bar (1-Stable), three stable bars (3-Stable), one bar moving with the target (1-With), three bars moving the target (3-With), one bar moving in the opposite direction as target (1-Against), and three bars moving in the opposite directions as target (3-Against). Note, the NB condition replicated Experiment 1 and acted as a control condition. See Table 3.1 for more detail on labelling of conditions.

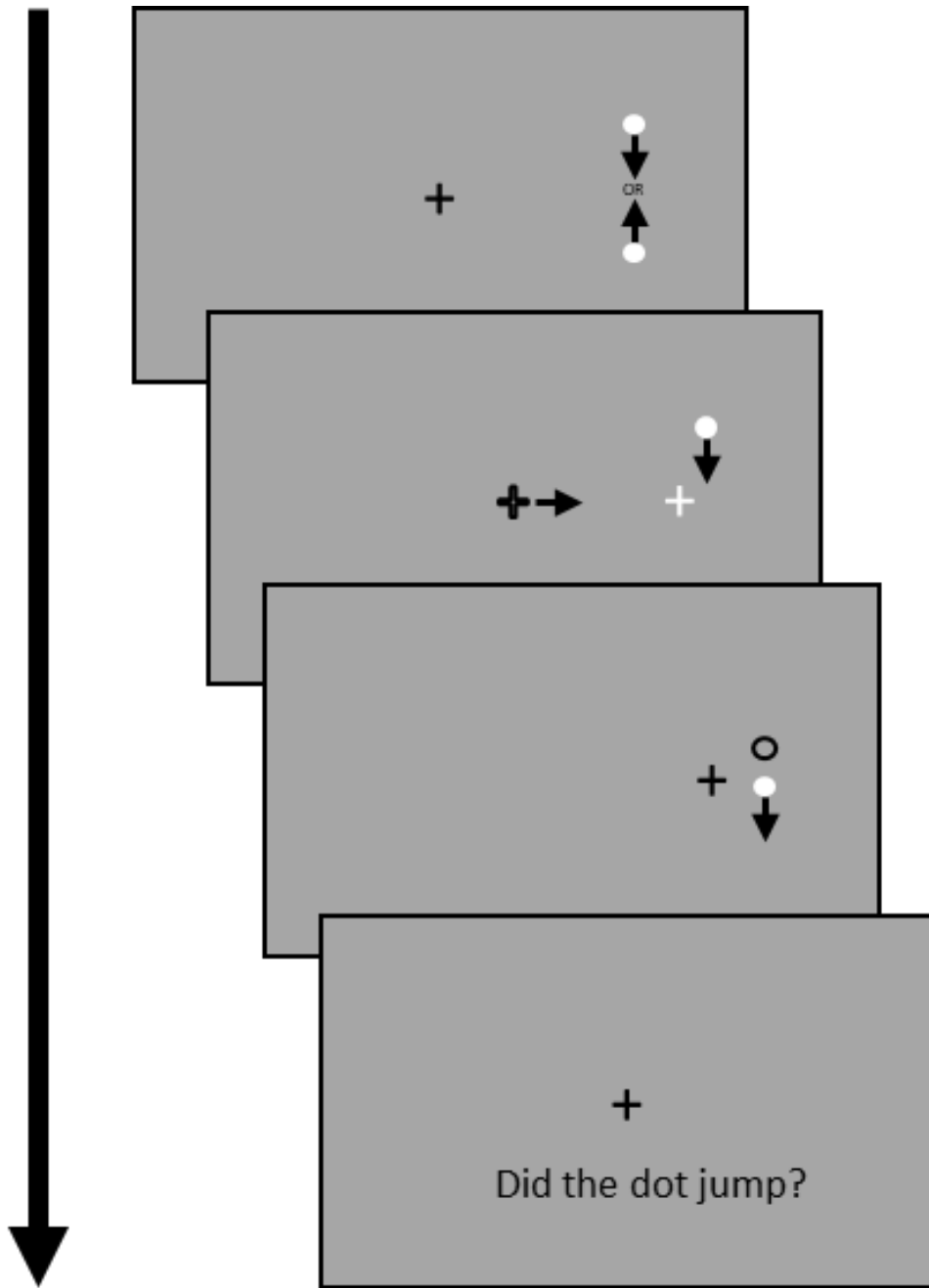


Figure 3.3. General experimental paradigm of Experiment 2. Trials began with a fixation-cross presented in the center of the screen and a target (white dot) presented to the right of fixation. The target immediately began its movement, either upward or downward. The initial fixation then disappeared and a new fixation-cross appeared to the right. Participants were instructed to saccade to the fixation-cross as soon as it moved, thus prompting a saccade. During the saccade the target could either be displaced, i.e., jump (as depicted), or it could continue its smooth movement (a displacement is depicted in the third screen). Finally, participants were prompted to answer whether the dot “jumped” with a yes or no response.

blocks which were counterbalanced between participants (i.e. A-B or B-A testing order). As in Experiment 1, both blocks contained short breaks after every 140 trials, during which they rested their eyes while maintaining chinrest contact. One long break was also included within each block as well as between the blocks, wherein participants were instructed to stand up, stretch and rest their eyes for several minutes before continuing.

Participants performed practice trials that were identical to the experimental trials, and therefore included the different target-bar combinations, until they felt comfortable with the task and the researcher confirmed they were following the fixation-cross with their eyes and not looking directly at the dot. Eye-tracker calibration-validation sequences were done at the beginning of the experiment as well as after each long break in order to maintain accurate eye coordinates. The entire experiment lasted 90 minutes including breaks and instructions.

Data Analysis

As in Experiment 1, eye data for every trial was analyzed offline, and trials which did not meet the same inclusion criteria defined in Experiment 1 were excluded from analysis. This resulted in a total loss of 33 participants prior to data analysis, resulting in a total of 8 participants retained for analysis (27 mean age, 5 female, 7 right-handed). JAMOVI statistical analysis software was used to conduct the data analysis utilizing the afex and emmeans R-packages (Lenth, 2018; R Core Team, 2018; Singmann, 2018; The jamovi project, 2019). Analysis was conducted on proportion yes responses, therefore, a yes response would only be correct in conditions where a displacement occurred. In trials where a displacement did not occur, i.e., the target continued its smooth movement, a yes response reflects a false positive. The variables used in the analysis were labeled as followed: target direction (up & down), target displacement (No-displacement, 1° backward, 0.5° backward, 1° forward, & 0.5° forward),

saccade-target combination (Small S-Close T, Small S-Far T, & Large S-Far T), and target-bar combination (NB, 1-Stable, 3-Stable, 1-With, 3-With, 1-Against, & 3-Against). Repeated measures ANOVAs and Tukey post-hoc tests were conducted within the analysis.

Results

Overall analysis. Before proceeding to the main analyses, preliminary repeated measures ANOVAs were conducted for each the NB, 1-Stable, and 3-Stable conditions to determine whether the displacement detection rates (i.e. proportion of yes responses) differed between target directions. The factors in these ANOVAs were saccade-target combination, target direction, and target displacement. In NB condition, the main effect of target direction was not significant nor did target direction significantly interact with the other variables (all $p > 0.072$), replicating the results of Experiment 1. Similar results were found in the ANOVAs for 1-stable (all $p > 0.609$) and 3-stable (all $p > 0.380$). Therefore, target direction was collapsed within these conditions (as illustrated in Figure 3.2 and Table 3.2) for all further analyses. Note that the target direction in 1-With and 3-With conditions was always upward and in 1-Against and 3-Against conditions was always downward because the moving bars always moved upward in these conditions. Thus, the conditions are defined by target's movement direction relative to the bar's.

Analysis of control trials. As was found in Experiment 1, the No-displacement condition was significantly different from all other displacement trials (all comparisons $p < 0.001$), confirming that the participants were completing the task as instructed. Therefore, the No-displacement trials were removed from further analysis to simplify the analyses and focus on the effects of displacement that occurred. For the sake of completeness, where necessary the No-displacement data is still shown in the main data figures.

Analysis of experimental trials. For the experimental trial analysis, a repeated measures ANOVA was conducted⁶ with the factors target displacement (after removal of the No-displacement), saccade-target combination, and target-bar combination.⁷ As with Experiment 1, there was a significant main effect of saccade-target combination ($F(2,14)=83.66, p<.001$; Figure 3.4 panel A) and target displacement ($F(4,28)=38.29, p<.001$; Figure 3.4 panel B). Post-hoc tests found that the highest detection rates occurred in Small S-Close T trials, followed by Small S-Far T, and finally Large S-Far T (all comparisons between these three saccade-target combinations $p<0.006$). Supporting Experiment 1, participants' performance also increased with target displacement with the highest detection rates occurring with 1° displacements compared to 0.5° (all comparisons $p<0.003$). However, the direction of the displacement (forward vs. backward) was not significant in this overall comparison (both comparisons $p>0.439$). That is, a 1° backward displacement was not significantly different from a 1° forward displacement when collapsing across all other factors.

Effect of target-bar combination. There was also a main effect of target-bar combination ($F(6,42)=4.74, p<.001$). Figure 3.5 shows the detection rates as a function of target-bar combination collapsed across the other factors. Post-hoc comparisons revealed that the highest detection rates occurred in the 3-With condition when compared against all other target-bar combinations (all comparisons $p<0.033$). There were also significant interactions between target-bar combination*saccade-target combination ($F(12,84)=3.51, p<0.001$), target-bar combination*target displacement ($F(18,126)=2.29, p=0.004$), and target-bar combination*saccade-target combination*target displacement ($F(36,252)=1.76, p=0.007$).

⁶ As stated, this analysis was collapsed across target direction within NB, 1-Stable, and 3-Stable conditions

⁷ All of these factors in the first overall analysis yielded similar significant or non-significant main effects and interactions between each other as reported in this simplified ANOVA.

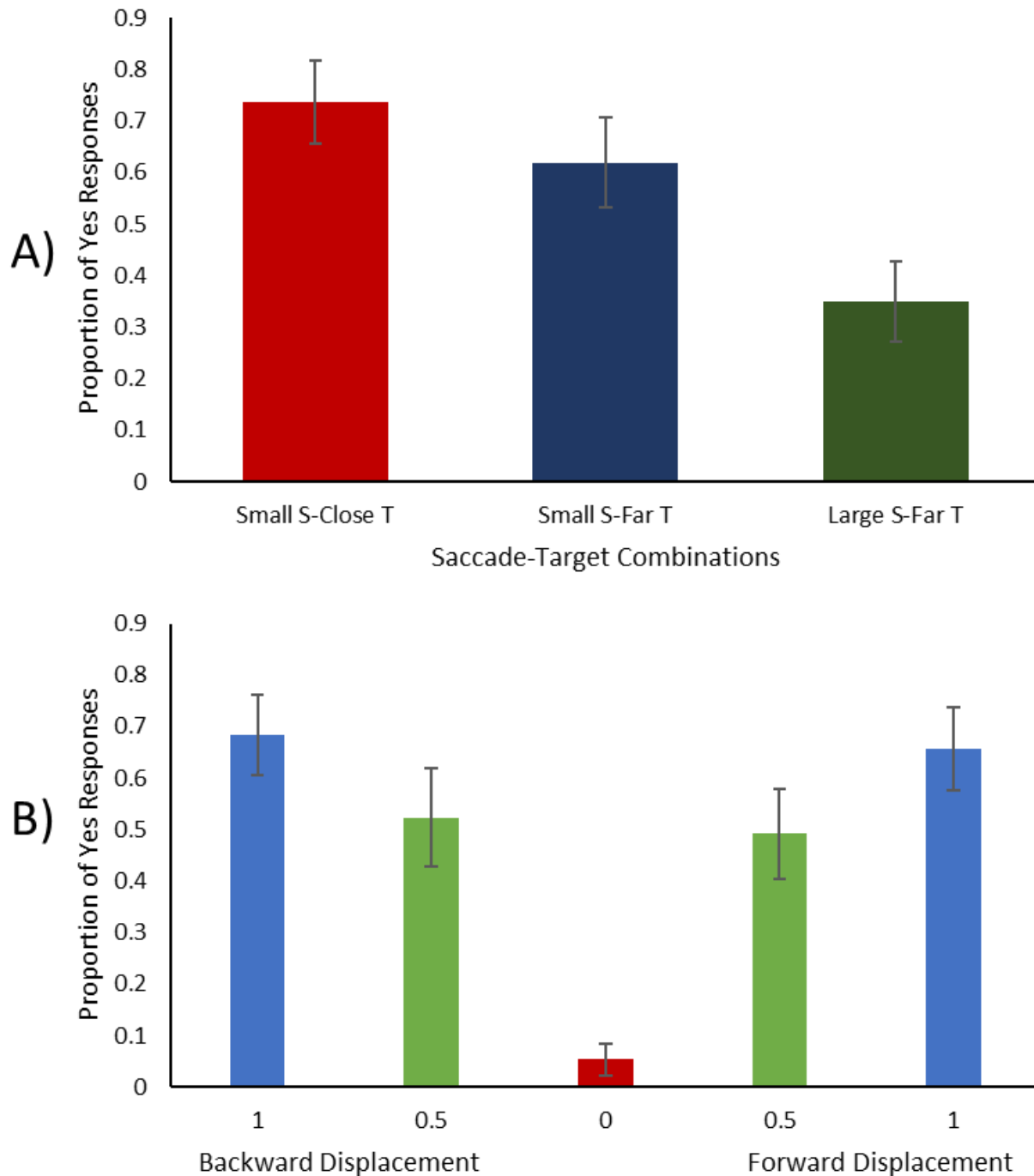


Figure 3.4. Displacement detection by saccade-target combination (panel A) or target displacement (panel B). As in Experiment 1, both the saccade-target combination and target direction influenced participants' accuracy on the task. Panel A, shows the overall main effect of saccade-target combination with the highest accuracy occurring Small S-Close T trials and lowest accuracy in Large S-Far T. Panel B, shows the overall main effect of target displacement, with 1° displacements resulting in the highest accuracy. Note, zero indicates a continued smooth movement of the target (0° displacement) and is included for completeness.

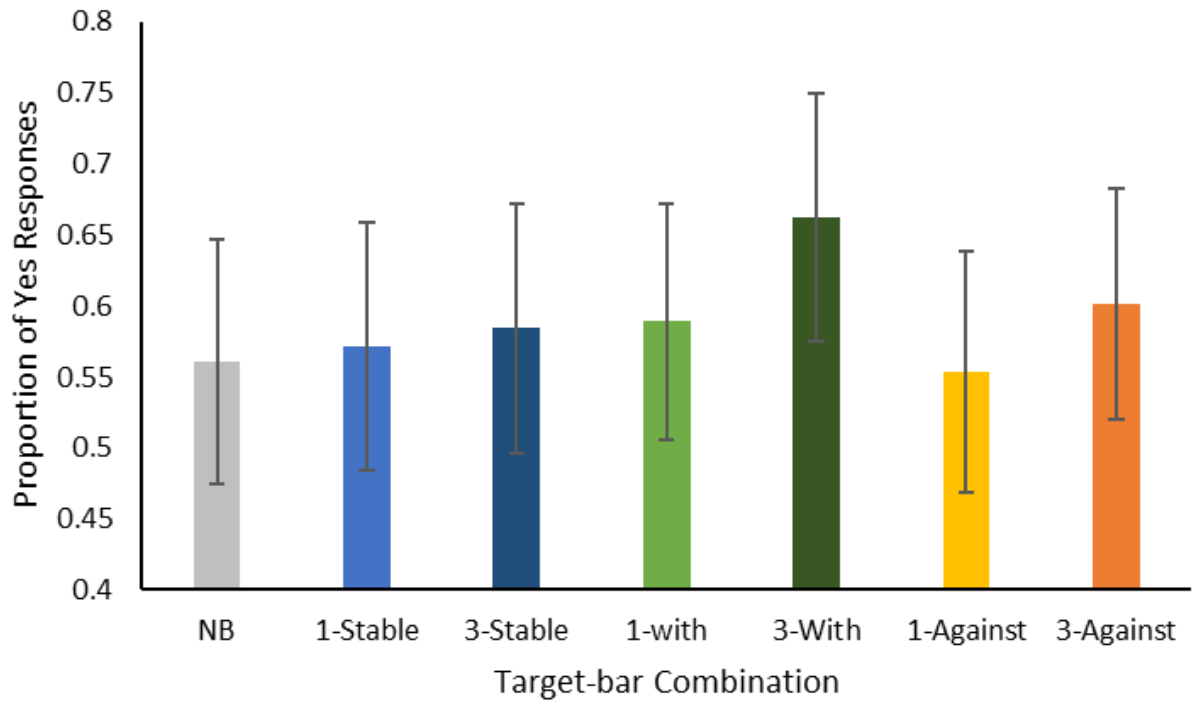


Figure 3.5. Displacement detection in the target-bar combinations, collapsed across target displacement and saccade-target combination. Overall the highest detection rates occurred in the 3-With condition (all comparisons $p < 0.033$). There was no significant difference between the other target-bar combinations when collapsing across all other factors.

Further post-hoc analyses were conducted to examine these interactions with a focus on differences between saccade-target combinations and target displacements within each target-bar combination.

Interactions between saccade-target and target-bar combinations. Figure 3.6 shows the overall results of Experiment 2, for each target-bar combination and saccade-target combination as a function of target displacement and proportion yes responses (displacement detection). This figure is presented to give the reader an overall view of all the data that can be referred to throughout this remaining results section. Note that zero on the x-axis indicates the No-displacement condition (i.e. 0° displacement) and is included for completeness but was not included in the main analysis due to the fundamental difference between required response in the displacement (experimental) and no displacement (control) trials. The panels in Figure 3.6 are labeled according to their target-bar combination condition, from left to right, top to bottom: A) solid grey background with no bars, B) one stable bar, C) three stable bars, D) one bar moving with the target, E) three bars moving with the target, F) one bar moving in the opposite direction as the target, G) and three bars moving in the opposite direction as the target. Note, the same saccade-target combinations occurred across all target-bar combinations and the legend is placed between the figures for ease of reading.

A visual inspection of Figure 3.6 shows the same general pattern of saccade-target combination and target displacement found in the overall analysis as well as in Experiment 1. In the saccade-target combinations we see Small S-Close T showing the greatest accuracy overall and Large S-Far T showing the lowest accuracy. Overall displacement detection was also proportional to the size of target displacement throughout the target-bar combinations, with 1° displacements typically resulting in higher detection accuracy. With this overall inspection of

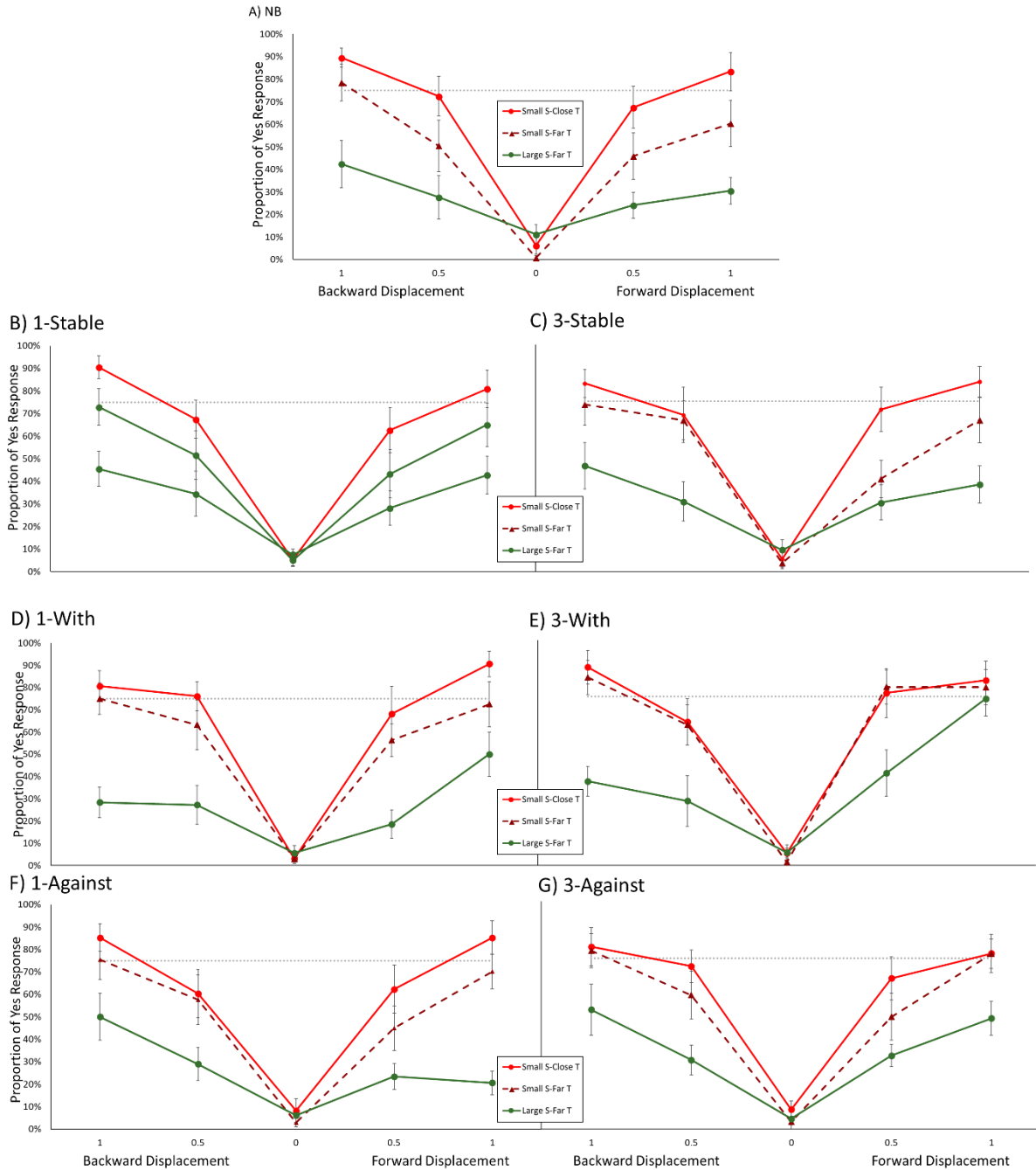


Figure 3.6. Displacement detection in the different target-bar combinations and saccade-target combinations as a function of target displacement. Panels are labeled according to their target-bar combination (see Table 3.2) and zero indicates no displacement (i.e. smooth movement) of the target. The NB, 1-Stable, and 3 Stable conditions were collapsed across dot direction. The light grey dotted line indicates Niemeier et al.'s (2003) 75% perceptual threshold. In all conditions, performance increased with target displacement, and Small S-Close T showed the most accurate performance while Large S-Far T was the most inaccurate. In some of the conditions an asymmetry between backward and forward displacements can be seen. A theoretical analysis of this asymmetry is expanded upon in the discussion.

Figure 3.6, the remaining analysis will examine the differences between these factors both within and between the target-bar combinations.

As mentioned, the NB conditions (panel A of Figure 3.6) was used as a control condition, since there were no allocentric cues presented, as well as a replication of Experiment 1 since the same egocentric paradigm was used. Post-hoc comparisons within the target-bar combinations showed the NB results were similar to those found in Experiment 1. Significant differences were found between all saccade-target combinations at each point the target was displaced (1° backward, 0.5° backward, 1° forward, or 0.5° forward; all comparisons $p < 0.05$), indicating performance was the best when saccades were small and the target was close to central fixation (solid red line) and lowest when saccades were large and the target was further in the periphery (dark green line). Similar overall differences between saccade-target combinations were found in 1-Stable (panel B; all comparisons $p < 0.006$), 3-Stable (panel C; all comparisons $p < 0.002$ except for the Small S-Close T vs. Small S-Far T at 0.5° backward displacement), and 1-with (panel D; all comparisons $p < 0.011$ except for the Small S-Close T vs. Small S-Far T at 1° backward displacement). In 3-With (panel E), 1-Against (panel F), and 3-Against (panel G), the Small S-Close T and Small S-Far T were not significantly different overall (all comparisons $p > 0.865$, 0.055 , & 0.393 respectively). However, both of the small saccade conditions were significantly different from Large S-Far T (all $p < 0.001$) in those target-bar combinations.

To further examine the differences between target-bar combinations, point-by-point post-hoc analyses were done on target displacement and target-bar combination within each saccade-target condition. In order to aid in the interpretation of these findings Figure 3.7 is provided which shows participants accuracy within each of the saccade-target combinations by target displacement and target-bar combinations. In the Small S-Close T condition (Figure 3.7 panel A)

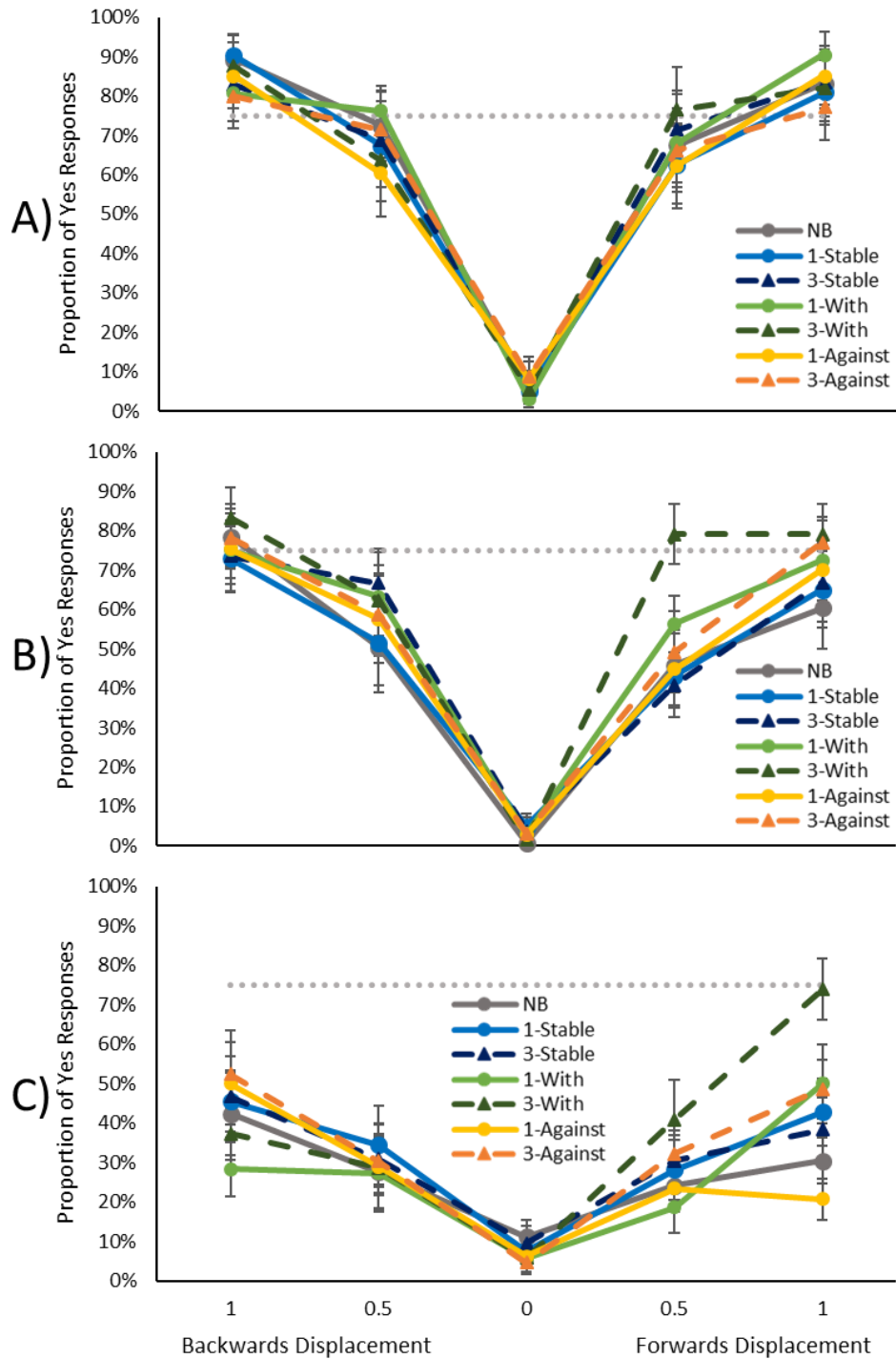


Figure 3.7. Displacement detection by target displacement and target-bar combination in each saccade-target combination. Panel A) The Small S-Close T condition exhibited the highest overall accuracy which remain consistent throughout all target-bar combinations. Panel B) The Small S-Far T condition showed more variability in accuracy due to target-bar combinations. Panel C) The Large S-Far T condition showed the most variability overall within target-bar combinations. The light grey dotted line indicates Niemeier et al.'s (2003) 75% perceptual threshold.

no differences in performance (all comparisons $p>0.744$) were found when comparing target-bar combinations within each target displacement. That is, participants performance was the same at each target displacement, regardless of target-bar combination (e.g. for the Small S-Close T conditions a 1° backward displacement in the NB condition was not significantly different than a 1° backward displacement in the 3-With). This indicates that overall performance in the Small S-Close T condition remained stable regardless of target-bar combination. In the Small S-Far T condition (Figure 3.7 panel B) performance was not as consistent compared to the Small S-Far C. When a 0.5° forward displacement occurred, performance was higher in the 3-With condition compared to all other target-bar combinations (all comparisons $p<0.05$). All other comparisons were not significant ($p>0.405$). In the Large S-Far T condition performance was the most variable as can be seen with a visual inspection of Figure 3.7 panel C. Performance was the highest in the 3-With condition when displacements were 1° forward (all comparisons $p<0.05$).

After this between target-bar combination analysis was completed a within condition point-by-point examination was conducted to examine the asymmetries in participants' accuracy across target displacements, as well as the increase in performance that can be seen in some of the target-bar combinations for Small S-Far T and Large S-Far T (see Figure 3.6) which, at times, raised participants' performance in these conditions to ceiling levels. In order to complete this analysis a benchmark for participants' performance had to be chosen in order to compare changes in participants' accuracy in the Small S-Far T and Large S-Far T conditions. For this, the Small S-Close T data was used as a standard for "ideal" performance within each target-bar combination. This condition was chosen since 1) the Small S-Close T exhibited the highest accuracy, both overall as well as within all the target-bar combinations; 2) it remained stable throughout all the target-bar combinations; and 3) it was found to result in the highest accuracy

in Experiment 1. Therefore, it was proposed that if allocentric cues did aid participants in their performance, then the influence of the allocentric cues should be evident in the other saccade-target combination when compared to the theoretically “ideal” condition of small saccades and close target eccentricities. That is, if allocentric cues aided in performance during large saccades, or far eccentricities, then we should see a corresponding increase in performance in the Small S-Far T and Large S-Far T conditions relative to Small S-Close T. The egocentric NB condition was used to set the standard with which to compare changes in performance. In this condition all comparisons between target displacement and saccade-target combination were significantly different (Figure 3.2 panel A). Therefore, in this experiment a performance increase was said to be significant if the difference between the saccade-target condition and the Small S-Close T condition became non-significant.⁸ To support this final analysis, and to replicate the analysis of Experiment 1, the data was also examined using Niemeier et al.’s (2003) perceptual threshold, which was set at 75% (see Table 3.3).

In the 1-Stable condition (Figure 3.6 panel B) all points remained significantly different ($p < .05$) and there was no difference when compared to NB (all comparisons $p > .119$). Therefore, adding a single allocentric cue did not appear to influence performance. Also, only the Small S-Close T condition exceeded the perception threshold (Table 3.3). In the 3-Stable condition (panel C), Small S-Far T showed a slight increase in performance when the target was displaced backward by 0.5° , resulting in a non-significant difference between Small S-Close T ($p = 0.6$). This increase was also found to be significant when compared to the NB condition ($p < 0.021$). This indicates that having three stable allocentric cues may have aided in participants

⁸ As found in the earlier analysis, no significant drops in participants’ accuracies occurred across the Small S-Close T conditions. Therefore, a significant change in differences between conditions would likely result from performance increases in the other saccade-target combinations.

Table 3.3.

Mean accuracy in saccade-target combination by target displacement and target-bar combination.

		Backward Displacement			Forward Displacement	
		1	0.5	0	0.5	1
NB	Small S-Close T	0.90	0.72	0.94	0.67	0.83
	Small S-Far T	0.78	0.50	0.99	0.46	0.60
	Large S-Far T	0.42	0.28	0.89	0.24	0.30
1-Stable	Small S-Close T	0.91	0.67	0.95	0.63	0.81
	Small S-Far T	0.73	0.52	0.95	0.43	0.65
	Large S-Far T	0.46	0.34	0.92	0.28	0.43
3-Stable	Small S-Close T	0.83	0.69	0.95	0.71	0.84
	Small S-Far T	0.74	0.67	0.96	0.41	0.67
	Large S-Far T	0.47	0.31	0.90	0.30	0.38
1-With	Small S-Close T	0.81	0.76	0.97	0.68	0.91
	Small S-Far T	0.75	0.63	0.97	0.56	0.72
	Large S-Far T	0.28	0.27	0.94	0.19	0.50
3-With	Small S-Close T	0.88	0.64	0.95	0.76	0.82
	Small S-Far T	0.83	0.62	0.99	0.79	0.79
	Large S-Far T	0.37	0.29	0.94	0.41	0.74
1-Against	Small S-Close T	0.85	0.60	0.92	0.62	0.85
	Small S-Far T	0.75	0.58	0.97	0.45	0.70
	Large S-Far T	0.50	0.29	0.94	0.23	0.21
3-Against	Small S-Close T	0.80	0.71	0.91	0.66	0.77
	Small S-Far T	0.78	0.59	0.97	0.49	0.77
	Large S-Far T	0.52	0.30	0.95	0.32	0.49

Note. Items bolded and shaded in gray exceed Niemeier et al.'s (2003) 75% displacement detection threshold, indicating target displacements were reliably detected. The "0" column shows accuracy of reporting no displacement occurring and was not analyzed with Niemeier et al.'s perception threshold.

performance dependent upon the direction and size of the target displacement. However, none of the target displacements in the Small S-Far T or Large S-Far T conditions exceeded the 75% displacement detection threshold.

In 1-With (Figure 3.6 panel D), performance in the Small S-Close T and Small S-Far T was the same for the 1° backward ($p=0.592$) and both 0.5° displacements (both $p=0.186$). Additionally, there was an asymmetry between backward and forward 1° displacements in Large forward displacements showing higher performance than backwards ($p<0.01$). Again, this change in performance indicates that having one allocentric cue can influence performance dependent upon target displacement. The asymmetry in performance can also be seen in the Small S-Close T condition, with a 0.5° backward displacement exceeding the perception threshold but not a 5° forward displacement. 3-With (panel E) showed similar accuracies between the small saccade conditions at each target displacement (all $p>0.460$) as well as the 1° forward displacement during large saccades (both $p>.255$). An asymmetry in performance can also be seen here in the Large S-Far T in Figure 3.6 panel E, as well as in perception thresholds in the small saccade conditions shown in Table 3.3.

In 1-Against (Figure 3.6 panel F), the small saccade conditions showed no significant difference when displacements were 1° in either direction ($p>.131$) or 0.5° backward ($p=0.548$). Here the asymmetry was found to be reversed when targets moved against the allocentric cues, with the backward displacements showing higher accuracy than the forward displacements. Finally, in 3-Against (panel G) there was no significant difference between the small saccade conditions for any of the displacements (all $p>0.159$), indicating that allocentric cues aided in performance when the target was further in the periphery. Unlike the other moving bar conditions, an asymmetry in performance is not apparent in this condition.

Due to the asymmetries in accuracy found in some of the target-bar combinations, but not Experiment 1 or the NB control condition, I reviewed the experimental paradigm. It was found that depending on the target-bar combination and direction of target displacement (forward or backward) the target would move outside of the boundary of the allocentric cue and onto the background (see Figure 3.8 for example). Therefore, this variation in performance is thought to be due to whether or not the target crossed a boundary between the edges of the allocentric cue and the background, thus creating a type of anchor for which to judge changes in the target. This ‘crossing over’ has been termed ‘boundary crossing’ and is further discussed below.

Discussion

Experiment 2 replicated Experiment 1 in that saccade amplitude and eccentricity of target both influenced detection rates. The interaction between saccade amplitude and target eccentricity found in Experiment 1 was quite evident in the control condition when no allocentric cues were presented. Participants showed the best performance when saccade amplitude and target eccentricity was small, while the worst performance occurred when saccades were large, and the target eccentricity was further in the periphery. Additionally, the extent to which target eccentricity or saccade size influence performance on their own was also shown, since small saccades benefitted from a close target (i.e. Small S-Close T > Small S-Far T) and targets with large eccentricities were monitored more accurately when saccades were small (i.e. Small S-Far T > Large S-Far T). Also, as was found in Experiment 1, the size of displacement heavily influenced participants’ performance on the task. In the control condition larger displacements were found to be more accurately detected, regardless of saccade amplitude and target eccentricity. These overall effects of saccade amplitude, target eccentricity, and target displacement were also shown throughout the target-bar combinations, indicating that our visual

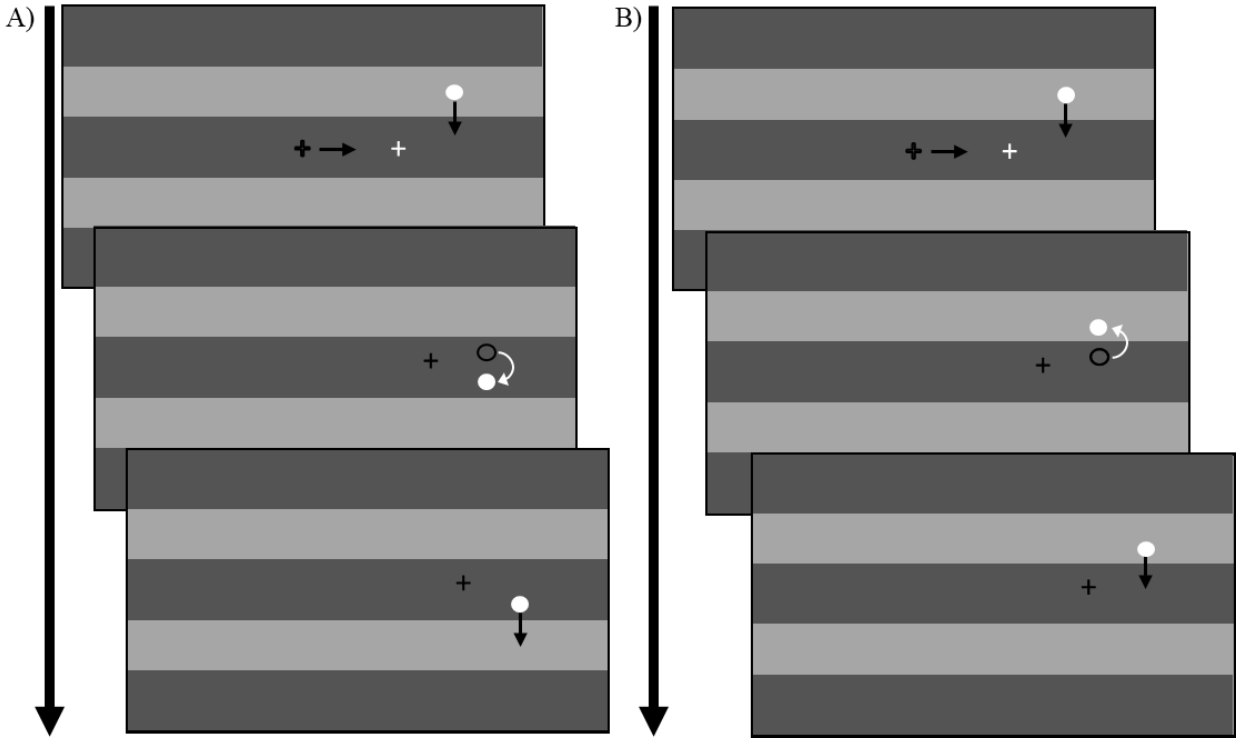


Figure 3.8. Example of boundary crossing when dot is moving downward and three stable allocentric cues are presented. Both examples show a trial in which three stable bars appear across the background. In both cases the target is moving downward, and a saccade is prompted to the right (indicated by the black and white cross in the first screen). In the center screen of Panel A, the target enters the center grey bar and is displaced forward along its path. After the displacement the target is still within the boundaries of the center grey bar, therefore this displacement did not result in any boundary crossing. The target then continues its downward motion. In Panel B, the target enters the center grey bar and is displaced backward along its path. Unlike the first example, this displacement results in the target crossing over the boundary between the bar and the light grey background. Therefore, in this example boundary crossing has occurred. After displacement the target then continues along its initial trajectory. The results from Experiment 2 indicate that participants were more likely to notice the targets displacement if it resulted in the boundary crossing shown in panel B, compared to no boundary crossing as shown in Panel A.

system relies heavily on its own internal processing (e.g. the motor efference copy) and information coming from the attended target (eccentricity and displacement).

At first it was unclear whether allocentric cues influenced participants' performance. While there was an overall main effect of target-bar combinations, this appeared to be mainly due to the condition wherein three cues moved with target motion. However, when examining background effects in more detail it appeared that the lack of effect may have been due to two factors. As mentioned earlier, detection rates were maximal when saccades were small and the eccentricity of the target was close. Since these conditions allowed for peak performance it may be the case that when these conditions arise we rely less on allocentric information, and therefore, the effect of allocentric cues would be less evident. Due to this it is necessary to examine the conditions that could lead to more errors in transsaccadic perception when evaluating the effect of allocentric cues, such as when we make large saccades or the target is further in our periphery.

Second, it was found that in some cases performance depended on the displacement direction (backward or forward) of the target, since in some cases the target's displacement could cause it to cross a boundary, as depicted in Figure 3.8. This boundary crossing seems to have aided in participants' performance by acting as a type of landmark by which the participants could judge the targets position. So, rather than the overall number of the targets being an important feature of the allocentric cue as expected, it is the ability to detect changes in position within or between the landmarks. If this is true it would suggest that the visual system uses a cost saving strategy when monitoring background information in our environment. Rather than processing the allocentric cue as a whole and the exact position the target is within it, the visual system may monitor boundaries of allocentric cues, therefore having a target cross a boundary

into another ‘area’ during a saccade, when we expected it to remain within landmark boundaries, could act as a signal that something changed in our environment. This boundary cross strategy would result in less processing demands on the system, since it would only be processing global information about the background and not fine details such as exact distance to an edge. This theory also fits several other studies which found that when allocentric information is presented the visual system will encode the targets position relative to the spatial coordinates of the background cues (Germeys et al., 2004; Hollingworth, 2007; Verfaillie, 1997; Verfaillie & De Graef, 2000).

With these factors taken into consideration we did find that number and motion of allocentric cues influences displacement detection of a target. When comparing performance in the other saccade conditions to the “ideal” condition of small saccades and a close target, it was found that allocentric cues can improve performance under three conditions. First, performance increased as the number of cues increased. This was true for both stable and moving target-bar combinations, since having more cues appeared to increase performance compared to having less or none. While this effect was minor, and only evident in some cases, the overall trend between conditions should be mentioned. This supports Verfaillie’s (1997) results who found that detection rates were lower when a target translated across a blank background compared to when it had one or more landmarks. As mentioned, Gysen, Verfaillie, and De Graef (2002) may not have found this effect since their presentations always held allocentric cues in the opposite visual field.

Second, detection rates increased when cues moved rather than staying stable. This was evident in both motion conditions when allocentric cues moved with the target trajectory as well as against. This finding supports the theory mentioned earlier that the visual system integrates

dynamic information more reliably and with greater detail than information regarding stationary stimuli. Rosenholtz (1999) found that participants perform better when detecting moving targets amongst stationary stimuli (Rosenholtz, 1999). This may be due to dynamic stimuli being more salient than stationary stimuli (Franconeri & Simons, 2003; Franconeri & Simons, 2005; Rosenholtz, 1999), therefore they could be processed preferably. However, it is also possible that since many of the cortical areas involved in spatial remapping are also superior at analyzing motion information, such as LIP neurons (Kusunoki et al., 2000), that this processing is enhanced when motion information is available.

Third, performance increased when allocentric cues moved with the targets trajectory, rather than against. When comparing the dynamic background conditions (1-With, 3-With, 1-Against, & 3-Against) in most cases performance was found to be better when target and cues moved in the same direction (see Figure 3.5). Therefore, overall, having allocentric cues move in the same trajectory as the target, rather than in opposite directions, allowed for more accurate detection rates. This novel finding offers new insights on how the visual system prioritizes dynamic information during spatial remapping. It is possible that when a target moves in the opposite direction as background information the spatial position of each item is harder to track, therefore causing the background information to be less reliable and thus ignored. It is also possible that detecting boundary crossing is more difficult when objects move in opposite trajectories. However, as can be seen in Figure 3.7 panel C, there are some cases in which performance was better when the target and bar moved in opposite trajectories. Therefore, the influence object momentum has on transsaccadic perception is still unclear. However, it does appear to play an important role during spatial remapping.

Overall, the effect of these three conditions can be best seen when combined, since compared to all other target-bar combinations, having 3 moving targets translate in the same direction as the target increase performance the most when saccades were large and target eccentricity was far. Just as small saccades and close target eccentricities appear to create the best scenario for detecting scene changes, so does having several allocentric cues which move in the same direction as the tracked object.

CHAPTER FOUR

General Discussion

The aim of this project was to provide exciting new information of the basic cognitive mechanisms underlying transsaccadic perception, and thus, gain more insight into a fundamental aspect of our visual conscious experience. In this discussion chapter I will summarize the purpose and procedure of each experiment, review the overall main findings in both studies, and discuss how these findings expand upon our current understanding of transsaccadic research. Throughout this will be a theoretical discussion of how the visual system may use different information in order to maintain stability across saccades. The chapter will conclude with a discussion of the limitations to this study, areas of future research, and a brief overall summary.

Overall this project had two main objectives:

1. Assess how well we track moving objects across saccades when relying solely on spatial information between the object's position relative to ourselves (i.e. egocentric information), and
2. Assess the extent to which other visual cues in our environment (i.e. allocentric information) contribute to transsaccadic motion tracking

The first study within this project aimed to extend the transsaccadic tracking work by Niemeier and colleagues (2003) and Gysen, De Graef, and Verfaillie (2002). Using a completely egocentric task, Niemeier et al. found that participants were most accurate in monitoring sudden changes in a static target (i.e. detecting displacements) when their saccades were small, and the target displacement was large. Building on this Gysen, De Graef, and Verfaillie examined how accurate participants were in detecting similar changes in a smoothly translating stimuli. Supporting Niemeier et al., they found that participants were better able to detect a target displacement if the displacement was large. Additionally, they found that performance was better

when the target was moving compared to remaining stationary before and after the displacement. This is surprising since the processes involved in tracking motion stimuli during a saccade are thought to be more complicated than those involved in tracking stationary objects. However, Gysen, De Graef, and Verfaillie did not vary saccade size and used relatively small, orthogonal saccades, relative to the target motion direction, which has been shown to increase performance on transsaccadic tasks (Niemeier et al., 2003). Additionally, it has yet to be examined how retinal eccentricity (how far the object is in the periphery) influences transsaccadic motion perception. Thus, Experiment 1 sought to examine how saccade size, eccentricity of targets, and the size of target displacement influences participants ability to track a moving target when only egocentric information⁹ is available.

In Experiment 1 participants viewed a moving dot (i.e. a target), which was always presented on the right side of the screen, while fixating on a fixation-cross. At set times the fixation-cross disappeared and reappeared in a new location on the screen, prompting subjects to make a saccade to follow the cross. During the saccade, the target either continued to move smoothly along its path or was suddenly displaced (either forward or backward) along its motion path. At the end of the trial participants were prompted to report whether they noticed the targets displacement during the saccade with either a 'yes' or a 'no'. To address the limitations in Gysen, De Graef, and Verfaillie (2002) the saccade size (how far the fixation-cross moved), saccade direction (where the cross moves to), target displacement (the size of the displacement), and target eccentricity (the position of the target relative to central fixation) were systematically manipulated.

⁹ Encoding the position of an object with relation to one's own physical position in space.

The second study evaluated whether allocentric information¹⁰ influences participants performance in a similar transsaccadic paradigm. Building on their previous study, Gysen, Verfaillie, & De Graef (2002), examined whether allocentric cues, additional objects within the visual field, aided participants' performance when monitoring a target for changes. In their study they found no difference in performance between their isolation and allocentric cue conditions. This led to the proposal that allocentric information is not used when tracking moving objects during a saccade. While this finding is contradictory to other transsaccadic research which used stable stimuli (Germeys et al., 2004; Hollingworth, 2007; Verfaillie, 1997; Verfaillie & De Graef, 2000), some studies have found similar results (Byrne & Crawford, 2010) indicating that allocentric cues may not always be relied upon when scanning our environments. However, Gysen, Verfaillie, & De Graef's findings may have been confounded by the way in which they defined their isolation and allocentric conditions, since allocentric cues were still available in their isolation condition. Due to this, participants may have used the allocentric information presented during both the isolation and allocentric conditions.

Therefore, Experiment 2 aimed to examine the effect of allocentric cues on transsaccadic motion perception by varying the number of allocentric cues available to participants. In addition to this, Experiment 2 examined how the stability of allocentric cues influences participants performance. This was done since a recent study by Byrne and Crawford (2010) found that participants were more likely to rely on their egocentric sense when judging of target location if the allocentric cues presented moved. Finally, Experiment 2 also included manipulations of saccade size, target eccentricity, and size of target displacement in order to 1) replicate Experiment 1, and 2) examine if these variables interact with the presentation of allocentric cues.

¹⁰ Encoding the position of an object with relation to the spatial position of other objects in the environment.

Using a similar transsaccadic paradigm as outlined above, Experiment 2 included the addition of allocentric cues (thick grey bars which spanned the length of the screen) to examine how additional environmental information might influence transsaccadic perception. These cues varied in the amount of information available to the participants (i.e. the number of horizontal bars presented), as well as their stability (i.e. stable versus slowly shifting vertically). These varied allocentric cues were considered to be analogous to real world contexts, such as running a marathon and tracking the objects around you as trees shift by with your pace.

The overall results from both Experiment 1 and 2 show a consistent influence of two variables on transsaccadic perception:

1. Size of target displacement
2. Size of the saccade and resulting changes in retinal eccentricity

Experiment 2 found that allocentric cues appear to be utilized by the visual system, but this use seems to be highly dependent upon how reliable the visual system determines they are. The remaining discussion in this section will examine each of these results in detail.

Target Displacement

In the case of displacement size, larger displacements (e.g. 1° or 2°) were detected more reliably compared to smaller displacements (0.5°). This was true across both experiments and occurred regardless of saccade size, target eccentricity, saccade direction, or presence of allocentric cues. This finding is supported by past research which has found that the larger the displacement of a tracked object (Gysen, De Graef, & Verfaillie, 2002; Niemeier et al., 2003) or the larger the change in the scene (Cavanagh, Hunt, Afraz, & Rolf, 2010; Fracasso et al., 2010; Higgins & Rayner, 2015), the more likely that change is to be detected. This effect seems to

support the idea that attention plays a role in transsaccadic perception, with large changes capturing attention and smaller changes going unnoticed.

It is possible that larger displacements are noticed more often because their displaced location exceeds some retinal shift “error” value our visual system allows for when tracking objects. Referring back to the subtraction model discussed in Chapter 1, if a 5° saccade is made and the object’s retinal coordinates shift by 6° in the opposite direction (5° retinal shift - 5° saccade size = 1° change) our visual system might assume that left over 1° is due to errors in the system and determine visual stability is maintained, thus ignoring what was actually a displacement of the stimulus. However, if the displacement is sufficiently large, for example a 5° saccade with a 8° retinal shift (8° retinal shift - 5° saccade size = 3° change). The remaining 3° is noticed, and the participant reports that the target jumped. This may be why past studies have found that attention influences transsaccadic perception. If the stimuli are approximately where we expected it to be it does not capture our attention, however if it is sufficiently outside of the expected retinal or spatial coordinates our attention is captured.

Saccade Amplitude and Retinal Eccentricity

When examining saccade amplitude both experiments found that small saccades (e.g. 4°) allow for more accurate displacement detection compared to larger saccades (e.g. 12°). This effect of saccade size has also been shown in previous transsaccadic experiments using static stimuli (Bridgeman, Hendry, & Stark, 1974; Li & Matin, 1997; Niemeier et al., 2003). As discussed in Chapter 1, the programming of a saccade (i.e. saccade latency) takes approximately 200ms. Additionally, the time it takes to complete a saccade depends on the saccade amplitude. In the current study the small (4°) saccades used took approximately 29.8ms to complete once

the eye was in flight, while the large (12°) saccades took approximately 47.4ms.¹¹ During these saccades the visual system needs to anticipate what could occur in the environment and predict what the visual scene will look like after the saccade is made (For a review of these processes see Figure 1.9). It is possible that with larger saccades, and thus longer time without viewing the environment (saccadic suppression lasting ~ 147.4 ms vs. 129.8ms for large and small saccades, respectively), the visual system's prediction allows for more errors or is less precise than when small saccades are made. Bridgeman et al. (1974) proposed that with static stimuli, displacements will not be noticed if the saccade amplitude is greater than ~ 3 times the targets displacement. While this exact ratio was not replicated in the present experiment, since 12° saccades were able to detect 2° displacements, it is possible that some threshold element exists in the visual system that aids in detecting changes during saccades.

It is important to note that when examining the effects of saccade size there will likely also be changes in retinal eccentricity, at least if the task is in a natural viewing condition such as when you are reading a paper. In the present study both experiments found that as saccade eccentricity increased (both pre- and post-), participants' performance decreased. The difficulty of monitoring targets with large pre-saccadic retinal eccentricities has been shown in several natural scene, change blindness, and transsaccadic tasks with static stimuli (Bosco, Lappe, & Fattori, 2015; Carrasco, 2011; Eymond, Cavanagh, & Collins, 2019; Li & Matin, 1997; O'Regan, Deubel, Clark, & Rensink, 2000; O'Regan & Noë, 2001; Paradiso & Carney, 1988; Richards, 1969; Vesia, Prime, Yan, Sergio, & Crawford, 2010; Whitaker, Latham, Mäkelä, & Rovamo, 1993). While a small effect of saccade direction was found, with performance decreasing when saccades were made away from the target versus towards, the resulting increase

¹¹ These calculations are based on Carpenter's (1988) formula $T = 2.2A + 21$

in post-saccade eccentricity due to these saccades did not appear to influence participants' performance to the same extent as large pre-saccade eccentricity did. It is possible that pre-saccade eccentricity plays a greater role in the spatial remapping of stimuli compared to post-saccade eccentricity. Theoretically, this makes sense when examining how transsaccadic integration is thought to occur as discussed in Chapter 1 (for review see the section on Transsaccadic Integration).

First, let's take for instance the case when there is a large pre-saccade eccentricity (the target is far from fixation) but after the saccade is made the post-saccade eccentricity is small, such as when participants saccaded toward the target (See Figure 4.1 image A₁). In the first step of transsaccadic integration (Panel A₂ pre-saccade) the peripheral information is captured. In this case the monitored target, a puffin, is far in the periphery, thus little information regarding the target can be captured due to the low acuity of peripheral vision. Once a saccade is prepared the pre-saccadic image is stored into memory as well as used to produce the predicted post-saccade image that will come into view after the saccade is completed (A₂ step 2). Since the pre-saccade input is used to create the predicted image, it is likely that the clearer the pre-saccade image is the more accurate the predicted post-saccade image could be. In this case the pre-saccade input is not clear, therefore, the predicted post-saccade image suffers from the low acuity of the pre-saccade input. This is reflected in the example via a high pixelation of the predicted image. In the final step, the memory and predicted image are compared to the post-saccade image (A₂ step 3).¹² Since the saccade brought the target closer to fixation in example A the post-saccade image of the puffin is clearer. However, the comparisons to determine whether something occurred

¹² Note, unlike the earlier example of transsaccadic integration, which used foveal input, these examples show what the post-saccade input may look like when tracked objects are not foveated. Therefore, the post-saccade image is less acute due to lack of foveation.

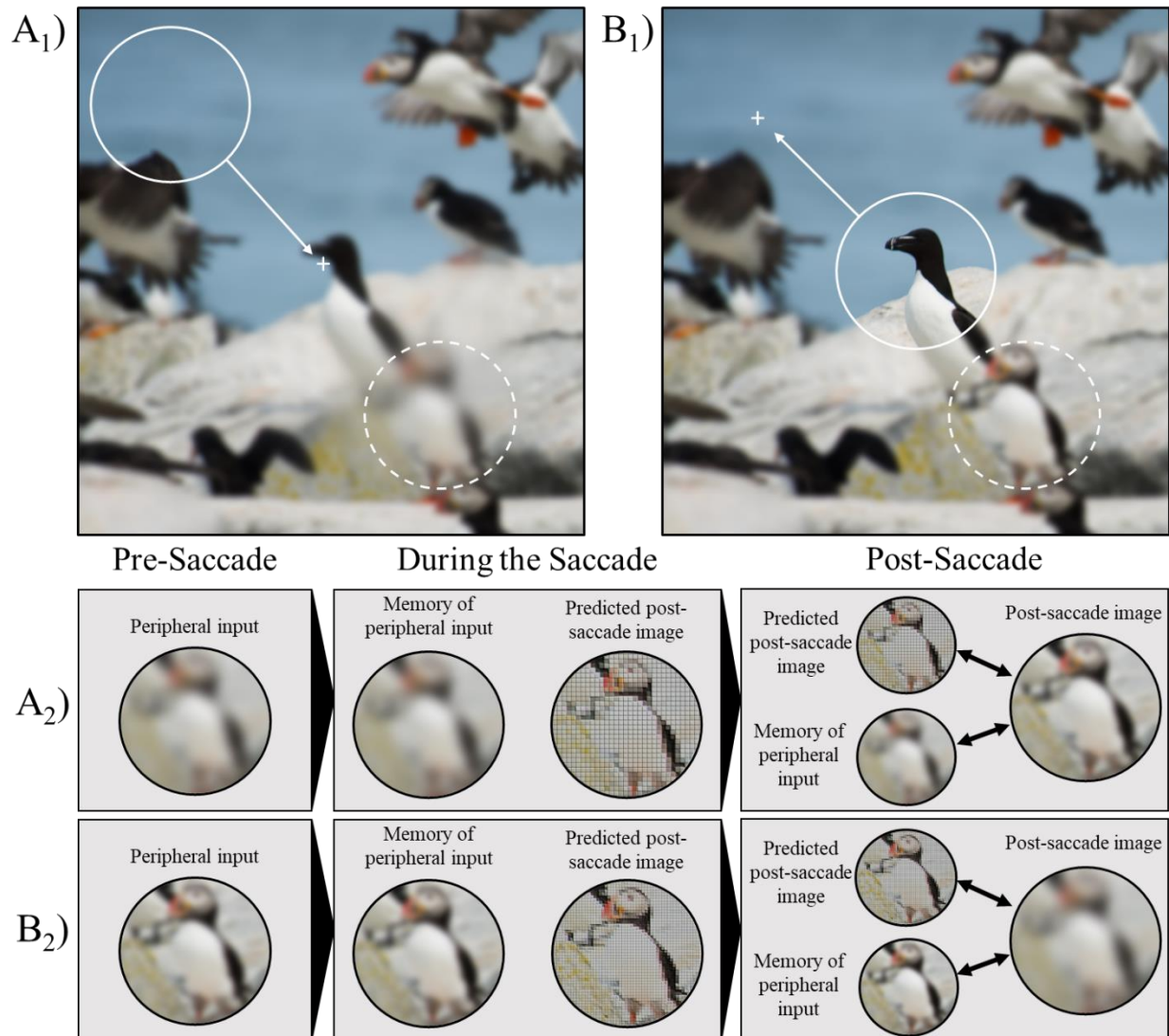


Figure 4.1. Example of transsaccadic integration in different saccade conditions. In the images A₁ and B₁ the solid circle indicates current fixation while the arrow and white cross indicates where the saccade will land. The dotted circle indicates the target that is being monitored in peripheral vision. In A₁ the saccade is made toward the target, resulting in a decrease of target retinal eccentricity (large pre-saccade eccentricity, small post-saccade eccentricity). While in B₁ the saccade is made away from the target resulting in an increased retinal eccentricity of the target (small pre-saccade eccentricity, large post-saccade eccentricity). Panels A₂ and B₂ show the processes of transsaccadic integration for their respective images. Images are shown with increased blur or pixelation to reflect the amount of acuity and accuracy available in the visual system with different retinal eccentricities, since acuity declines the further a target is in the periphery. In panel A₂, the memory and predicted images are less acute and therefore the post-saccadic comparisons are less reliable. In panel B₂, the pre-saccadic memory and predictions are more acute and therefore more reliable. So even though the post-saccade input is less acute, the two reliable sources (memory and prediction) allow for more accurate comparisons between the three images. Therefore, the pre-saccadic eccentricity appears to be more important for transsaccadic integration than the post-saccadic eccentricity.

during the saccade are still difficult, since the pre-saccade image and resulting prediction do not contain reliable information due to the low acuity. Without a reliable basis on which to judge changes the saccade integration task becomes more difficult.

Now take for example the second scenario, when there is little pre-saccade eccentricity (the target is close to fixation) but after a saccade is made there is a large amount of post-saccade eccentricity, such as when you saccade away from a target (see Figure 4.1 image B₁). Again, the pre-saccadic image (panel B₂ step 1) is created. Here the target is close to central fixation, thus the image is created with enough detail to distinguish general features. Due to this higher pre-saccadic acuity, the predicted post-saccade image also benefits and is more detailed (indicated by less pixelation). The saccade is then made away from the monitored target (i.e. Puffin, image B₁). Finally, the memory of the image and image prediction is compared to the post-saccade input (B₂ step 3). While the post-saccade image is now less acute than the previous example, due to the increased post-saccade retinal eccentricity, the two compared images are more reliable. This may allow for more accurate detection of changes, since there are two reliable sources relaying information about the compared visual image rather than two unreliable sources of what occurred before the saccade was made. Additionally, in the second example, the reliable post-saccade information can be compared while still actively attending to the peripheral target. Thereby giving a live feed of information, all be it low acuity information, to compare to the reliable memory and prediction.

Allocentric Information

In Experiment 2 it was first unclear whether allocentric cues influenced participants' performance since performance did not appear to substantially differ overall between the egocentric and allocentric conditions. While some studies have found that allocentric information

is ignored when viewing a scene (Byrne & Crawford, 2010; Yarbus, 1967), others find that the use of allocentric information depends on the extent to which it can be relied upon to aid in tracking the object (Byrne & Crawford, 2010; Germeys et al., 2004; Verfaillie, 1997) or if the background information becomes salient and thus captures attention (O'Regan & Noe, 2001; Simons & Rensink, 2005). In the current study, when the task and data was examined closer, subtle effects of the allocentric information became apparent. From these nuanced effects we concluded three main ways in which allocentric information influences transsaccadic performance.

1. The amount of allocentric information,
2. The stability of allocentric information, and
3. The relative motion of allocentric information and tracked objects.

In the current study participants performance was at its best when more cues were available, cues were moving, and that movement was in the same trajectory as the target. The effect of number of allocentric cues is also supported by other studies, such as Verfaillie (1997) who found that displacement detection rates increased with the proportion of allocentric information presented. Byrne and Crawford (2010) found that when judging displacements of a static target's position, participants relied more heavily on their egocentric sense of the target location compared to allocentric cues. This finding is partially supported by the current study, since overall participants performance was not drastically influenced by allocentric cues. However, the influence of allocentric cues should not be discounted all together since the current study did illustrate instances when participant's performance did increase due to the presentation of allocentric information.

Byrne and Crawford (2010) also found that participants relied more on their sense of self when the allocentric cues were moving. They suggested that the visual system regards moving allocentric cues as an unreliable landmark with which to judge the relative position of the target, and therefore the allocentric visual information is disregarded. This finding was not supported by Experiment 2, since in several cases moving cues resulted in higher displacement detection accuracy, regardless of allocentric motion direction. In Byrne and Crawford's examination of egocentric and allocentric weightings they used a reaching task to determine the extent to which background cues will be relied upon. It is possible that this task would result in some influence from other systems, rather than purely visual encoding, since the vestibular system would be engaged in a reaching/grasping task. This system is dedicated to allowing for a sense of orientation in our environment and aids in balance (Goldberg, Walker, & Hudspeth, 2013), therefore, it may naturally be more egocentric than the visual system. Thus, the results of this study may not be as reflective of the sole processes in the visual system as suggested.

The current study also found that when the target and cues travelled in the same direction, at the same speed, performance was increased compared to if they travelled in opposite directions. It may be that the visual system relies less on allocentric cues when the relative motion between tracked object and background is incongruent. Theoretically this is plausible since a disparity in relative motion would result in more visual processing in order to track the separate velocities of the objects. This increase in processing could then result in more errors within the transsaccadic calculations. In order to avoid these complications, the visual system may not use the allocentric cues in this case, or, it may still track the background but put more weight on the egocentric calculations during transsaccadic integration. This latter explanation seems more plausible, since even when relative motion was incongruent there were still some

trials in which participants' performance increased. Therefore, the background information did not appear to be totally disregarded during spatial remapping.

As mentioned in Chapter 3, the differences between the allocentric conditions appear to be due to whether or not the target crossed a boundary between the allocentric cue and background (for a review see Figure 3.8). Past studies have found that, when examining a scene, participants become more sensitive to changes in the background when those changes violate the general layout or expected progression of the scene (O'Regan & Noe, 2001; Simons & Rensink, 2005). Due to this it is thought that background information is only processed superficially, with enough detail to get the general layout (or gist) of the scene. However, when there is a violation of this overall layout our attention is captured, and we analyze the visual field more critically. It is possible that when the target crossed a boundary this general layout of the presented background was changed beyond what the visual system would allow for, and participants' attention was captured making them more likely to notice that the target was displaced. So while the visual system may not prioritize integrating background information across saccades, compared to more salient visual stimuli, it does appear to encode the allocentric information and use some type of weighting system to determine when the information is reliable, or attention capturing, enough to be used during saccade integration. Due to this, it is likely the way in which our visual system uses allocentric information is more nuanced than other studies have shown.

Limitations and Future Directions

In this project participants completed a transsaccadic perception task in both egocentric and allocentric conditions. During an egocentric task it is important to ensure the screen is impoverished of all other information other than the tracked target, thereby ensuring participants rely on their own, egocentric, sense of self. In this study, in addition to the target, a fixation-cross

was also presented during egocentric conditions. Therefore, presentation of the fixation-cross could have acted as an allocentric cue with which participants judged the relative position of the target. However, without this fixation-cross it would not be possible to direct participants' gaze to the required positions. Thus, the inclusion of a single fixation-cross is necessary during egocentric transsaccadic experiments and is overall accepted within the community (Byrne & Crawford, 2010; Gentilucci, Daprati, Gangitano, & Toni, 1997; Klatzky, 1998; Prime, Tsotsos, Keith, & Crawford, 2007; Prime et al., 2011).

Some studies have show that vertical displacements, as conducted in the present study, are easier to detect than horizontal displacements (Heywood & Churcher, 1981). In these transsaccadic studies static targets shifted either horizontally or vertically and it was found that vertical intrasaccadic movements resulted in higher accuracy than horizontal displacements. However, other studies have found that horizontal displacements are easier to detect than vertical changes (Ilg & Hoffman, 1993). Therefore, it is unclear how these results would relate to conditions in which a tracked object shifted horizontally, and the current results should not be assumed to apply to other transsaccadic displacement until further research examines whether displacement direction truly influences transsaccadic integration.

For the allocentric conditions, horizontal bars were chosen as the allocentric cues. Here several different options of non-target options could have been chosen, such as other dot stimuli, boxes around the target, or backgrounds of varying texture. In this project bars were chosen to represent real world stimuli that may occur, such as passing trees or transitions from cement to grass. Due to the wide variety of possible allocentric cues it is possible that the results collected are specific to that type of allocentric stimuli and presentation of different allocentric cues, such as more dots, may result in different effects on displacement detection. In the second experiment

relative motion between the target and allocentric cues was found to influence participants performance. In these allocentric motion trials the cues always moved at the same speed as the target ($2.7^\circ/s$), regardless of trajectory. While this was done in order to avoid the confound of different trajectories and speeds, it is possible that if the speeds differed the visual system may not find allocentric information as reliable. Therefore, an interesting area of transsaccadic research would be to examine what influence relative speed has on transsaccadic perception in addition to relative motion. Another limitation to the second experiment is that saccades were only made toward the target, resulting in a decrease in post-saccade eccentricity while in the first experiment saccades were made in either direction. Therefore, the effects of allocentric cues are limited to cases where retinal eccentricity is reduced and cannot be generalized to instances when retinal eccentricity may increase (such as when you saccade away from an object).

In the present study it was found that displacements were more likely to be detected if a displacement caused a target to cross a boundary between an allocentric cue and the background. This novel finding supports the etcetera principle, or gist theory, which states that the background of a scene is not processed in great detail and instead the overall layout of the scene is analyzed. While the present study showed that when boundary crossing resulted in a violation of the general “gist” of the scene, it is still unclear what other changes could cause the visual system to use background information during transsaccadic perception. For example, would performance increase if the boundaries between stimuli were more salient, such as in the case of a large tree viewed against a blue sky? Or would an increase in the number of boundaries result in less use of the background information, for instance when watching a deer run through a forest? In relation to this, Prime and colleagues (2007) proposed that the amount of information retained across a single saccade is akin to visual working memory, ~3-4 items. In the second

study the amount of information available to the participants was, at its lowest, 2 objects (fixation-cross and target) and, at its highest, 5 objects (3 bars, fixation-cross, and target). While the present study was not specifically examining the memory size of transsaccadic perception, the results indicate that when all 5 objects were presented participants were able to use this additional allocentric information to increase their performance on the task. Therefore, these results seem to support an upper limit of at least ~5 objects in transsaccadic memory. Future studies should examine the true extent of transsaccadic memory and whether an increase in tracked objects decreases the efficiency and accuracy of the visual system.

Conclusion

Overall this project's novel findings suggest that the basic processes involved in transsaccadic perception of static stimuli are also involved in the transsaccadic perception of dynamic stimuli. During egocentric tracking, the visual system uses the location of the image on the retina, sensory information regarding the velocity of the tracked object, and the motor efference copy to integrate information across saccades. While the calculations that occur during these processes have been found to be flawed (Dassonville, Schlag, & Schlag-Rey, 1992; Honda, 1997), the visual system seems to use some type of mechanism that can account for some of the errors within the system and may occasionally use allocentric cues to help maintain visual stability across saccades. If a culmination of errors occurs, for example due to large saccades and retinal eccentricities, our visual system is less likely to notice changes in the environment when relying on egocentric information and therefore reliance on allocentric cues may be more likely. During allocentric tracking, the visual system appears to use boundaries between stimuli and the general layout of a scene to aid in tracking of stimuli across saccades. The present study sheds light on some of the aforementioned transsaccadic theories, as well as some other theories

regarding vision, eye movements, and brain function. Due to the natural viewing conditions of the tasks in this study it may be possible to apply some of the findings of this research to real-world problems where eye-movement and visual processing are a key aspect to the task, such as vehicle operation (texting and driving) and athletics (a quarterback misjudging the position of their receiver).

References

- Albright, T.D. (2013). *High-level visual processing: Cognitive influences*. In E.R. Kandel, J.H. Schwartz, T.M. Jessell, S.A. Siegelbaum, & A.J. Hudspeth (Eds.), *Principles of neuroscience* (pp. 621-637). USA: McGraw-Hill Companies, Inc.
- Andersen, R.A. (1989). Visual and eye movement functions of the posterior parietal cortex. *Annual Review of Neuroscience*, *12*, 377-403. doi: 10.1146/annurev.ne.12.030189.002113
- Andersen, R.A. (1987). *The role of the inferior parietal lobule in spatial perception and visual-motor integration*. In F. Plum, V.B. Mountcastle, & D.R. Geiger (Eds.), *The handbook of physiology* (pp. 483-518). Bethesda, MD: American Physiological Society.
- Anderson, E.J., Dakin, S.C., & Rees, G. (2009). Monocular signals in human lateral geniculate nucleus reflect the Craik-Cornsweet-O'Brien effect. *Journal of Vision*, *9*(12), 1-18. doi: 10.1167/9.12.14
- Anzai, A., Peng, X., & Van Essen, D.C. (2007). Neurons in monkey visual area V2 encode combinations of orientations. *Nature Neuroscience*, *10*(10), 1313-1321. doi: 10.1038/nn1975
- Bays, P.M., & Husain, M. (2007). Spatial remapping of the visual world across saccades. *Neuroreport*, *18*(12), 1207-1213. doi: 10.1097/WNR.0b013e328244e6c3
- Beckers, G., & Zeki, S. (1995). The consequences of inactivating areas V1 and V5 on visual motion perception. *Brains*, *118*, 49-60.
- Bedell, H.E., & Lott, L.A. (1996). Suppression of motion-produced smear during smooth pursuit eye movements. *Current Biology*, *6*(8), 1032-1034.

- Betts, J.G., Desaix, P., Johnson, E., Johnson, J.Y., Korol, O., Kruse, O., ... Young, K.A. (2017). *Anatomy & physiology*. Houston, Texas: OpenStax.
- Bosco, A., Lappe, M., & Fattori, P. (2015). Adaptation of saccades and perceived size after trans-saccadic changes of object size. *The Journal of Neuroscience*, *35*(43), 14448-14456. doi: 10.1523/JNEUROSCI.0129-15.2015
- Breitmeyer, B.G., Kropfl, W., & Julesz, B. (1982). The existence and role of retinotopic and spatiotopic forms of visual persistence. *Acta Psychologica*, *52*, 175-196.
- Bridgeman, B., Hendry, D., & Stark, L. (1975). Failure to detect displacement of the visual world during saccadic eye movements. *Vision Research*, *15*(6), 719-722. doi: 10.1016/0042-6989(75)90290-4
- Bridgeman, B., Van der Heijden, A., & Velichkovsky, B.M. (1994). A theory of visual stability across saccadic eye movements. *Behavioral and Brain Sciences*, *17*(2), 247-257.
- Brotchie, P.R., Andersen, R.A., & Goodman, S.J. (1995). Head position signals used by parietal neurons to encode locations of visual stimuli. *Nature*, *375*(6528), 232-235. doi: 10.1038/375232a0
- Byrne, P.A., & Crawford, J.D. (2010). Cue reliability and landmark stability heuristic determine relative weighting between egocentric and allocentric visual information in memory-guided reach. *Journal of Neurophysiology*, *103*, 3054-3069. doi: 10.1152/jn.01008.2009
- Calvert, G.A., Hansen, P.C., Iversen, S.D., & Brammer, M.J. (2001). Detection of audio-visual integration sites in humans by application of electrophysiological criteria to the BOLD effect. *NeuroImage*, *14*, 427-438. doi: 10.1006/nimg.2001.0812
- Carpenter, R.H.S. (1988). *Movements of the eyes* (2nd ed.). London: Pion Press.

- Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*, 1484-1525. doi: 10.1016/j.visres.2011.04.012
- Cavanaugh, J., Berman, R.A., Joiner, W.M., & Wurtz, R.H. (2016). Saccadic corollary discharge underlies stable visual perception. *The Journal of Neuroscience*, *36*(1), 31-42.
- Cavanagh, P., Hunt, A.R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of attentional pointers. *Trends in Cognitive Science*, *14*(4), 147-135. doi: 10.1016/j.tics.2010.01.007
- Chelazzi, L., Miller, E.K., Duncan, J., & Desimone, R. (1993). A neural basis for visual search in inferior temporal cortex. *Nature*, *363*, 345-347.
- Colby, C.L., Duhamel, J., & Goldberg, M.E. (1995). Oculocentric spatial representation in parietal cortex. *Cerebral Cortex*, *5*(5), 470-481. doi: 10.1093/cercor/5.5.470
- Colby, C.L., & Goldberg, M.E. (1999). Space and attention in parietal cortex. *Annual Review of Neuroscience*, *22*(1), 319-349. doi: 10.1146/annurev.neuro.22.1.319
- Collins, T., Rolfs, M., Deubel, H., & Cavanagh, P. (2009). Post-saccadic location judgment reveal remapping of saccade targets to non-foveal locations. *Journal of Vision*, *9*(5), 1-9.
- Dassonville, P., Schlag, J., & Schlag-Rey, M. (1992). Oculomotor localization relies on a dampened representation of saccadic eye movement displacement in human and nonhuman primates. *Visual Neuroscience*, *9*, 261-269.
- Deubel, H. (1995). Separate adaptive mechanisms for control of reactive and volitional saccadic eye movements. *Vision Research*, *35*(23-24), 3529-3540. doi: 10.1016/0042-6989(95)00058-M
- Deubel, H., Bridgeman, B., & Schneider, W.X. (1998). Immediate post-saccadic information mediates space constancy. *Vision Research*, *38*, 3147-3159.

- Deubel, H., Schneider, W.X., & Bridgeman, B. (1996). Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Research*, 7, 985-996.
- Diamond, M.R., Ross, R., & Morrone, M.C. (2000). Extraretinal control of saccadic suppression. *The Journal of Neuroscience*, 20(9), 3449-3455.
- Duhamel, J., Bremmer, F., BenHamed, S., & Graf, W. (1997) Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature*, 389, 845-848.
- Duhamel, J., Colby, C.L., & Goldberg, M.E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, 255, 90-92.
- Eymond, C., Cavanaugh, P., & Collins, T. (2019). Feature-based attention across saccades: Pop-out in color search is spatiotopic. *Attention, Perception, and Psychophysics*, 81(1), 85-97. doi: 10.3758/s13414-018-1597-5
- Fabius, J.H., Fracasso, A., & Van der Stigchel, S. (2016). Spatiotopic updating facilitates perception immediately after saccades. *Scientific Reports*, 6(34488), 1-11. doi: 10.1038/srep34488
- Festinger, L., & Holtzman, J.D. (1978). Retinal image smear as a source of information about magnitude of eye movement. *Journal of Experimental Psychology: Human Perception and Performance*, 4(4), 573-585.
- Fournier, J., Müller, C.M., Schneider, I., & Laurent, G. (2018). Spatial information in a non-retinotopic visual cortex. *Neuron*, 97(1), 164-180. doi: 10.1016/j.neuron.2017.11.017
- Fracasso, A., Caramazza, A., & Melcher, D. (2010). Continuous perception of motion and shape across saccadic eye movements. *Journal of Vision*, 10(13), 1-17. doi: 10.1167/10.13.14
- Franconeri, S.L., & Simons, D.J. (2003). Moving and looming stimuli capture attention. *Perception & Psychophysics*, 65(7), 999-1010.

- Franconeri, S.L., & Simons, D.J. (2005). The dynamic events that capture visual attention: A reply to Abrams and Christ (2005). *Perception & Psychophysics*, *67*(6), 962-966.
- Gallati, C., Battaglini, P.P., Fattori, P. (1993). Parietal neurons encoding spatial locations in craniotopic coordinates. *Experimental Brain Research*, *96*, 221-229.
- Gandhi, N.J., & Katnani, H.A. (2011). Motor functions of the superior colliculus. *Annual Review of Neuroscience*, *34*, 205-231. doi: 10.1146/annurev-neuro-061010-113728
- Gattas, R., Sousa, A.P., Mishkin, M., & Ungerleider, L.G. (1997). Cortical projections of area V2 in the macaque. *Cerebral Cortex*, *7*(2), 110-129. doi: 10.1093/cercor/7.2.110
- Gegenfurtner, K.R., Kiper, D.C., & Levitt, J.B. (1997). Functional properties of neurons in macaque area V3. *Journal of Neurophysiology*, *77*(4), 1906-1923. doi: 10.1152/jn.1997.77.4.1906
- Gentilucci, M., Daprati, E., Gangitano, M., & Toni, I. (1997). Eye position tunes the contribution of allocentric and egocentric information to target localization in human goal-directed arm movements. *Neuroscience Letters*, *222*, 123-126.
- Germeys, F., De Graef, P., Panis, S., van Eccelpeol, C., & Verfaille, K. (2004). Transsaccadic integration of bystander locations. *Visual Cognition*, *11*, 203-234. doi: 10.1080/13506280344000301
- Gilbert, C.D. (2013). *Intermediate-level visual processing and visual primates*. In E.R. Kandel, J.H. Schwartz, T.M. Jessell, S.A. Siegelbaum, & A.J. Hudspeth (Eds.), *Principles of neuroscience* (pp. 602-619). USA: McGraw-Hill Companies, Inc.
- Goldberg, M.E., & Bruce, C.J. (1990). Primate frontal eye fields. III. Maintenance of a spatially accurate saccade signal. *Journal of Neurophysiology*, *64*(2), 489-508. doi: 10.1152/jn.1990.64.2.489

- Goldberg, M.E., Colby, C.L. & Duhamel, J.R. (1990). Representation of visuomotor space in the parietal lobe of the monkey. *Cold Spring Harbour Symposia on Quantitative Biology*, 55, 729-739. doi: 10.1101/SQB.1990.055.01.068
- Goldberg, M.E., & Walker, M.F. (2013). *The control of gaze*. In E.R. Kandel, J.H. Schwartz, T.M. Jessell, S.A. Siegelbaum, & A.J. Hudspeth (Eds.), *Principles of neuroscience* (pp. 894-915). USA: McGraw-Hill Companies, Inc.
- Goldberg, M.E., Walker, M.F., & Hudspeth, A.J. (2013). *The vestibular system*. In E.R. Kandel, J.H. Schwartz, T.M. Jessell, S.A. Siegelbaum, & A.J. Hudspeth (Eds.), *Principles of neuroscience* (pp. 917-933). USA: McGraw-Hill Companies, Inc.
- Goldberg, M.E., & Wurtz, R.H. (2013). *Visual processing in action*. In E.R. Kandel, J.H. Schwartz, T.M. Jessell, S.A. Siegelbaum, & A.J. Hudspeth (Eds.), *Principles of neuroscience* (pp. 638-653). USA: McGraw-Hill Companies, Inc.
- Gombruch, E.H. (1979). *The sense of order: A study in the psychology of decorative art*. Great Britain: Phaidon Press limited.
- Gottlieb, J.P., Kusunoki, M., & Goldberg, M.E. (1998). The representation of visual salience in monkey parietal cortex. *Nature*, 391, 481-484.
- Grimes, J. (1996). *On the failure to detect changes in scenes across saccades*. In K. Akins (Ed.), *Vancouver Studies in Cognitive Science (Vol. 2): Perception* (pp. 89-110). New York, NY: Oxford University Press.
- Herwig, A. (2015). Transsaccadic integration and perceptual continuity. *Journal of Vision*, 15(16), 1-6. doi: 10.1167/15.16.7
- Henderson, J.M. (2003). Human gaze control during real-world scene perception. *TRENDS in Cognitive Sciences*, 7(11), 498-504. doi: 10.1016/j.tics.2003.09.006

- Henderson, J.M., & Hollingworth, A. (1999). The role of fixation position in detecting scene changes across saccades. *Psychological Science*, *52*, 175-196. doi: 10.1111/1467-9280.00183
- Hennessy, H. (2017). *A group of atlantic puffins and razorbills all takeoff from the rocks on Machias Seal Island with the Atlantic Ocean in the background*. [Photograph]. Retrieved from <https://unsplash.com/photos/dXHKxkPgAA8>.
- Heywood, S., & Churcher, J. (1981). Direction-specific and position-specific effects upon detection of displacements during saccadic eye movements. *Vision Research*, *21*, 255-261.
- Higgins, E., & Rayner, K. (2015). Transsaccadic processing: Stability, integration, and the potential role of remapping. *Attention, Perception, and Psychophysics*, *77*, 3-27. doi: 10.3758/s13414-014-0751-y
- Hollingworth, A. (2007). Object-position binding in visual memory for natural scenes and object arrays. *Journal of Experimental Psychology: Human Perception and Performance*, *33*(1), 31-47. doi: 10.1037/0096-1523.33.1.31
- Honda, H. (1997). Interaction of extraretinal eye position signals in double-step saccade task: Psychophysical estimation. *Experimental Brain Research*, *113*, 327-336.
- Ibbotson, M., & Krekelberg, B. (2011). Visual perception and saccadic eye movements. *Current Opinion in Neurobiology*, *21*, 553-558. doi: 10.1016/j.conb.2011.05.012
- Ilg, U.J., & Hoffman, K.P. (1993). Motion perception during saccades. *Vision Research*, *33*(2), 211-220.

- Irwin, D., Brown, J., & Sun, J. (1988). Visual masking and visual integration across saccadic eye movements. *Journal of Experimental Psychology General*, *117*(3), 276-287. doi: 10.1037//0096-3445.117.3.276
- Irwin, D., Yantis, S., & Jonides, J. (1983). Evidence against visual integration across saccadic eye movements. *Perception and Psychophysics*, *34*(1), 49-57.
- Joiner, W.M., Cavanaugh, J., & Wurtz, R.H. (2011). Modulation of shifting receptive field activity in frontal eye field by visual salience. *Journal of Neurophysiology*, *106*(3), 1179-1190.
- Jonas, J.B., Schneider, U., & Naumann, G.O. (1992). Count and density of human retinal photoreceptors. *Graefe's Archive for Clinical and Experimental Ophthalmology*, *230*(6), 505-510.
- Jones, E.G. (1985). *The thalamus*. New York: Plenum.
- Jonides, J., Irwin, D.E., & Yantis, S. (1982). Integrating visual information from successive fixations. *Science*, *215*(4529), 192-194. doi: 10.1126/science.7053571
- Jovicich, J., Peters, R.J., Koch, C., Braun, J., Chang, L., & Ernst, T. (2001). Brain areas specific for attention load in a motion-tracking task. *Journal of Cognitive Neuroscience*, *13*(8), 1048-1058.
- Kerschensteiner, D., & Guido, W. (2017). Organization of the dorsal lateral geniculate nucleus in the mouse. *Visual Neuroscience*, *34*(e008), 1-9. doi: 10.1017/S0952523817000062
- Klatzky, R.L. (1998). *Allocentric and egocentric spatial representations: Definitions, distinctions, and interconnections*. In C. Freksa, C. & C. Habel (Eds.), *Spatial cognition. An interdisciplinary approach to representing and processing spatial knowledge*. (pp. 1-17). Berlin, Heidelberg: Springer.

- Kusunoki, M., Gottlieb, J., & Goldberg, M.E. (2000). The lateral intraparietal area as a salience map: The representation of abrupt onset, stimulus motion, and task relevance. *Vision Research*, 40, 1459-1468.
- Land, M., Mennie, N., & Rusted, J. (1999). The roles of vision and eye movements in the control of activities of daily living. *Perception*, 28, 1311-1328.
- Latour, P. (1962). Visual threshold during eye movements. *Vision Research*, 2, 261-262.
- Lenth, R. (2018). Emmeans: Estimated marginal means, aka least-squares means. [R package]. Retrieved from <https://cran.r-project.org/package=emmeans>.
- Leo, F., Bertini, C., di Pellegrino, G., & Làdavas, E. (2008). Multisensory integration for orienting responses in humans requires the activation of the superior colliculus. *Experimental Brain Research*, 186(1), 67-77. doi: 10.1007/s00221-007-1204-9
- Li, W., & Matin, L. (1990). The influence of saccade length on the saccadic suppression of displacement detection. *Perception & Psychophysics*, 48(5), 453-458.
- Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science*, 240(4853), 740-749.
- MacKay, D.M. (1967). *Ways of looking at perception*. In W. Wathen-Dunn (Ed.), *Models for the perception of speech and visual form* (pp. 25-43). Cambridge, MA: MIT Press.
- Maruko, I., Zhang, B., Tao, X., Tong, J., Smith III, E.L., & Chino, Y.M. (2008). Postnatal development of disparity sensitivity in visual area 2 (V2) of macaque monkeys. *Journal of Neurophysiology*, 100, 2486-2495. doi: 10.1152/jn.90397.2008
- Matin, E. (1974). Saccadic suppression: A review and an analysis. *Psychological Bulletin*, 81, 899-917.

- McConkie, G., & Rayner, K. (1976). *Identifying the span of the effective stimulus in reading: Literature review and theories of reading*. In H. Singer & R.B. Rudell (Eds.), *Theoretical models and processes in reading* (pp. 137-162). Newark, DE: International Reading Association.
- McConkie, G., & Zola, D. (1979). Is visual information integrated across successive fixations in reading? *Perception & Psychophysics*, *25*(3), 221-224.
- Meister, M., & Tessier-Lavigne, M. (2013). *Low-level visual processing: The retina*. In E.R. Kandel, J.H. Schwartz, T.M. Jessell, S.A. Siegelbaum, & A.J. Hudspeth (Eds.), *Principles of neuroscience* (pp. 577-600). USA: McGraw-Hill Companies, Inc.
- Melcher, D. (2008). Dynamic, object-based remapping of visual features in trans-saccadic perception. *Journal of Vision*, *8*(14), 1-17. doi: 10.1167/8.14.2
- Melcher, D. (2005). Spatiotopic transfer of visual-form adaptation across saccadic eye movements. *Current Biology*, *15*, 1745-1748. doi: 10.1016/j.cub.2005.08.044
- Melcher, D., & Colby, C.L. (2008). Trans-saccadic perception. *Trends in Cognitive Sciences*, *12*(12), 466-473. doi: 10.1016/j.tics.2008.09.003
- Melcher, D., & Morrone, M.C. (2003). Spatiotopic temporal integration of visual motion across saccadic eye movements. *Nature*, *6*(8), 877-881.
- Meredith, M.A., & Stein, B.E. (1986). Visual, auditory, and somatosensory convergence on cells in superior colliculus results in multisensory integration. *Journal of Neurophysiology*, *56*(3), 640-662. doi: 10.1152/jn.1986.56.3.640
- Merriam, E.P., Genovese, C.R., & Colby, C.L. (2007). Remapping in human visual cortex. *Journal of Neurophysiology*, *97*(2), 1738-1755.

- Mirpour, K., & Bisley, J. (2012). Anticipatory remapping of attention priority across the entire visual field. *The Journal of Neuroscience*, *32*(46), 16449-16457. doi: 10.1523/JNEUROSCI.2008-12.2012
- Monty, R.A., & Senders, J.W. (1976). *Eye movements and psychological processes*. New York, USA: Lawrence Erlbaum Associates, Inc.
- Moore, T., Tolias, A.S., & Schiller, P.H. (1998). Visual representations during saccadic eye movements. *PNAS*, *95*(15), 8981-8984. doi: 10.1073/pnas.95.15.8981
- Nakamura, K., & Colby, C.L. (2000). Visual, saccade-related, and cognitive activation of single neurons in monkey extrastriate area V3A. *Journal of Neurophysiology*, *84*, 677-692.
- Nakamura, K., & Colby, C.L. (2002). Updating of the visual representation in monkey striate and extrastriate cortex during saccades. *PNAS*, *99*, 4026-4031.
- Niemeier, M., Crawford, D., & Tweed, D. (2003). Optimal transsaccadic integration explains distorted spatial perception. *Nature*, *422*, 76-80.
- Ong, W.S., Hooshvar, N., Zhang, M., & Bisley, J.W. (2009). Psychophysical evidence for spatiotopic processing in area MT in short-term memory for motion task. *Journal of neurophysiology*, *102*(4), 2435-2440.
- O'Regan, J.K. (1992). Solving the "real" mysteries of visual perception: The world as an outside memory. *Canadian Journal of Psychology/Revue Canadienne De Psychologie*, *46*(3), 461.
- O'Regan, J.K., Deubel, H., Clark, J.J., & Rensink, R.A. (2000). Picture changes during blinks: Looking without seeing and seeing without looking. *Visual Cognition*, *7*, 191-211.

- O'Regan, J.K., & Levy-Schoen, A. (1983). Integrating visual information from successive fixations: Does trans-saccadic fusion exist? *Vision Research*, 23(8), 765-768. doi: 10.1016/0042-6989(83)90198-0
- O'Regan, J.K., & Noë, A. (2001). A sensorimotor account of vision and visual consciousness. *Behavioral and Brain Sciences*, 24, 939-1031. doi: 10.1017/S0140525X01000115
- Ostendorf, F., Kiliyas, J., & Ploner, C.J. (2012). Theta-burst stimulation over human frontal cortex distorts perceptual stability across eye movements. *Cerebral Cortex*, 22, 800-810. doi: 10.1093/cercor/bhr143
- Paradiso, M.A., & Carney, T. (1988). Orientation discrimination as a function of stimulus eccentricity and size: Nasal/temporal retinal asymmetry. *Vision Research*, 28(8), 867-874.
- Payman, G.A., Meffert, S.A, Chou, F., & Conway, M.D. (Eds.). (2001). *Vitreoretinal Surgical Techniques*. London, England: Martin Dunitz Ltd.
- Pitzalis, S., Fattori, P., & Galletti, C. (2012). The functional role of the medial motion area V6. *Frontiers in Behavioral Neuroscience*, 6(91), 1-13. doi: 10.3389/fnbeh.2012.00091
- Pouget, A., Sejnowski, T.J., & Hughes, H. (1999). Spatial representation in the parietal cortex may use basis functions. *Advances in Neural Information Processing Systems*, 7, 157-164.
- Prime, S.L., Niemeier, M., & Crawford, J.D. (2006). Transsaccadic integration of visual features in a line interaction task. *Experimental Brain Research*, 169, 532-548. doi: 10.1007/s00221-005-0164-1

- Prime, S.L., Niemeier, M., & Crawford, J.D. (2007). *Trans-saccadic memory of visual features*. In L. Harris & M. Jenkins (Eds.) *Computational Vision in Neural and Machine Systems* (pp167-182). Cambridge University Press, UK.
- Prime, S.L., Tsotsos, L., Keith, G.P., Crawford, J.D. (2007). Visual memory capacity in transsaccadic integration. *Experimental Brain Research*, 180, 609-628. doi: 10.1007/s00221-007-0885-4
- Prime, S.L., Vesia, M., & Crawford, J.D. (2011). Cortical mechanisms for trans-saccadic memory and integration of multiple object features. *Philosophical Transactions of the Royal Society B*, 366(1564), 540-553. doi: 10.1098/rstb.2010.0184
- Purves, D., Augustine, G.J., Fitzpatrick, D., Hall, W.C., LaMantia, A.S., McNamara, J.O., & Williams S.M. (Eds.). (2004). *Neuroscience* (3rd ed.). MA, USA: Sinauer Associates, Inc.
- Qiu, F.T., & von der Heydt, R. (2005). Figure and ground in the visual cortex: V2 combines stereoscopic cues with gestalt rules. *Neuron*, 47, 155-166. doi: 10.1016/j.neuron.2005.05.028
- Quaia, C., Optican, L., & Goldberg, M.E. (1998). The maintenance of spatial accuracy by the perisaccadic remapping of visual receptive fields. *Neural Networks*, 7(8), 1229-1240. doi: 10.1016/S0893-6080(98)00069-0
- R Core Team. (2018). R: A language an environment for statistical computing. [Computer software]. Retrieved from <https://cran.r-project.org/>.
- Rayner, K., McConkie, G., & Zola, D. (1980). Integrating information across eye movements. *Cognitive Psychology*, 12(2), 206-226. doi: 10.1016/0010-0285(80)90009-2

- Rayner, K., & Pollatsek, A. (1983). Is visual information integrated across saccades? *Perception & Psychophysics*, *34*(1), 39-48.
- Remington, R.W. (1980). Attention and saccadic eye movements. *Journal of Experimental Psychology: Human Perception and Performance*, *6*(4), 726-744.
- Richard, C.M., Wright, R.D., Ee, C., Prime, S.L., Shimizu, Y., & Vavrik, J. (2002). Effect of concurrent auditory task on visual search performance in a driving-related image-flicker task. *Human Factors*, *44*(1), 108-119. doi: 10.1518/0018720024494874
- Richards, W. (1969). Saccadic suppression. *Journal of the Optical Society of America*, *59*(5), 617-623.
- Rizzolatti, G., & Strick, P.L. (2013). *Cognitive functions of the premotor systems*. In E.R. Kandel, J.H. Schwartz, T.M. Jessell, S.A. Siegelbaum, & A.J. Hudspeth (Eds.), *Principles of neuroscience* (pp. 412-425). USA: McGraw-Hill Companies, Inc.
- Rolls, E.T., Aggelopoulos, N.C., & Zheng, F. (2003). The receptive fields of inferior temporal cortex neurons in natural scenes. *Journal of Neuroscience*, *32*(1), 339-348.
- Rosenholtz, R. (1999). A simple saliency model predicts a number of motion popout phenomena. *Vision Research*, *39*, 3157-3163.
- Ruff, C.C., Bestmann, S., Blankenburg, F., Bjoetomt, O., Josephs, O., Weiskopf, N.,... Driver, J. (2008). Distinct causal influences of parietal versus frontal areas on human visual cortex: Evidence from concurrent TMS-fMRI. *Cerebral Cortex*, *18*(4), 817-827. doi: 10.1093/cercor/bhm128
- Shatz, C.J. (1996). Emergence of order in visual system development. *Proceedings of the National Academy of Sciences of the United States of America*, *93*(2), 602-608. doi: 10.1073/pnas.93.2.602

- Simons, D.J. (1996). In sight, out of mind: When object representations fail. *Psychological Science*, 7(5), 301-305.
- Simons, D.J., & Rensink, R.A. (2005). Change blindness: Past, present, and future. *Trends in Cognitive Sciences*, 9(1), 16-20.
- Singmann, H. (2018). Afex: Analysis of factorial experiments. [R package]. Retrieved from <https://cran.r-project.org/package=afex>.
- Sommer, M.A., & Wurtz, R.H. (2002). A pathway in primate brain for internal monitoring of movements. *Science*, 296(5572), 1480-1482.
- Sommer, M.A., & Wurtz, R.H. (2004). What the brain stem tells the frontal cortex. I. oculomotor signals sent from superior colliculus to frontal eye field via mediodorsal thalamus. *Journal of Neurophysiology*, 91(3), 1381-1402.
- Sommer, M.A., & Wurtz, R.H. (2006). Influence of the thalamus on spatial visual processing in frontal cortex. *Nature*, 444, 374-377. doi: 10.1038/nature05279
- Sommer, M.A., & Wurtz, R.H. (2008). Brain circuits for the internal monitoring of movements. *Annual Review of Neuroscience*, 31, 317-338.
- Spiske, M. (2017). *Light Dieting*. [Photograph]. Retrieved from <https://unsplash.com/photos/TnKcYzVa2Js/info>.
- Tatler, B.W. (2001). Characterising the visual buffer: Real-world evidence for overwriting early in each fixation. *Perception*, 30(8), 993-1006. doi: 10.1068/p3121
- Tobimatsu, S., & Celesia, G.G. (2006). Studies of human visual pathophysiology with visual evoked potentials. *Clinical Neurophysiology*, 117(7), 1414-1433.

- Tolias, A.S., Moore, T., Smirnakis, S.M., Tehovnik, E.J., Siapas, A.G., & Schiller, P.H. (2001). Eye movements modulate visual receptive fields of V4 neurons. *Neuron*, 29, 757-767. doi: 10.1016/S0896-6273(01)00250-1
- The jamovi project. (2019). Jamovi (Version 1.0) [Computer Software]. Retrieved from <https://www.jamovi.org>
- Thier, P., & Erickson, R.G. (1992). Responses of visual-tracking neurons from cortical areas MST-I to visual, eye and head motion. *European Journal of Neuroscience*, 4(6), 539-553. doi: 10.1111/j.1460-9568.1992.tb00904.x
- Umeno, M.M., & Goldberg, M.E. (1997). Spatial processing in the monkey frontal eye field I. Predictive visual responses. *Journal of Neurophysiology*, 78, 1373-1383.
- Umeno, M.M., & Goldberg, M.E. (2001). Spatial processing in the monkey frontal eye field: II Memory responses. *Journal of Neurophysiology*, 86(5), 2344-2352. doi: 10.1152/jn.2001.86.5.2344
- Ungerleider, L.G., & Desimone, R. (1986). Cortical connections of visual area MT in the macaque. *The Journal of Comparative Neurology*, 248, 190-222.
- Valsecchi, M., & Gegenfurtner, K.R. (2016). Dynamic re-calibration of perceived size in fovea and periphery through predictable size changes. *Current Biology*, 26, 59-63. doi: 10.1016/j.cub.2015.10.067
- van Donkelaar, P., & Müri, R. (2002). Craniotopic updating of visual space across saccades in the human posterior parietal cortex. *Proceedings of the Royal Society B*, 269, 735-739. doi: 10.1098/rspb.2001.1935

- Verfaillie, K. (1997). Transsaccadic memory for the egocentric and allocentric position of a biological-motion walker. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 23(3), 739-760. doi: 10.1037/0278-7393.23.3.739
- Verfaillie, K., & De Graef, P. (2000). Transsaccadic memory for position and orientation of saccade source and target. *Journal of Experimental Psychology: Human Perception and Performance*, 26(4), 1243-1259. doi: 10.1037/0096-1523.26.4.1243
- Vesia, M., Prime, S.L., Yan, X., Sergio, L.E., & Crawford, J.D. (2010). Specificity of human parietal saccade and reach regions during transcranial magnetic stimulation. *The Journal of Neuroscience*, 30(39), 13053-13065. doi: 10.1523/JNEUROSCI.1644-10.2010
- von der Heydt, R., Peterhans, E., & Baumgartner, G. (1984). Illusory contours and cortical neuron responses. *Science*, 224(4654), 1260-1262. doi: 10.1126/science.6539501
- von der Heydt, R., Zhou, H., Friedman, H.S. (2000). Representation of stereoscopic edges in monkey visual cortex. *Vision Research*, 40, 1955-1967.
- Walker, M.F., Fitzgibbon, E.J., & Goldberg, M.E. (1995). Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements. *Journal of Neurophysiology*, 73, 1988-2003.
- Wallace, M.T., Meredith, M.A., & Stein, B.E. (1988). Multisensory integration in the superior colliculus of the alert cat. *Journal of Neurophysiology*, 80(2), 1006-1010. doi: 10.1152/jn.1998.80.2.1006
- Whitaker, D., Latham, K., Mäkelä, P., & Rovamo, J. (1993). Detection and discrimination of curvature in foveal and peripheral vision. *Vision Research*, 33(16), 2215-2224. doi: 10.1016/0042-6989(93)90101-2

- Wolf, C., & Schütz, A. (2015). Trans-saccadic integration of peripheral and foveal feature information is close to optimal. *Journal of Vision, 15*(16), 1-18. doi: 10.1167/15.16.1
- Wurtz, R.H., (2008). Neuronal mechanisms of visual stability. *Vision Research, 48*(20), 2070-2089.
- Yamasaki, T., Muranaka, H., Kaseda, Y., Mimori, Y., & Tobimatsu, S. (2012). Understanding the pathophysiology of alzheimer's disease and mild cognitive impairment: A mini review on fMRI and ERP studies. *Neurology Research International, 2012*, 2090-1852. doi: 10.1155/2012/719056
- Yang, Q., Bucci, M.P., & Kapoula, Z. (2002). The latency of saccades, mergence, and combined eye movements in children and in adults. *Investigative Ophthalmology and Visual Science, 43*, 2939-2949.
- Yanoff, M., & Sassani, J.W. (2009). *Ocular pathology* (6th ed.). Amsterdam: Elsevier.
- Yantis, S. (2014). *Sensation and perception*. New York, USA: Worth Publishers.