CUE CONFLICTS IN SPATIAL UPDATING

CUE CONFLICTS IN OPTIC FLOW AND BODY ORIENTATION DURING SPATIAL UPDATING

By LAURA YAN JIN, B.SC.

A Thesis Submitted to the School of Graduate Studies in Partial Fulfillment of the Requirements of the Degree Master of Science

McMaster University MASTER OF SCIENCE (2020) Hamilton, Ontario

TITLE: CUE CONFLICTS IN OPTIC FLOW AND BODY ORIENTATION DURING SPATIAL UPDATING

AUTHOR: Laura Jin, B.Sc. (McMaster University)

SUPERVISOR: Professor Hong-jin Sun

NUMBER OF PAGES: viii, 65

Abstract

When spatial updating tasks are performed in a real-world setting, participants usually complete it with ease (e.g., Klatzky et al., 1998). However, in virtual reality (VR), when tasks are presented using optic flow, participants tend to exhibit one of two response patterns, with some participants correctly updating their headings ("turners") and others pointing consistently in the opposite direction ("non-turners") (e.g., Gramann et al., 2005). While research has looked at the stability and pointing characteristics of these two groups (e.g., Gramann et al., 2012; Riecke, 2008), we still do not know why non-turners exist. The following thesis studied two potential sources of cue conflict—stationary versus central visual information and sensorimotor interference—that could impact participants' strategies using the Starfield task (Gramann et al., 2012). Occluding stationary peripheral information increased pointing errors, especially for turners. It is thus possible that turners require the peripheral information to correctly parse and process the central optic flow. Alternatively, manipulating body orientation to decrease sensorimotor interference seemed to decrease error and increase strategy consistency for both turners and non-turners. It is possible that the orientation changes allowed participants to ignore the stationary body-based cues, thereby improving spatial updating. Although these manipulations did not remove the non-turner group altogether, they provided important insights into how cue conflicts may play a role in spatial updating for VR tasks.

Acknowledgements

To my supervisor, Dr. Hong-jin Sun, for providing me with the foundation and support to complete independent research. Thank you for supporting my independence and constantly pushing me to be a better student and researcher. I am incredibly grateful for this experience and the skills I have acquired along the way.

I'd also like to thank my committee members, Dr. Judith Shedden and Dr. Suzanna Becker, for providing me with guidance and encouragement along the way as well as detailed thesis edits. I am extremely grateful for their validation and input.

Special gratitude goes to the students and volunteers whom helped me collect data for my research, as well as my fellow lab mates for bringing positivity and laughter to every day.

Finally, I'd like to extend thanks to my parents and friends, who have provided me with an immense amount of emotional and mental support over the past few years. This accomplishment would have not been possible without them.

Thanks for all of your encouragement!

Table of Contents

List of Figures and Tables

List of Abbreviations and Symbols

PTO = point-to-origin
VR = virtual reality
RT = reaction time

1 GENERAL INTRODUCTION

Imagine running errands downtown. After getting off the subway, we travel to three different stores before heading home. But how do we get back to the subway station? All of us have innate navigational abilities and a reasonable capacity to update our current direction and orientation when travelling through a given environment. This process, termed spatial updating, is the integration of spatial information during travel to form a holistic representation of the environment (e.g., Rieser et al., 1994). Successful spatial updating leads to path integration, the process of combining various travel segments to create a representation of one's current trajectory relative to their starting location (e.g., Etienne & Jeffery, 2004; McNaughton et al., 2006). The combination of spatial updating and path integration therefore allows us to travel back to the subway station without much conscious effort.

1.1 Cues in Navigation

Navigation involves the integration of numerous sensory cues and cognitive processes. These sensory cues could be interoceptive (i.e., body-based) or exteroceptive (i.e., environment-based). Two important body-based cues for navigation arise from the vestibular and proprioceptive systems.

1.1.1 Interoceptive Cues

The vestibular system is located within the inner ear and provides us with information about head positioning and spatial orientation (e.g., Purves et al., 2001). It is important for maintaining balance and posture during motion. Within the vestibular system, the otolith organs respond to changes in linear motion. Hair cells within the otolith organs can be transiently displaced based on changes in linear accelerations. Segments of hair cells can respond to changes in both the horizontal and vertical plane, thus providing a three-dimensional field of linear change information. The semicircular canals, on the other hand, are responsible for detecting changes in angular acceleration (e.g., Purves et al., 2001). The hair cells are contained in a structure called the cupula which is encased in endolymph fluid. Any angular change of the head creates disturbances in the endolymph and therefore displaces the hair cells. This physical displacement then is transduced into neural signals that are sent to the brain.

While the vestibular system provides cues about linear and angular acceleration, the proprioceptive system provides information about the positioning of the body in the local environment (e.g., Proske & Gandevia, 2012). Proprioceptive receptors can be found across the body in the muscles, joints, and skin. The afferent receptors constantly provide neural information about where each limb is and the velocity each part of the body is moving at. The proprioceptive system provides an intuitive sense of where each of our limbs are. Importantly, the proprioceptive system can work without visual input, allowing us to touch our hand to our nose, even with our eyes closed. The maturation of the proprioceptive system is closely linked to motion imitation via the mirror neurons, which begins shortly after birth (Proske & Gandevia, 2012). The sensitivity of the proprioceptive system is therefore established very early on.

1.1.2 Exteroceptive Cues

While interoceptive cues are extremely salient and important, exteroceptive cues also provide information about travel. In humans, environment-based cues arise in the form of visual cues. In the case where someone is a passenger in a car, there is very little vestibular or proprioceptive information during travel. Most of the time, the body is stationary relative to the vehicle. Despite the lack of body-based cues, the passenger is still aware that they are travelling, and can use visual cues such as optic flow to maintain a sense of relative direction.

Visual cues can either be monocular, binocular, or external to the navigator. One salient form of visual information is the use of landmarks, also called recognition-based navigation (Loomis et al., 1993). Landmarks can be distal or proximal to the observer. Interestingly, these are also processed in different brain regions. Distal landmarks are processed by the hippocampus and entorhinal cortex (Save & Poucet, 2000; Parron et al., 2004). Distal landmarks are encoded by place cells (O'Keefe & Dostrovsky, 1971; Moser et al., 2007), grid cells (Hafting et al., 2005; Moser et al., 2007), and head direction cells (Taube, 2007), which collectively support a global orientation and allocentric processing. Navigation using distal landmarks—piloting—uses external environmental features to determine one's current position. The landmarks act as a point of reference for other, less salient, items in the local environment. For instance, the CN Tower is often used as a salient point of reference in Toronto. For travelers new to Toronto, the CN Tower is a structure that is easily visible from many parts of downtown. Then, as individuals become more familiar with an environment, the landmarks they choose may change. Having more landmarks allows for more points of reference within a given environment. Piloting is therefore typically used more for long-range navigation in larger environments (Loomis et al., 1993).

In contrast, proximal landmarks are used for stimulus-response strategies and building up an egocentric representation of the environment. Proximal, or local, landmarks are processed by the associative parietal cortex (APC) (Save & Poucet, 2000). An individual travelling to a new restaurant might be told to "turn left at the fountain". However, this fountain is only visible at a specific range, and is therefore less useful for local travel. Distal and proximal landmarks are therefore both used during wayfinding. When one landmark type is unavailable, we are able to effortlessly switch to using the other (Steck & Mallot, 1997).

During travel, navigators also receive visual information through optic flow, defined by the motion of the environment across the retina as the navigator moves. The direction and magnitude of optic flow allows the individual to determine the extent of their travel and relative direction they are headed. Interestingly, optic flow alone, when integrated across time, is sufficient to allow for successful spatial updating of information about the extent and relative direction of travel over time and therefore can be used to study navigation (e.g., Gramann et al., 2005; Riecke et al., 2002).

1.2 Cue Weighting in Navigation

To aid in navigation, environmental information is simultaneously gathered via myriad sensory modalities. Body-based and visual cues can be used holistically or individually. However, certain cues appear to take precedence. In determining one's travel direction and velocity, cue weighting occurs. When both visual and body-based cues are available, individuals integrate both information sources but rely on the cues perceived to be more reliable (Chen et al., 2017).

Cue weighting in navigation differs depending on whether the traveler is experiencing linear or rotational motion. During linear motion, body-based cues are weighted more heavily than optic flow cues (Campos, Byrne & Sun, 2010). This is supported by findings that spatial updating can also occur without any history of visual input (Rieser et al., 1994; Wang, 2004; Klatzky et al., 1990). In studies of blind and blindfolded-sighted individuals, both groups of participants can successfully travel back to their origin after being led through a travel path (Loomis et al., 1993).

Even though certain cues appear to have greater importance, information from other cues are not ignored. This is especially apparent when cues are in conflict. Evidence for cue conflict comes from spatial updating experiments, where competing information can result in decreased accuracy (e.g., May, 2004). Sensorimotor interference occurs, for example, when the visually simulated motion and body-based information are in competition (May, 2004; Kesler et al., 2010; Wang, 2005), thereby increasing the error of heading updates or preventing spatial updating altogether. Research from EEG even supports that there are individual differences in the relative weighting of cue stimuli. In fact, some participants are unable to ignore visual cues when they are in conflict with vestibular or proprioceptive cues (Townsend et al., 2019).

1.3 Cues Used in Spatial Updating

1.3.1 Spatial Updating and Body-Based Cues

Exteroceptive cues appear to take greater precedence when determining relative position (Mou & Zhang, 2014). When participants received conflicting visual rotation information to disorient them, their knowledge of their current position was unaffected. However, large degrees of heading error were found. Participants also made larger errors when they were in a visually simulated motion condition than a self-locomotion condition. It appears that updating one's position does not necessarily require body-based cues and is a process that is resistant to disorientation. On the other hand, heading updates are much more accurate when body-based cues of self-locomotion are available. But heading updates are also more susceptible to disorientation from conflicting visual information (Mou & Zhang, 2014).

When all visual information is occluded, body-based cues allow for seemingly effortless heading updates (Wang, 2004). Wang (2004) tested participants in a physical environment while simultaneously asking them to imagine themselves in a familiar environment such as their kitchen. Participants were told to point to the locations of various objects in the environment with their eyes closed. The reaction times and accuracy for pointing to objects do not differ between the physical and in the imagined environment

(Wang, 2004). Conscious, imagined spatial updating was also as successful as physically updating. When asked to picture themselves rotating to face a new direction in their imagined environment (e.g., their kitchen), their direction in their real environment was also updated despite no physical rotation.

Although spatial updating in the absence of physical cues is possible, it may not be as successful. Grant and Magee tested participants' ability to transfer information learned from a virtual environment into a real-world one (1998). Groups were instructed to learn the floorplan of a building in virtual reality (VR). To move around the virtual space, one group used a joystick while the other had to physically walk. When tested in the actual environment, participants who were in the walking-VR condition outperformed those in the joystick condition, reaching their destinations faster. In comparing these participants to those who were both trained and tested in the real-world environment, those who trained in VR made more disorientation errors. Information transfer is thus more enhanced when participants are given proprioceptive feedback (Grant & Magee, 1998).

1.3.2 Spatial Updating Through Visual Cues – Point to Origin (PTO) Tasks

Spatial updating can occur when any visual information is available (Gramann et al., 2005; Riecke et al., 2004; Richardson et al., 1999). However, when motion information is only provided visually via optic flow, more response errors are found, with some participants getting disoriented and greater degrees of error than in real-world tasks (Riecke et al., 2002; Gramann et al., 2005; Riecke, 2008).

PTO tasks are one way that the efficacy of visual cues in spatial updating can be measured. The Tunnel task is a modified PTO paradigm using a desktop VR paradigm in which participants watched simulated motion through a tunnel displayed on a computer screen (Gramann et al., 2005). In a typical condition, motion included (1) one straight traversal (moving in the direction perpendicular to the surface of the computer screen), (2) a simulated turn using a combination of translation and rotation (i.e., left or right), and (3) another linear motion. To vary task difficulty, participants experienced either 1, 2, or 3 turns during motion and the eccentricity of each turn varied from 15 to 60 degrees. At the end of the travel, an arrow appeared, and the participant was asked to rotate the response arrow so that it pointed towards their origin location.

Interestingly, participants tended to respond in one of two distinct ways. One group of participants successfully pointed back to their origin location with the mean vector matching that of the direction of origin (i.e., pointing left when experiencing left turns). In contrast, another group of participants pointed in the opposite direction, which would be predicted if they were to not rotate their body orientation during travel (Riecke, 2008) (i.e., moving "into" the screen). It appears that this second group can successfully update their position, but not their relative orientation, thereby exhibiting a left-right reversal during the response phase (Gramann et al., 2005; Riecke, 2008). This second group was categorized as "non-turners", as they appear to be unable to update their heading during the simulated motion, while the first group was categorized as "turners". A small subset of participants seemed to switch between both strategies and were termed "switchers". Both turners and non-turners were consistent in their strategy selection, pointing consistently in opposite directions, despite viewing the same simulated path of motion.

1.3.3 Spatial Updating via Solely Optic Flow – The Starfield Task

In addition to the Tunnel task, another PTO task has been used with similar findings. In the Tunnel task, participants could predict the movement direction for the immediate future as the approaching tunnel structure is visible. The Starfield task, instead, displays many stationary dots of random sizes dispersed in a 3D space (Gramann et al., 2012). There are no landmarks in this environment, nor is there a relative "ground" for participants to travel on. Instead, participants appear to be suspended in space. The location of the dots themselves do not provide a hint to the future direction of travel. Only during simulated self-motion, different dots exhibit different movement speed and directions, simulating their unique locations in a 3D space. For example, the as the viewpoint moves forward, all the dots formed a pattern of movement in a radial direction. Therefore, the Starfield task produces a much more select representation of navigation using only optic flow.

The Starfield task was used to measure the efficacy of optic flow during spatial updating in both the yaw (left/right) and pitch (up/down) planes (Gramann et al., 2012). While species that fly or swim may travel equally in both planes, humans mostly experience changes in only left or right. Humans therefore have a gravity-based orientation, in which we expect the force of gravity to always be below our feet. When rotating in the pitch plane, the direction of gravity relative to our bodies is thus altered, producing greater errors. Furthermore, although humans do experience slight changes in altitude, these are typically gradual (e.g., hiking up a hill) and rarely are combined with rotational motions. They therefore expected to find faster and more accurate point-to-origin responses in the yaw plane. Therefore, it is likely that both planes would produce a visuo-vestibular conflict, since the information provided visually conflicts with the lack of body-based motion cues (Gramann et al., 2012).

Results showed almost perfect dichotomous split in response strategy, which could again be separated into turners and non-turners. Most participants were consistent in their response patterns in both yaw and pitch. However, 18% of participants switched from a turner strategy in the yaw plane to a non-turner strategy in pitch trials (Gramann et al., 2012). It is possible that this shift in strategy revealed the increased difficulty in spatial updating in an unfamiliar plane rather than a complete loss of orientation. Both turners and non-turners also experienced errors that increase with an increase in turn angle. However, these errors were significantly larger for non-turners. Errors were also significantly larger in pitch than in yaw. Similar to the Tunnel task (Gramann et al., 2005), they found that participants tended to overestimate small turn angles and underestimate larger ones.

1.4 Present Study

Across the studies described above, findings from both the Tunnel task (Gramann et al., 2005) and the Starfield task (e.g., Gramann et al., 2012) demonstrated that motion simulated via optic flow can be sufficient for spatial updating in the laboratory setting. Spatial updating can therefore be possible even in the absence of body-based motion cues. However, spatial updating via optic flow seems to only be successful in less than half of a given sample of participants. If we assume that these tasks effectively revealed individual differences in spatial updating ability, we still do not know which aspects of the task led to the different pointing responses seen in turners and non-turners. Furthermore, both groups of participants appear to be highly consistent in their response strategies (e.g., Gramann et al., 2005). Thus, one might wonder why only one group of individuals, the non-turners, appear to be disoriented and continuously fail to update their heading.

Identifying the aspects of the task that prompt the dichotomous response patterns might provide insight into the critical factors that determine individual differences in cue weighting during spatial updating. As previously discussed, when observers are exposed to visually simulated travel, they need to effectively process the extent of linear and rotational motion from optic flow. At the same time, they need to ignore the interference from the conflicting visual and body-based information about lack of self-motion.

One potential explanation for the lack of heading updating could be a difference in processing the turns themselves or recognizing the overall trajectory. In particular, the final heading direction of a travel path requires idiothetic body-based cues and suffers when only visual rotation is provided (Mou & Zhang, 2014). However, it has been shown that if participants are asked to select from different configurations when shown a birds-eye view (view from directly above) of potential trajectories, both turners and non-turners can correctly identify their trajectory (Wong et al, unpublished work). Importantly, this shows that both groups of participants can correctly identify whether they made a left or a right turn and can also recognize the orientation of their last heading relative to their initial heading. Participants are likely able to process the optic flow information in a way that generates correct heading information prior to making a homing response. Thus, it rules out the possibility that the participants cannot process information about the optic flow. The difference between the two groups is likely found in the response phase.

The next logical step is to examine the contribution of conflicting information that prevents one group of participants from correctly updating their heading. There are two possible sources of confusion. Unlike real world self-motion, the Starfield task presents optic flow over a limited field of view surrounded by a stationary background. Furthermore, motion information presented from optic flow conflicts with the vestibular and proprioceptive cues that tell the participant they are stationary.

An important factor of note is that in desktop virtual reality (VR), participants view a simulated environment through a computer monitor (e.g., Riecke et al., 2002; Gramann et al., 2005). A caveat to using desktop VR is that it inherently produces a significant amount of cue conflict (Riecke et al., 2002), which has not been extensively examined in navigation paradigms. In this thesis, we examined the contribution of two potential sources of cue conflict to spatial updating using the Starfield task (i.e., Gramann et al., 2012). The response patterns of the non-turners suggest that they make responses as if they do not update their heading. At the time of response, they point as if they are maintaining the heading direction which is the same as their heading during initial travel. Their perceived heading is also their physical heading relative to the visual surround (e.g., perpendicular to the frame of computer monitor in particular). In addition, maintaining such a heading is also congruent with observers' body orientation (facing the computer monitor).

Since the task is presented in desktop VR, optic flow can only be presented partially across the retina. One source of conflict thus comes from the peripheral visual field, which is stationary. Another source of cue conflict comes from sensorimotor interference. Since proprioceptive and vestibular cues are so salient, it is possible that for some individuals, these body-based cues override any visual cues provided. Therefore, despite viewing rotations through optic flow, some participants may be unable to spatially update when they are not receiving any body-based rotation cues. By comparing the same task when different amounts of information are available, we can gain insight into the relative weighing of cues during spatial updating. In each of those two tasks we examined whether each experimental condition mentioned above would lead to (1) reduction of the proportion of non-turners and (2) improvement in non-turners' response accuracy in contrast to a control condition where the Starfield task is typically administered in literature (Gramann et al., 2012).

2 EXPERIMENT 1: Replication of Dichotomous Updating Strategy

The purpose of this experiment was to replicate the findings of Gramann et al. (2005) to look for individual differences in strategy in a virtual point-to-origin task. Participants completed the Starfield task, implemented similar to that described by Gramann et al. (2012). The Starfield task was used since it provides pure optic flow without any landmarks. The random dot configuration was chosen instead of a natural scene because it allows us to present optic flow without other environmental information (e.g., the ground or sky). When Gramann et al. first presented the Starfield task, rotations were completed in both the yaw (left/right) and pitch (up/down) planes (2012). The present study uses only yaw rotations since it is the plane that is most familiar to us. Since rotational errors can accumulate, all trials contained only one rotation.

While Gramann focused on categorization, one should also examine the extent of strategy selection for a particular participant. While different cut-offs can be used for turner or non-turner categorization, not all participants are 100% consistent in their strategy selection between trials. It is also important to define different sources of error. Variable error is an individual's consistency in pointing response for a given turn direction. Constant error is the amount of deviation from the theoretically predicted correct answer based on the travel direction. In the Starfield task, the true correct answer is what the turners would make. For non-turners, the theoretically predicted correct answer - if it is assumed that non-turners do not update their heading - is of the same magnitude but opposite in direction across the midline.

2.1 Methodology

2.1.1 Participants

Forty undergraduate participants recruited from McMaster University completed the study and received course credit for their participation. All participants reported normal or corrected-to-normal vision. Their ages ranged from 18–23 (M=18.33). Two participants were excluded from analyses as they exhibited direction reversals during the control trials (N=38). This study was approved by the McMaster Research Ethics Board.

2.1.2 Materials and Procedure

Participants were seated in front of a computer monitor. Participants viewed motion simulated through optic flow using a white dot cloud. Each trial contained three segments: a straight motion, a yaw rotation/translation combination, and another straight segment. Following the motion, a dart (homing vector) appeared with the tip pointing towards the participant. Participants were told to use the left and right arrow keys to rotate the tip of the dart to point towards their origin location. Following the dart rotation, participants pressed the spacebar to begin the next trial. Prior to the experimental phase, participants were given three practice trials in which there was no rotation. Participants completed 90 total trials during the experimental phase, with 18 being control trials (no rotation). During the control trial, a correct response would be to press the spacebar without any dart rotation, as the starting location is directly behind the participant. Each trial contained one yaw turn (left or right). Task difficulty was varied through the eccentricity of the turn (25, 50, 75, 90 degrees).

2.1.3 Categorization

Responses were measured on a per-trial basis. To designate a trial as having a turner response, the participant would have to point the dart in the same direction as the rotation of the turn angle during the trial. Therefore, if the trial contained a right turn (+) and the individual also pointed the homing vector towards the right, it would be categorized as a turner response trial. If the individual exhibited a left-right reversal on a trial, it would be categorized as a non-turner response trial (Figure 1).

To categorize individuals into turners or non-turners, participants had to respond consistently with one strategy on ≥75% of rotation trials (ignoring the control trials). Therefore, participants would have to respond with a consistent strategy for at least 44 turn trials. Individuals who demonstrated inconsistent responses were categorized as switchers and subsequently removed from analyses, as they appeared not to have a consistent preference for a given spatial reference frame.

2.1.4 Measures

Per-trial and total response time as well as the angle of each dart response were recorded. To compare the degree of error between turners and non-turners, the analogous correct response for non-turners was defined as the angle magnitude a turner would make, but opposite in direction. For example, for a 25-degree left turn, a correct response for a turner is -12.8 degrees, while the analogous correct answer for a non-turner is +12.8 degrees. Therefore, measures of error are calculated using the two potential "correct" pointing angles.

Since the correct answer for each trial was determined by the participant's pointing direction, error was calculated relative to participant strategy categorization. Error was calculated in three ways. For each pointing response, we can obtain a measure of absolute error, signed error, or variable error. Absolute error is the absolute magnitude difference between an individual's pointing response and their respective correct answer. Signed error takes into account the direction as well as magnitude of error, with positive values signifying an overestimation of angle while negative values signified an underestimation. Finally, variable error is the standard deviation of participant response angles for a given turn angle.

Mixed-model ANOVAs were conducted with turn angle as the within-participants factor and strategy categorization as the between-participants factor. Mauchly's tests of sphericity were conducted on all repeated-measures variables and adjusted p-values were reported using Greenhouse-Geiser corrections. All post-hoc comparisons used Tukey-HSD adjusted p-values. Data from experiment 1 was also used as the control group for subsequent experiments (2a and 2b).

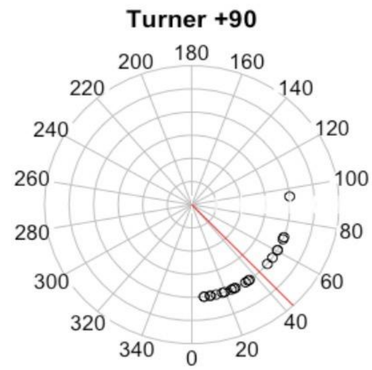

Figure 1. *Average participant pointing responses for a 90-degree right turn. Participants can be grouped as responding either to the left or right of the midline. The red lines represent the two respective "correct" answers for* ***a)*** *turners and* ***b)*** *non-turners*

2.2 Results

2.2.1 Strategy Categorization

Participants were categorized as turners, non-turners, or switchers based on the percentage of total turn trials they would respond with using a given strategy. However, participants differed in their strategy consistency (Figure 2). A 2-sample test for equality found no significant differences between proportions at the 60% or 75% cut-off levels, and thus the 75% level was used for the remainder of the analyses. A 3-sample test for equality of proportions was conducted across strategy groups and revealed a significant increase in the number of switchers across categorization cut-offs. The proportion of turners and non-turners did not significantly differ, meaning that the significant increase of switchers was likely driven by changes in both the proportion of turners and non-turners.

2.2.2 Absolute, Signed, and Variable Error

Absolute error is defined as the average of the absolute difference between an individual's pointing response and the correct answer for their given strategy. A mixed-measures ANOVA revealed a significant main effect of turn angle ($F(3,105) = 45.0$, $p<0.001$). However, there were no strategy differences, with marginals means being 14.23 (SD=11.22) and 14.22 (SD=9.54) for turners and non-turners, respectively.

Signed error takes into consideration the magnitude and direction of error made across trials and was averaged across participants for each angle magnitude. A mixed-measures ANOVA revealed a significant main effect of turn angle ($F(3,105) = 5.5$, $=0.002$), with both turners and non-turners tending to under-estimate turn angle magnitudes. The average signed error was -3.04 degrees (SD=16.6) for non-turners and -4.86 degrees (SD=17.6) for turners.

Variability in pointing responses was averaged for each participant. Left and right turns were compiled for each angle to measure effects of angle magnitude. A mixed-measures ANOVA revealed significant main effects of turn angle ($F(3,105) = 3.19$, $p=0.027$) and strategy ($F(1,35) = 7.31$, $p=0.010$) qualified by a turn angle by strategy interaction ($F(3,105) = 18.8$, $p<0.001$). While non-turners vary greatly in their response variability across turn angles, turners' variation in responses are comparable across turning angles.

2.2.3 Reaction Time (RT)

Average trial RT was compiled for turners and non-turners. Trials were separated into three blocks and average RT was calculated for each block to look for differences in time-course across the experiment. Each block contained 30 trials and contained an equal number of each turn angle type. A mixed-measures ANOVA was conducted and found significant main effects of block ($F(2,66) = 21.7$, $p<0.001$) and strategy ($F(1,33) = 6.80$, $p=0.014$). The block by strategy interaction was not significant. Non-turners were significantly faster than turners for each block, and overall reaction time decreased across the time course of the experiment.

2.3 Discussion

We replicated the findings by Gramann et al. (2005) and Gramann et al. (2012) in that the point to origin task effectively produced two distinct groups of participants with opposite pointing responses. Some participants pointed in the correct direction back to origin (turners), suggestive of successful spatial updating, while others did not (non-turners). A small subset of participants did not exhibit a consistent pointing response and were therefore categorized as switchers.

Like Gramann et al. (2012), we found a difference in pointing response variability across turn angle. Non-turners had greater variability for larger turn angles while turners' variability did not significantly differ. We also found main effects of turn angle for both absolute and signed error. However, in contrast to the Gramann et al. (2012) findings, there was no effect of strategy on signed error, both groups tended to under-estimate all angle magnitudes. Finally, while Gramann et al. (2012) failed to find a significant effect of strategy across RT, we found that non-turners were faster than turners across the entire experiment, with both groups responding faster over time. The increased RT for turners may be evidence for increased cognitive effort resulting from successful spatial updating. Perhaps turners are taking more time to consider each rotation and fully integrating the cues of each turn.

The Starfield task effectively separated participants into groups based on their dominant pointing response. An interesting question is therefore why there is this disparity in strategy despite all participants viewing the same stimuli. In experiment 2, we explored two effects of cue conflict on turners and non-turners.

3 EXPERIMENT 2: Cue Conflicts in Spatial Updating Via Optic Flow

3.1 Influence of the Stationary Surround (Experiment 2a)

It is typically presumed that the decline in accuracy during virtual spatial updating tasks is solely due to the lack of body-based motion cues (Chance et al., 1999; May, 2004). However, if this were true, all participants would show similar reductions in performance during spatial updating when only visual information is provided. Yet what we find in optic flow motion simulation tasks is that only about half of participants appear to fail to update their headings (e.g., Gramann et al., 2005) . To further challenge this presumption, Riecke et al. (2004) investigated the role of visual cues in real-world spatial updating using peripheral blinders. When participants wore these blinders to limit their peripheral vision in a navigation task, performance declined (Riecke et al., 2004). In this situation, both visual and body-based motion cues were available. Perhaps, then, it is the lack of optic flow in the visual periphery that is causing a performance deficit for the non-turners.

Optic flow is one cue which can be used to estimate one's heading direction (Lappe et al., 1999; Foulkes et al., 2013). Following retinal image stabilization, optic flow is parsed into self-locomotion and object-locomotion components (Rushton et al., 2007; Warren & Rushton, 2007). The self-locomotion components are therefore used to build up representations of relative travel direction and velocity. In desktop VR tasks, the various components of the visual field have conflicting levels of motion. Since participants view simulated motion on a computer monitor, any motion cues provided through optic flow is only available to the participants' central visual field. This central visual motion-information might compete then with stationary peripheral visual information about the environment outside of the computer screen.

One reason some participants appear not to update their heading may be due to the inconsistent visual information between the central and peripheral visual fields. When we are physically travelling, optic flow occurs consistently across the entire visual field. Any other incongruent motion is then parsed as object-locomotion. The limits of presenting the task using a laboratory computer screen are that it forces the optic flow to be restricted to a small part of the participants' central visual field. Perhaps when optic flow is not presented across the entire retina, some participants cannot perceive the motion self-motion correctly. Therefore, instead of sensing that they are travelling, participants may feel as if they are stationary, and watching stars travel past them. It is possible that this conflict may especially affect the non-turner group, thus preventing them from experiencing the simulated rotation and updating their heading.

In Experiment 2a, we tested whether the stationary surround produces any cue interference for the observer. We minimized the external visual information that was available from the laboratory environment. Participants viewed the display through a large circular aperture placed in front of the computer screen. A chin rest was used to ensure that the only visual information would come from inside the aperture. Any conflicting visual information outside the display was thus occluded. Instead of changing the size of the screen itself, the aperture modification was designed to occlude conflicting information instead of altering the field of view. The optic flow was thus restricted to the participants' central visual field.

If the cue conflict from the stationary surround is the only source of information producing interference, the minimization of external visual information would produce successful heading updates in all participants. We therefore would see a much smaller proportion of non-turners in the aperture condition compared to the control condition. Alternatively, non-turners may still be unable to update their headings, but the reduction of cue interference would increase accuracy. Therefore, the second hypothesis is that the aperture condition would reduce the amount of error (i.e., absolute, signed, or variable) for non-turners (and maybe even for turners). Participants may maintain the same strategy but experience less error and variability in their pointing responses.

3.2 Sensorimotor Interference (Experiment 2b)

While optic flow alone is a powerful indicator of one's travel direction and velocity, it may not be sufficient for successful spatial updating in all participants (e.g., Riecke et al., 2007). Another reason non-turners may use this strategy is due to the cue conflict between visual and body-based cues. When proprioceptive cues are missing during movement or rotation, participants may fail to update their heading orientation (Klatzky et al., 1998). This is because the lack of motion information from body-based cues causes greater interference for rotations than translations (Presson & Montello, 1994; Chance et al., 1998). Updating is still possible when imagining rotations (Easton & Sholl, 1995; May, 1996), but it is susceptible to a high degree of error and requires conscious effort.

When visual and body-based cues conflict, participants may experience disorientation and inaccurate responses (Mou & Zhang, 2014). Interestingly, presenting conflicting optic flow information seems to impact an individual's heading but not their position. Adopting a new perspective appears to be less effortful when disorientation occurs (May, 1996).

Visual motion cues presented during the Starfield task conflict with proprioceptive information since the participant's body is not also physically travelling. When the simulated motion is forward (i.e., into the screen), the information from the visually simulated motion and stationary body-based cues are congruent. However, during a simulated left or right turn, sensorimotor interference creates greater conflict, as the rotational information presented visually now conflicts with body-based cues. Since physical cues are more important for rotations than translations, the cue conflict during the rotation may prevent spatial updating.

In Experiment 2b, we wanted to test whether participants were affected by sensorimotor interference. The conflict between visual and body-based cues may explain the decreased performance when spatially updating in virtual reality. We tested the effects of sensorimotor interference using a within-subjects design, where participants experienced three trial types of seating orientations while completing the task. One condition served as the neutral control while in the other two, participants were seated oriented either 90 degrees to the left or the right of the computer monitor, with their heads turned towards the monitor.

If sensorimotor interference accounts for the existence of the non-turner group, we would see a smaller proportion of non-turners in experiment 2b than in experiment 1. In particular, non-turners' body-based cues in Experiment 1 may be more heavily weighted compared to that of turners, thus preventing spatial updating based on optic flow. Since the body and head orientations are incongruent for two-thirds of the trials, this may decrease the weighting of the body-based cues for non-turners because it is no longer perceived as a reliable source of heading information, allowing them to perform as turners.

Alternatively, sensorimotor interference would affect accuracy for both turners and non-turners instead of affecting strategy selection. Reducing this interference could decrease the relative weighting of body-based cues, thereby decreasing the amount of error (i.e. constant and variable) for both groups. The reduction in error would also be greater for non-turners if they rely more heavily on body-based cues.

Finally, it is possible that the body rotations will increase confusion and that the weighting of body-based cues cannot be altered. This may result in differences between the three seating orientations. For example, when the participant is seated facing towards the right, a visually simulated right turn would produce the highest amount of heading congruency between visual and body-based cues. In contrast, a left turn would produce the greatest amount of cue conflict. We would then see the degree of error for left and right rotations vary depending on seating orientation.

3.3 Methodology

3.3.1 Participants

Participants recruited from McMaster University completed the study and received course credit for their participation. All participants had self-reported normal or corrected-to-normal vision. A total of 49 participants (32 female) completed experiment 2a and 60 participants (39 female) completed experiment 2b. One participant was removed from experiment 2b analyses as they exhibited direction reversals in the control trials (N=59). Ages ranged from 18–24 (M=18.77). This study was approved by the McMaster Research Ethics Board.

3.3.2 Materials

Participants were either seated in front of a computer monitor or in front of the same monitor with a black circular aperture placed in front of it (diameter=12"). The aperture was placed in a manner to reduce visibility of external stimuli such as the computer monitor frame. In experiment 2a, a chin rest was used to ensure participants remained 60 cm away from the monitor throughout the duration of the experiment. In 2b, chair rotations were completed so their heads were maintained at a distance of 60 cm away from the monitor.

3.3.3 Procedure 2a – Aperture Experiment

Participants completed the same Starfield task as experiment 1, beginning with three practice trials followed by 90 experimental trials. Task difficulty was varied through the eccentricity of the turn (25, 50, 75, 90 degrees). The only difference from experiment 1 was that participants viewed the experiment through the circular aperture. Data from experiment 1 served as the control group.

3.3.4 Procedure 2b – Body Orientation Experiment

Participants underwent three within-subject conditions of the Starfield task. The stimuli were identical to that in Experiment 1. In condition (N), the participant was seated neutrally, or facing towards the screen, which is the same seating orientations as Experiments 1 and 2a. Alternatively, the participant was seated at an orientation of 90 degrees to the right (condition R) or 90 degrees to the left (condition L) of midline. The left and right body rotation conditions were counterbalanced with the neutral condition always second. Each condition had a total of 60 trials: 24 left rotations, 24 right rotations, and 12 control trials with no rotation. Each participant experienced each condition once, for a total of 180 trials. Task difficulty was varied through the eccentricity of the turn (25, 50, 75, 90 degrees); the 90-degree physical rotation encompassed the greatest potential heading rotation. Each participant held a keyboard to make their responses and were instructed to keep their back and shoulders against the chair with their head turned to face the monitor for the duration of the task. Following each condition, participants were allowed a brief rest while the chair was rotated. Again, data from experiment 1 served as the control group.

3.3.5 Analyses

All of the following analyses compared data across three experiments (i.e., Experiment 1, Experiment 2b, Experiment 2b). Data from Experiment 1 served as a control group, while Experiments 2a and 2b served as the experimental groups. Participants were removed as outliers if they were two or more standard deviations away from the mean for all angle magnitudes.

Mixed-model ANOVAs were conducted with turn angle as the within-participants factor and strategy (i.e., turner versus non-turner) and experiment (i.e., Experiment 1, 2a, 2b) as the between-participants factors. Mauchly's tests of sphericity were conducted on all repeated-measures variables and adjusted p-values were reported using Greenhouse-Geiser corrections. All post-hoc comparisons used Tukey-HSD adjusted p-values with an alpha of 0.05. All participants categorized as switchers were removed from analyses.

3.4 Results

3.4.1 Proportions of Turner and Non-Turners

Participants were classified as turners if they displayed turning responses for $\geq$75% of trials, or as non-turners if they displayed non-turning responses for $\geq$75% of trials. All other participants were categorized as switchers. One participant, who demonstrated a direction reversal during control trials, rotating the dart into the screen instead of towards the participant, was removed from analyses since they seemed to not understand the task. As was done in Experiment 1, switchers were removed from further analyses.

Figure 2 shows the relative proportions of participants categorized as each strategy using three different consistency values as cut-offs. Independent sample t-tests for equality of proportions were conducted to look for differences in categorization between the three experiments as well as differences in strategy proportions across three arbitrary cut-offs.

Values are summarized in Table 1. There were no differences in strategy proportions at the 60 % or 75% cut-offs. As seen in Figure 2, the proportion of participants between the control and body orientation experiments were almost identical, with about half of participants categorized as turners and about 40% categorized as non-turners. In the aperture experiment, we see 36.7% of participants categorized as turners and 53.1% as non-turners. However, this apparent increase in the number of non-turners was non-significant.

In Experiment 2b, the majority of participants (79.7%) maintained the same strategy across all three viewing conditions. Twenty-seven participants were consistently categorized as turners while 20 participants were categorized as non-turners. The remaining twelve participants switched strategies between conditions. For the remainder of analyses, only participants who were consistently turners or non-turners across all three orientation conditions were used for analyses.

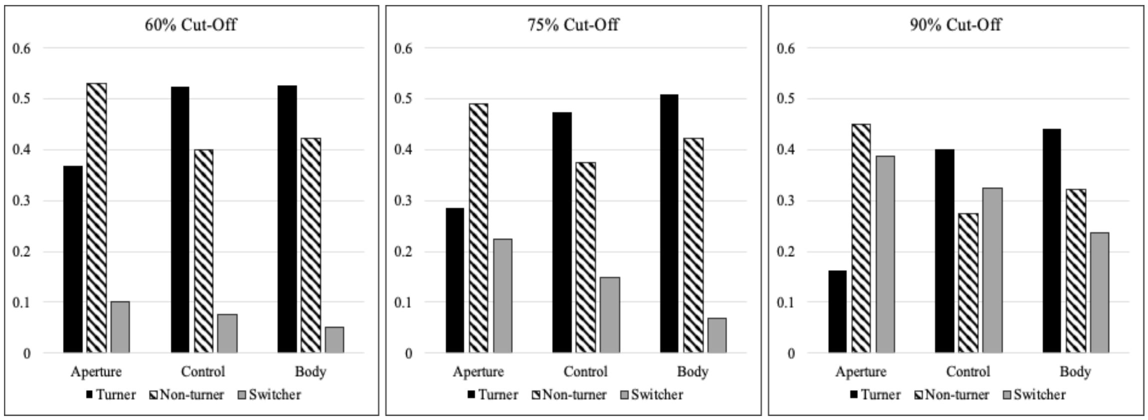

Figure 2. *Comparison of participant strategy categorization proportions between experiments.*

Turners		**75% Cut-Off**			**90% Cut-Off**		
		Control	Aperture	Body	Control	Aperture	Body
60% Cut-Off	Control				N.S.	–	–
	Aperture		N.S.		–	*	–
	Body				–	–	N.S.
75% Cut-Off	Control	–	N.S.	N.S.			
	Aperture	–	–	*		N.S.	
	Body	–	–	–			
Switchers		75% Cut-Off			90% Cut-Off		
		Control	Aperture	Body	Control	Aperture	Body
60% Cut-Off	Control				*	–	–
	Aperture		N.S.		–	**	–
	Body				–	–	**
75% Cut-Off	Control	–	N.S.	N.S.			
	Aperture	–	–	*		N.S.	
	Body	–	–	–			

Table 1. *A summary of independent sample t-tests for equality of proportions. Significant values are labeled as *<0.05 and **<0.01. There were no significant differences at the 60% cut-off. There were also no significant differences in the proportion of non-turners.*

3.4.2 Strategy Consistency

Since categorization is classified using a cut-off, we can define participants' tendency towards a certain strategy by the proportion of trials they used that specific strategy (Figure 3). A factorial ANOVA was conducted and revealed a main effect of experiment ($F(2,122) = 8.67$, $p<0.001$), quantified by a significant strategy by experiment interaction ($F(2,122) = 3.15$, $p=0.046$). The simple main effect of experiment was only significant for turners ($p<0.001$). Post-hoc tests of the strategy by experiment interaction confirmed that turners in the aperture experiment were less consistent in their strategy choice than turners in the control ($p=0.040$) and body orientation experiments ($p<0.001$). In contrast, turners and non-turners' strategy consistency did not significantly differ in the body orientation (Exp. 2b) ($p=0.997$) and control experiments (Exp. 1) ($p=0.999$).

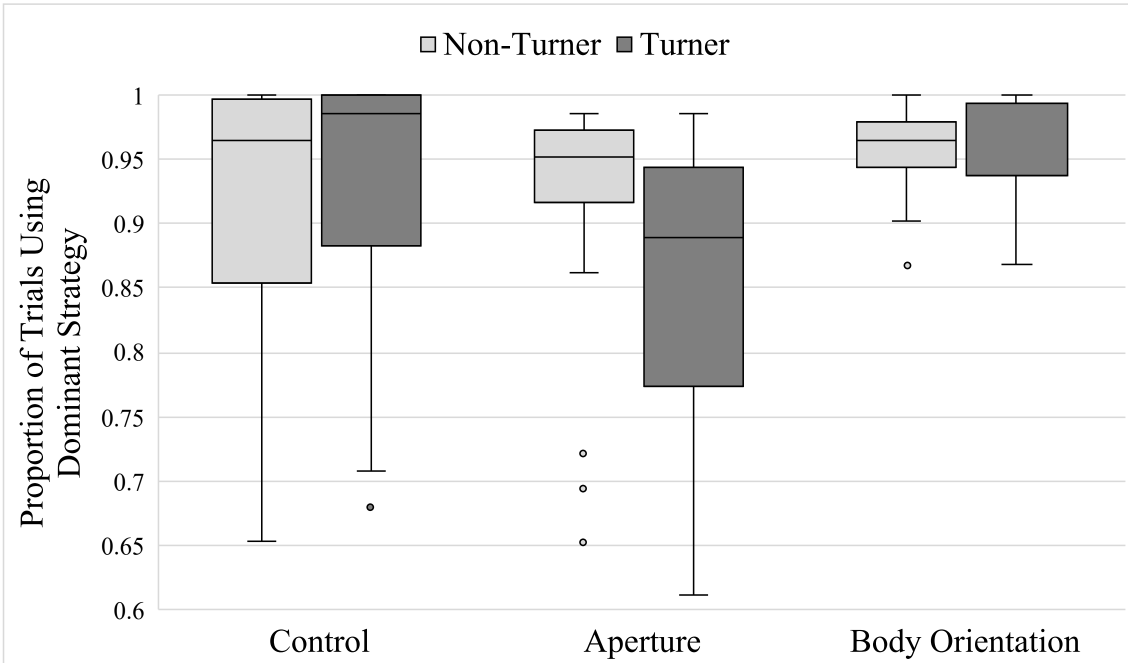

Figure 3. *Proportion of trials that participants use their dominant strategy across experiments with median lines visible. The whiskers and outliers show the distribution of consistency among participants.*

3.4.3 Effect of Viewing Conditions on Heading Response

The heading response for each turn angle was averaged across participants between the three experiments, separated by strategy (Figure 4). A mixed-measures ANOVA using absolute values for average heading responses found a significant main effect of turn angle ($F(8,967) = 84.7$, $p<0.001$) quantified by the strategy by turn angle interaction ($F(8,967) = 278.7$, $p<0.001$). Both turners and non-turners across all three experiments displayed larger pointing responses for larger turn angle magnitudes. The main effects of condition and strategy were not significant. There were also no significant differences in mean heading response between participants in the body and control conditions.

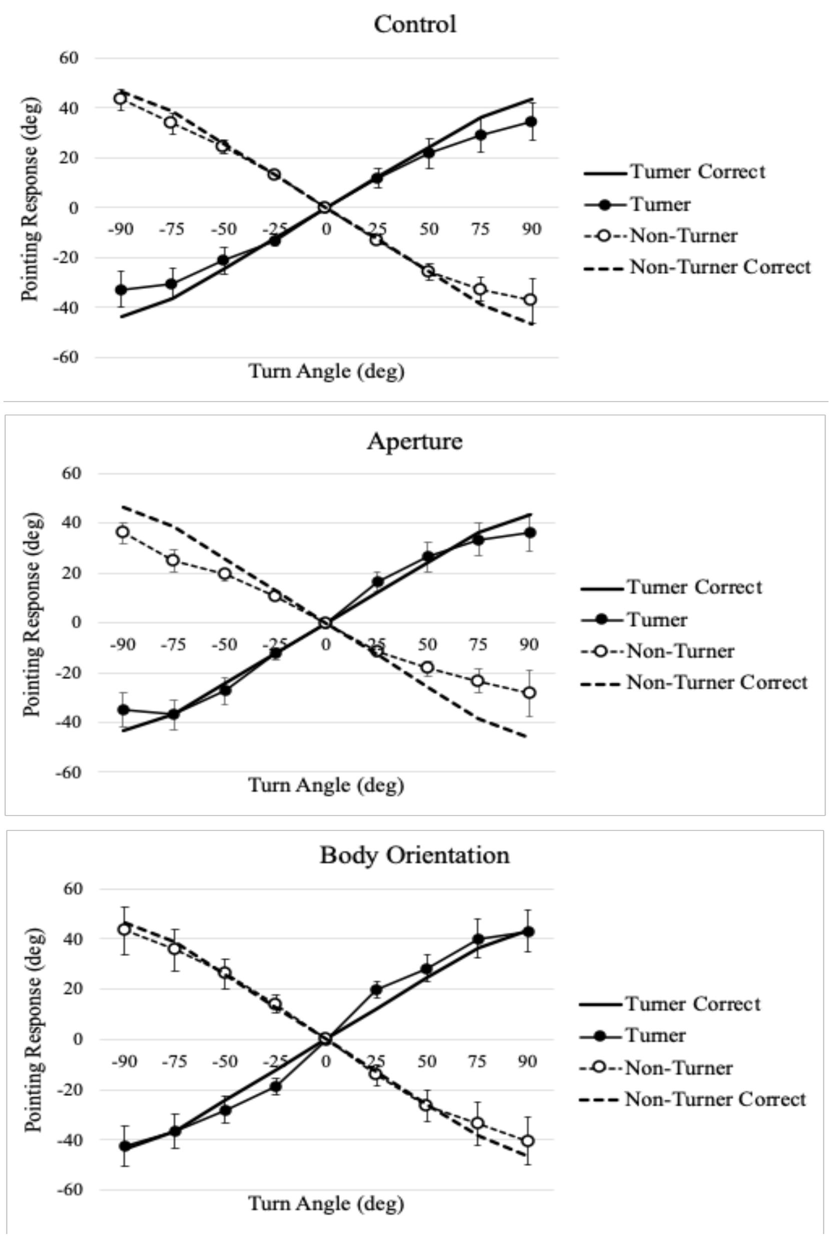

Figure 4. *Average heading response is plotted for each angle separated by strategy. The correct homing response for turners (solid line) and non-turners (dotted line) is plotted against average participant responses.*

3.4.4 Absolute Error

A mixed-measures ANOVA for absolute error using strategy and experiment as the between-participants factors and eccentricity as the within-participants factor found a main effect of turn angle ($F(3,366)=70.73$, $p<0.001$) (Figure 5a). The turn angle by strategy interaction approached significance ($p=0.058$). Turners tended to make smaller degrees of absolute error than non-turners.

We were particularly interested in whether the aperture or body orientation experiments produced any significant differences from the control. A mixed-measures ANOVA of absolute error comparing the body orientation and control experiments revealed a significant main effect of turn angle ($F(3,240)=56.68$, $p<0.001$) and the ANOVA comparing the aperture and control experiments revealed a significant main effect of turn angle as well ($F(3,231)=50.20$, $p<0.001$) (Figure 5a).

3.4.5 Signed Error

A mixed-measures ANOVA for signed error (2x3x4) using strategy and experiment as the between-participants factors and eccentricity as the within-participants factor found a main effect of turn angle ($F(3,366)=19.09$, $p<0.001$) (Figure 5b). As seen in Figure 5b, all non-turner groups had a tendency to under-estimate angle magnitudes across all turn angles.

Again, we were interested in between-experiment effects between each manipulation and the control experiment. A mixed-measures ANOVA of signed error comparing the body and control experiments found a significant main effect of turn angle ($F(3,240)=11.30$, $p<0.001$). A mixed-measures ANOVA of signed error comparing the aperture and control experiments confirmed a main effect of turn angle as well ($F(3,231)=13.06$, $p<0.001$). Post-hoc tests of signed error found that a main effect of strategy was marginally significant for the aperture experiment (Exp. 2a) ($p=0.072$).

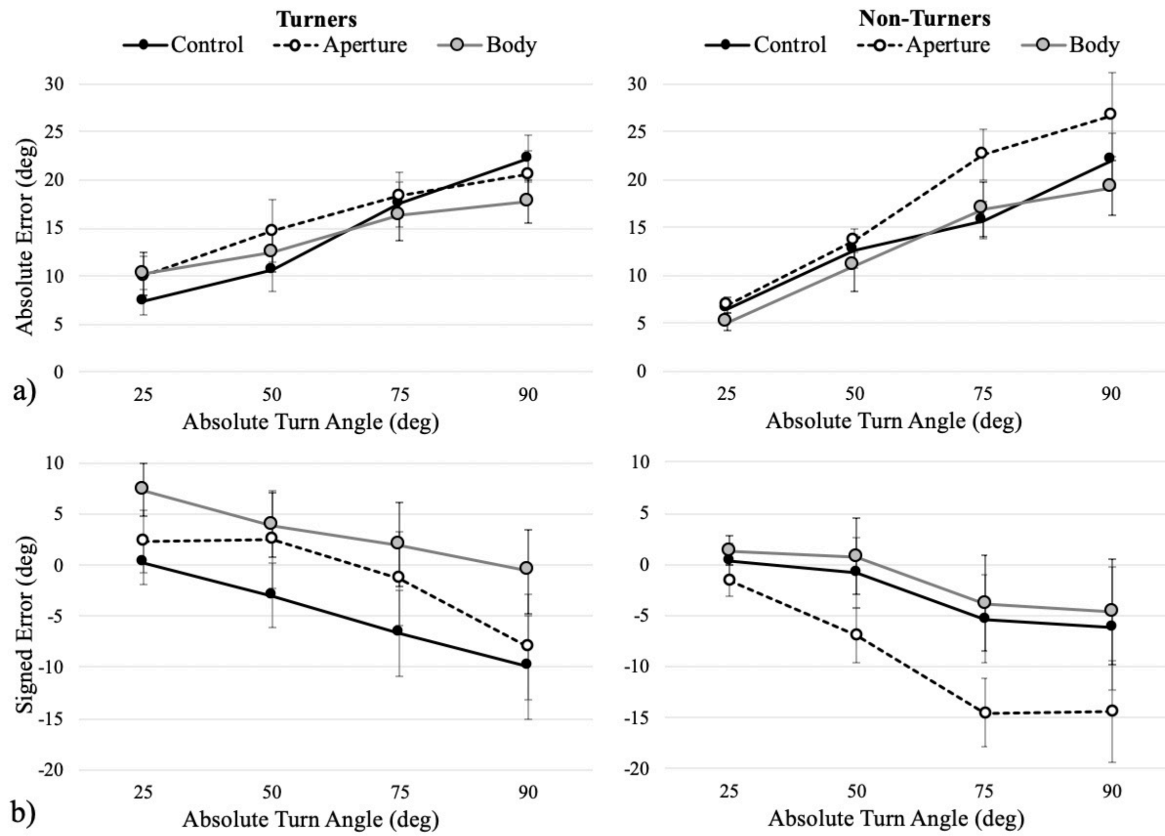

Figure 5. *Average absolute **(a)** and signed error **(b)** was calculated for turners and non-turners. For signed error, values above zero represent a tendency to over-estimate the angle magnitude, while values below zero represent a tendency to under-estimate the angle.*

3.4.6 Variable Error

The standard deviation for each participants' responses was calculated across each angle magnitude and averaged as a measure of variable error (Figure 6). Two participants from the non-turner group and one from the turner group in the aperture experiment were removed from analyses as outliers. A mixed-measures ANOVA comparing across all three conditions revealed a significant main effect of turn angle ($F(3,357) = 60.2$, $p<0.001$, $\eta^2 = 0.160$). Participants tend to have larger variability in their responses for larger angle magnitudes. The main effect of strategy was also marginally significant ($p=0.064$). Post-hoc analyses confirmed that the simple main effect of strategy was significant for the control group ($p=0.010$) and marginally significant for the body orientation group ($p=0.063$). Turners and non-turners in the aperture group were not statistically different ($p=0.255$). However, Figure 6b does show a distinct pattern in the aperture experiment where turners seem to display larger variations in pointing responses than non-turners, which is opposite to the pattern found in the control and body orientation experiments.

The experiment by strategy interaction was significant ($F(2,119) = 3.79$, $p=0.025$, $\eta^2 = 0.058$) while the turn angle by strategy interaction was marginally significant following sphericity correction ($p=0.068$). As seen in Figure 6b, turners and non-turners in the aperture condition experienced similar patterns of variable error, with greater variation for larger turn angles. In the control and body orientation conditions, non-turners displayed more variation in pointing responses for a given angle than turners, who did not significantly vary in their variable error based on angle magnitude. However, these were not statistically significant following pair-wise comparisons.

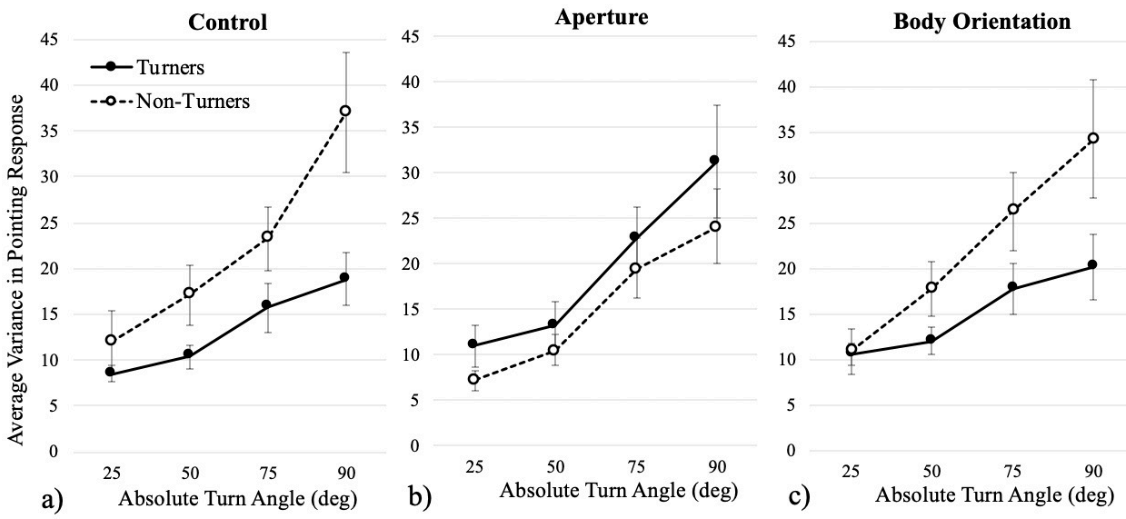

Figure 6. *Variation in pointing response for each experiment separated by turners and non-turners. The average standard deviation per turn angle was plotted for each participant and averaged across strategy groups.*

3.4.7 Reaction Times (RT)

The mean RT per trial across all participants was 3.60 seconds (SD=1.79s). The average reaction time was 4.10s for turners and 3.11s for non-turners. A factorial ANOVA revealed a significant condition by strategy interaction ($F(1,77) = 6.16$, p=0.015, η^2=0.058) and main effects of condition ($F(1,77) = 14.63$, p<0.001, η^2=0.138) and strategy ($F(1,77)$ = 8.17, p=0.005, η^2=0.077). The simple main effect of condition was significant for turners ($F(1,77) = 19.68$, p<0.001) but not for non-turners.

RT for each participant were averaged across three time sections of trials (i.e., 0-30, 31-60, 61-90) (Figure 7). A mixed-measures ANOVA was conducted comparing the aperture and control conditions and revealed a significant main effect of time ($F(2,156)$ = 54.3, p<0.001, η^2=0.107), condition ($F(1,78) = 5.63$, p=0.020, η^2 =0.061), and strategy ($F(1,78) = 6.17$, p=0.015, η^2 =0.067). No two or three-way interactions were significant.

A mixed-measures ANOVA using turn angle as the within-participants factor instead revealed significant main effects of turn ($F(3,366) = 54.06$, p<0.001, η^2 =0.055), condition ($F(2,122) = 7.34$, p<0.001, η^2 =0.096), and strategy ($F(1,122) = 6.46$, p=0.012, η^2 =0.042). These were quantified by significant interactions between turn angle and strategy ($F(3,366) = 5.21$, p=0.004, η^2 =0.005), condition and strategy ($F(2,122) = 4.52$, p=0.013, η^2 =0.059), and the three-way interaction ($F(6,366) = 2.70$, p=0.024, η^2 =0.005).

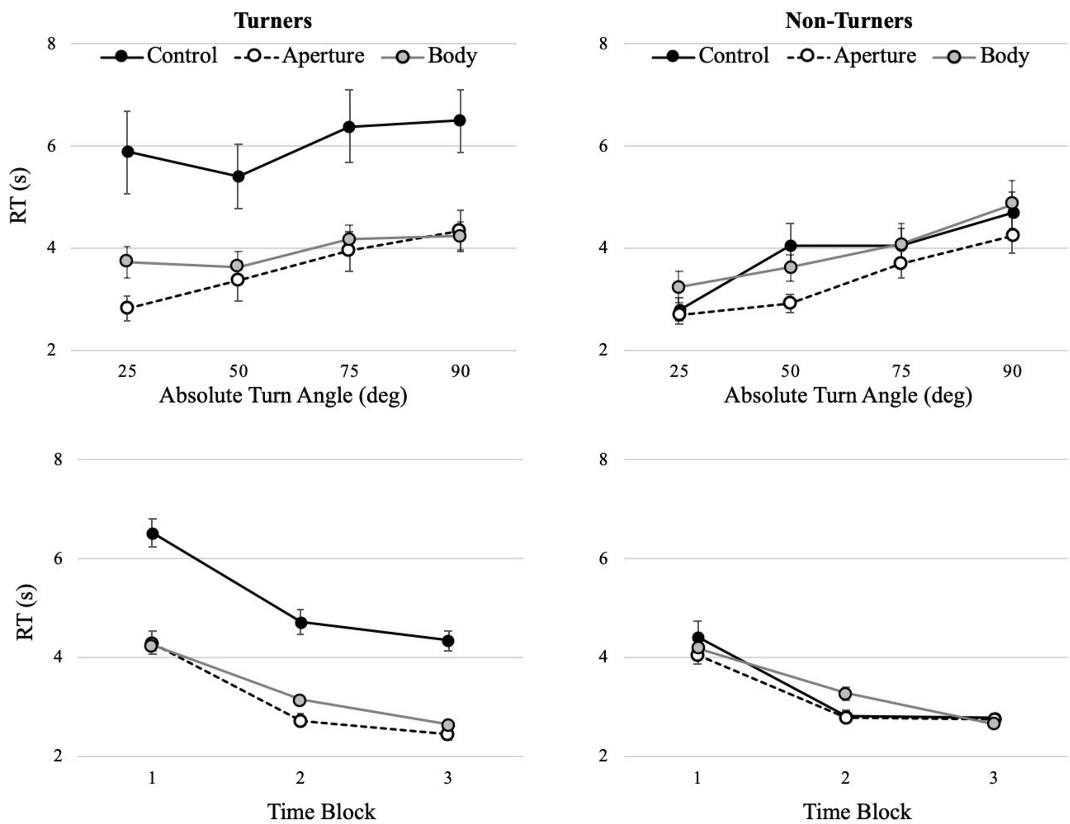

Figure 7. *Reaction time is separated into three time blocks for the aperture and control conditions. The aperture and control conditions saw a significantly slower response for turners compared to non-turners. This response was not found in participants in the body orientation experiment.*

3.4.8 Additional Analyses – Body Orientation (2b)

During the first condition (counterbalanced facing left or right across participants), 5.4% of participants were categorized as switchers, while only 3.3% of participants were switchers during the final condition of the task (Figure 8). For participants who were categorized as the same strategy across conditions, a repeated-measures ANOVA revealed a significant main effect of condition number ($F(2,90) = 5.80$, $p=0.009$) but not strategy. The Greenhouse-Geiser corrected p-value was reported. Both turners and non-turners become more consistent in their strategy across conditions.

A mixed-measures ANOVA was conducted with turn angle as the within-participants factor and strategy and seating orientation as the between-participants factors. The ANOVA revealed a main effect of turn angle ($F(3,405) = 85.7$, $p<0.001$) quantified by a turn by strategy interaction ($F(3,405) = 8.52$, $p<0.001$). Post-hoc tests confirmed that non-turners made larger errors than turners at the 90-degree angle magnitude ($p=0.039$). There were no significant differences in signed error across the three conditions (Figure 9). Mixed-model ANOVAs were conducted with turn angle as the within-participants factor and either condition number or viewing direction as the between-participants factor. No significant main effects or interactions were found.

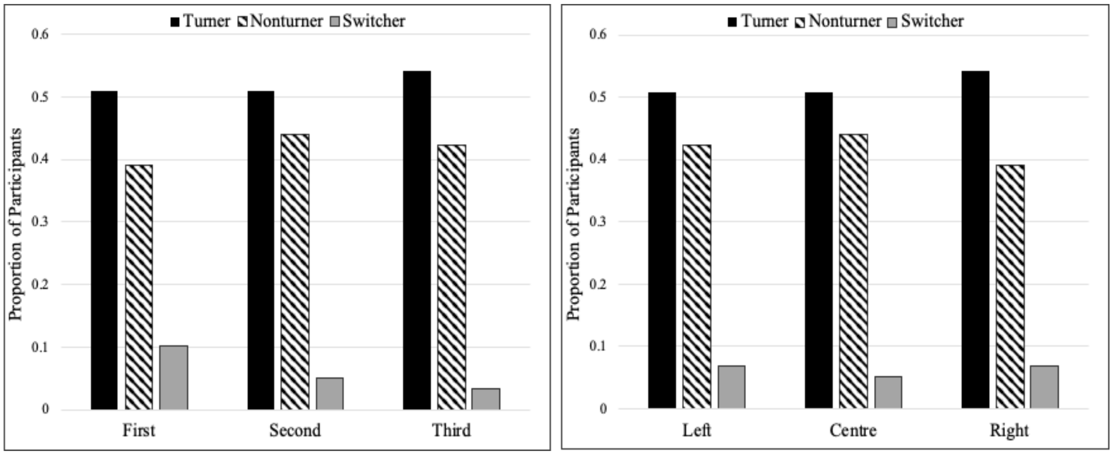

***Figure 8**. Strategy categorization across three trial types in the body orientation experiment. The left, centre, and right viewing conditions were counterbalanced across participants. **A)** Proportions were corrected for the participants' respective first viewing trial type, second, and third. The number of switchers decreased across trial types**.** **B)** Proportions plotted based on orientation. There are no significant differences in strategy across the three viewing orientations.*

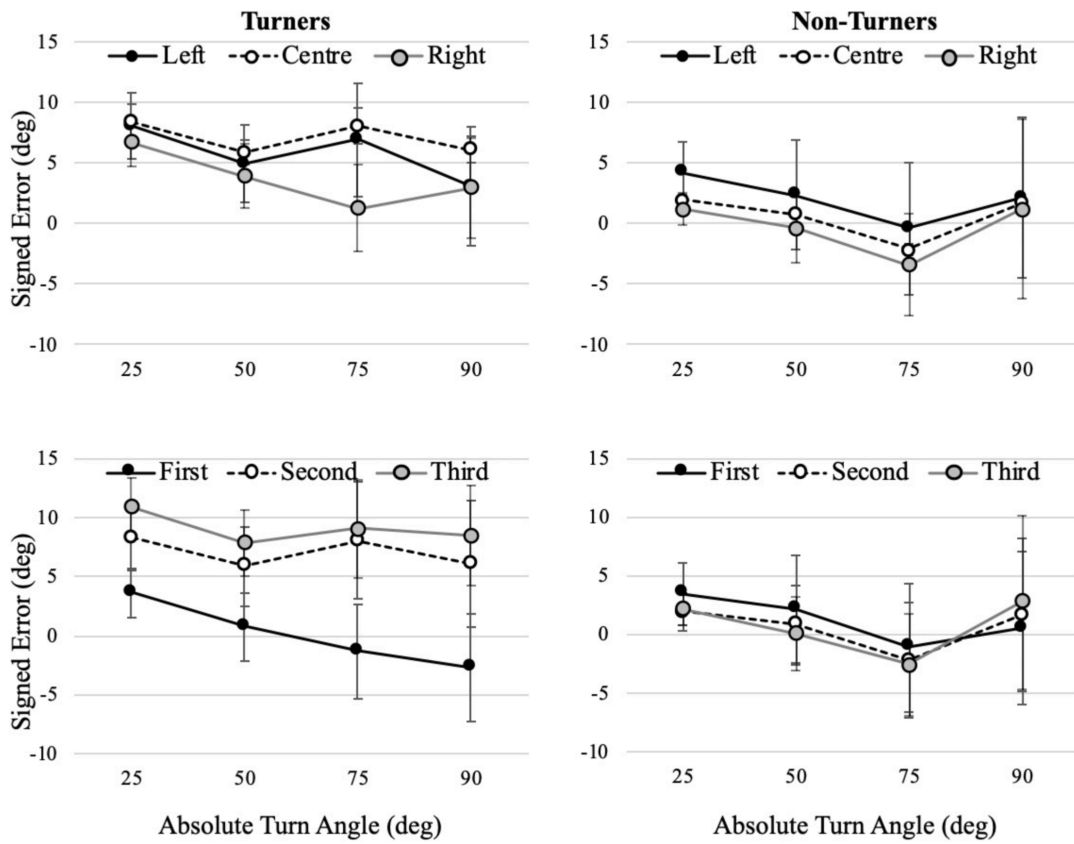

Figure 9. *Signed error separated by the three trial types of experiment 2b. Since orientation was counterbalanced, the two sets of graphs show error by **a)** seating orientation and **b)** trial type order.*

3.5 Discussion

3.5.1 Measures of Strategy Consistency

While it is clear that participants seem to prefer one of two distinct strategies, the designation of participants into these two categories relies on somewhat arbitrary measures. Most groups (e.g., Gramann et al., 2012, Riecke et al., 2008) use percent cut-offs as a way to separate participants into turners or non-turners. We see from Figure 2 (pg. 32) that the relative proportions of participants in each category vary based on the value we choose for this cut-off. When comparing proportions between 60% and 75% cut-offs, there were no significant changes between the experiments. At the 90% cut-off, we see a huge increase in the number of "switchers" across all experiments, and the relative proportions for each experiment now look very different. Therefore, we need more precise measures of strategy differences to truly look at individual differences in spatial updating.

One way we can accomplish this is by looking at an individual's tendency towards a particular strategy. Since each trial is categorized as a turner or non-turner trial based on pointing direction, we can calculate an overall proportion of trials for each strategy. When looking strategy consistency, we can see that participants' averages vary across experiments (Figure 3, pg. 35). In the body orientation and control experiments, turners and non-turners exhibited similar levels of strategy consistency. However, turners in the aperture experiment had less strategy consistency than non-turners. It appears that occluding peripheral vision caused only the turners to question their strategy, while manipulating body orientation may have caused both turners and non-turners to favour their strategy more strongly. One explanation is that manipulating body orientation reduced the weighting of body-based cues, decreasing the amount of confusion and strategy switching in all participants.

3.5.2 Error Measurements

Within each strategy group, participants also differed in terms of their constant (i.e., absolute error and signed error) and variable error (variance of responses within individuals) across experiments. Since spatial updating is considerably more difficult without vestibular cues, we naturally expect greater amounts of error for larger turn angles (Klatzky, 1998). This is also in line with studies of sensorimotor interference, which support that larger simulated turn angles would produce more interference with the current body's heading orientation (May, 1996). When comparing absolute error across experiments, turners exhibited comparable levels of error across experiments (Figure 5, pg. 40). However, non-turners in the aperture group appeared to have greater degrees of error than the control or body orientation groups.

The pattern of turner responses in the aperture condition is what we expect for participants who understood the task. Plots of signed error revealed a pattern of over-estimation for small angles and under-estimation for larger angels, which is also found in other studies (e.g., Gramann et al., 2012). Although non-significant, non-turners in the aperture condition appeared to perform worse than those in the control condition, showing a pattern of larger errors and a tendency to under-estimate all angles. However, sign error also has another important implication, in that a tendency to continuously under-estimate angles means that participants are starting to behave more like those in the other strategy. Therefore, the pattern of under-estimation for non-turners in the aperture group may signify a tendency for them to begin behaving like turners.

When measuring variable error, Experiment 1 revealed a main effect of strategy for those in the control condition. Non-turners experienced greater variability in pointing responses for larger angle magnitudes, while turners' variability remained relatively consistent. This consistency suggests that turners' heading updates are less affected by angle magnitude. This pattern was also found in the body orientation experiment (Figure 6, pg. 43). However, for the aperture condition, turners also exhibited this effect of turn angle. Although non-significant, it appears that the non-turners now have less variable error, becoming more like turners in the control group. This provides another piece of evidence that the aperture non-turners are now behaving more like turners.

3.5.3 Reaction Time (RT)

We expect all participants to respond faster across the course of the experiment. Interestingly, turners tend to be slower in their RT than non-turners. While all groups get faster over time, turners consistently respond slower than non-turners, with those in the aperture condition responding faster than those in the control condition. It is possible that this increase in response time is reflective of increased cognitive effort in imagining correct heading updates, translating into accuracy differences.

Since participants make responses by rotating a dart on-screen, we naturally expect to see a main effect of turn angle in RT, with higher RTs for larger angle magnitudes. This effect was seen in non-turner averages across all three experiments, but only in the aperture experiment for turners. Surprisingly, we do not see this effect in turners for the control group or body orientation group, but rather there are no significant differences in RT for turn angle (Figure 7, pg. 45). This would only occur if participants were spending longer thinking about smaller angles to make up for the time required to rotate the dart.

3.5.4 Changes Across Body Orientation

Unlike other iterations of point-to-origin tasks, Experiment 2b allowed us to see changes in strategy over time. Each participant completed the Starfield task three separate times in three different seating orientations. Although each condition can be categorized as either favouring the turner or non-turner strategy overall, analyses of the proportion of turner trials in each condition also revealed changes. For participants who were consistently categorized as turners or non-turners across all three conditions, there was a significant increase in the percentage of trials using their preferred strategy across conditions. Thus, they became more consistent in their strategy over time. Furthermore, participants who switched strategy across the conditions were likely to end up as turners in the final condition.

4 GENERAL DISCUSSION

It is clear that participants perceive and interpret the rotation in different ways. Individuals experiencing a left turn trial will consistently point in either the left (turners) or right (non-turners) directions back to origin. Furthermore, participants can correctly interpret the optic flow patterns to discriminate between various magnitudes of turning angles, since all groups display a positive correlation between turn angle and dart response angle. This supports the findings from Gramann, Sharkawy, and Deubel (2009) in that individuals who prefer different frames of reference do not differ in the encoding of motion.

4.1 Central vs. Peripheral Cue Conflict

In Experiment 2a, we measured whether the occlusion of the stationary surround could impact the proportion of turners and non-turners. Participants viewed the task through a black circular tunnel that blocked peripheral visual information. The proportion of turners, non-turners, and switchers were similar to those found in Experiment 1, suggesting that the existence of the non-turner group is likely not due to the cue conflict between the central and peripheral visual fields. Interestingly, however, occlusion of the periphery visual information increased the variable error for only the turners while increasing absolute error and decreasing variable error for non-turners.

Previous findings suggest that successful spatial updating can be generated through optic flow alone. However, when the peripheral environment was occluded, turners experienced more pointing error than those in the control condition. One potential explanation is that the turners were more likely to use the stationary environment as a reference point to compare against the magnitude of the simulated turn. During travel, optic flow allows us to gather information about velocity and direction of our motion by parsing object-locomotion and self-locomotion (Warren & Rushton, 2007).

In a PTO experiment, we expect participants to correctly parse the motion on screen as self-locomotion and the surrounding stationary environment a lack of object-locomotion. Alternatively, we can process the stationary environment as an extension of self-movement. For example, when we are driving a car, the dashboard and steering wheel are not in motion. This stationary aspect of the environment is expected because of the nature of our self-motion. We thus expect to only see optic flow in one part of our visual field. Perhaps this illusion is stronger for turners than non-turners and they can therefore successfully update with only central optic flow. When we occluded the stationary surround, that information was no longer available, which may have hindered turners' ability to effectively process the turns.

4.2 Visual vs. Body-Based Cue Conflict

Experiment 2b tested whether sensorimotor interference had any effect on strategy selection or performance (i.e., accuracy and/or consistency). Sensorimotor interference has a greater effect on rotations than translations (May, 2004). The Starfield task thus uses a rotation/translation combination to see if participants can correctly interpret the turn angle despite the cue conflicts. The methods of this study allowed us to compare turners and non-turners across the entire experiment as well as across each condition, looking for differences in performance at different body orientations.

In the control study (Experiment 1), non-turners made larger absolute error magnitudes for each angle than turners, replicating findings from Gramann et al. (2012). In the body orientation experiment, turners tended to make larger magnitudes of errors for smaller angles while non-turners made larger errors for bigger angles (Figure 9, pg. 48). In comparing pointing responses (Figure 4, pg. 37), both turners and non-turners consistently underestimated the angle magnitude in the control group. However, we found that turners as a group in the body orientation experiment tended to over-estimate the angle. Absolute error for turners was also reduced across all turn angles compared to the control.

One explanation is that since the experiment always began with participants seated at an angle to the screen, perhaps the relative weighting of body-based cues was reduced, allowing some participants to ignore their body orientation. It is also possible that this unnatural seating arrangement served as a form of disorientation for the viewers, supporting research that adopting a new spatial heading is easier when disorientation occurs (e.g., May, 1996).

Turners in the neutral condition (i.e., facing the monitor) appeared to perform the worst. When participants are seated facing the screen, their initial travel direction is the same as their current body orientation. This initial congruence between visual and body-based orientation may then cause problems during the rotation phase of the trial, where the vestibular cues no longer match the visually presented motion cues. The manipulation of body-based cues seemed to increase strategy consistency for both groups, therefore reducing the amount of strategy switching that participants tended to engage in. This is in support of the notion that sensorimotor interference affects all participants, regardless of strategy.

4.3 Why Do Non-Turners Exist?

This study tested whether cue conflicts had any effects on spatial updating. When only optic flow is available, participants must effectively overcome conflicting information to successfully spatially update. It appears that turners are more impacted by experimental manipulations in both Experiments 2a and 2b. When peripheral information was occluded (Experiment 2a), turners were less consistent in their strategy selection and had greater variability in their pointing responses. Turners also exhibited highly accurate pointing responses when their seating orientation was rotated (Experiment 2b) and an improvement in strategy consistency.

The measures of RT revealed important differences between turners and non-turners. The control group (Experiment 1) demonstrated a distinct difference between these groups. While non-turners' RTs vary by angle magnitude, turners' RTs do not. Furthermore, while both groups get faster over time, turners consistently respond slower than non-turners across the duration of the experiment. One explanation could be that this reveals another difference in task strategy between the two groups. Perhaps turners are putting more cognitive effort into the task and updating their heading correctly. On the other hand, non-turners may be comparing the time of simulated rotation against the time it takes to rotate the dart. Longer turn angles thus translate into longer dart rotations. We therefore see less absolute and variable error for turners than non-turners across all angles.

This is supported by findings when sensorimotor interference was manipulated. In Experiment 2b, participants began the experiment either facing the left or right of the monitor. Since the participant's physical heading is initially incongruent with the visual travel direction, it may have caused increased awareness of the cue conflict and therefore allowed participants to ignore body-based cues entirely. This may have led to the lack of RT differences between strategy groups across the course of the experiment.

When peripheral visual information was occluded (Experiment 2a), we also saw no differences between turners and non-turners across the time course of the experiment. However, we now see that both groups' RTs vary by turn angle (Figure 7, pg. 45). One explanation is that the removal of peripheral information actually reduced turners' ability to spatially update, causing them to use another strategy. They may rely less on heading updates and more on the time it takes to rotate the dart, much like the non-turners. This is further supported by findings that turners in the aperture group had larger variable error as well as less strategy consistency.

4.4 Future Directions and Limitations

Since the present study had a between-subjects design across three experiments, we cannot draw any conclusions about the potential individual strategy changes when different cues are available. It is entirely possible that participants who performed as non-turners in the control experiment would choose a turner strategy in the aperture or body orientation experiments. It is also possible that we would see individual differences in response error if using a within-participants design.

The use of the circular aperture to block environmental information was also problematic in that it inherently also narrowed the available field of view. Therefore, while it occluded peripheral information, it also occluded some optic flow information that would have been available in the control (Experiment 1). A potential solution would be to project the Starfield onto a wall in a completely dark room with no other objects. This would still allow for the minimization of stationary peripheral information, without changing the field of view and amount of optic flow available. This could then be compared to a group that views the Starfield through an aperture, to test the effects of occluding peripheral vision versus increasing the congruency between central and peripheral vision.

A limitation for Experiment 2b is the method of participant rotation between each condition. Since participants had to be rotated to a specific orientation and distance away from the monitor, it required an experimenter to physically rotate the chair between conditions. Since the participant had to stand up sit back down in a new orientation for each condition, it is possible that this transition caused them to re-orient themselves within the laboratory, thereby influencing their headings representations.

Finally, an important assumption we held was that the apparent failure to spatially update by the non-turner group was caused by unconscious cognitive differences. To gain further insight into why this group exists, a qualitative questionnaire about participant strategies may be useful. It is possible that turners and non-turners simply employ different conscious strategies to complete the task. When participants are trained to respond using a particular strategy, they are able to complete the task using their non-preferred strategy (Gramann et al., 2005). However, it appears that participants who are categorized as turners are better able to engage in strategy-switching, producing smaller magnitudes of errors using the non-preferred strategy than non-turners. Therefore, the difference in groups may not be entirely due to a difference in cognitive ability, but rather of a combination of task strategy and individual differences.

5 CONCLUSIONS

This thesis sought to understand why some individuals appear to fail to spatially update when only optic flow motion information is presented. We examined the effects of two sources of cue conflict in virtual reality (VR) point to origin (PTO) experiments using the Starfield task (e.g., Gramann et al., 2012). One source of conflict was the stationary visual information in the peripheral field, which was hypothesized to impact parsing of object versus self-locomotion information. The other source of cue conflict we manipulated was body-based cues of orientation.

While the manipulations to reduce two types of cue conflict did not alter the overall proportions of turners and non-turners within the sample, Experiments 2a and 2b did reveal important differences in the degree of error participants make when different types of cue conflict do occur. While reducing peripheral visual information (2a) decreased performance, especially for turners, manipulating body orientation improved performance for turners and caused both strategy groups to respond more consistently. New reaction time analyses corroborated these findings. Perhaps the difference between strategy groups is not of updating ability, but rather cognitive strategy used to complete the task.

REFERENCES

Busettini, C., Masson, G. S., & Miles, F. A. (1997). Radial optic flow induces vergence eye movements with ultra-short latencies. *Nature*, *390*, 512–515. https://doi.org/10.1038/37359

Campos, J. L., Byrne, P., & Sun, H. J. (2010). The brain weights body-based cues higher than vision when estimating walked distances. *European Journal of Neuroscience*, *31*(10), 1889–1898. https://doi.org/10.1111/j.1460-9568.2010.07212.x

Chance, S. S., Gaunet, F., Beall, A. C., & Loomis, J. M. (1998). Locomotion mode affects the updating of objects encountered during travel: The contribution of vestibular and proprioceptive inputs to path integration. *Presence: Teleoperators and Virtual Environments*, *7*(2), 168–178.

Chen, X., McNamara, T. P., Kelly, J. W., & Wolbers, T. (2017). Cue combination in human spatial navigation. *Cognitive Psychology*, *95*, 105–144. https://doi.org/10.1016/j.cogpsych.2017.04.003

Easton, R. D., & Sholl, M. J. (1995). Object-array structure, frames of reference, and retrieval of spatial knowledge. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *21*(2), 483–500. https://doi.org/10.1037/0278-7393.21.2.483

Etienne, A. S., & Jeffery, K. J. (2004). Path integration in mammals. *Hippocampus*, *14*(2), 180–192. https://doi.org/10.1002/hipo.10173

Foulkes, A. J., Rushton, S. K., & Warren, P. A. (2013). Flow parsing and heading perception show similar dependence on quality and quantity of optic flow. *Frontiers in Behavioral Neuroscience*, *7*, 1–10. https://doi.org/10.3389/fnbeh.2013.00049

Gramann, K. (2013). Embodiment of Spatial Reference Frames and Individual Differences in Reference Frame Proclivity. *Spatial Cognition and Computation*, *13*(1), 1–25. https://doi.org/10.1080/13875868.2011.589038

Gramann, K., Müller, H. J., Eick, E. M., & Schönebeck, B. (2005). Evidence of separable spatial representations in a virtual navigation task. *Journal of Experimental Psychology: Human Perception and Performance*, *31*(6), 1199–1223. https://doi.org/10.1037/0096-1523.31.6.1199

Gramann, K., Wing, S., Jung, T. P., Viirre, E., & Riecke, B. E. (2012). Switching spatial reference frames for yaw and pitch navigation. *Spatial Cognition and Computation*, *12*(2–3), 159–194. https://doi.org/10.1080/13875868.2011.645176

Hafting, T., Fyhn, M., Molden, S., Moser, M. B., & Moser, E. I. (2005). Microstructure of a spatial map in the entorhinal cortex. *Nature*. https://doi.org/10.1038/nature03721

Kessler, K., & Thomson, L. A. (2010). The embodied nature of spatial perspective taking: Embodied transformation versus sensorimotor interference. *Cognition*, *114*(1), 72–88. https://doi.org/10.1016/j.cognition.2009.08.015

Klatzky, R. L., Loomis, J. M., Beall, A. C., Chance, S. S., & Golledge, R. G. (1998). Spatial updating of self-position and orientation during real, imagined, and virtual locomotion. *Psychological Science*, *9*(4), 293–298. https://doi.org/10.1111/1467-9280.00058

Klatzky, R. L., Loomis, J. M., Golledge, R. G., Cicinelli, J. G., Doherty, S., & Pellegrino, J. W. (1990). Acquisition of route and survey knowledge in the absence of vision. *Journal of Motor Behavior*, *22*(1), 19–43. https://doi.org/10.1080/00222895.1990.10735500

Lappe, M., Bremmer, F., & Van Den Berg, A. V. (1999). Perception of self-motion from visual flow. *Trends in Cognitive Sciences*, *3*(9), 329–366. https://doi.org/10.1016/S1364-6613(99)01364-9

Loomis, J. M., Klatzky, R. L., Golledge, R. G., Cicinelli, J. G., Pellegrino, J. W., & Fry, P. A. (1993). Nonvisual Navigation by Blind and Sighted: Assessment of Path Integration Ability. *Journal of Experimental Psychology: General*, *122*(1), 73–91. https://doi.org/10.1037/0096-3445.122.1.73

May, M. (1996). Cognitive and embodied modes of spatial imagery. In *Psychologische Beitraege*.

May, M. (2004). Imaginal perspective switches in remembered environments: Transformation versus interference accounts. *Cognitive Psychology*, *48*(2), 163–206. https://doi.org/10.1016/S0010-0285(03)00127-0

McNaughton, B. L., Battaglia, F. P., Jensen, O., Moser, E. I., & Moser, M. B. (2006). Path integration and the neural basis of the "cognitive map." *Nature Reviews Neuroscience*, *7*(8), 663–678. https://doi.org/10.1038/nrn1932

Mou, W., & Zhang, L. (2014). Dissociating position and heading estimations: Rotated visual orientation cues perceived after walking reset headings but not positions. *Cognition*, *133*, 553–571. https://doi.org/10.1016/j.cognition.2014.08.010

Moser, E. I., Kropff, E., & Moser, M.-B. (2008). Place Cells, Grid Cells, and the Brain's Spatial Representation System. *Annual Review of Neuroscience*. https://doi.org/10.1146/annurev.neuro.31.061307.090723

O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, *34*, 171–175. https://doi.org/10.1016/0006-8993(71)90358-1

Parron, C., Poucet, B., & Save, E. (2004). Entorhinal cortex lesions impair the use of distal but not proximal landmarks during place navigation in the rat. *Behavioural Brain Research*. https://doi.org/10.1016/j.bbr.2004.03.006

Presson, C. C., & Montello, D. R. (1994). Updating after rotational and translational body movements: coordinate structure of perspective space. *Perception*, *23*(12), 1447–1455. https://doi.org/10.1068/p231447

Proske, U., & Gandevia, S. C. (2012). The proprioceptive senses: Their roles in signaling body shape, body position and movement, and muscle force. *Physiological Reviews*, *92*(4), 1651–1697. https://doi.org/10.1152/physrev.00048.2011

Purves, D., Augustine, G., Fitzpatrick, D., Katz, L., LaMantia, A.-S., McNamara, J., & Williams, M. (2001). *Neuroscience. 2nd edition*. Sunderland (MA): Sinauer Associates; 2001.

Richardson, A. E., Montello, D. R., & Hegarty, M. (1999). Spatial knowledge acquisition from maps and from navigation in real and virtual environments. In *Memory & Cognition* (Vol. 27, Issue 4).

Riecke, B. E., van Veen, H. A. H. C., & Bülthoff, H. H. (2002). Landmarks: A path integration study in virtual reality. *Presence*, *11*(5), 443–473.

Riecke, B. E. (2008). Consistent left-right reversals for visual path integration in virtual reality: More than a failure to update one's heading? *Presence: Teleoperators and Virtual Environments*, *17*(2), 143–175. https://doi.org/10.1162/pres.17.2.143

Riecke, B. E., Cunningham, D. W., & Bülthoff, H. H. (2007). Spatial updating in virtual reality: The sufficiency of visual information. *Psychological Research*, *71*(3), 298–313. https://doi.org/10.1007/s00426-006-0085-z

Riecke, B. E., Von Heyde, M. Der, & Bülthoff, H. H. (2004). Spatial updating in real and virtual environments - Contribution and interaction of visual and vestibular cues. *Proceedings - 1st Symposium on Applied Perception in Graphics and Visualization, APGV 2004*, 9–17.

Rieser, J. J., Garing, A. E., & Young, M. F. (1994). Imagery, Action, and Young Children's Spatial Orientation: It's Not Being There That Counts, It's What One Has in Mind. *Child Development*, *65*(5), 1262–1278. https://doi.org/10.1111/j.1467-8624.1994.tb00816.x

Rushton, S. K., Bradshaw, M. F., & Warren, P. A. (2007). The pop out of scene-relative object movement against retinal motion due to self-movement. *Cognition*, *105*(1), 237–245. https://doi.org/10.1016/j.cognition.2006.09.004

Save, E., & Poucet, B. (2000). Involvement of the hippocampus and associative parietal cortex in the use of proximal and distal landmarks for navigation. *Behavioural Brain Research*, *109*(2), 195–206. https://doi.org/10.1016/S0166-4328(99)00173-4

Steck, S. D., & Mallot, H. A. (2000). The role of global and local landmarks in virtual environment navigation. *Presence: Teleoperators and Virtual Environments*. https://doi.org/10.1162/105474600566628

Taube, J. S. (2007). The Head Direction Signal: Origins and Sensory-Motor Integration. *Annual Review of Neuroscience*. https://doi.org/10.1146/annurev.neuro.29.051605.112854

Townsend, B., Legere, J. K., O'Malley, S., Mohrenschildt, M. V., & Shedden, J. M. (2019). Attention modulates event-related spectral power in multisensory self-motion perception. *NeuroImage*, *191*, 68–80. https://doi.org/10.1016/j.neuroimage.2019.02.015

Wang, R. F. (2005). Beyond imagination: Perspective change problems revisited. *Psicólogica: International Journal of Methodology and Experimental Psychology*, *26*(1), 25–38.

Wang, R. F. (2004). Between reality and imagination: When is spatial updating automatic? *Perception and Psychophysics*, *66*(1), 68–76. https://doi.org/10.3758/BF03194862

Warren, P. A., & Rushton, S. K. (2007). Perception of object trajectory: Parsing retinal motion into self and object movement components. *Journal of Vision*, *7*(11), 1–11. https://doi.org/10.1167/7.11.2

Warren, P. A., Rushton, S. K., & Foulkes, A. J. (2012). Does optic flow parsing depend on prior estimation of heading? *Journal of Vision*, *12*(11), 8. https://doi.org/10.1167/12.11.8