

**THE INFLUENCE OF ALLOCENTRIC CUES ON
TRANSSACCADIC INTEGRATION OF MULTIPLE OBJECTS**

George Tomou

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ABSTRACT

This thesis explores the role of stable allocentric information on the integration of visual information across eye movements. In this series of studies, I tested transsaccadic integration of multiple objects each with varying orientations in the presence or absence of reliable landmarks. Participants compared the orientations of two target stimuli presented before (amongst distractors) and after an eye movement. The orientation of the target stimulus changed during the eye movement and participants were required to indicate if the change was clockwise or counterclockwise. On a given block, the stimuli were either presented in isolation, or in the along with visual landmarks. In the first experiment, the landmarks were *intrinsic* (directly related to the spatial location of the stimuli), while in the second experiment the landmarks were *extrinsic* (spatially independent that provided indirect location information). Results showed that performance without landmarks dropped as the number of distractors increased. The intrinsic landmarks were not able to temper this decrease in performance, but the extrinsic landmark had a significant effect. A control experiment was conducted to explain the extrinsic landmark's role of as a spatial cue. These results show that extrinsic visual landmarks can aid the visual system's ability to integrate visual information across eye movements.

DEDICATION

*This thesis is dedicated to my wonderful wife, Vivi.
Thank you for your patience, love, and support.*

*It is also dedicated to my family, Kosta, Jeannie, and Lenna.
Thank you for your endless encouragement.*

“We did it!”

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Introduction

Humans largely rely on their vision to navigate and make sense of complex environments. While the distribution of complex information in the environment may be spread over a large area, the acuity of incoming information is not evenly distributed on the retina (Osterberg, 1935). Highly detailed information is processed when the information falls on a very small region called the fovea; outside of the fovea, the peripheral regions of the retina provide less detailed visual information (Bouma, 1970). Thus, in order to process the complex visual world, we move our eyes to situate locations of interest on the fovea (Walls, 1962). These eye-movements, also called saccades, are executed several times a second (Rayner, 1978, 1998), during which vision is suppressed (Matin, 1974; Nakamizo 1974; Volkman, 1986), and as a result our visual experience is comprised of the stringing together of discrete snapshots of information acquired at each fixation. Because of this snapshot acquisition, the image that falls on the retina at each fixation is different from the last, yet our visual perception is that of a global percept. This unified percept of the environment arises because our visual system takes these independent images and combines them. The process of retaining and synthesizing visual information across saccades is called *transsaccadic integration* (Irwin, 1991; Melcher & Colby, 2008).

Previous research on transsaccadic integration has attempted to understand the integration of object features and locations across saccades (Irwin, 1996; Prime, Tsotsos, Keith, & Crawford, 2007), to identify the neural correlates of transsaccadic integration (Duhamel, Colby, & Goldberg, 1992; Prime, Vesia, & Crawford, 2011), and to investigate the influence of internal egocentric information on the process outlined above (Melcher & Morrone, 2003; Prime et al., 2011; Sommer & Wurtz, 1998). However, the role of allocentric visual information in

transsaccadic integration has not been investigated. As such, the aim of this thesis was to investigate the influence of exogenous allocentric information on this process. In particular, I was interested in both *intrinsic* and *extrinsic* allocentric landmarks; intrinsic landmarks directly relate to the spatial location of the target and can highlight interobject relationships and grouping (Mou & McNamara, 2002; H. Wang, Sun, Johnson, & Yuan, 2005), whereas extrinsic landmarks are items that convey spatial information in an indirect manner.

1.2 Saccades

Eye movements are an essential aspect of visual processing and human perception, and as such have had a lengthy history in several different research areas and disciplines (Wade, 2010). The jerky motion of eye movements caused by nystagmus first emphasized the importance of recording eye position, and it was in this context that the first systematic studies of eye movements were conducted (Wells, 1792). With the focus on recording eye position growing, research was conducted to determine the correlation between fixation position and perceptual experience (Stratton, 1902), and eventually evolved toward understanding what characteristics drive eye movement positioning within a scene in real-world contexts (Buswell, 1935, 1937). Since then, saccadic eye movements have received extensive attention and today we understand that saccades are often goal-directed and executed towards items of interest within a scene (Underwood & Radach, 1998).

During the 19th century, a lot of focus was put on a specific type of jerky eye movement. In English, these movements were described as ‘jerk’ (Brown, 1895), while ‘saccade’ was first used at around the same time in France (Javel, 1878; Wade, 2010). The term saccade eventually became the prominent term used to describe these movements when they were distinguished

from other eye movements (Dodge, 1903), such as smooth pursuit movements used for tracking (Fuchs, 1967). Several different types of saccades were defined including voluntary, predictive, memory-guided, and reflexive to name a few (Yarbus, 1968). Because of their easy classification, saccades are widely used as a research tool today (Leigh & Kennard, 2004).

Saccadic eye movements are classified as such based on their stereotypical characteristics (Liversedge, Gilchrist, & Everling, 2012). During a saccadic movement, the eye moves rapidly from one stable fixation to another in a very short period of time, and the relationships between saccade velocity, duration, and amplitude are mathematically defined such that they produce a normal range of values (Lebedev, Van Gelder, & Tsui, 1996; Sharpe, Troost, Dell'Osso, & Daroff, 1975; Sharpe & Zackon, 1987). Peak velocities of saccades can range between 30-700 degrees per second, and their duration can range between 30-100 ms for saccade amplitudes of 0.5-40° (Bahill, Clark, & Stark, 1975; Smeets & Hooge, 2003; Smit, Van Gisbergen, & Cools, 1987). Indeed, the relationship between duration and amplitude is called the *main sequence* (Bahill et al., 1975) and represents a trade off between accuracy and duration of the saccade (Harris & Wolpert, 2006). These relationships between velocity, duration, and amplitude can be affected by factors such as fatigue, target predictability, and age (Becker & Fuchs, 1969; Fletcher & Sharpe, 1986; Munoz, Broughton, Goldring, & Armstrong, 1998; Sharpe et al., 1975; Smit et al., 1987), but are otherwise quite reliable.

Another characteristic of saccades is latency, which is the time required to initiate a saccade (Liversedge et al., 2012). Saccade latency is approximately 150-200 ms following the command to execute a saccade (Leigh & Zee, 2005; Sharpe & Wong, 2005), and can be affected by several factors such as object features (i.e., luminance, contrast, size, etc.) (Doma & Hallett, 1988; Groner & Groner, 1989) as well as motivation and attention (Carpenter, 2004; Reddi,

Asrress, & Carpenter, 2003). Finally, saccade accuracy is another studied characteristic of these eye movements. While saccadic eye movements are generally quite accurate, our eyes can miss the target of the saccade by up to 10% of the total saccade amplitude (Becker & Fuchs, 1969; Troost, Weber, & Daroff, 1974; Weber & Daroff, 1971). These errors occur because the eye falls short of the target (undershooting or hypometria) or falls beyond the target (overshooting or hypermetria), and are dependent on where in the visual field the target of the saccade lies. For saccade targets presented in the periphery, observed errors are consistently hypometric, whereas for targets presented centrally, observed errors are reliably hypermetric (Collewyn, Erkelens, & Steinman, 1988). As with latency, saccade accuracy can be affected by target size and luminance, biasing saccade end-points to more salient targets (Deubel, 1989). Additionally, accuracy is influenced by the presence or absence of the target prior to the initiation of the saccade. Specifically, when the target is visible prior to initiation (visually-guided), saccades tend to be more accurate than when the target vanishes before saccade initiation (memory-guided) (Opris, Barborica, & Ferrera, 2003).

1.2a Neural Correlates of Saccades

Since humans rely so heavily on visual information to experience and navigate the world, it is no surprise that a significant amount of the brain revolves around visual processing. After light enters the eye and falls on the retina, photoreceptor cells that are highly concentrated in the fovea (Osterberg, 1935) begin a relay of visual information to several cortical and subcortical destinations. This convergence of photoreceptors in the fovea results in the need to make eye movements and direct the fovea to parts of a visual scene or specific items of interest (Underwood & Radach, 1998; Westheimer, 1987). Hence, many of the cortical and subcortical

areas involved in general visual processing are also involved in preparation and generation of saccades.

Several areas have been associated with the control and initiation of saccadic eye movements, including areas of the brainstem, the superior colliculus, the thalamus, frontal and parietal cortices, and the cerebellum (Bruce & Goldberg, 1985; Goldberg & Bruce, 1985; Leigh & Zee, 1999, 2006; Mohler, Goldberg, & Wurtz, 1973; Munoz & Coe, 2011; Munoz & Wurtz, 1995; Optican & Quaia, 2002; Sparks, 2002; Wurtz & Goldberg, 1971). Brainstem structures are involved in saccade generation by providing the signals that determine saccade direction (Horn & Büttner-Ennever, 1998; Horn, Büttner-Ennever, Suzuki, & Henn, 1995). These areas receive information from the superior colliculus, which plays a role in determining saccade direction, velocity, and amplitude, and is credited with generating the commands that initiate a saccadic eye movement (Munoz, 2002; Sparks & Mays, 1990; Walker, FitzGibbon, & Goldberg, 1995). To generate these commands, the superior colliculus encodes specific target locations (Glimcher & Sparks, 1992) in retinotopic (eye-centered) coordinates (DeSouza et al., 2011; Klier, Wang, & Crawford, 2007). Besides driving the eyes, the superior colliculus is also involved in maintaining eye fixation (Goldberg & Wurtz, 1972; Sparks & Mays, 1980) and mediating how visual attention is directed to stimuli in the environment (Wurtz, Goldberg, & Robinson, 1982).

Cortical regions are also involved in the planning and generation of saccadic eye movements. One such area, the parietal eye field, is found in the parietal lobe of the brain (Müri, Iba-Zizen, Derosier, Cabanis, & Pierrot-Deseilligny, 1996; Vesia, Prime, Yan, Sergio, & Crawford, 2010) and is involved in generating reflexive movements of the eye as well as voluntary eye movements with accuracy (Gaymard, Ploner, Rivaud-Péchoux, Vermersch, & Pierrot-Deseilligny, 1998; Gnadt & Andersen, 1988). In addition to the parietal lobe, areas in the

frontal lobe such as the frontal eye fields and the supplementary eye fields play an important role in eye movements as well (Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981; Schlag, Schlag-Rey, & Pigarev, 1992; Umeno & Goldberg, 2001). The frontal eye fields transform visual signals into saccade motor commands (Bruce & Goldberg, 1985; Schall, 2015) and the supplementary eye fields are involved in motor programming (Isoda & Tanji, 2002). Importantly, these saccade related areas are interconnected (Pouget, Emeric, Stuphorn, Reis, & Schall, 2005; Sommer & Wurtz, 1998).

1.3 Visual Working Memory

One of the earliest views of visual working memory theorized that sensory information was very briefly held in a sensory storage, and if the information was attended to, it would then eventually be passed to longer memory stores (Atkinson & Shiffrin, 1971). This was later adapted and altered to a model that more closely resembles the contemporary view of working memory; one that highlights the processes involved in integrating and processing information that was held in a temporary buffer (Baddeley, 1986; Baddeley and Hitch, 1974). Following encoding of visual information by the brain, this temporary store would allow the information to be used and integrated with other items such as object features and locations (Baddeley, 1986, 2003), and that the temporary store and the processes required to manipulate the information was the recipe for working memory (Jonides et al., 1993). Some held that this temporary store was sustained because of groups of neurons that continued firing together after the stimulus was no longer visible (Varela, Lachaux, Rodriguez, & Martinerie, 2001).

Since the establishment of a visual working memory, researchers have tried to determine the characteristics of the memory store. Such characteristics include its capacity, rate of delay,

and its ability to maintain information about objects independently from the object's fixed location in space (Phillips, 1974). The capacity of visual working memory is thought to be similar to that of simple working memory (i.e. working memory that doesn't involve eye movements). That is, several studies support that the capacity of visual working memory is 3-4 items (Baddeley, 2003; Irwin, 1992; Luck & Vogel, 1997; Prime et al., 2007; Vogel, Woodman, & Luck, 2001), which includes feature and spatial information (Baddeley, 2003). Retention of object features deteriorated when more than 4 items were presented (Luck & Vogel, 1997; Prime et al., 2007), and it was shown that participants remembered objects with multiple features, a finding that suggests integration of objects and their features (Luck & Vogel, 1997). As with number of items, the number of visual features to be memorized also affected visual working memory capacity (Alvarez & Cavanagh, 2004; Olson & Jiang, 2002). The nature of decay from this memory store has also been investigated, with early theories supporting a rapid loss of information (Posner & Keele, 1967), while others provided evidence pointing toward a gradual decline (Lee & Harris, 1996). More recent research indicates that object features can be maintained for several seconds before they are promptly discarded (Zhang & Luck, 2009).

Investigating individual features maintained in visual working memory, researchers manipulate the number of features per stimulus, and have found that the more features required to be remembered, the fewer overall objects could be retained (Alvarez & Cavanagh, 2004). Interestingly, it has been shown that memory for the features of an object are represented in different cortical areas than the memory for spatial information (Chafee & Goldman-Rakic, 1998; Desimone and Ungerleider, 1989; Ungerleider & Haxby, 1994). Despite this difference in cortical resources, it has been shown that different types of information can be integrated (Luck & Vogel, 1997; Prime, Niemeier, & Crawford, 2006), and it has been proposed that integration

occurs because visual working memory utilizes both internal signals about eye position (egocentric) and interobject representations (allocentric) (Hayhoe, Moller, Ballard, & Albano, 1990). Closer to the aim of this thesis lies the questions of how this integration of object features and locations is integrated across eye movements, and which reference frames are utilized to accomplish this goal.

To examine the memory capacity of transsaccadic integration specifically, an early study calculated that participants could recall 3-4 items (Irwin, 1992). However, this study had participants attend to arrays of at least 6 items and found that performance was sub-optimal. Follow-up studies supported the proposed 3-4 capacity memory store for transsaccadic integration, mirroring findings of working memory (Irwin & Andrews, 1996; Irwin & Gordon, 1998). Some of these studies investigating transsaccadic memory used complex items requiring the activation of semantic memory (Deubel, Schneider, & Bridgeman, 2002; Irwin & Zelinsky, 2002), thus potentially engaging higher order mechanisms further down the visual processing streams. In an attempt to uncover the integration of simple object features across saccades available in earlier visual systems, Prime and colleagues (2007) had participants report changes of object luminance and orientation across eye movements. The results from this study indicated that participants were able to recall 3-4 objects, supporting Irwin's early estimation (Prime et al., 2007).

1.3a Models of Visual Working Memory

The aforementioned findings from studies investigating visual working memory have lead to the establishment of two prominent models. The traditional model of visual working memory, referred to as the '*fixed slot model*' assumes that there is a fixed capacity limit to this

type of memory. According to this model, only a fixed number of items can be maintained, and any number of items surpassing the capacity limit are discarded from visual working memory (Cowan, 2011; Luck & Vogel, 1997; Pashler, 1988). An integral aspect of the fixed slot model is that the slots are considered all-or-nothing; an observer either remembers all of the presented items with the same accuracy and that the precision of items remains the same whether items are presented alone or in a group of up to four items (Schurgin, 2018). Support for this theory came from an early study that demonstrated similar performance for a fixed number of objects, regardless if whether participants were required to remember a single feature or a conjunction of object features (Luck & Vogel, 1997). However, several studies that attempted to replicate this finding have failed to do so, finding instead that as feature load increases, visual working memory capacity is reduced (Fougnie, Asplund, & Marois, 2010; Olson & Jiang, 2002; Wheeler & Treisman, 2002).

Alternatively, the '*continuous resource model*' posits that visual working memory capacity is information based and is a limited, finite resource. Within this framework, the finite resource is shared between objects, rather than having all of the features of a few select objects remembered (Bays & Husain, 2008). This model provides more flexibility as there can be an unequal division toward different items within a given display, a division that may differ due to any number of factors (Schurgin, 2018). Such a division of visual working memory is in direct contrast to a strict, fixed slot model, and has been supported by several studies (Donkin, Kary, Tahir, & Taylor, 2016; Huang, 2010; Jie Li, Shao, Xu, Shui, & Shen, 2013).

Finally, there may be a middle ground between these two polarized views. The third model proposes that visual working memory capacity is constrained to 3-4 item representations, like the fixed slot model, but that the capacity within these slots is limited by the amount of

information load in a given display, similar to the continuous resource model (Schurgin, 2018). Support for such a hybrid comes from a study that found varying capacity estimates for different stimulus classes, demonstrating that visual working memory is limited to both the number of items and the amount of information within each (Alvarez & Cavanagh, 2004).

1.4 Spatial updating

Spatial updating is the process that maintains a unified global percept of the environment by taking into account the changes between the observer and the environment that arise by movements of the observer (R. F. Wang et al., 2006). In other words, spatial updating is a mechanism that keeps track of an object's location in space despite changes due to the observer's movements. Studies have demonstrated the visual system's ability to perform spatial updating spanning as far back as the 19th century when Helmholtz (Helmholtz, trans. 1963) observed that our perceived stability of the world quickly falls apart when the eyes were passively moved. He concluded that in order for the stability to persist during eye movements, the brain must use internal saccade metrics to rapidly calculate and compensate for the displacement of the eyes.

Since we move our eyes frequently (Rayner, 1978), spatial updating is an important process as it maintains visual constancy (Klier & Angelaki, 2008; McConkie & Currie, 1996; Prime et al., 2011) and helps us remember where things are so that we can interact with them despite our constant movement around the environment. A significant component of spatial updating is the use of intrinsic information regarding the movement of our eyes, including the size and direction of a saccade. This internal signal of saccade metrics is known as an *efference copy*, or corollary discharge, and is used by the brain to define the location of an object independently of the observer (Sperry, 1950; von Holst & Mittelstaedt, 1950). Researchers have

found that spatial constancy depends on the number of objects in the visual scene (R. F. Wang et al., 2006), while others have reported that feature information can be updated across eye movements (Melcher, 2007). Saccade-specific mechanisms are involved in remapping visual information such that the representations of the items in space are updated based on internal signals of motion (Crawford, Medendorp, & Marotta, 2004; Sommer & Wurtz, 2008). When a given saccade has been planned, prior to its initiation, the efference copy brings about a change in an object's internal representation, updating it to the new location, and it has been shown that receptive fields of neurons adjust in order to include the new location even prior to the saccade execution (Duhamel et al., 1992; Nakamura & Colby, 2002).

Spatial remapping has been viewed as the vehicle of spatial constancy because of a theorized creation of a salience map. That is, each retinal snapshot was part of, and contributed to, a larger percept, and the salience map is updated and remapped as new information comes to the visual system via saccades (Pisella & Mattingley, 2004). There are two views as to how this is accomplished. The first view focused on the similarities between remapping and spatial working memory, highlighting that remapping is the first mechanism required for spatial updating as it is quick and occurs as the eyes move around a visual scene. Following remapping is spatial working memory, a slower mechanism required to retain the images acquired across eye movements and to integrate them into a single percept. The authors argued that while they work on different time scales, each of these mechanisms requires and enhances the other (Pisella & Mattingley, 2004). The second view, however, focused on dissimilarities of these two mechanisms and identified dissociations (Vasquez & Danckert, 2008). To illustrate the dissociations between remapping and spatial updating, they had participants compare changes in trials with saccades and trials without, and showed that spatial updating occurred and was

stronger in the absence of remapping. Others also showed that spatial working memory was not related to remapping, and that deficits in spatial working memory was due to rapid forgetting of spatial information (Danckert & Ferber, 2006).

1.5 Transsaccadic Integration

Following the dual structure of spatial working memory mentioned above, transsaccadic perception is also driven by two complementary processes. Visual information must first be stored in some type of transsaccadic memory that maintains visual information acquired at separate fixations, and second, the retained information must be integrated to form a global percept. There have been numerous studies dedicated to understanding the integration of visual information across eye movements that have lead to multiple theories of transsaccadic integration.

Early theories of transsaccadic integration, such as the *spatiotopic fusion hypothesis*, maintained that the brain retained detailed visual information across saccades in an *integrative visual buffer* (Jonides & Yantis, 1988; McConkie & Rayner, 1976). This theory was supported by experiments that had participants make saccades while viewing arrays of dots in the same spatial location pre- and post-saccade. The results allowed the researchers to claim that visual information was perfectly aligned in spatiotopic coordinates in this spatial buffer, and that the transsaccadically-fused image was instantly available for further processing (Jonides & Yantis, 1988). Further evidence for the spatiotopic fusion hypothesis came from studies that found that information that occupied the same spatial location could be retained and integrated across eye movements (Breitmeyer, Kropfl, & Julesz, 1982; Jonides, Irwin, & Yantis, 1982; Ritter, 1976). The *integrative visual buffer* theory was short-lived as experimenters began testing the detection

of changes that occurred during saccades, and realized that participants were largely unaware of such changes (Bridgeman & Mayer, 1983; O'Regan, Deubel, Clark, & Rensink, 2000; Rensink, O'Regan, & Clark, 1997). Results from these studies found that participants were insensitive to change detection and lead to theories that supported the idea that transsaccadic memory didn't exist at all (Bridgeman, 1981; Bridgeman, Van der Heijden, & Velichkovsky, 1994), and that instead the visual world was acquired anew at each fixation with the external world acting as a memory store (O'Regan, 1992). Studies using large amounts of highly detailed information provided some support for this theory, since participants were unable to rely on the external world as a memory store (O'Regan et al., 2000; Simons & Levin, 1997).

Irwin and colleagues (Irwin, 1992, 1996; Irwin & Andrews, 1996) proposed a hybrid of the two theories outlined above. They put forward an *object-file* theory of transsaccadic integration whereby the visual system maintains an object features map and a locations map, and argued that objects were coded in these two coordinates. Further, because attention is required to combine object features and locations, a limited number of object files can be obtained between saccades (Irwin, 1996). This view attempted to reconcile the two aforementioned extreme theories of transsaccadic integration. In addition, researchers have proposed that internal representations of object features can be spatially updated relative to gaze (Golomb & Kanwisher, 2012; Melcher & Colby, 2008; Prime et al., 2006, 2011). These studies indicate that gaze-centered remapping plays a role in updating feature information across saccades. Interestingly, others have argued that feature information does not need to be attended across eye movements because it remains unchanged over time – and thus across eye movements – and that attended locations are all that need to be attended to (Cavanagh, Hunt, Afraz, & Rolfs, 2010). This theory of '*attention pointers*' maintains that there are predictive shifts of location pointers to

attended targets in space that are linked to object identify information. Ultimately, it appears that transsaccadic integration occurs between the two previously discussed extreme views, with the brain making optimal inferences about events that occur across saccades (Niemeier, Crawford, & Tweed, 2003).

1.5a Neural Correlates of Transsaccadic Integration

Beyond the general discussion of cortical areas involved in eye movements, physiological studies have attempted to identify the neural correlates of transsaccadic integration. Evidence of spatial updating in the brain has come from studies in both primate and human physiology. Duhamel and colleagues (1992) reported spatial updating in the primate lateral intraparietal cortex – a homolog of the human parietal eye field. Merriam and colleagues (2003) later found evidence of remapping in the parietal eye field in humans. Studies have provided evidence of spatial updating in the posterior parietal cortex, the frontal eye fields, and earlier visual areas (Goldberg & Bruce, 1990; Medendorp, Goltz, Vilis, & Crawford, 2003; Nakamura & Colby, 2002). More recently, researchers have used transcranial magnetic stimulation (TMS) to investigate the contribution of these regions in transsaccadic integration. TMS over the right posterior parietal cortex, and both right and left frontal eye fields, disrupted memory capacity in a task where participants were required to compare the orientations of multiple objects across saccades, indicating that the right posterior parietal cortex and both frontal eye fields are heavily involved in the spatial processing of visual features across eye movements (Prime, Vesia, & Crawford, 2008, 2010). Conversely, TMS over the dorsolateral prefrontal cortex significantly improved performance on similar tasks, suggesting a disinhibition of spatial processing and updating via TMS, and thus indicating the dorsolateral prefrontal cortex's role in spatial updating

across eye movements (Tanaka, Dessing, Malik, Prime, & Crawford, 2014). To my knowledge, all of these studies have investigated the neural correlates of transsaccadic integration without systematic manipulation of allocentric cues.

1.7 Reference Frames

To retain and integrate information across eye movements, the brain must maintain representations of the observer and of the environment within which the observer finds themselves. A reference frame can be defined as the coordinate system with which the location of an object in space can be represented (Crawford, Henriques, & Medendorp, 2011; Klatzky, 1998). Two spatial reference frames the visual system utilizes to accomplish this are egocentric and allocentric reference frames; an egocentric reference frame is one where objects in the world are represented relative to the observer, whereas an allocentric reference frame is one where objects are represented relative to each other (i.e. such as reliable landmarks) in the environment (Byrne, Becker, & Burgess, 2007; Howard & Templeton, 1966; Proulx, Todorov, Aiken, & de Sousa, 2016; Vogele & Fink, 2003). An example of an egocentric frame of reference would be coding the location of an object relative to eye position, while an example of an allocentric reference frame would be coding the location of an object on a table relative to the other objects on the table. This example of allocentric information is of particular interest because it can be used to highlight two sub-systems. If the object of interest is coded relative to an anchor in the environment such as the table, we can say that the coding is occurring based on *extrinsic* information (‘external’ to the target), whereas if it is coded relative to all of the other objects on the table, highlighting the interobject relationships and grouping, we can say that the coding occurs based on *intrinsic* allocentric information (Mou & McNamara, 2002; H. Wang et al., 2005). The terms ‘intrinsic’ and ‘extrinsic’

here refer to the relationships between the target object and the environment, not to be confused with the egocentric and allocentric reference frames.

In addition to egocentric references, allocentric information can influence the recollection of object location (Hayhoe, Lachter, & Feldman, 1991; Obhi & Goodale, 2005). It has been shown that the brain combines information from both of these reference frames (Diedrichsen, Werner, Schmidt, & Trommershäuser, 2004; Sheth & Shimojo, 2004) depending on the reliability of each (Byrne & Crawford, 2010; Fiehler, Wolf, Klinghammer, & Blohm, 2014; Thompson & Henriques, 2010). Furthermore, updating information across eye movements has been shown to be a noisy process (Byrne & Crawford, 2010; Prime et al., 2006, 2007), but allocentric information typically remains stable during eye movements (Byrne & Crawford, 2010; Redon & Hay, 2005). In studies investigating the influence of allocentric cues on spatial updating for reach, research indicates that the brain integrates egocentric and allocentric information after the completion of a given eye movement (Byrne, Cappadocia, & Crawford, 2010).

Previous research has demonstrated that allocentric information leads to increased spatial recall precision of stimuli at fixation (Aagten-Murphy & Bays, 2019), but the influence of reliable allocentric information on the integration of visual information across eye movements has not yet been tested. For transsaccadic integration, beside the retinal information acquired at a given location, it has been proposed that extra-retinal information is also used to identify changes across saccades (Melcher & Morrone, 2003). More specifically, efference copies of an executed eye movement may provide egocentric information about saccade metrics that serve spatial updating of visual information (Duhamel et al., 1992; Sommer, 2003). In another line of research, participants were asked to indicate the intersecting point of two lines that were shown in isolation at two separate fixations. Participants fixated on a point in one hemifield and were

presented with a line of one orientation. Following a saccade to a location in the opposite hemifield, they were presented with another line of a different orientation such that the two lines would have intersected had they been presented at the same time (Prime et al., 2006). The results of this and other studies (e.g., Prime et al., 2007) indicate that the visual system is able to integrate visual information across eye movements relying on egocentric mechanisms alone. Due to the abundance of stable and reliable allocentric information under natural viewing conditions, it stands to reason that providing systematic allocentric information should improve transsaccadic integration.

1.8 Aims of Present Study

While several studies have investigated the mechanisms of transsaccadic integration, there is still much to be uncovered about this process. In the above introduction, I summarized studies that highlight the visual system's ability to retain and integrate visual information such as object features and locations across eye movements. In the next chapter, I provide quantitative data that illustrates the influence of allocentric landmarks on transsaccadic integration. In a series of experiments, I investigated the processes of memory and integration across saccades as they pertain to a memory task utilized previously by Prime and colleagues (2007). Importantly, I was interested in the different frames of reference – egocentric and allocentric – involved in transsaccadic integration. Previous results have shown that the brain is competent in integrating visual information across saccades using egocentric mechanisms alone (Prime et al., 2006, 2007). Here, I introduced allocentric information in a systematic manner to identify the influence of reliable external information from the environment on memory and spatial updating across eye movements. In the first experiment, the *intrinsic* landmarks were in the form of circles that occupied the location of the stimuli and provided direct spatial information regarding their

positions in space. In the second experiment, the *extrinsic* landmarks provided cues to stimulus locations relative to an independent visual anchor. I hypothesized that as the amount of items increased and working memory was taxed, performance in the task would decrease. Further, I hypothesized that the allocentric landmarks would mitigate this by providing reliable spatial information.

CHAPTER 2

THE INFLUENCE OF ALLOCENTRIC CUES ON TRANSSACCADIC INTEGRATION OF MULTIPLE OBJECTS

(A manuscript in preparation for submission)

George Tomou, Xiaogang Yan, and J. Douglas Crawford

2.1 Abstract

It has been shown that humans can rely on egocentric information to retain and integrate visual objects across saccades, but the role of allocentric information is unknown. Here, we tested the influence of stable visual landmarks. Participants compared the orientation change of a stimulus that was briefly presented before (amongst 0-6 distractors) and after a saccade. We manipulated the presence of allocentric spatial information by providing participants with two types of landmarks. *Intrinsic* landmarks were low-contrast circles that remained at the target and distractor locations, providing explicit cues to both their absolute and relative locations, whereas the *extrinsic* landmark was a large, stable cross that provided cues to stimulus locations relative to an independent visual anchor. As expected, performance without landmarks decreased as the number of distractors increased. Intrinsic landmarks failed to mitigate this effect, but the extrinsic landmark significantly increased performance in the presence of distractors. A control experiment showed that the cross did not benefit transsaccadic orientation sensitivity, instead supporting its role for transsaccadic space constancy. These results show that extrinsic visual landmarks can supplement egocentric location cues to improve transsaccadic memory and integration of oriented objects, especially when memory of larger set-sizes is required.

2.2 Introduction

Humans make several eye movements – called saccades – every second in order to bring objects of interest into the fovea (Rayner, 1978, 1998). However, with each saccade, the visual system acquires a new, highly detailed snapshot of visual information. The snapshot nature of this acquisition means that the image on the retina is likely to be vastly different at each fixation, and, yet, we perceive a unified and stable percept. This global percept of the environment arises because our brains take these disjointed snapshots, remember them, and integrate them with the information acquired at the next fixation. The process of retaining and synthesizing visual information across saccades is called *transsaccadic integration* (Irwin, 1991; Melcher & Colby, 2008). Key questions in transsaccadic integration research include what types of information can be retained and integrated across saccades (Hayhoe et al., 1991; Prime et al., 2007) and what types of cues does the brain use to accomplish successful transsaccadic integration (Byrne et al., 2007; Melcher & Morrone, 2003; Prime et al., 2011). The following series of experiments focused on the latter question, in particular the role of allocentric visual cues.

Previous psychophysical research on transsaccadic integration has investigated the retention and integration of object features across saccades (Ganmor, Landy, & Simoncelli, 2015; Hayhoe et al., 1991; Irwin, 1996; Melcher & Morrone, 2003; Prime et al., 2006, 2007; Wolf & Schütz, 2015), and the role of attention on this process (Cavanagh et al., 2010; Jonikaitis, Szinte, Rolfs, & Cavanagh, 2013; Mathôt & Theeuwes, 2011; Prime et al., 2007; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011; Stewart & Schütz, 2018). Transsaccadic integration appears to be attention-dependent, and shows a limited capacity for retention and integration of features such as location, luminance, and orientation (Prime et al., 2007). Most studies agree transsaccadic memory degrades as set-size increases (Irwin, 1992; Irwin &

Andrews, 1996; Prime et al., 2007), and this may be influenced by other factors such as saccade magnitude, visual field, and distance of the visual stimulus from the fovea before and/or after the saccade.

Another stream of inquiry has been to identify the spatial frames used for this integration (Burr & Morrone, 2011; Deubel, Schneider, & Bridgeman, 1996; Melcher & Morrone, 2003; Tatler & Land, 2011). Two general types of reference frames might be used to integrate information across saccades; egocentric reference frames, where objects are represented relative to the observer, and allocentric reference frames, where objects are represented relative to some reliable landmarks (Burgess, 2006; Byrne et al., 2007; Prime et al., 2011; Proulx et al., 2016). Most previous investigations have focused on the role of internal egocentric information in transsaccadic integration, in particular the use of saccade efference copies to update retained visual information in an eye-centered frame (Hamker, 2003; Hamker & Zirnsak, 2006; Melcher & Morrone, 2003; Prime et al., 2011; Sommer & Wurtz, 1998).

It has also been shown that allocentric information can have a strong influence on the memory of target location (Lemay, Bertram, & Stelmach, 2004; Neggers, Schölvink, van der Lubbe, & Postma, 2005; Obhi & Goodale, 2005; Sheth & Shimojo, 2004; Sun & Wang, 2010). In situations where both egocentric and allocentric information are available but conflict, the brain appears to optimally weigh these two sources of information (Byrne & Crawford, 2010; Fiehler et al., 2014; Jirui Li et al., 2017; Thompson & Henriques, 2010). The balance of this weighting depends on different factors such as perceived reliability of the landmark, but generally tends to favor the egocentric course (Byrne & Crawford, 2010). But of course, in normal situations allocentric landmarks tend to be stable and agree with egocentric cues, so that their integration should lead to the best estimate of object location. Since allocentric cues also

influence the spatial updating of point targets (Byrne et al., 2010) and are readily available under natural viewing conditions, it stands to reason that they would also augment performance in transsaccadic integration. In some special cases (such as a group of objects like a flock of birds) intrinsic information and grouping might also provide cues to remembering the location of individual elements (Mou & McNamara, 2002; H. Wang et al., 2005). It is also possible that external landmarks might provide reference cues for the object features, such as luminance, color, and orientation. However, these factors have not previously been tested in a transsaccadic integration task.

The aim of the current research project was to investigate the influence of allocentric information on transsaccadic integration. In particular, I investigated the processes of memory and integration across saccades in a task similar to that used by Prime and colleagues (2007). The results from Prime and colleagues (2007) supported the idea that the brain is successful in integrating object location and orientation across saccades using egocentric mechanisms alone. Here, I introduced allocentric information in a systematic manner to identify their influence on transsaccadic memory and integration. In particular, I tested the influence of intrinsic spatial cues to object location (i.e., cues at the location of the object) versus an extrinsic (spatially independent) landmark, and further investigated whether their influence was specific to object location or remembering orientation. The results suggest that – under the conditions tested here – stable allocentric cues do augment performance in a transsaccadic integration task, extrinsic landmark have more influence than intrinsic cues, and this influence is primarily on object location memory rather than feature retention.

2.3 Methods

2.3a Participants

A total of 15 students (7 males and 8 females; 18-30 years of age) provided informed consent and took part in this study. All participants had normal or corrected-to-normal vision, and none reported any history of neurological disorders. Data from 3 participants was excluded due to poor baseline performance, resulting in a total of 12 participants (7 males and 5 females; 18-30 years of age). Experimental procedures were approved by the York University Human Participants Review Subcommittee.

2.3b Apparatus

A customized computer network was used for stimulus presentation and data collection. Figure 1 illustrates the experimental set-up. Visual stimuli were back-projected onto the display area (1.84 m x 1.38 m, spanning 119.2° visual angle horizontally by 103.8° visual angle vertically) by a video projector. Participants sat in a darkened room with their heads stabilized by a personalized bite plate made with dental compound situated such that their eyes were approximately 50 cm from the center of the display and 115 cm from the ground. Positions of the right eye were recorded using *EyeLink II* (SR Research, Mississauga, Ontario, Canada) which was calibrated prior to each experimental block to ensure optimal positioning, and eye movements were analyzed offline; trials with eye movements during stimulus presentation, blinks during the trials, or failure to execute the saccade when prompted were excluded from further analysis.

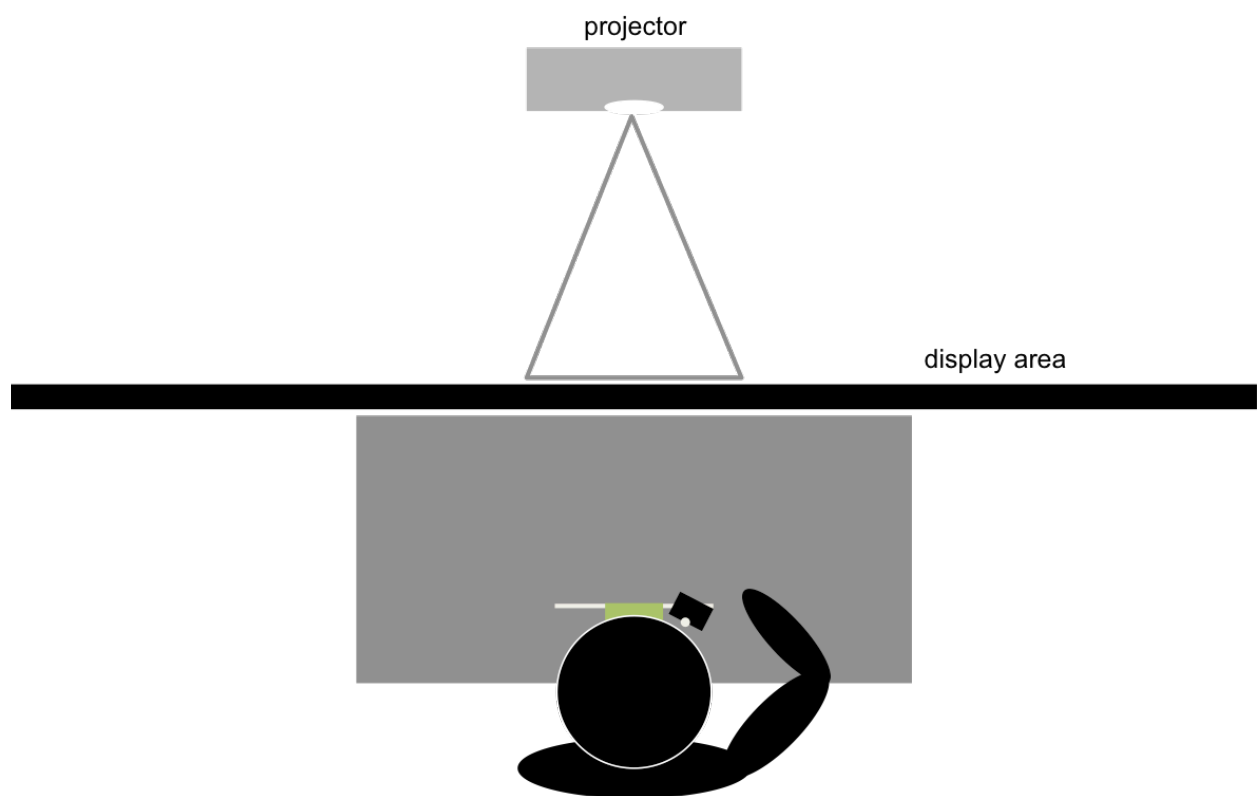


Figure 1. Bird's eye representation of the experimental set-up. From top to bottom: a video projector back-projected visual stimuli onto the display area. The display area was 1.84 m x 1.38m (119.2° visual angle x 103.8° visual angle). Participants sat at a desk in a darkened room with their heads stabilized by a personalized bite plate (green) such that their eyes were approximately 50cm from the center of the display area. The *EyeLink II* eye-tracking camera was affixed to the table and trained on the right eye.

2.3c General Procedure

I explored the effect of allocentric landmark cues on transsaccadic integration in 3 experiments all of which followed the same general procedure. The experimental paradigm for these experiments was an adapted transsaccadic integration task (Prime et al., 2007, 2008, 2010) and is illustrated in Figure 2. In the control *No Landmark* task (essentially the same as Prime et al., 2007), participants were asked to keep their eyes trained on a fixation cross that was randomly presented at one of 12 possible spatial locations (a ‘cross’ grid with 5° between adjacent points) within the center of the display area. They were instructed to remember the location and orientation of target stimuli presented to their periphery during initial fixation, and to compare the orientation of the probe stimulus presented post-saccade to the orientation of the pre-saccade stimulus presented in the same spatial location.

During the *Target Display* phase, participants were presented with either a single target stimulus, or the target among distractors; the total set-size of the target plus distractors ranged between 1-7, and the number of stimuli per trial differed randomly between trials. When multiple stimuli were presented pre-saccade, the participants did not know which one was the probe stimulus and were thus required to remember the location and orientation of as many of the targets as they could. Stimuli were Gabor-like patches (4.8° in diameter; spatial frequency 0.42 cpd; mean luminance 19.57 cd/m²) of alternating black and white bars. The orientation of each stimulus was selected randomly between 10 possible orientations: $\pm 25^\circ$, 35° , 45° , 55° , and 65° clockwise or counterclockwise from vertical; cardinal orientations were purposely avoided because discrimination sensitivity of these angles has been shown to be very high (Girshick, Landy, & Simoncelli, 2011; Pratte, Park, Rademaker, & Tong, 2017; Regan & Price, 1986). The target stimuli occupied random positions within the ‘cross’ grid and did not overlap with one

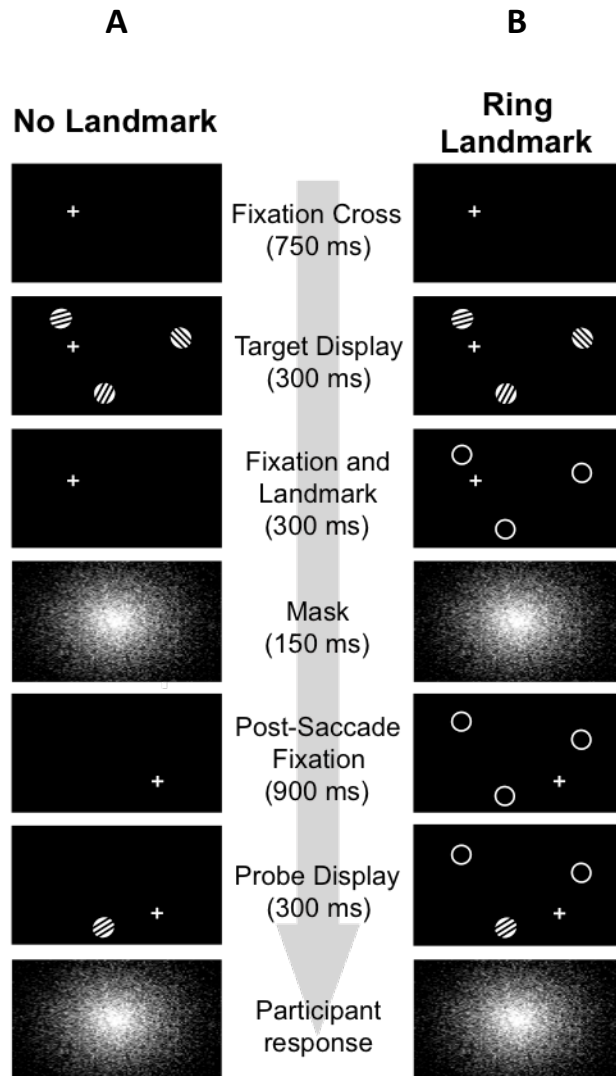


Figure 2. The experimental paradigm for Experiment 1, adapted from Prime et al., (2007). The figure depicts the order of a typical trial. **A.** *No Landmark* condition. Participants fixated on the fixation cross during the Probe Display phase while target stimuli (1-7) were presented. After a mask, participants executed an eye movement to the new fixation-cross location where the probe stimulus was presented at the same spatial location as it was prior to the eye movement, but with a new orientation. Participants compared the orientation of the post-saccade probe stimulus with the orientation of the pre-saccade stimulus. **B.** *Circle Landmark* condition. Similar to the *No Landmark* condition, except following the initial Target Display phase, circles remained on display in the same spatial location as the targets in order to provide additional allocentric spatial cues. Stimuli are not drawn to scale.

another nor with the fixation cross. After a given position had been occupied by either the fixation cross or a target stimulus, that position was unavailable until all 12 possible positions had been cycled through.

Following the presentation of the target stimuli during the *Target Display* phase, participants were presented with a brief mask (150 ms) to reduce visual afterimages of the previously seen stimuli. The mask was a full screen display of randomized pixel noise that faded to black toward the edges of the display area in order to reduce the contrast of the display's contours – this was important because the aim of the *No Landmark* condition was to present the target stimuli in isolation and reduce as much allocentric visual information as possible.

After the presentation of the mask, the fixation cross was presented in a new location within the grid of potential positions, cueing participants to execute a saccadic eye movement. Participants had 900 ms to saccade to the new fixation cross before they were presented with the lone probe stimulus for 300 ms. The probe was in the same spatial location as it was prior to the eye movement but had a new orientation ($\pm 15^\circ$ from its initial pre-saccadic orientation). The new orientation could bring the post-saccadic orientation closer to cardinal orientations, and as such any trials with post-saccadic stimuli oriented at $\pm 10^\circ$ or $\pm 80^\circ$ were removed from analysis. The presentation of the probe stimulus (300 ms) was immediately followed by another mask, during which participants were required to indicate the nature of the orientation change in a two alternative forced choice task. Responses were provided via a mouse button, indicating a counterclockwise orientation change by pressing the left mouse key or a clockwise orientation change by pressing the right mouse key. Participants were instructed to provide their best guess if they were unsure about the direction of the orientation change.

2.3d Experiment 1: Circle Landmark

The purpose of Experiment 1 was to test the influence of intrinsic cues to the locations of objects that disappeared after the saccade in the basic task described above. Participants were required to compare the orientation of the probe stimulus to the target stimulus that was previously presented in the same spatial location in the presence or absence of allocentric circle landmarks. This *Circle Landmark* condition differed from the *No Landmark* condition in that following the disappearance of the pre-saccadic stimuli as seen in Figure 2, circles (4.8° in diameter to match the Gabor-like patch targets) occupied the spatial location of the previously presented stimuli for 300 ms prior to the presentation of the mask. Circle stimuli were chosen rather than discs with the mean luminance of the Gabor-like stimuli because in preliminary tests participants found the latter to be distracting from the test stimulus. This period of 300 ms following the presentation of the stimuli was included in both the *Circle Landmark* and *No Landmark* conditions in order to match the temporal sequence of trials.

Following the presentation of the mask, the fixation cross was presented in a new location within the grid of potential positions cueing participants to execute their saccade. Participants had 900 ms to make their eye movement to the new fixation cross. During this time, the landmark circles were present on the screen in the same spatial location as they were prior to the mask. Following the period of 900 ms for fixation, one of the landmark circles was populated with the probe stimulus. As described in the *General Procedure*, the probe stimulus was presented in the same spatial location as it was pre-saccade, but with a new orientation 15° clockwise or counterclockwise from its initial orientation.

The *No Landmark* and *Circle Landmark* tasks were presented in a block design with a total of 8 blocks over two 1-hour sessions. The order of the blocks was counter-balanced

between data collection sessions (A-B-B-A / B-A-A-B), as well as between participants, and each block consisted of 91 trials for a total of 728 trials per participant. I hypothesized that the presence of allocentric landmark information would provide the visual system with additional spatial cues relating the stimuli to the environment that would improve the participant's ability to update the stimulus location and orientation across the saccade, and thus mitigate the predicted effect of set-size resulting in increased performance compared to the *No Landmark* condition.

2.3e Experiment 2: Cross Landmark

The purpose of Experiment 2 was to provide participants with an extrinsic landmark independent from the stimuli, but in other respects it was similar to Experiment 1. Here, the stimuli were accompanied by an allocentric cross landmark that extended across the entire display was present throughout the trial in a pseudorandom position within the stimulus array (see Figure 3). This large landmark was used because previous research has suggested that local landmarks have less influence than global landmarks (Uchimura, Nakano, Morito, Ando, & Kitazawa, 2015) and because this laboratory has previously shown that the same landmark has an influence on saccade programming (Jirui Li et al., 2017). The landmark did not intersect with either of the fixation crosses but could intersect with the visual stimuli because restraining the location of the landmark in such a manner was too restricting, especially for trials with higher set-sizes.

Similarly to Experiment 1, *No Landmark* and *Cross Landmark* conditions were presented in a blocked design with a total of 8 blocks over two 1-hour sessions, counter-balancing blocks between data collection sessions as well as participants. Each block consisted of 91 trials for a total of 728 trials per participant. As with Experiment 1, I hypothesized that the presence of allocentric information would mitigate the predicted effect of set-size resulting in increased performance compared to the *No Landmark* condition.

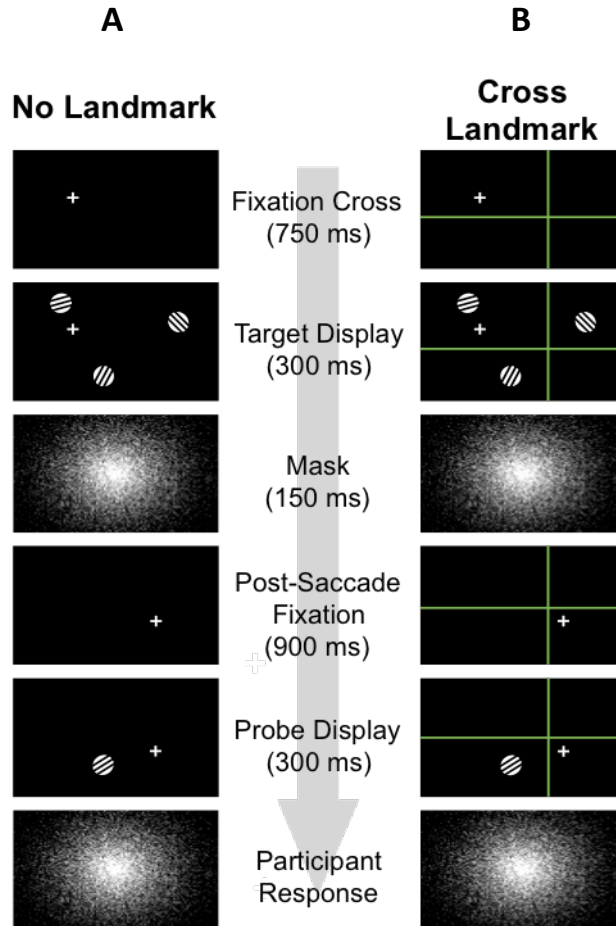


Figure 3. The experimental paradigm for Experiment 2. The figure demonstrates the order of a typical trial. **A.** *No Landmark* condition. Participants fixated on the fixation cross during the Probe Display phase while target stimuli (1-7) were presented. After a mask, participants executed an eye movement to the new fixation-cross location where the probe stimulus was presented at the same spatial location as it was prior to the eye movement, but with a new orientation. Participants compared the orientation of the post-saccade probe stimulus with the orientation of the pre-saccade stimulus. **B.** *Cross Landmark* condition. Similar to the *No Landmark* condition, but with the presence of an allocentric landmark for the duration of the trial. The landmark was a cross positioned pseudorandomly within the stimulus array and extended across the screen. Stimuli are not drawn to scale.

2.3f Experiment 3: Orientation Sensitivity

The purpose of Experiment 3 was to test whether the benefits, if any, of the cross landmark in Experiment 2 arose from its potential role as a spatial reference as opposed to a reference for the orientation feature. I reduced the set-size from seven such that there was only one stimulus in every trial and varied the amount of orientation change between pre-saccadic and post-saccadic stimuli, as shown in Figure 4. In Experiments 1 and 2, the degree of change between target display and presentation of the probe was constant at 15° , but in this task the orientation was randomly changed between trials from a range between 0° to 20° in steps of 2° (i.e., $\pm 0^\circ, 2^\circ, 4^\circ, 6^\circ, 8^\circ, 10^\circ, 12^\circ, 14^\circ, 16^\circ, 18^\circ$, and 20°). These step-wise increases in change allow us to identify each participant's sensitivity to stimulus orientation changes. Participants were presented with a cross landmark in 50% of trials in a block design that was counter-balanced across sessions and participants, with each block consisting of 147 trials for a total of 1176 trials per participant.

I hypothesized that if the cross landmark had an effect on sensitivity of orientation discrimination, performance would improve when the landmark was present, providing an alternative explanation for any effect found in Experiment 2.

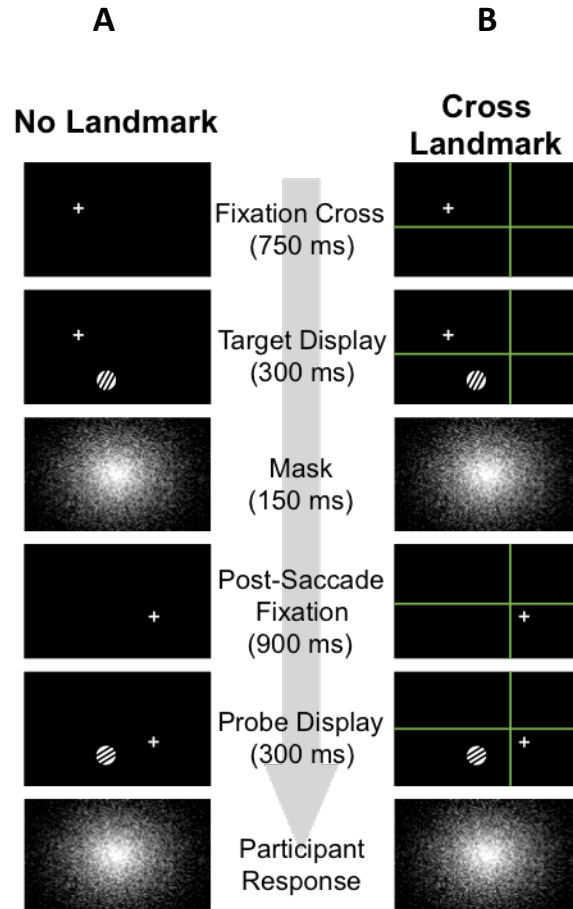


Figure 4. The experimental paradigm for Experiment 3. The figure demonstrates the order of a typical trial. **A.** *No Landmark* condition. Participants fixated on the fixation cross during the Probe Display phase while a single target stimulus was presented. After a mask, participants executed an eye movement to the new fixation-cross location where the probe stimulus was presented at the same spatial location as it was before the eye movement, but with a new orientation. Participants compared the orientation of the post-saccade probe stimulus with the orientation of the pre-saccade stimulus. **B.** *Cross Landmark* condition. Similar to the *No Landmark* condition, but with the presence of an allocentric landmark for the duration of the trial. The landmark is a cross positioned pseudorandomly within the stimulus array and extended across the screen. Stimuli are not drawn to scale.

2.3g Analysis

Prior to data collection, participants were brought to the lab and underwent training sessions until they achieved 90% accuracy for trials with a set-size of 1 stimulus. In addition, participants received a brief training block of 21 trials prior to data collection for each experimental session, the data for which was not included in the analyses.

The objective in this series of experiments was to examine the effect of stable, reliable allocentric landmark cues on transsaccadic integration. To ensure that participants were correctly completing the task, eye position was inspected following data collection. Individual trials were excluded from further analysis if participants failed to maintain fixation on the fixation crosses during stimulus presentation or to execute their saccade during the cued duration. The total data excluded due to the analysis of eye position was less than 5% for each experiment.

I performed a main analysis for each of the three experiments, and additional analyses if there was a significant effect of landmark in order to further investigate under which conditions the landmark had an effect. For Experiments 1 and 2, a generalized linear mixed-model (GLMM) was performed in RStudio using the *nlme* package (Pinheiro et al., 2016). The GLMM was conducted because such models are robust to violations of the assumptions of traditional ANOVAs (Field, 2005). If either of these analyses revealed a significant effect of landmark, I conducted repeated-measures ANOVAs in SPSS (Chicago, Illinois, USA) additional factors such as saccade amplitude and distance between fixation and probe stimulus (described in detail below). For Experiment 3, I fitted Weibull functions to each participant's data to obtain their discrimination threshold defined at 75% performance for each condition and conducted pairwise t-tests to determine if the cross landmark provided significant advantage on orientation sensitivity.

2.4 Results

2.4a Experiment 1: Intrinsic Landmark

Figure 5 shows the results of Experiment 1. Plotted here is the mean performance averaged across all participants for both *No Landmark* (blue) and *Circle Landmark* (orange) conditions. In both conditions, performance decreased as the number of distractors (set-size) increased, and the intrinsic circle landmarks did not appear to have any effect on performance.

A 2 (landmark) x 7 (set-size) generalized linear mixed-model revealed a significant effect of set-size, $t_{(4960)} = -5.770$, $p < .001$, but not a significant effect of landmark, $t_{(4960)} = -0.456$, $p = .648$. These results show that as set-size increases, performance significantly decreases, but contrary to our expectations, the presence of the locations cues intrinsic to the stimuli did not mitigate the effect of set-size.

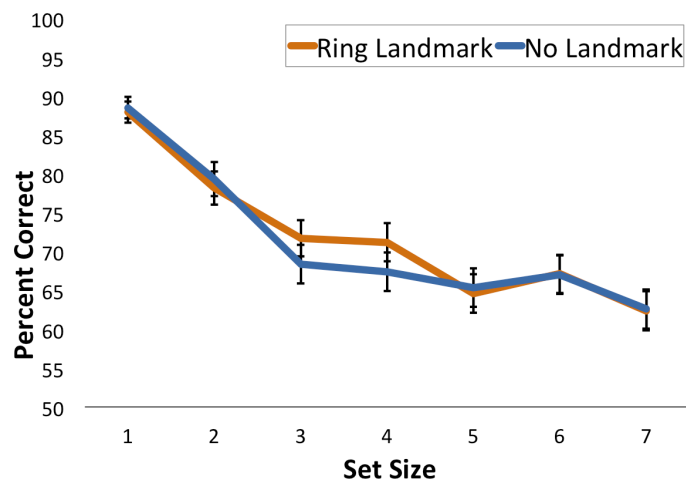


Figure 5. Mean performance across participants for Experiment 1. The blue line represents performance of the *No Landmark* condition, and the orange line represents performance of the *Circle Landmark* condition. The error bars are standard error of the mean.

2.4b Experiment 2: Extrinsic Landmark

Figure 6 shows the mean performance across participants for each set-size in both the *No Landmark* and *Cross Landmark* conditions. Plotted here is the mean performance averaged across all participants for both *No Landmark* (blue) and *Circle Landmark* (orange) conditions. In both conditions, performance decreased as the number of distractors (set-size) increased, but here the extrinsic cross landmark appeared to mitigate the decrease in performance. Qualitatively, this effect appeared at a set-size of two, peaked at three, and remained constant for higher set-sizes.

A 2 (landmark) x 7 (set-size) generalized linear mixed-model that revealed a significant effect of set-size, $t_{(4887)} = -7.780$, $p < .001$, confirming once again that as set-size increases, performance decreases. In Experiment 2, unlike the results of Experiment 1, there was a significant effect of landmark, $t_{(4887)} = 2.488$, $p = .013$, indicating that extrinsic location cues in the form of the cross landmark aided the visual system in the transsaccadic integration task. Post-hoc comparisons were conducted to further probe the landmark effect, and revealed that for a set-size of 3, the landmark lead to increased performance, $t_{(4787)} = 2.313$, $p = .028$.

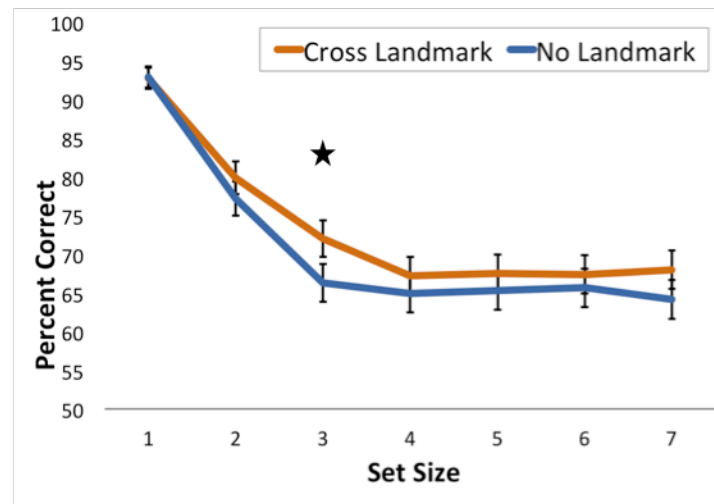


Figure 6. Mean performance across participants for Experiment 2. The blue line represents performance of the *No Landmark* condition, and the orange line represents performance of the *Cross Landmark* condition. The error bars are standard error of the mean. The (*) denotes statistical significance of $p < .05$.

Having established a significant effect of the extrinsic cross landmark, we were interested in identifying how the landmark's effect on performance varied as a function of saccade amplitude; saccade direction; the distance between the probe stimulus and landmark, the initial fixation, and the end fixation; and the visual field of the probe stimulus relative to the initial fixation and the end fixation. Repeated-measures ANOVAs were run for these factors. A p -value of 0.05 was adopted for significance and all post-hoc comparisons were Bonferroni corrected.

2.4.b. i Distance. I was also interested in determining if the landmark provided a benefit to transsaccadic integration as a function of relative distances between aspects of the visual scene. Specifically, analyses were conducted to understand the influence of the distance of the landmark to the probe stimulus, as well as a function of the distance of the probe stimulus to the fixation points. Figure 7 above shows the results of these analyses.

Distance between the probe stimulus and the cross landmark. Figure 7a shows the mean performance across participants as a function of binned distances between the probe stimulus and the cross landmark. Here, the lines represent performance for different set-sizes. To make the results clearer and to reduce the number of comparisons, set-sizes were binned into three groups, and performance for 1-2 *Distractors* is shown in gray, 3-4 *Distractors* in green, and 5-6 *Distractors* in yellow. Additionally, the distance between the probe stimulus and the cross landmark was quantified as the distance between the center of the probe stimulus and the intersecting point of the cross landmark in visual degrees. To test the influence of the relative distance between the landmark and the probe stimulus, we conducted a 3 (binned set-size) x 4 (binned distances between probe stimulus and the landmark) repeated-measures ANOVA.

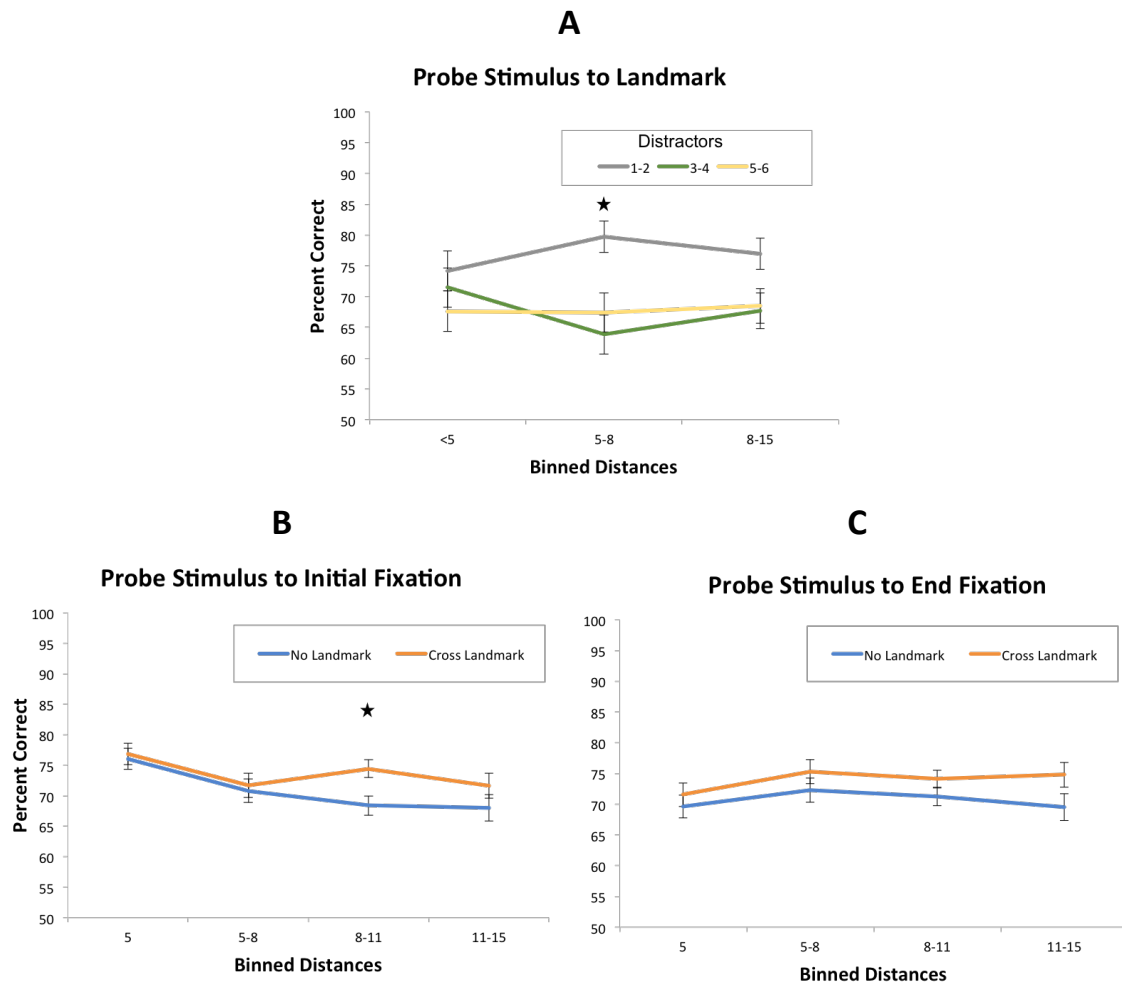


Figure 7. Results of additional analyses on relative distances conducted for Experiment 2, depicting mean performance averaged across participants. **A.** Distance between probe and landmark, lines show binned distractors. **B.** Distance between probe stimulus and initial fixation. **C.** Distance between probe stimulus and end fixation. The (*) denotes statistical significance of $p < .05$.

There was no significant main effect of distance probe stimulus to the landmark, $F_{(2,16)} = 0.180$, $p = .073$, and no significant interaction between binned set-sizes and binned distance of probe stimulus to the landmark, $F_{(4,32)} = 1.513$, $p = .414$. Post-hoc comparisons with Bonferroni corrections revealed that the landmark lead to improved performance at intermediate distances (between 5-8°) for the smallest set-size compared to the larger set-sizes: performance was greater for 1-2 distractors vs. 3-4 distractors, ($p = .038$) and for 1-2 distractors vs. 5-6 distractors, ($p = .030$), but not for 3-4 distractors vs. 5-6 distractors, ($p = .1.000$). For largest distances (greater than 8°), performance trended towards significance for 1-2 distractors vs. 5-6 distractors, ($p = .056$), but not for 1-2 distractors vs. 3-4 distractors, ($p = .108$) or for 3-4 distractors vs. 5-6 distractors, ($p = 1.000$). The comparisons revealed that for the smallest distances (below 5°), performance for all three set-size bins was similar: 1-2 distractors vs. 3-4 distractors, ($p = 1.000$); 1-2 distractors vs. 5-6 distractors, ($p = .398$); 3-4 distractors vs. 5-6 distractors, ($p = 1.000$). These results indicate that the landmark provided a benefit for trials with the fewest distractors when the probe stimulus was at intermediate distances from the landmark.

Distance between the probe stimulus and the initial fixation cross. Figure 7b shows mean performance across participants as a function of distance between the probe stimulus and the initial fixation. This occurred during the *Target Display* phase, where the probe stimulus was presented among distractors. The cross landmark, shown in orange, appeared to have an effect on performance for greater distances. To test the influence of the landmark on distances between the probe stimulus to the initial fixation, we conducted a 2 (landmark) x 4 (binned distances between probe stimulus and initial fixation) repeated-measures ANOVA. Distances were binned into four groups 5°, 5.01-8°, 8.01-11°, and 11.01-15 to keep analyses consistent with those above.

There was a significant main effect of distance between the probe stimulus and initial fixation, $F_{(3,24)} = 5.526$, $p = .005$, $\eta^2 = .409$, but no significant interaction between the distances and the landmark, $F_{(3,24)} = 1.398$, $p = .268$. Post-hoc comparisons revealed a significant effect of the landmark on performance for intermediate distances of 8.01-11° ($p = .001$). There was no significant effect for the smallest distances of 5° ($p = .639$), distances between 5.01-8° ($p = .579$), nor for the largest distances of 11.01-15° ($p = .114$). These results indicate that the landmark provided a benefit to performance when the probe stimulus is at an intermediate distance from the fovea during the *Target Display* phase.

Distance between the probe stimulus and the end fixation cross. Figure 7c shows mean performance across participants as a function of distance between the probe stimulus and the end fixation. This occurred during the *Probe Display* phase, where the probe stimulus was presented in isolation. The cross landmark, shown in orange, appeared to have an effect on performance at the greatest distances. To test the influence of the landmark on distances between the probe stimulus to the end fixation, we conducted a 2 (landmark) x 4 (binned distances between probe stimulus and end fixation) repeated-measures ANOVA.

There was no significant main effect of distance between the probe stimulus and the end fixation, $F_{(3,24)} = 1.016$, $p = .403$, nor a significant interaction between distances and the landmark, $F_{(3,24)} = .403$, $p = .752$. Post-hoc comparisons revealed that there was a difference in performance that trended towards significance for the greatest distance 11.01-15° ($p = .051$), but no difference in performance for the shorter distances 5° ($p = .385$), 5.01-8° ($p = .414$), or 8.01-11° ($p = .085$). These results indicate that the landmark may provide a benefit to performance when the probe stimulus is at large distances from the fovea during the *Probe Display* phase.

2.4.b. ii Saccade Metrics. I was interested in determining if the landmark provided a benefit to transsaccadic integration as a function of different saccade metrics. Specifically, analyses were conducted to understand the influence of the landmark as a function of saccade amplitude and saccade direction. Figure 8 above shows the results of these analyses.

Saccade Amplitude. Figure 8a shows mean performance across participants as a function of saccade amplitude. The cross landmark, shown in orange, appeared to have an effect on performance for some of the saccade amplitudes. To test the influence of the landmark on saccade amplitude, we conducted a 2 (landmark) x 4 (binned saccade amplitudes) repeated-measures ANOVA. Amplitudes were binned in four groups 5°, 5.01-8°, 8.01-11°, and 11.01-15° to keep the size of the group relatively equal so that results would be clear and easy to interpret. These same bins were previously used by Prime (2007), and were the same for all subsequent analyses.

There was no significant main effect of amplitude, $F_{(3,24)} = 1.116$, $p = .358$, nor was there a significant interaction between landmark and amplitude, $F_{(3,24)} = 2.414$, $p = .091$. Post-hoc comparisons indicated that the landmark lead to significantly greater performance for saccade amplitudes of 5.01-8° ($p = .046$) and 11.01-15° ($p = .037$). There was no effect of the landmark for the smallest saccade amplitude of 5° ($p = .420$), or for the amplitudes of 8.01-11° ($p = .454$). These results indicate that the presence of extrinsic location cues did not affect transsaccadic integration for small saccades, but that they provide some benefit to performance as saccade sizes grow.

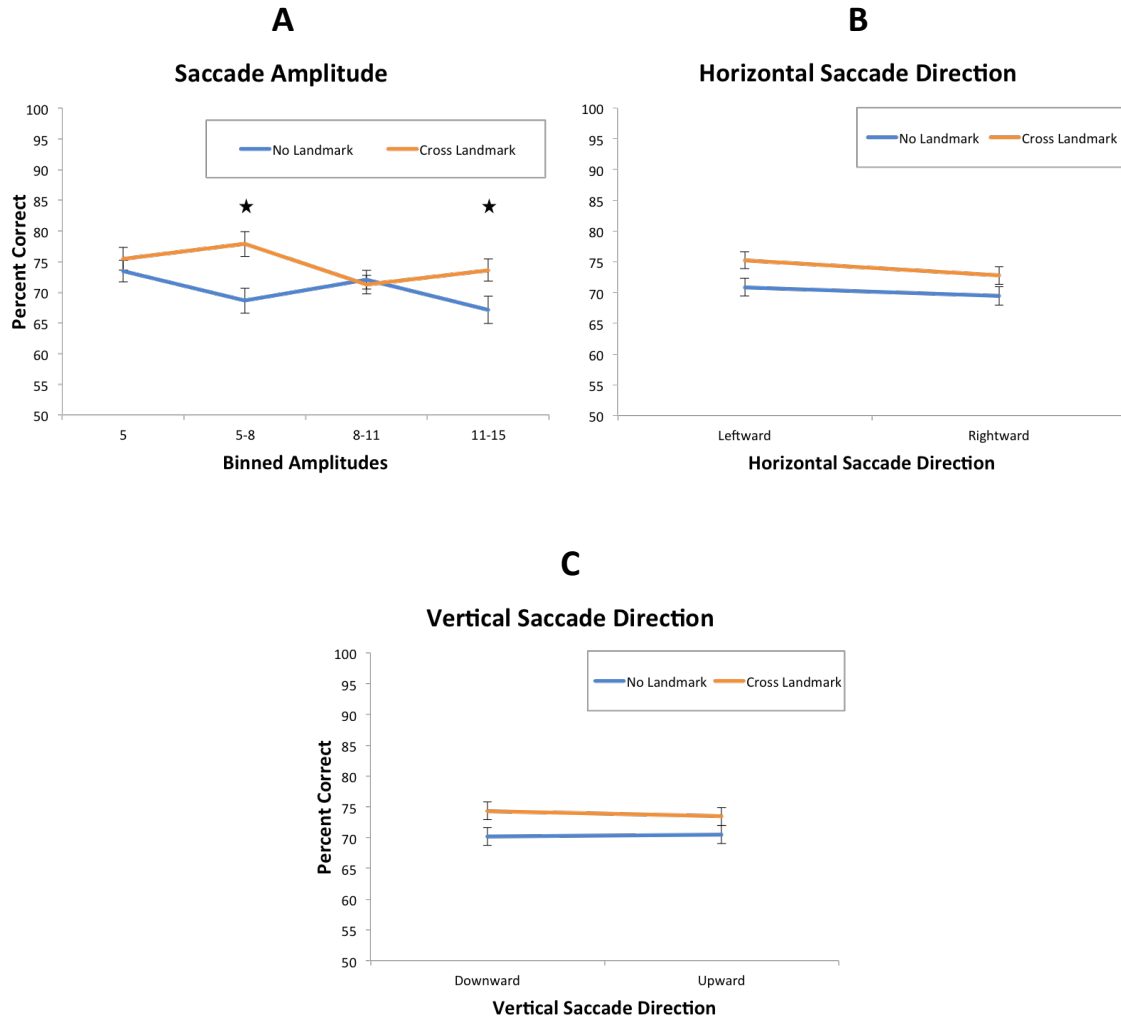


Figure 8. Results of additional analyses on saccade metrics conducted for Experiment 2. Mean performance averaged across participants. The blue line represents performance of the *No Landmark* condition and the orange line represents performance of the *Cross Landmark* condition. The error bars are standard error of the mean. **A.** Saccade amplitude. **B.** Horizontal saccade direction. **C.** Vertical saccade direction. The (*) denotes statistical significance of $p < .05$.

Saccade Direction. Figures 8b and 8c show mean performance across participants as a function of horizontal and vertical saccade amplitude respectively. Once again, the no landmark data is shown in blue and the cross landmark was shown in orange. To test the influence of the landmark on saccade direction, we conducted two 2 (landmark) x 2 (saccade direction) repeated-measures ANOVAs, one for horizontal and one for vertical saccade direction.

The analysis of horizontal direction (Figure 8b) revealed no significant main effect of horizontal saccades, $F_{(1,8)} = 3.447$, $p = .100$, nor a significant interaction between landmark and horizontal direction, $F_{(1,8)} = 0.116$, $p = .743$. The analysis of vertical direction (Figure 8c) also failed to reveal a significant main effect of vertical saccades, $F_{(1,8)} = 0.164$, $p = .696$, or a significant interaction between landmark and vertical direction, $F_{(1,8)} = 0.031$, $p = .864$. These results indicate that saccade direction did not influence transsaccadic integration.

2.4.b iii Visual Field. Finally, I was interested in determining if the visual field of the probe stimulus had an effect on performance, and if the landmark mediated this effect. These analyses were separated into visual field of the probe stimulus relative to initial fixation, and relative to end fixation. Additionally, the analyses at each fixation cross were separated into vertical and horizontal visual fields for a total of four repeated-measures ANOVAs. Figure 9 above shows the results of these analyses.

Initial fixation. The first set of visual field analyses were conducted for the probe relative initial fixation. This occurred during the *Target Display* phase, where the probe stimulus was presented among distractors.

Vertical visual field. Figure 9a shows mean performance across participants as a function of vertical visual field of the probe stimulus relative to the initial fixation. To test the influence of the landmark on vertical visual field, we conducted a 2 (landmark) x 2 (vertical visual field) repeated-measures ANOVA.

There was no significant main effect of vertical visual field, $F_{(1,8)} = 1.033$, $p = .339$, nor did the ANOVA reveal a significant interaction, $F_{(1,8)} = 3.296$, $p = .107$. Post-hoc comparisons revealed a significant difference between the *No Landmark* and *Landmark* conditions when the probe stimulus was below the initial fixation ($p = .001$), but no difference in performance between these conditions when the probe stimulus was above the initial fixation ($p = .968$). These results indicate that the presence of location cues extrinsic to the stimuli provided a benefit to performance when the probe stimulus was below the fixation cross during the *Target Display* phase (Figure 9a).

Horizontal visual field. Figure 9b shows mean performance across participants as a function of horizontal visual field of the probe stimulus relative to the initial fixation. To test the influence of the landmark on horizontal visual field, we conducted a 2 (landmark) x 2 (horizontal visual field) repeated-measures ANOVA.

There was a significant main effect of horizontal visual field, $F_{(1,8)} = 94.021$, $p = .001$, partial $\eta^2 = .763$, such that performance was greater when the probe stimulus was presented to the left of initial fixation than when it was presented to the right of initial fixation. The ANOVA failed to reveal a significant interaction, $F_{(1,8)} = 1.743$, $p = .730$. Together, these results indicate that the presentation of the probe stimulus to the left of fixation during the *Target Display* phase lead to greater performance on the task, and that the presence of the cross landmark did not influence this horizontal visual field effect.

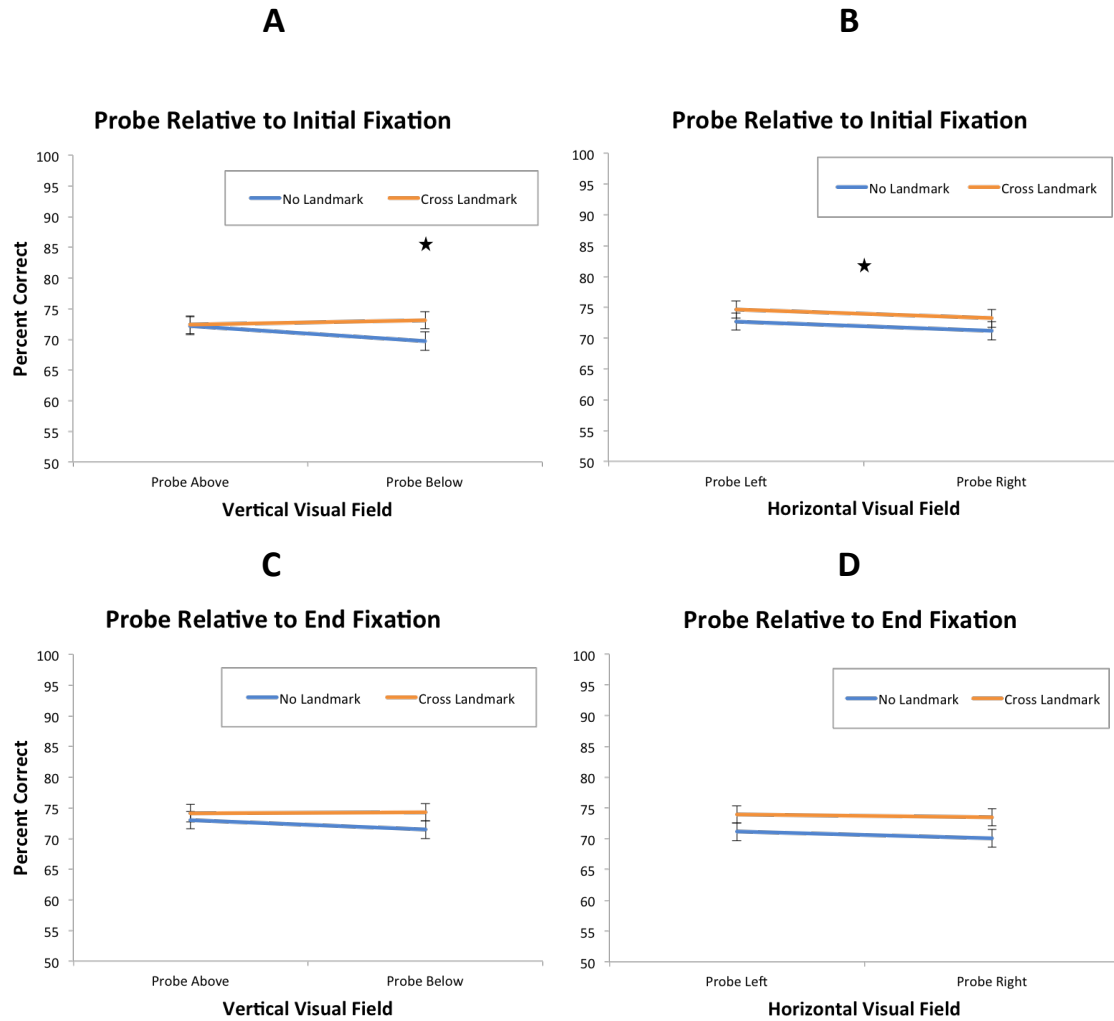


Figure 9. Results of additional analyses on visual field conducted for Experiment 2, depicting mean performance averaged across participants. The blue line represents performance of the *No Landmark* condition and the orange line represents performance of the *Cross Landmark* condition. The error bars are standard error of the mean. **A.** Vertical visual field of stimulus probe relative to initial fixation. **B.** Horizontal visual field of stimulus probe relative to initial fixation. **C.** Vertical visual field of stimulus probe relative to end fixation. **D.** Horizontal visual field of stimulus probe relative to end fixation. The (*) denotes statistical significance of $p < .05$.

End fixation. The second set of visual field analyses were conducted for the probe relative to the end fixation. This occurred during the *Probe Display* phase, where the probe stimulus was presented among distractors.

Vertical visual field. Figure 9c shows mean performance across participants as a function of vertical visual field of the probe stimulus relative to the end fixation. To test the influence of the landmark on vertical visual field, we conducted a 2 (landmark) x 2 (vertical visual field) repeated-measures ANOVA.

There was no significant main effect of vertical visual field, $F_{(1,8)} = 0.696, p = .428$, nor a significant interaction $F_{(1,8)} = 0.816, p = .393$. The results for vertical visual field for the probe stimulus relative to the end fixation in the presence of the landmark appear to follow a similar pattern as the vertical visual field results for initial fixation (see Figures 9a and 9c), but failed to reach significance ($p = .097$). These results indicate that while the presence of a location cue extrinsic to the stimuli provided a benefit to performance when the probe stimulus was below fixation during the *Target Display* phase, it did not provide a benefit to performance during the *Probe Display* phase.

Horizontal visual field. Figure 9d shows mean performance across participants as a function of horizontal visual field of the probe stimulus relative to the end fixation. To test the influence of the landmark on horizontal visual field, we conducted a 2 (landmark) x 2 (horizontal visual field) repeated-measures ANOVA.

There was no significant main effect of horizontal visual field $F_{(1,8)} = 2.352, p = .164$, and no significant interaction $F_{(1,8)} = 0.642, p = .446$, indicating that the presentation of the probe stimulus to the right or left of end fixation did not influence accuracy on the task, and that the presence of the landmark did not shift performance in one direction over another.

2.4c Experiment 3: Orientation Sensitivity

As the main analyses of Experiment 1 and Experiment 2 provided conflicting reports of the influence of allocentric landmarks on transsaccadic integration, we conducted Experiment 3 as a control to account for the cross landmark's potential influence on orientation. In this experiment, we determined psychometric curves for orientation sensitivity based on transsaccadic changes to orientation of a single object. For each observer, I fitted Weibull functions to the data from the *No Landmark* and *Cross Landmark* and estimated their orientation sensitivity by using a 75% performance threshold conditions using psignifit 4.0 (Schütt, Harmeling, Macke, & Wichmann, 2016). Psychometric functions for one typical observer are shown in Figure 10a, and for the mean data across all participants in Figure 10b. I compared these orientation sensitivity thresholds between *No Landmark* and *Cross Landmark* conditions using paired-sample *t*-tests, which revealed that the allocentric cross landmark did not have a significant effect on participant's orientation sensitivity, $t(8) = 0.393$, $p = .704$. Based on these results, we are confident that the cross landmark effect that was observed in Experiment 2 was due to the cross landmark's potential role as a spatial reference as opposed to a reference for the orientation feature.

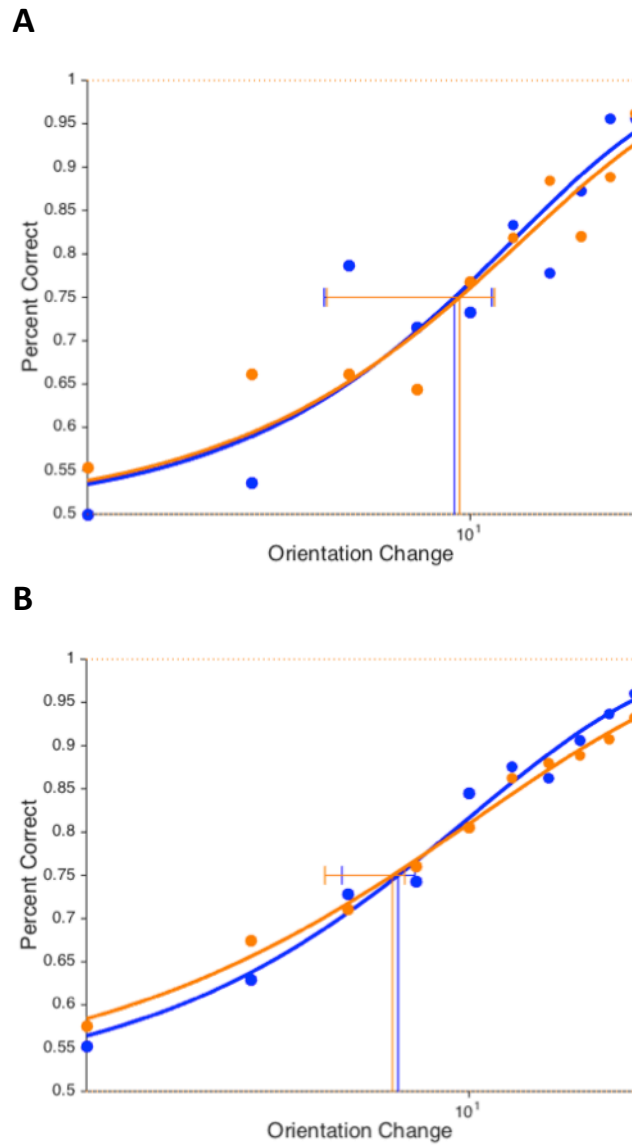


Figure 10. 75% performance thresholds were used as estimates of orientation sensitivity in the presence and absence of allocentric landmarks. The blue line is fitted to the *No Landmark* data, and the orange line is fitted to the *Landmark* data. **A.** Psychometric functions fitted to data of one typical observer. **B.** Psychometric functions fitted to mean data for all participants.

2.5 Discussion

In this study, a series of experiments were used to investigate the influence of multiple distractors and allocentric location cues on transsaccadic integration. In both Experiments 1 and 2, participants' ability to compare stimuli across saccades decreased as set-sizes increased. This was true both for our control *No Landmark* task, as well as our landmark tasks. In the case of the intrinsic circle landmark task (Experiment 1) we found no advantage in performance relative to controls. However, the extrinsic cross landmark (Experiment 2) did provide an advantage, especially for moderate and large saccade amplitudes, moderate distances of the probe stimulus to the landmark and to the initial fixation, and when the probe stimulus was in the lower visual field. Finally, the cross landmark did not have any influence on performance in a transsaccadic orientation discrimination task, suggesting that its major benefit was providing a spatial memory reference. We will consider these results in more detail in the following sections.

2.5a Transsaccadic memory capacity

The transsaccadic integration task used in this study required participants to retain the location and orientation of multiple objects and compare those stimuli across saccades in the presence or absence of allocentric landmarks (Prime et al., 2007, 2008, 2010). In the case of the *No Landmark* control condition, participants were required to do this based on egocentric mechanisms such as extra-retinal signals about the amplitude and direction of their saccades (Prime et al., 2007). As expected, transsaccadic performance decreased with set-size in both Experiments 1 and 2, indicating that transsaccadic memory and transsaccadic integration are hampered as working memory load is taxed. This was an anticipated finding based on previous studies (Irwin, 1992; Irwin & Andrews, 1996; Prime et al., 2007, 2008, 2010).

Curiously, performance in our control task dropped off faster and plateaued higher than observed in some similar previous studies (Prime et al., 2007, 2008, 2010), although not all (Tanaka et al., 2014). Possibly, the presence of additional stimuli influenced participants to adopt a more global memory strategy (Mou & McNamara, 2002; H. Wang et al., 2005), as opposed to remembering the items independently, leading to consistent performance as set size increased past 4 items. This finding argues against the ‘*fixed slot model*’ of visual working memory, indicating that the visual system is able to maintain item representations for set sizes greater than 3-4 items, supporting instead flexible models of visual working memory that integrate a role for spatial ensemble representations (Schurgin, 2018). Such a model could incorporate situations where items are clustered by type, and where changes to individual items are perceived as changes to the ensemble cluster. In either case, our control data served their purpose as to provide a baseline pattern to examine the influence of an additional landmark. Overall, the presence of a landmark did not fundamentally alter this pattern, but in the case of the extrinsic cross landmark, the presence of additional spatial information shifted the plateau up slightly (Figure 6). This seems to suggest that in our task the extrinsic cross landmark might help to reduce noise in storing and representing visual information, but could not overcome fundamental limits in storage capacity.

2.5b Intrinsic vs. extrinsic allocentric cues

The aim of the landmark conditions was to investigate whether allocentric landmark cues would aid transsaccadic integration by providing the visual system with additional location information as it has been shown that such allocentric information can influence the memory of target locations (Lemay et al., 2004; Neggers et al., 2005; Obhi & Goodale, 2005). We separated

our allocentric cues into two categories: the intrinsic cues that provided information about both the absolute locations and the interobject spatial organization of the stimuli (Mou & McNamara, 2002; H. Wang et al., 2005), and extrinsic cues that represented the stimuli in relation to other independent objects in the environment (Sheth & Shimojo, 2004). As such, it was expected that the intrinsic circle landmarks in Experiment 1 would alleviate working memory load, allowing the visual system to focus on the object features, leading to enhanced performance compared to the *No Landmark* condition where participants were required to retain both orientation and location information. The results from Experiment 1 indicated that the intrinsic location cues (*circle landmark*) had no benefit on transsaccadic integration.

Previous research has shown that intrinsic landmarks that provide additional information on the overall layout of the stimulus array by providing salient landmarks aid in recollection of object location in space (Sun & Wang, 2010). However, in our task it may be that since the visual system is trying to remember a certain set of locations, it may automatically discount these locations as unreliable as additional allocentric cues and instead resort to independent stimuli that it judges as stable and reliable as landmarks (Uchimura & Kitazawa, 2013; Uchimura et al., 2015). Further, the change in the stimulus (from an oriented patch to a circle) may have been distracting or even influenced the visual system to ‘dump’ this information. In fact, when we tried another version of this experiment (where the stimuli changed to a neutral grey) participants performed even worse and complained that the change was distracting.

In contrast to the results of Experiment 1, the presence of the extrinsic location cue (*cross landmark*) lead to a modest yet significant benefit on performance in Experiment 2, providing some support to the hypothesis that allocentric landmark information aids the visual system in transsaccadic integration. These contrasting results between the two experiments could be

explained in part due to the nature of the presentation of the allocentric information. The circle landmarks in Experiment 1 appeared following the *Target Display* phase, *after* the visual system began encoding the location of the stimuli, in contrast to the cross landmark in Experiment 2 which was presented from the beginning of the trial, perhaps providing the opportunity for the visual system to encode the location of the stimuli with respect to the extrinsic cross landmark. Since stimulus encoding may have occurred prior to the presence of the landmarks, it could be that the retroactive intrinsic cues failed to provide a benefit (Sheth & Shimojo, 2004). Retroactive cues have been shown to increase performance for both feature and spatial-based stimuli (Heuer, Schubö, & Crawford, 2016; Q. Li & Saiki, 2015), but our transsaccadic task may be recruiting egocentric mechanisms in such a way that participants perform equally well in egocentric and intrinsic allocentric landmark conditions.

Another plausible explanation for this result is that as set size increased, so too did the number of intrinsic ring landmarks. These additional landmark cues may have provided additional complexity in the overall display, a complexity that was not present in the extrinsic landmark condition that had only one landmark – and by extension the same level of complexity – in every trial. Future research investigating the influence of simple visual landmarks on the integration of simple visual features across saccades may consider running ‘mini blocks’ whereby the location of the cross landmark remains stable for a number of trials to reinforce the landmark’s reliability.

2.5c Location vs. feature allocentric cues

The conflicting results between Experiments 1 and 2 location cues provided by the allocentric landmarks, we were concerned that the cross landmark, in addition to being a spatial

reference, was providing the visual system with additional references for orientation information and that this potential orientation benefit of the cross landmark was driving the effect of Experiment 2. As such, I ran a control experiment to probe the cross landmark's effect on orientation sensitivity. Results from Experiment 3 indicated that there was no increase in orientation sensitivity in the presence of the cross landmark. This finding provides additional support to the conclusion that extrinsic allocentric landmarks lead to increased performance in transsaccadic integration by providing spatial references.

The experimental task used in these experiments was designed to probe the visual system's ability to retain and integrate object location and orientation across saccades. We found that the extrinsic allocentric landmark in Experiment 2 provided an additional spatial reference, but not a feature reference (Experiment 3), that lead to an increase in performance. A potential explanation for this could be that the visual system is optimally integrating feature information via egocentric mechanisms alone, while the integration of location information may benefit from the presence of allocentric landmark information. While near-optimal integration of orientation information across saccades in the absence of landmarks has been demonstrated in several studies (Ganmor et al., 2015; Prime et al., 2007; Wolf & Schütz, 2015), the efficiency of location integration across saccades has been shown to decline as saccade-size grows (Prime et al., 2006). An extrinsic landmark could help reduce the extra-retinal noise for larger saccades, similar to effect of the cross landmark observed here (Figure 8). Thus, transsaccadic integration may be optimal when both egocentric feature-based and extrinsic allocentric location information are present before, during, and after the saccade.

2.5d Possible Neural mechanisms

Brain regions specialized in egocentric coding have been identified with several techniques. Early studies interested in visual processing and saccade programming have implemented the superior colliculus (Walker, Fitzgibbon, & Goldberg, 1995), extrastriate areas (Melcher & Morrone, 2003; Nakamura & Colby, 2002), and frontal eye fields (Sommer & Wurtz, 2006; Umeno & Goldberg, 2001). Previous research has shown that the both the right and left FEF, known for their role in providing saccade efference copies to the visual system (Colby, Duhamel, & Goldberg, 1995; Moore & Armstrong, 2003), are involved in spatial processing during transsaccadic integration (Prime et al., 2010). Previous transcranial magnetic stimulation research in our lab has also demonstrated the involvement of the early visual cortex (Malik, Dessing, & Crawford, 2015), the posterior prefrontal cortex (Vesia, Prime, Yan, Sergio, & Crawford, 2010), and the dorsolateral prefrontal cortex (Tanaka, Dessing, Malik, Prime, & Crawford, 2014). A more recent functional resonance imaging adaptation experiment has specifically implicated the right supramarginal gyrus and extrastriate cortex in transsaccadic integration of visual orientation (Dunkley, Baltaretu, & Crawford, 2016).

Nothing is known about the cortical areas involved in allocentric coding for transsaccadic integration, but one might speculate based on areas that have been implicated in allocentric coding for perception, short-term visual memory, and action. Chen and Crawford (2017) used fMRI to identify cortical areas such as the precuneus and midposterior intraparietal sulcus that showed a preference for landmark-centered saccade target coding. The precuneus was also implicated in coding passively presented stimuli relative to background landmarks (Uchimura et al., 2015). Other research has found allocentric activation in the lateral occipital cortex, and the posterior parietal cortex in perceptual judgments (Neggers, van der Lubbe, Ramsey, &

Postma, 2006) and manual judgments (Thaler & Goodale, 2011). Temporal cortex and inferior occipital cortex have also been implicated in landmark-centred coding of reach targets (Chen et al., 2014; Chen, Monaco, & Crawford, 2018). Some or all of these areas could provide inputs to saccade areas and areas involved in transsaccadic integration, stabilizing the system's location estimate.

2.5e Conclusions

In conclusion, we set out to test the influence of intrinsic and extrinsic allocentric information on the retention and integration of multiple objects across eye movements. Our results indicate that extrinsic, but not intrinsic, allocentric information leads to increased performance on our transsaccadic integration task. Further investigations are required to more fully understand the influence of allocentric landmark information on transsaccadic integration. The work described in this chapter investigated the influence of simple landmarks on the integration of simple visual features, and the results support that some forms of allocentric landmark information (i.e., location cues that are extrinsic to stimuli of interest) provide beneficial spatial cues that enhance the integration of orientation across saccades.

CHAPTER 3

GENERAL DISCUSSION

3.1 Summary

In this thesis, I investigated the influence of stable, reliable allocentric landmarks on transsaccadic integration of multiple objects. The series of studies described above showed the extent to which both *intrinsic* and *extrinsic* allocentric landmarks influence the visual system's ability to retain and integrate object locations and features (i.e., orientation) across eye movements. Namely, intrinsic circle landmarks failed to provide a benefit to performance on our task, but the extrinsic cross landmark had a modest, yet significant effect by providing an additional spatial reference. A control experiment provided further evidence for our interpretation of the results of the main experiments, indicating that the effect of the extrinsic cross landmark was not due to a feature reference.

In the present chapter, I will discuss the implications of this series of studies and how the observed results expand on previous studies on transsaccadic integration of object features and locations. I will then address any potential limitations of the studies conducted here, as well as any outstanding questions that remain and potential future directions.

3.2 Contributions to Transsaccadic Integration Literature

Previous studies on transsaccadic integration have aimed to uncover what types of information acquired during stable fixations (and how much of it) can be retained and integrated across saccadic eye movements. In a task requiring participants to acquire spatially relevant information at one fixation, and integrate it with similarly relevant spatial information at another fixation, it was shown that participants retained and integrated such information across eye movements and successfully identified the intersecting point of two lines that were presented in succession (Prime et al., 2006). Further, it has been shown that the visual system can retain

simple object features such as colour, luminance, spatial frequency, orientation, and size in order to integrate them based on their relative spatial locations (Jeyachandra, Nam, Kim, Blohm, & Khan, 2018; Luck & Vogel, 1997; Moore, Tolias, & Schiller, 1998; Prime et al., 2011; Verfaillie, De Troy, & Van Rensbergen, 1994). Additionally, more high-level cognitive functions such as reading have been investigated, as reading involves transsaccadic integration (McConkie & Rayner, 1976). The results from these studies indicate that the visual system can successfully integrate object features across eye movements by maintaining some sort of spatial representation.

It has been shown that the visual system can successfully remember simple object features and locations, and integrate this information across eye movements, and that allocentric information leads to increased spatial recall precision of stimuli at fixation (Aagten-Murphy & Bays, 2019), but the influence of reliable allocentric information on transsaccadic integration hasn't been thoroughly investigated. The series of studies presented in this thesis elaborated on the transsaccadic literature by systematically introducing stable allocentric landmarks on a transsaccadic integration task. I asked participants to compare the orientation of stimuli presented pre- and post-saccade in the presence or absence of reliable allocentric landmarks. The results of the first experiment show that the intrinsic circle landmarks that were directly related to the spatial location of the stimuli and highlighted the interobject spatial relationships within the set-size failed to improve performance on the task. In contrast, the second experiment revealed a significant increase in performance in the presence of the extrinsic cross landmark that provided cues to stimulus locations relative to an independent visual anchor. This was especially true when the stimulus was presented in a set-size of 3 items. Taken together, the results of these

experiments show that some types of allocentric landmarks aid the visual system in integrating object features and locations across saccades.

In addition to the influence of allocentric landmarks, additional analyses on the data from the second experiment revealed the conditions under which the allocentric cross landmark was most influential. Specifically, the cross landmark lead to increased performance for the smallest set-sizes compared to the larger set-sizes when the probe stimulus was at moderate distances from the landmark, when the probe was at moderate to larger distances from the fovea during the initial presentation (i.e., at the initial fixation), and trended towards increased performance when the probe was at the largest distances from the fovea during the presentation of the altered probe stimulus post-saccade (i.e., at the end fixation).

Beyond the analyses of probe-related distances, the cross landmark provided a benefit to performance for moderate and large saccade amplitudes. These results indicate that the presence of reliable extrinsic allocentric information could help reduce the extra-retinal noise in the visual system produced by larger saccades. Finally, analyses of visual field effects revealed that the presence of the landmark provided a benefit when the probe stimulus was presented in the lower visual field during initial fixation, and was trending toward better performance when the probe stimulus was presented in the below the end fixation as well. These visual field results could be attributed to the different processing of upper and lower visual field information in different visual-processing streams (Silson, Reynolds, Kravitz, & Baker, 2018). Taken together, these results indicate that reliable extrinsic landmark information leads to better performance in a transsaccadic integration task.

3.3 Limitations

Great effort was placed into optimizing the experimental paradigm to minimize potential effects of unexpected reference cues. We recorded in complete darkness, while participants were seated approximately 50 cm from the center of a large display (1.84 m x 1.38 m, spanning 119.2° visual angle horizontally by 103.8° visual angle vertically). The purpose of such a large display was to remove the edges of the monitor from participants' periphery as the monitor's position in space could serve as an allocentric landmark. An additional step toward reducing the monitor's edges was creating a mask that was a full screen display of randomized pixel noise that faded to black toward the edges to reduce the contrast of the monitor's contours. However, one possible limitation of this work was the brightness of the monitor. The mean luminance of the Gabor-like stimuli (19.57 cd/m²) was significantly brighter than previously reported in studies that used a similar paradigm (mean luminance 17 cd/m²; Prime et al., 2007). This difference may emphasize more of the participants' surroundings than intended, and can be avoided in the future by filtering the projected image before it reaches the display area to dim it further. In a similar vein, the eye's adaptation to darkness may also serve to increase participants' sensitivity to their surroundings in the darkened room (Lamb & Pugh, 2004); as such, smaller blocks to avoid habituation to darkness, or flashes of light between trials at pseudorandom intervals, could help reduce dark adaptation.

Another potential limitation of the series of studies presented here was the different time scale of the two paradigms in Experiments 1 and 2. While Experiment 2 followed the time course of the original paradigm (Prime et al., 2007), an additional 300 ms between the *Target Display* phase and the mask was included in Experiment 1. This was required in order to present participants with the circle landmarks immediately following the disappearance of the stimuli.

The timing between the two experiments was originally the same, but participants had difficulty executing correct saccades when the appearance of the circle landmarks occurred at the same time as the post-saccadic fixation cross. In addition, the simultaneous presentation of circle landmarks and post-saccadic fixation cross may not have provided the visual system with sufficient allocentric landmark when it occurred so late in the trial. Because of this timing discrepancy, we cannot draw direct conclusions between our two allocentric conditions, but this did not affect our interpretation of each experiment as the data from the *No Landmark* control condition within each experiment served the purpose of providing a baseline pattern to examine the influence of each allocentric landmark.

Finally, the reasons behind the absence of an allocentric landmark effect in Experiment 1 are unclear. During preliminary testing, the allocentric landmarks were grey discs rather than circles that appeared in the spatial location of the stimuli following the disappearance of the Gabor-like oriented patches. Participants reported that these filled-in discs were distracting, and preliminary analyses showed that participants performed even worse in the *Landmark* condition than in the *No Landmark* condition, perhaps because the filled-in discs acted as masks of the oriented stimuli. To account for this, we altered the landmarks from filled-in discs to circles with low luminance, but perhaps the nature of the presentation continued to be distracting, causing the visual system to ‘dump’ the information.

3.4 Unresolved Questions and Future Directions

While I have demonstrated that certain types of allocentric information provide the visual system with spatially relevant information that aids in the integration of simple visual features across eye movements, several questions remain. First, we only manipulated a single object

feature (orientation) while focusing on the effect of landmark as set-size, and by extension working memory load, increased. Although some studies have investigated the capacity of working memory load (i.e., multiple objects) in transsaccadic integration (Prime et al., 2007), and others have investigated integration of multiple feature changes of a single object across saccades (Jeyachandra et al., 2018), not many studies have investigated both varying set-sizes and multiple feature changes. Future research could focus on the influence of allocentric landmarks on transsaccadic integration of multiple objects while multiple features (i.e., orientation, location, luminance, and size) change between saccades.

Additionally, the experiments described in this thesis investigated the influence of simple allocentric cues on transsaccadic integration of simple visual stimuli. There have been studies that have investigated transsaccadic integration of more complex, natural objects, but to my knowledge, none of these have systematically studied the influence of allocentric landmarks on natural stimuli across eye movements. Therefore, future research could attempt to answer similar questions as those posed at the beginning of this thesis using complex landmarks and stimuli rather than simple landmarks and object features.

Finally, having established the influence of allocentric landmark information on transsaccadic integration of multiple objects, both simple and complex, future research can endeavor to uncover the cortical mechanisms of allocentric landmarks and transsaccadic integration. Specifically, targeting areas known for their egocentric transsaccadic integration mechanisms such as the frontal eye fields (involved in providing egocentric signals for transsaccadic integration) (Prime et al., 2010) and the supramarginal gyrus (Dunkley et al., 2016) with transcranial magnetic stimulation (TMS) may lead to disrupted performance on transsaccadic integration tasks, whereas the presence of allocentric information may mitigate the

TMS effects. Likewise, targeting areas implicated in allocentric coding (Chen & Crawford, 2017) may degrade the hypothesized allocentric advantage.

3.5 Conclusion

Since we rely on the snapshot acquisition of visual information across multiple eye movements, it is important to research the visual system's ability to maintain spatial constancy and a unified global percept. One way our brains may accomplish this is by using remembering the location of items in space and determining whether or not they are stable and reliable. It may evaluate landmarks from the external world, anchor our visual perception on those that are deemed stable, and update internal representations of the environment according to that perceived stability. In this thesis, I presented a series of experiments that investigated the influence of reliable *intrinsic* and *extrinsic* allocentric information on the integration of multiple objects across saccades. Our results suggest that reliable extrinsic allocentric information benefits transsaccadic integration of multiple objects.

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APPENDICES

Appendix A: Author Contributions

George Tomou contributed to experimental design, laboratory preparation, data collection and analysis, and wrote the paper. Dr. Yan contributed to laboratory preparation and provided technical support. Dr. Crawford contributed to experimental design, provided advice and feedback on experiments and analyses, editorial comments, and funding support.