Allocentric and egocentric navigational strategies are adopted at comparable rates in a virtual MWM: an eye-tracking study

by

Megan Yim
B.A., Vancouver Island University, 2010

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

MASTER OF SCIENCE

in the Department of Psychology

Supervisory Committee

Allocentric and egocentric navigational strategies are adopted at comparable rates in a virtual MWM: an eye-tracking study

by

Megan Yim
BA, Vancouver Island University, 2010

Supervisory Committee

Dr. Ronald W. Skelton, Department of Psychology
Supervisor

Dr. Anthony Robertson, Department of Psychology
Departmental Member

Dr. James B. Hale, Department of Psychology
Departmental Member

Abstract

Supervisory Committee
Dr. Ronald W. Skelton, Department of Psychology
Supervisor
Dr. Anthony Robertson, Department of Psychology
Departmental Member
Dr. James B. Hale, Department of Psychology
Departmental Member

Considerable research has examined strategies involved in spatial navigation, and what factors determine which strategy an individual will use. The little research that has examined strategy adoption has produced conflicting results. The present study investigated the relative rate of adoption of allocentric and egocentric strategies in an environment that allowed individuals to adopt one or the other, or switch between them. Results indicated that by the end of testing nearly all participants had adopted one strategy or the other. Also, more participants were using an allocentric strategy than an egocentric strategy. However, strategy selection was not related to gender, or the relative efficiency of the two strategies. Analysis of gaze position at the start of trials showed that those who adopted an allocentric strategy tended to focus their attention on the distal (landscape) features of the environment whereas those who adopted an egocentric strategy tended to focus their attention on the proximal object features. However, vertical gaze position could not be used to reveal the rate of adoption of an egocentric strategy, because this did not vary over trials. Analysis of gaze position using "regions of interest" overcame this problem and showed that both strategies are adopted at a similar rate early in trials. Comparison of strategy by gaze position and strategy by navigation probe indicated that these two metrics were measuring two different stages of navigation. Finally, analysis of the navigational efficiency of different strategies indicated that the best navigators were those who

used both strategies. These findings indicate allocentric and egocentric strategies are adopted at a similar rate and that within the space of a few seconds, individuals may use different strategies for orientation and navigation.

Key words: Spatial navigation, eye tracking, allocentric, egocentric, strategy use, strategy adoption, orientation strategy, navigational strategy, gaze position

Table of Contents

Supervisory Committee ii

Abstract iii

Table of Contents v

List of Figures vii

Acknowledgments ix

Introduction 1

- Strategy definition 1
- Strategy Adoption 5
- Human research: Strategy Adoption 6
- Research Approach: Environment 8
- Research Approach: Gaze Position 10

Methods 12

- Participants 12
- Apparatus 13
- Procedure 15
- Ancillary Tasks 19
- Behavioural data analysis 20
- Eye tracking data analysis 20
- Analysis of strategy acquisition from gaze data 23
- Strategy adoption 24
- Orientation Strategy 25

Results 25

- Behavioural results 25
- Eye movement results 33
  - Overall Navigational Strategy 33
- Gender 36
- Strategy 36
- Horizontal gaze position 37
- Regions of Interest (ROI) 38
- Strategy adoption 39
  - Strategy grouped by dDTS 39
- ROI 41
- Separation of participants by vertical GP 44
- ROI Strategy Adoption 47

Discussion 49

- Attentional Focus and Navigational Strategy 54

Attentional Focus and Adoption of Navigational Strategy 55
Emergent construct: Multiple strategies during single trials 58
Attentional Focus and Adoption of Orientation Strategy 59
Theoretical implications 60
Future applications 63
Conclusions 64
References 67

Appendix A: X data 76

X data- overall strategy 76
Methods 76
Results 77
Overall strategy: Horizontal distribution 77
Strategy adoption: Horizontal gaze 78

Appendix B: Gender 79

Methods: data analysis 80
Behavioural 80
Gaze position 81
Results 81
Overall strategy: Gender 81
Adoption: Gender 83

List of Figures

Figure 1. Virtual environments: 14

Figure 2. Start positions in the Dual-strategy maze 17

Figure 3. The DTS Trial and scoring 18

Figure 4 The horizon. 22

Figure 5. Regions of Interest 23

Figure 6. Strategy Selection 26

Figure 7. Navigational Performance 28

Figure 8. Adoption by behavioural performance. 29

Figure 9. Performance by Gender. 31

Figure 10. Behavioural Adoption by Gender Performance 31

Figure 11. Behavioural Performance, Strategy by Gender. 32

Figure 12. Behavioural Adoption, Strategy by Gender. 32

Figure 13. Average Vertical Gaze Position 34

Figure 14. Average Frequency Distribution above the Horizon. 34

Figure 15. Heatmaps by Strategy Group. 35

Figure 16. Average Vertical Gaze Position. 37

Figure 17. Proportion of Gaze within Regions of Interest 38

Figure 18. Average Vertical Gaze Position Over Trials 40

Figure 19. Average Frequency of Gaze Above the Horizon 40

Figure 20. Proportion of Gaze Spent in Regions of Interest Over Trials 42

Figure 21. Trial of First Asymptote 43

Figure 22. Trial of Second Consecutive Asymptote. 43

Figure 23. Strategy Selection by Orientation Strategy..... 45

Figure 24. Average gaze between orientation strategy groups 46

Figure 25. Average frequency of gaze above the horizon..... 47

Figure 26. Percentage of Gaze Spent in Regions of Interest..... 48

Figure 27. Trial of Adoption after grouping by orientation strategy 48

Figure 28. Performance between groups by gaze position..... 49

Figure 29. Horizontal Gaze by Strategy..... 77

Figure 30. Strategy Adoption According to Horizontal Gaze..... 78

Figure 31. Average gaze position and percentage by gender..... 81

Figure 32. Horizontal Gaze Position by Gender 82

Figure 33. Gaze Spent in Regions of Interest by Gender..... 83

Figure 34. Strategy Adoption by Gender 84

Figure 35. Trial of Adoption by Gender 84

Acknowledgments

First and foremost I would like to express my sincerest gratitude to my supervisor, Dr. Ronald Skelton, who has supported me throughout my thesis with his patience and experience while still allowing me to express my own ideas and opinions. During the running of the current study I was kindly supported by several research assistants and wish to extend my gratitude to them as well. Specifically, Sonja Murchison, Allison McGerrigle and Dustin van Gerven for their assistance in running participants and entering data. Finally, I would like to thank the Department of Psychology for providing the necessary lab space and equipment for completing this project.

Introduction

Spatial navigation is the process of getting from one place to another without getting lost along the way. It requires multiple cognitive processes including those involved in locating oneself and other objects in space, perceiving relative distances, assessing directional relationships between objects and being able to translate this information into a behaviour that enables movement and attainment of a goal within an environment (Humphreys, 1998; Committeri, Galati, Paradis, Pizzamiglio, Berthoz, & LeBihan, 2004; Knaugg, Rauh, & Renz, 1997). Gaining an understanding of spatial navigation would provide key insights into understanding a high level cognitive function and would advance our understanding of the cognitive processes involved. A large portion of the research on spatial navigation has focused on the cognitive strategies people use to navigate (see Maguire, Burgess, Donnet, Frackowiak, Frith, & O'Keefe, 1998). However, little research has examined factors that influence strategy selection, and even less has looked at the process of strategy acquisition. Accordingly, the present study proposes to focus on how and when people adopt these strategies.

Strategy definition

To a large extent, the foundation of work on spatial navigation strategy derives from Tolman's work in the early 1940s (Tolman, 1948). This work showed that sometimes, navigation was by simple stimulus response similar to conditioning. However, in other circumstances, spatial navigation seemed to be more complex than a simple stimulus response reaction. Instead it could be a complicated interaction where the brain, while navigating, forms multiple connections and by analyzing incoming spatial information, compiles a "cognitive map". It has been suggested that a "unitary spatial framework," much like a cognitive map, is

present innately in all organism and that it is intimately related to activation of the hippocampus (O'Keefe & Nadel, 1978).

Neuroimaging technology has led to further advancements towards the visualization of the brain during navigation. It has shown activation in brain areas specific to navigation in general as well as specific regions activated during tasks that require different types of navigation strategies (stimulus response versus cognitive map), providing anatomical support for the theory of multiple navigation strategies (Maguire, Burgess, & O'Keefe, 1999). In the case of stimulus response navigation, the posterior parietal lobe and more specifically the caudate, have been implicated (Maguire, Burgess, Donnett, Frackowick, Frith, & O'Keefe, 1998), whereas navigating by cognitive map tends to activate the hippocampus and retrosplenium (Iaria, Chen, Guariglia, Ptito, & Petrides, 2003). These two areas as well as the prefrontal cortex, have been proposed to be interconnected in a neural circuit underlying many aspects of spatial cognition and memory (Floresco, Seamns, & Phillips, 1997). This circuit is proposed to integrate different spatially mediated behaviours, specifically delayed versus nondelayed spatial navigation. Although this study suggests an integration of information for the purposes of spatial memory, it is also likely that the success of navigation is influenced by the connections between the two navigation systems with the prefrontal cortex.

Two types of spatial navigation strategy have now been defined including allocentric and egocentric navigation strategies. They are characterized and defined according to differing behavioural patterns and are dependent on separable cognitive processes originating in different brain regions (Gr\ön, Wunderlich, Spitzer, Tomczak, & Riepe, 2000). These strategies include the cognitive map, or allocentric strategy, which involves referencing knowledge of the relationships between landmarks in our environment (O'Keefe & Nadel, 1978; Jordan, Schadow,

Wuestenberg, Heinze, & J\äncke, 2004) and egocentric navigation, which involves simple stimulus-response learning leading to automatic responses to environmental cues independent of any spatial relationships between objects (Harley, Maguire, Spires, & Burgess 2003; Moghaddam & Bures, 1996a).

Allocentric navigation employs a cognitive map requiring the encoding of the relationships between external stimuli, independent of the position of the observer (Andersen, & Enriquez, 2006). Allocentric navigation uses the relation between distal and proximal landmarks and the target location to calculate a vector (distance and direction) to the target. It requires constant updating position within the cognitive map while keeping track of orientation within the map (Wang & Spelke, 2002). Importantly, allocentric navigation is viewer independent and a path to the destination can be found from multiple perspectives because it requires orienting according to general landmarks (global focus) like cardinal directions (North South East West), the positionn of the sun or other large distant object (like mountains or the Eiffel tower).

Cognitive map building and the use of the allocentric strategy occurs in a progressive manner with an increasing level of complexity and information being included in the map over time (Trullier, Wiener, Berthoz, & Meyer, 1997). Once a certain level of complexity and information content has been added to the cognitive map, the individual is able to use this information to take detours and shortcuts successfully, which is an advantage over an egocentric method. This strategy is effective in more complex situations because it is flexible to differing locations of the navigator within the environment and does not depend on the orientation or position of the navigator in relation to the goal (Jordan, Schadow, Wuestenberg, Heinze, & Jancke, 2004).

In contrast, egocentric navigation incorporates the spatial relationship between the navigator and the goal object as a series of interim stimulus-response associations between single landmarks that lead to certain body-based responses such as “turn left at that corner” (O’Keefe & Nadel, 1978). This method leads to a coding of relative space (Moghaddam & Bures, 1996b). With every step made by the navigator, egocentric parameters must be updated. This is done by adding any displacement vector, created by various objects and movement, to the previous vector, resulting in the navigator remaining spatially fixed in the center of the reference system (Wang & Spelke, 2002). This spatial representation is therefore characterized as highly dynamic and transient. With more complex navigation tasks, egocentric updating becomes more and more challenging, leading to more errors and increased response time (Loomis, Klatzky, Golledge, Cicinelli, Pellegrino, & Fry, 1993). Most research regarding egocentric navigation has emphasized the role of visual-perception, however, kinaesthetic and motor skills acquired incrementally have also been implicated. This finding possibly explains the difficulty in reversing and modifying an egocentric strategy when presented with a novel starting position in a similar environment (Maguire, Burgess, & O'Keefe, 1999).

Spatial navigation research has sought to separate the two navigation strategies and to understanding the mechanisms of navigation by studying the factors that influence strategy use (eg. Cutmore et al., 2000; Moffat, Zonderman, & Resnick, 2001; Maguire et al., 1999). These factors include gender, age experience etc. There is overwhelming research suggesting that people predominantly use one strategy in many situations (Holdstock et al., 2000), however, it is likely that in real-world situations strategies are more integrated and may be employed in parallel as well as singly.

Gender has long been considered a factor in spatial navigational (Astur, Ortiz, & Sutherland, 1998). For example, males have been shown to be better at completing navigation tasks that require an allocentric strategy while females seem to be better at navigation tasks that require an egocentric strategy (Driscoll, Hamilton, Yeo, Brooks, & Sutherland, 2005). This gender specific propensity for different navigation strategies has suggested to researchers that perhaps because males are better at allocentric navigation, they will choose to navigate allocentrically more often whereas because females are better at egocentric navigation, they will choose to navigate egocentrically more often (Levy, Astur , & Frick, 2005). However, there is contention within the area as to whether there is indeed a gender bias in strategy selection or simply performance when using one strategy over the other (van Gerven et al., 2012).

Strategy Adoption

Adoption rate has been shown (by animal research) to differ depending on the strategy required by the task. Adoption rate of rats in a maze reinforced for allocentric navigation was faster when compared to rats in a maze reinforced for egocentric navigation (Tolman, Ritchie & Kalish, 1946). This suggests that acquisition may be faster and easier for an allocentric strategy than an egocentric one. However, in another classic study, acquisition was fastest and easiest for rats forced to navigate by directional navigating (consistently going the same directions despite new orientation) rather than allocentric or egocentric navigation (Blodgett, McCutchan, & Mathews, 1949). More modern research also finds little evidence for more easy acquisition of allocentric navigation and instead concludes that egocentric and directional navigation are both acquired easier than allocentric navigation (Skinner et al., 2003).

Adoption rate is also different by strategy when rats are able to spontaneously choose which strategy to use. A study assessing strategy acquisition in a maze that supported either

allocentric or egocentric navigation measured acetylcholine (Ach) release simultaneously in the hippocampus and striatum (Chang & Gold, 2003). Depending on strategy choice, adoption was different, indicated by differing levels of Ach in both structures. Rats that chose an allocentric strategy (determined by behavioural data) showed an early increase of ~ 60% Ach in the hippocampus. In contrast, rats that chose an egocentric strategy showed a later 30-40% increase in Ach in the striatum. After an early adoption of an allocentric strategy, some rats showed a later increase in Ach in the striatum corresponding to a behavioural shift to egocentric navigation. Other studies measuring adoption have found similar results when using behavioural measures (Packard, & McGaugh, 1996). A key aspect of these strategy adoption studies was the advancement in methodology allowing assessment of adoption by first grouping rats according to their spontaneously chosen strategy, within an environment that supported both strategies, and then observing changes in strategy use over time.

Human research: Strategy Adoption

Few studies involving humans allows spontaneous strategy choice to allow the direct comparison of strategy adoption and the little research that exists show conflicting results. For example, a study assessing spontaneous strategy selection and adoption incorporated functional magnetic resonance imaging (fMRI) with behavioural paradigms and found a difference in adoption indicated by activation in strategy specific brain regions (Iaria et al., 2003). Initially, participants selected strategies in similar proportions, half chose to navigate allocentrically and half chose to navigate egocentrically, and exhibited typical activation in the hippocampus and caudate respectively. The difference in adoption between these two groups was shown by an early activation of the hippocampus in the allocentric group in contrast to a later activation of the caudate in the egocentric group. Also there was later activation in the caudate for some of those

participants who had started navigating allocentrically, this switch corresponded with a behavioural strategy switch as well. It was inferred that adoption was easier for an allocentric strategy and that once this strategy had been adopted, participants were able to switch to an egocentric strategy. Another study on adoption also found a late switch from an allocentric to an egocentric strategy and in addition found that the most effective performances were seen in participants who were able to switch strategies depending upon task demands (Etchamendy & Bohbot, 2007). Both of these studies on adoption suggest that spontaneous strategy selection occurs in an approximately equal division but that this occurs because an allocentric strategy is easier to adopt. However, strategy selection and adoption is generally documented by self-report or by a behavioural strategy probe trial and both of these methods are subject to confounding variables (subjectivity and using strategy during a final trial to infer strategy of all trials).

Strategy adoption has also been shown to occur in parallel (Igloi et al., 2009). In an adoption study in which both an allocentric or an egocentric strategy could be used to solve the task, information for both strategies was adopted in parallel. In this study, participants first completed blocks of four training trials followed by a strategy probe; however, during some strategy probe trials all features for one type of navigation were eliminated. Acquisition was thought to be similar because both strategy groups were equally successful at navigating even when cues for their chosen strategy were eliminated. According to this study, navigation strategies are acquired at the same rate and that spatial knowledge for either strategy is encoded in parallel, allowing participants to use either strategy depending on task demands. Again, this conclusion was reached using behavioural methods and information gathered at intervals during training and cannot be generalized to navigation during each individual trial.

In sum, over the past few decades, spatial navigation research has made progress in the work of determining and classifying strategies and even showing trends in spontaneous strategy selection and adoption. However, only a little is known about the process of strategy adoption, but this may be due to methodological limitations. Strategy in humans has thus far been measured using self-report, error counts and forced strategy switch tasks (behavioural measures) (e.g. Etchamendy & Bohbot, 2007; Iaria et al., 2003; Igloi et al., 2009). It is very difficult to infer strategy adoption using these methods; researchers are able to determine strategy use at the end of a group of trials and to infer participants' ability to switch when forced, however, they do not capture the progression of strategy adoption on a trial-by-trial basis.

Research Approach: Environment

Mazes are the most often used method for studying spatial navigation strategies. The Morris water maze (MWM) has proven particularly valuable in assessing allocentric navigation and the factors that influence its successful use (e.g. Morris, 1984; Sutherland & Dyck, 1984; Whishaw, 1985). Within this maze, rats are placed in a pool of opaque water with the escape platform rendered invisible, thus offering no local cues to guide behaviour. The maze requires the ability of rats to use accurate directional information to guide escape behavior and to learn by using spatial position of the platform relative to distal cues (Brandeis, Brandys, & Yehuda, 1989). Also, the MWM allows qualitative information to be gathered from trials during which the platform is moved and dwell time in the correct area of the pool provides information regarding spatial learning that is unconfounded by the motoric capacity of the rats being tested (Rapp, Rosenberg, & Gallagher, 1987). Although this maze paradigm was originally designed to study place navigation the argument has also been made that rats may learn to solve the maze

using nonspatial strategies such as sequence of movements or the use of some specific local cues (Sutherland & Dyck, 1984).

Since the MWM's development, this basic procedure has become one of the most widely used laboratory tools in behavioural neuroscience. Many methodological variations of the MWM have been developed in an attempt to study spatial navigation in the human population. The MWM was adapted to test humans by being simulated in a virtual environment and has successfully been used in quite a few studies that elicit allocentric (see Astur, Ortiz, & Sutherland, 1998; Jacobs, Thomas, Laurance, & Nadel, 1998;Skelton, Bukach, Laurance, Thomas, & Jacobs, 2000; Hamilton, Driscoll, & Sutherland, 2002) and even egocentric navigation (Feigenbaum, & Morris, 2004; Skelton, Ross, Nerad, & Livingstone, 2006; Livingstone-Lee et al., 2011). Again, most of the research using the vMWM has been concerned with identifying ultimate strategy rather than the process of strategy acquisition.

A strategy probe has been developed to determine which strategy participants are using to navigate (Skelton, Ross, Nerad, & Livingstone, 2006). It taps into the cognitive processes that people are using to find their way to the goal location and integrates the movement trajectory taken to reach the goal. In this paradigm, there is an arena within a room containing features for both allocentric and egocentric navigation. At the end of a series of test trials there is a strategy probe trial where participants must place a marker in the location that they think the virtual platform has been in previous trials. According to where they place the marker, either using allocentric or egocentric stimuli, researchers are then able to determine the strategy that has been chosen. The strategy probe forces participants to choose which environmental features have been used to find the platform in relation to the navigator and the surrounding features but only at the

end of trials. This can be used to infer navigational strategy or the way in which individuals localize the goal within the environment.

Research Approach: Gaze Position

Eye movements have long been used to infer certain cognitive processes due to gazes' intrinsically cognitive and task based nature (Yarbus, 1967). That is, gaze tends to be fixated on objects or features that individuals cognitively require to complete a task. Indeed, gaze and its resultant fixations are the central means by which we sequentially acquire information from our environment (Shagass, Roemer, & Amadeo, 1976). Many theories regarding gaze fixation are image based, and they suggest that our eye is drawn to fixate on scenes that contain discontinuities in image features such as motion, colour and texture (Marr, 1982). However, evidence gathered from more recent eye movement data are showing that fixations are extracting very specific information from the environment, information that is directly relevant to the task at hand (Droll, Hayhoe, Triesch, & Sullivan, 2005). For example, if participants are told to search for a specific item in a multitude of items, fixation will be restricted to items that resemble the specific target item only (Swain & Ballard, 1991). Eye movements in relation to spatial navigation research could be attracted to specific local features or may also be attracted to more holistic information in the environment (Tatler & Vincent, 2009).

Attention as indicated by gaze is focused on specific environmental feature when navigating allocentrically versus egocentrically and analyzing the features being attended to may allow inferences regarding strategy use. Attention during egocentric navigation tends to be on proximal features in order to make a series of decisions about a navigational path to a goal (Maguire et al., 1999). In contrast, attention during allocentric navigation tends to be on distal landmarks or beacons that can be seen for longer periods of time and from further distances

(Maguire, Burgess, & O'Keefe, 1999). That is, they simultaneously rely on multiple elements of their cognitive maps. During a study assessing gaze during spatial navigation strategy selection using the virtual Morris Water Maze (VMWM), Livingstone-Lee and colleagues showed that there were specific patterns in gaze position that correlated with specific environmental feature use. Gaze during allocentric navigation was largely dedicated above the horizon with more central fixation, where the landscape features were located, whereas using egocentric navigation was correlated with gaze below the horizon and more dispersed along the x axis, where the proximal objects were located. This study confirms that eye tracking can be used to detect difference in gaze fixation according to strategy choice. This difference in attention to environmental features and resultant gaze positions is potentially a source of differentiation between strategies and the way that individuals process their surroundings.

Eye tracking and gaze analysis enables an indication of how participants are orienting, or finding their own position, within the environment. Eye movement analysis can be quite overwhelming due to the large volume of data produced during each trial. However, gaze during the first second of each trials can be analyzed as vertical, horizontal or as a percentage of time spent in specific regions (Holmqvist, Holsanova, Barthelson, & Lundqvist, 2003). Gaze during this time is focused on features that are used to orient or locate the participants' own position within the environment. We can infer that these features are also used when navigating to the goal in the environment.

In our task, two main types of navigational strategy can be adopted when people engage in the task; allocentric, and egocentric. Our aim was to investigate the rate and ease of adoption between an allocentric and an egocentric strategy. To that purpose, we used a previously tested maze in which allowed efficient learning of the task using either strategy. We defined

spontaneously chosen strategy through the strategy probe trial in which participants choose which cues to place a marker according to. Finally, we documented adoption of allocentric and egocentric strategies using eye tracking as an indication of environmental feature use during the first second of each trial.

The current study will directly compare spatial navigation strategy selection in the virtual MWM paradigm and will determine whether there are differences in adoption rate depending on strategy choice. There is little research to date that allows participants to spontaneously select a strategy, and even less research has been able to index both allocentric and egocentric strategy adoption together on a trial by trial basis. This study will provide indications of how individuals adopt a strategy on a trial-by-trial basis using a combination of the vMWM and eye tracking. Because the maze environment used in this study was solvable using either an allocentric or an egocentric strategy, we were able to see spontaneous strategy selection and adoption separately for each navigational strategy groups. The study also compares groups according to orientation strategy.

Methods

Participants

A sample of 80 undergraduate students (approximately equal numbers of males and females) volunteering for course credit participated in the study however due to technological complications only 55 (30 males, 25 females) were included in analysis. They were screened for a history of brain injury or neurological disease. Also they were required to speak English as a first language so that everyone understood the instructions similarly and had normal or corrected to normal vision. Participants were given full written informed consent before completing the experiment.

Apparatus

Spatial navigation was investigated using three versions of a specialized virtual Morris water maze, visible, Dual-strategy and Place, designed using the computer program Unreal (Epic Megagames). The maze was presented on an 800x600 computer monitor. A modified joystick with the backwards and jump functions disabled was used to navigate within the virtual environment to mimic the movements of rats in a real MWM. Participant's heads were stabilized in a chin rest to ensure accuracy of eye tracking.

The initial maze is the visible maze designed as a practice task in which participants can become accustomed with the joystick and movement within the maze as well as to ensure that they understand the task instructions presented in the rest of the experiment. The visible maze environment is composed of a large room with windows on each of the four walls and an arena in the centre of the room; participants were allowed to move within this arena. Mountains are visible from the north facing window, hills sloping down towards water are visible from the East and West windows and an island in a body of water is visible from the south window as allocentric landmark stimuli. In addition, there are eight objects perched on the arena wall as egocentric stimuli (see Figure 1). The Dual-strategy testing maze also has both allocentric and egocentric stimuli therefore allowing participants to choose between using landmarks for allocentric navigation and objects for egocentric navigation. Finally, the place maze only has landmarks for allocentric navigation and does not have the objects perched on the wall. This maze provides an example of average allocentric gaze patterns that we can compare gaze from the Dual-strategy maze to.

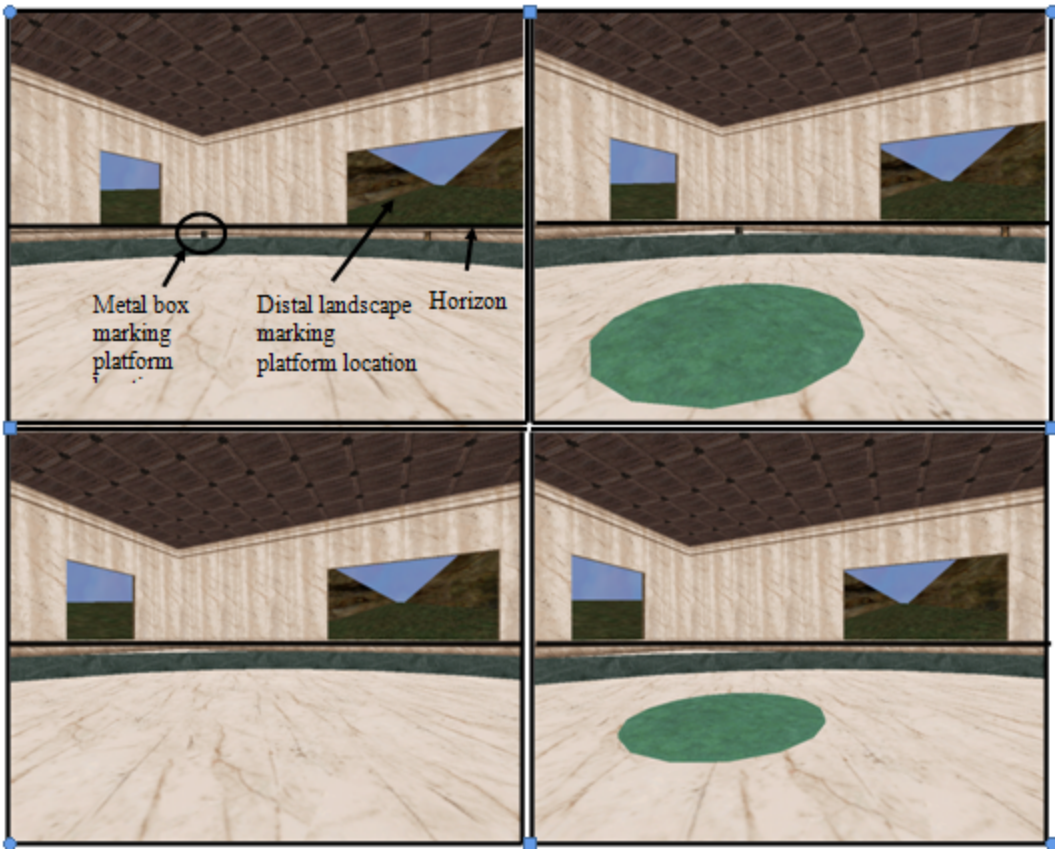


Figure 1. Virtual environments:

A. View of the mazes. (A) The Dual-strategy maze from the start position in the South East corner with landscape visible through the windows above the horizon and object cues below the horizon. (B) The Dual-strategy maze after the platform has been stepped on. Notice that the horizon is below the landscape and the objects are above the objects. (C) The Place maze with no object cues from the start position in the South East corner. (D) The Place maze once the platform has been stepped on.

The eye tracker, developed by CanAssist (Canadian Institute for Accessibility and Inclusion) at the University of Victoria, consisted of a digital camera (Flea Firewire, Point Grey Research, Vancouver, BC) fitted with an LED-infrared lighting system (Hamamatsu Corp.) with a frame of lights placed around the lens. The camera was mounted on an adjustable metal swivel. In order to determine the angle of the eye fixating on the screen and therefore the location of gaze fixations, infrared light from the camera is reflected from the cornea of the dominant eye. The eye tracking computer records the eye movements of participants as positional ‘x’ and ‘y’

coordinates at a frequency of 60 Hz. Eye fixations were recorded on one computer (the "eye tracking computer") while the game was run on a separate computer (the "game computer") and both were fed to one monitor. The maze tasks and eye tracking red ball were overlaid and presented on a television monitor where the second researcher was able to monitor while the participant navigated the mazes ensuring that any problems with eye tracking could be observed and corrected immediately (Figure 2). Eye tracking during the task was also recorded on a DVD with no individual identifying information except a participant code.

Procedure

After participants gave written consent and complete the demographics questionnaire, their dominant eye was determined using the Miles test of ocular dominance (Miles, 1930). During the maze tasks participants were seated so that their eyes were level with the midpoint on the computer monitor at a distance of 24" from the screen. They were stabilized with a chin rest to reduce movement throughout the experiment. The participants completed a calibration task comprised of a 5x5 grid of dots appearing on the screen to ascertain the relation between the participant's eye positions and their gaze fixations on the computer screen. They were instructed to fixate on the dot at all points on the screen so that the eye tracker could confirm gaze position while participants were looking at a pre-defined series of points. In addition, they completed a baseline task during which they followed a point across the midpoint on the computer monitor. This provided a measurement of the midpoint of individual participants' gaze and allowed researchers to correct for any 'y' axis lag. Once calibration was achieved participants moved on to the vMWM on the game computer.

Training trials: The first trials during the training phase were designed to enable the participant to explore the environment as well as to become comfortable with the joystick.

During the first exploration trial participants were free to move throughout the room surrounding the arena and they were encouraged to approach each window and look out as well as notice the objects surrounding the arena. When the participants indicated that they had completed exploring the room, the visible trials commenced. There were four "visible platform" trials in which a large circular green platform was present on the floor of the arena that the participants were instructed to go to. They also completed a practice drop-the-seed (DTS) trial. Participants picked up seeds by walking over them and moved to the still-visible platform to plant the tree. These visible maze trials tested understanding and mastery of the non-spatial aspects of the task as well as operating the joystick.

Strategy Choice Test (Dual-strategy Maze): The Dual-strategy trials were designed to test the participant's ability to navigate to a location utilizing landmark allocentric or object egocentric stimuli. Participants completed 10 trials in the Ambig maze so as to give ample opportunity for the strategy to be chosen and efficiently adopted. Similar to the MWM, participants were required to repetitively navigate to a stationary invisible platform (either the center of the SE or NW quadrant) from random starting positions. This discouraged memorizing motor patterns and required use of a navigational strategy (see Figure 2).

In order to indirectly measure knowledge of the platform location when navigating utilizing landmark or object stimuli, a probe trial was conducted at the end of the invisible trials and was quantified as dwell time spent in the correct quadrant. This trial was the same as the invisible trials however the platform did not appear, even when the participant walked over it, until 50 seconds into the trial. Participants were reminded to continue searching until they had found the platform.

To determine strategy selection, during the final test (a differential drop-the-seed: dDTS) in the Dual-strategy maze, participants were instructed to pick up several seeds off of the floor

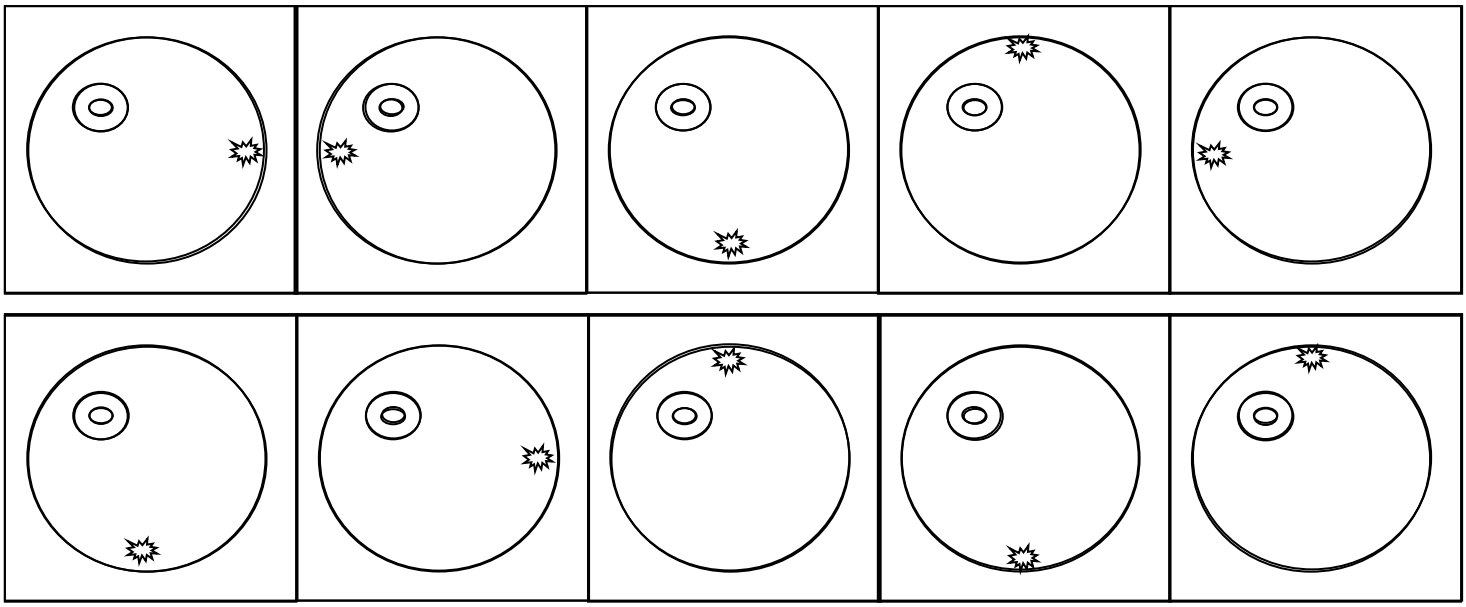


Figure 2. Start positions in the Dual-strategy maze
Start positions change for each trial. The large circle marks the invisible platform location, the small circle shows the constant location of the platform and the asterisk marks the different start positions.

and to plant the seeds (similar to the "practice drop the seed trial") as close to the platform as possible, as it never rose up out of the floor. This task determined strategy because the surrounding landscape remained the same in this trial however the objects were rotated 180^{o} along the arena wall, so that the cue object (steel box) was located in the quadrant opposite the location of the platform in all previous trials (see Figure 3). The dDTS required the participants to plant the seed marker according to the strategy they were using during the last trials, either according to landmarks (allocentric) or objects (egocentric) Thus, it was used as a relatively objective measure of preferred strategy (object-oriented vs. place-oriented) at the end of all invisible trials. The dDTS was scored by the second researcher from 0 to 7 using one of two bull's eye target scoring systems either over the platform according to allocentric or egocentric

stimuli. If placed according the allocentric landmarks participants were given a score from zero to seven; in contrast, if the seed was placed according to the egocentric object stimuli the participant was given a score of zero to minus seven. Participants who scored between three and minus three on this task were determined to show unclear strategy selection and were not included in analysis.

Figure 3. The DTS Trial and scoring

On drop-the-seed (DTS) trials, participants indicated where they thought the platform was located by picking up a seed from near the start location and moving to where they thought the platform was on previous trials. Bull's eye targets fill two opposite quadrants and are not visible during the trial. Target on right is in location of platform relative to room cues; target on left is in front of the object which on previous trials had been located on the opposite side of the arena. Performance is scored by according to whether participant dropped the seed relative to room cues, or object on wall, with a score ranging from 7 (bull's eye) to 1 for the outer ring and 0 for outside the target (and quadrant).

Place Navigation Test (Place Maze): In order to assess allocentric gaze patterns after all trials in the visible and Dual-strategy maze were finished, participants completed ten trials in the Place maze. The Place maze trials only provided landmark cues therefore forcing participants to learn and exhibit allocentric strategy gaze fixation. Participants again completed a knowledge probe trial implicitly testing knowledge of the platform location using only landmark cues as

well as a DTS trial that explicitly tested knowledge of the platform location using only landmark cues.

The platform was always situated in the center of either the South East (SE) or North West (NW) quadrant in each trial of the Dual-strategy maze and was countered with the platform in the NW or SE corner in the Place maze. For example, if a participant started with the platform in the SE quadrant of the Ambig maze it was countered with the platform in the NW quadrant of the Place maze, and the next person started with the platform in the NW quadrant in the Ambig maze countered with the platform in the SE quadrant of the place maze. This measure was taken to account for any differences in ease of finding the platform in one quadrant over the other.

Ancillary Tasks

Where's-the-Water: In order to test the participants' sense of "presence" within the virtual environment after all of the maze trials are completed, the participants were asked several questions relating to where the water was while facing different directions within the virtual maze.

Room reconstruction: To test the quality of participants' cognitive map they were provided with eight laminated images of the landscape surrounding the virtual maze, four images of the room walls, and a scale-image of the platform in order to reconstruct their environments topographically. They also received an image of the arena floor containing the arena wall and the eight proximal objects.

Object recognition: Participants' object memory was also tested with the object recognition task. They were presented with 16 objects and asked to pick the objects that appeared in the Ambig maze and it was scored according to correct, incorrect, flanking and cue objects identified.

Questionnaire: In order to determine whether results were influenced by confounding variables, participants were asked to complete a questionnaire on background information specifically their experience with computer games such as preference for two- or three-dimensional games, how often they play these types of games, and their overall familiarity with game controllers. There was also a self-report questionnaire on strategy and cue use.

Behavioural data analysis

Participants were grouped by strategy selected during the dDTS task following the Dual-strategy maze (either placing the marker according to the room or object). The simple main effects in performance between the Allo and Ego strategy groups were analyzed using independent samples t-tests on latency, distance and dwell time. These dependent variables were analyzed by averaging over Dual-strategy maze trials 2 to 10. Performance data from the first trial was excluded because at this point participants were searching for an unknown platform location, in contrast to subsequent trials where participants were returning to a previously encountered place and are therefore using different cognitive processes. This data was analyzed by independent samples t-tests. Gender was also analyzed as a factor influencing performance. The simple main effect between males and females was analyzed by independents samples t-tests. The interaction between gender and strategy was analyzed also analyzed using a 2x2 ANOVA.

Eye tracking data analysis

Gaze position (GP) data was analyzed during the first second of each trial. The first second of each trial has previously been found to be the interval during which participants are gathering task relevant information in order to successfully find the hidden platform (Livingstone-Lee et al., 2011). Data from the first second was analyzed as vertical coordinates

('y' values) and by combining horizontal and vertical coordinates into regions of interest (ROIs). Individual participants' GP was organized separately as 'x' coordinates and 'y' coordinates on a spreadsheet; 'x' data ranged from 0 to 800 and 'y' ranging from 0 to 600, (0, 0 equal to the top left hand corner of the screen). After the initial analysis of horizontal and vertical data separately we defined six regions of interest (regions measuring 160x100). We further condensed the data into on and off center and specified the high on center ROI as important for individuals navigating allocentrically and the low off-center region as important for individuals navigating egocentrically.

The first step in organizing the vertical GP data was to correct the data for vertical lag. Subtracting the individual participants' y-midpoint from the computers y-midpoint on the screen did this. The difference value was then subtracted from all other vertical gaze points. After baseline correction was complete we were able to establish individual vertical gaze position averages for each participant. For vertical position analysis the important information was whether participants were looking above (0-300) or below (301-600) the horizon because the strategy specific stimuli were separated by the vertical midpoint on the computer screen (see Figure 4). Data was also individually converted to frequency distributions in each 5x5 pixel region on the screen. This data allowed the calculation of percentage of gaze spent above the horizon, greater than 50%. An independent samples t-test was conducted to determine whether there was a significant difference in vertical GP between the Allo and Ego groups.

Finally, horizontal and vertical GP was combined and binned to create six regions high or low, left, center and right regions (160x100) (see Figure 5). This data was then condensed into frequency of gaze spent in hi or low, on or off-center regions. Specific regions were defined as strategy specific and most interesting in analysis. These regions included the High on-center

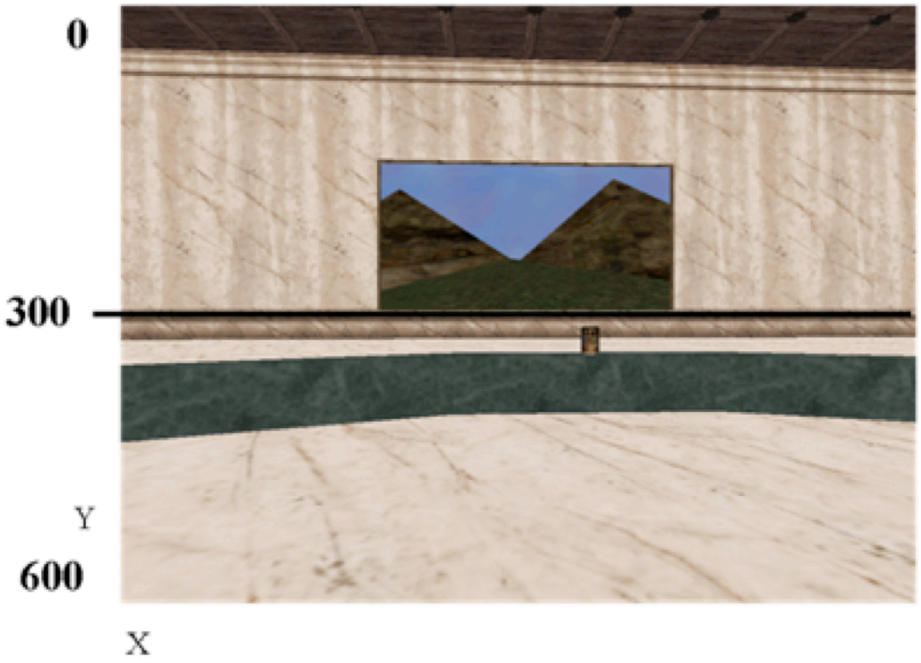


Figure 4 The horizon.
The horizon line was located at vertical coordinate 300. Allocentric landscape features were located above the horizon while all egocentric object features were located below the horizon.

region, localized at a position where participants could see the surrounding landscape allowing allocentric navigation, and the low off-center regions, localized at a position where participants could see the object cues allowing egocentric navigation.

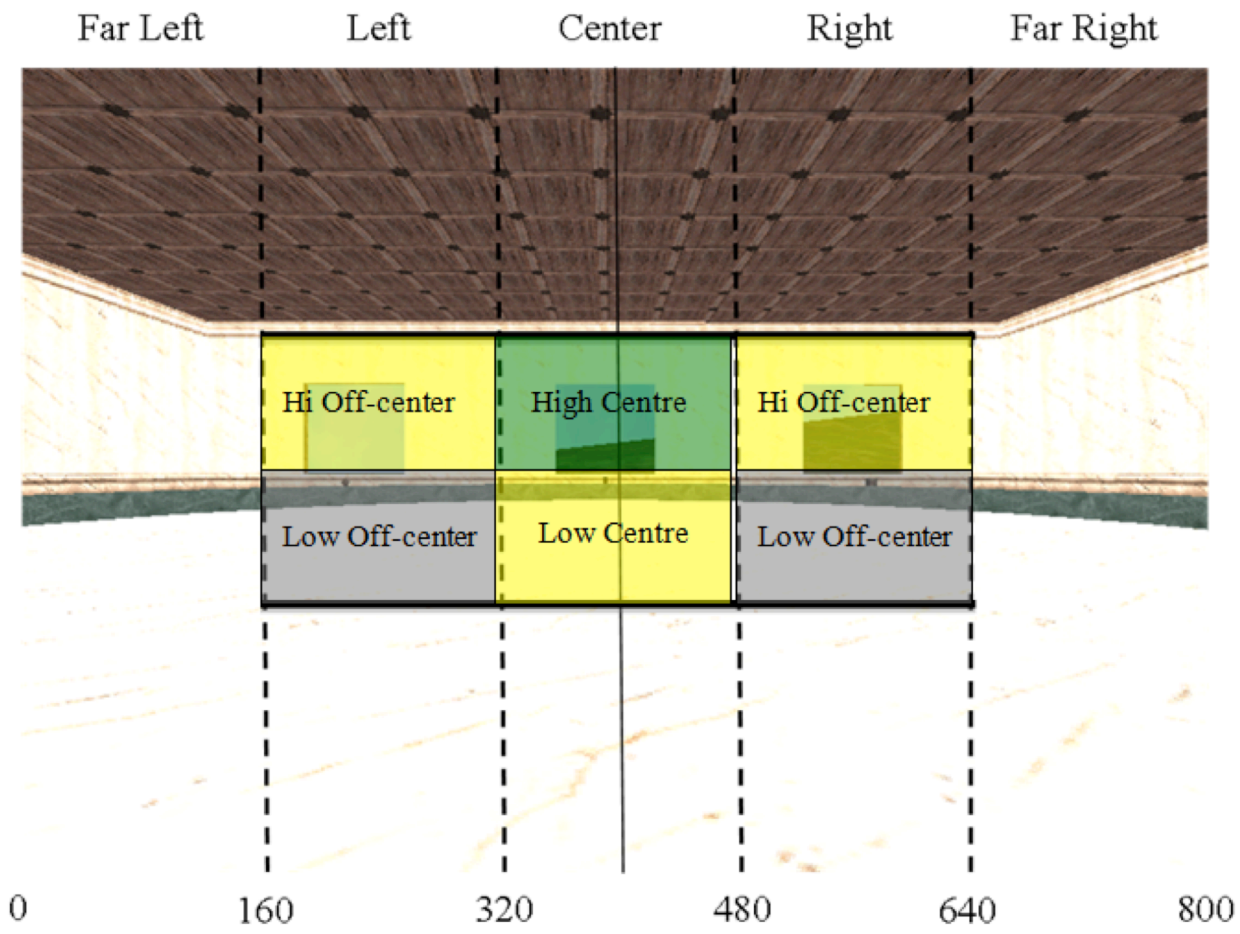


Figure 5. Regions of Interest

The landscape cue was located in the hi-center of the screen at the start of every trial while the object cue was located in either the low right or left off-center region.

Analysis of strategy acquisition from gaze data

In order to determine differences in gaze based on strategy use, gaze during the first second of trials 2-10 were compared between strategy groups (as determined by dDTS score). Vertical gaze was compared as the average vertical gaze between the two groups but also as average percentage of gaze spent above the horizon, statistically analyzed by independent samples t-test. Also, gaze spent in ROI's was analyzed by determining the discriminant ratio of time spent in the high on center region compared to the low off center regions, again using an independent samples t-test.

Gaze between groups was also compared to gaze in the place maze where an allocentric strategy was forced. If there are indeed two strategies being used then the Allo group's gaze patterns should be similar to gaze in the place maze while the egocentric group's gaze pattern should not be similar to gaze in the place maze. Horizontal, vertical and regions of interest during the first second were compared between the two strategy groups using an independent samples t-test.

Strategy adoption

The purpose of the current study was to analyze strategy adoption using gaze patterns to show environmental feature use on a trial-by-trial basis. In order to measure adoption, average gaze patterns were measured for individual trials during the first second, and the trial averages were compared between strategy groups. Strategy adoption was analyzed as the change in vertical gaze position and percentage above the horizon. Adoption was also measured as ratios of GP spent in the ROIs, particularly the hi on-center and low off-center regions. Due to the close proximity of the egocentric cues to the horizon in comparison with the allocentric cues, vertical gaze position could not be accurately compared. Instead the change in ratio of time spent in regions of interest was taken as a measure of adoption. For each individual 80% of the asymptote of gaze spent in ROIs was used as a critical value for acquisition. The trial at which asymptotic gaze was reached and maintained (second consecutive trial during which asymptotic gaze had been achieved) was taken for each individual participant. This trial was averaged for each strategy group to determine whether one strategy was adopted earlier than the other.

Gender was also analyzed as a factor in gaze however it was secondary so results were included in the appendices. All analyses were conducted in the same way as for strategy. Comparisons were conducted between horizontal, vertical and gaze in regions of interest using

independent samples t-tests. Data was again compared to determine overall differences (tr 2-10) as well as to determine differences in acquisition (over trials). The interaction between gender and strategy on overall gaze as well as acquisition was also analyzed using an ANOVA.

Orientation Strategy

An emergent analysis of the gaze position data suggested a difference in strategy measured by the strategy probe trial and that indicated by vertical gaze position. We defined a criterion using vertical gaze position during the last three trials. If participants maintained more than 50% of gaze above the horizon in each of the last three trials during the Dual-strategy maze they were categorized as Hi-Lookers in contrast to Lo-Lookers who maintained less than 50% of gaze above the horizon on the last three trials. A third group was comprised of participants who switched proportions of gaze spent above the horizon from, above to below, during the last three trials, this group was named the Switchers. Overall differences in vertical gaze were not compared since vertical gaze was used as criteria for defining the groups however vertical gaze as well as gaze in regions of interest were analyzed over trials to determine differences in strategy adoption. Performance was also analyzed between participants grouped by orientation strategy. Similar analyses were conducted on latency distance and dwell between the groups using independent samples t-tests.

Results

Behavioural results

Out of 80 participants, only 55 (30 males, 25 females) were included in analysis due to technological difficulties as well as unmet experimental criteria (English as a first language, no history of brain trauma). Average age of these participants was 20.47 (Females = 19.95, Males 21.09).

All participants successfully completed the visible platform trials. Mean latency to the platform on the visible trials was 4.05 (*SEM* = 0.23). Performance during visible platform trials showed that all participants were able to use the joystick and understand the instructions necessary to complete the virtual tasks.

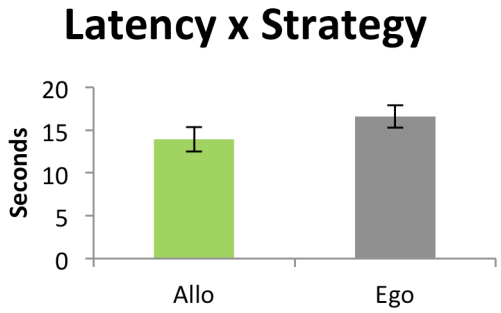
Based on how participants navigated during the strategy probe, more participants chose to navigate allocentrically than chose to navigate egocentrically. (see Figure 6). Out of 55 participants included in analysis, 32 (58%) chose to navigate allocentrically (placed the marker according to the room/landscape) while only 16 (29%) chose to navigate egocentrically (placed their marker according the repositioned object cue). An additional 8 (14%) participants did not place the marker in either correct quadrant, indicating they did not learn the platform location and therefore have been excluded from further analysis.

Figure 6. Strategy Selection
Most participants chose to navigate allocentrically. There was no gender bias, indicated by similar proportions of males and females choosing to navigate both allocentrically and egocentrically.

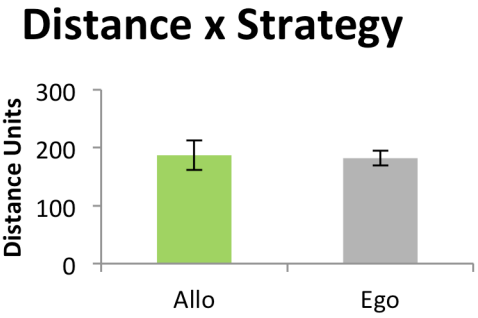
Navigational strategy was not clearly indicated by self-reports of strategy use. Many participants listed multiple features used to navigate by, making it very difficult to separate participants into strategy groups by self-report alone. However, this could be an indication that

one strategy is not used throughout the entire task, rather both strategies are adopted and one simply predominates. Regardless, the strategy probe trial allows a more objective way to indicate the strategy predominately used and is preferred to self-report measures.

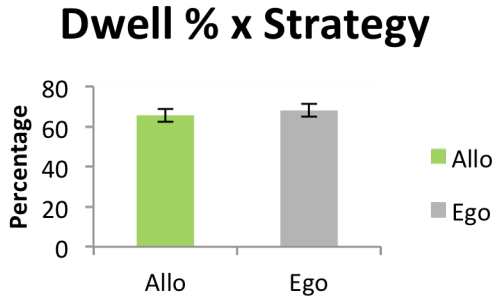
Strategy determined by dDTS was not a main factor determining performance which was expected since the maze was designed to allow navigation using either strategy (see Figure 7). Overall performance on trials 2-10 was similar between the Allo (latency: M = 12, *SEM* = 0.89, distance: M = 168, SEM = 14.98, dwell: M = 66%, SEM = 3.28%) and Ego groups (latency: M = 16, *SEM* = 0.99, distance: M = 187, SEM = 12.62, dwell: M = 68%, SEM = 3.15%) (latency: $t(47) = 1.23$, $p < .22$, distance: $t(47) = 0.17$, $p < 0.87$, dwell: $t(47) = 0.34$, $p < 0.74$). Also, both groups showed typical learning curves for distance and latency (see Figure 8), though the Allo group achieved asymptotic latency slightly earlier (trial 6) than the Ego group (trial 7) (see Figure 8).



a)



b)



c)

Figure 7. Navigational Performance

These figures show the performance between strategy groups from trials 2-10. There was no significant difference in performance between strategy groups. (a). There was no significant difference between mazes in latency, (b), distance traveled to the platform, (c), or time spent searching the correct quadrant on the probe trial.

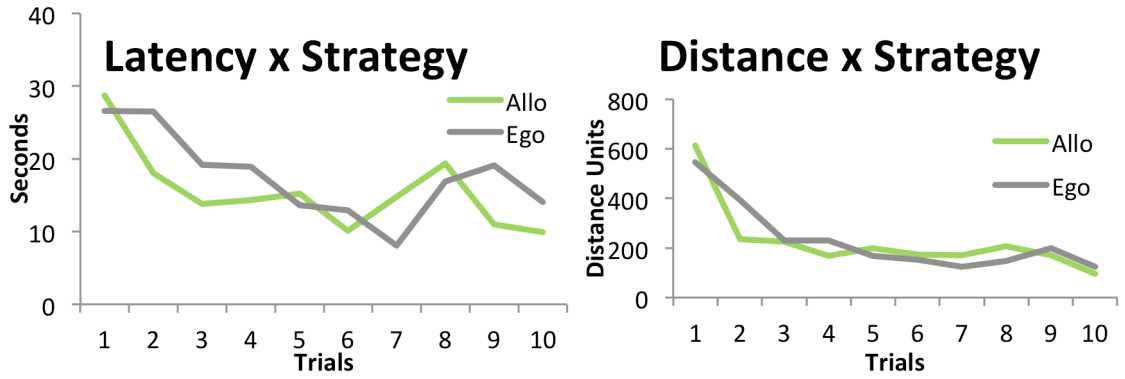


Figure 8. Adoption by behavioural performance.

Change in behavioural performance over trials as shown by latency (A) and distance (B) averaged by strategy groups. Note that performance was asymptotic for both Latency and Distance around trial 5-7 in both allocentric (Allo) and egocentric (Ego) strategy groups.

Somewhat surprisingly, there was no gender bias in strategy selection (see Figure 9). On the strategy probe trial that determined environmental feature use, 18 out of 30 men (53%) selected an allocentric strategy, whereas 9 out of 30 men (30%) selected an egocentric strategy. In contrast, 13 out of 25 women (52%) selected an allocentric strategy, whereas 7 out of 25 women (28%) selected an egocentric strategy. Three males and five females did not place the marker in either correct quadrant, indicating they did not learn the platform location and therefore have been excluded from further analysis. Note that of those who had learned the platform location, a similar proportion of males and females chose to use an allocentric and an egocentric strategy (Allo: 53% males, 52% females vs. Ego 30% males, 28% females) indicating no gender bias and perhaps indicating that the maze itself was allocentrically biased.

Navigational performance seemed to be influenced more by gender when gender and strategy were combined, rather than by each factor individually. Similar to between strategy groups, there were no differences in performance between genders; both took similar amounts of time and traveled similar distances to the platform (Male: Lat: M = 13 *SEM* = 2.24, Dis: M =

190, *SEM* = 38.94, Dwell: M = 66%, *SEM* = 4.92%, Female: Lat, M = 17, *SEM* = 3.07, Dis: M = 251, *SEM* = 63.86. Dwell: M = 67%, *SEM* = 4.48) (Latency: $t(47) = 0.39$, $p < 0.70$) (Distance: $t(47) = 1.89$, $p < 0.07$)(fig 5 a, b, and c). Both genders also had similar knowledge of the platform location ($t(47) = 0.07$, $p < 0.94$) (see Figure 9). Adoption as indicated by performance seemed to be similar by gender however males did seem to reach asymptotic performance slightly earlier than females (see Figure 10).

In terms of an interaction between strategy and gender, males navigating allocentrically tended to be more efficient than all other groups (see Figure 11). Males navigated slightly faster than females in both the Allo and Ego groups (Allo: Males: M = 12, *SEM* = 3, Females: M = 16, *SEM* = 4, Ego: Males: M = 15, *SEM* = 4, Females: M = 19, *SEM* = 6) although there was a close to significant difference in latency between males and females navigating allocentrically (latency: $t(47) = 1.86$, $p < 0.07$). Gender and strategy for distance and dwell percentage was also not significant, although Ego females traveled less distance and spent more time in the correct quadrant than Allo females (Distance: Allo: M = 257, *SEM* = 86, Ego: M = 240, *SEM* = 87, Dwell: Allo: M = 69%, *SEM* = 6%, Ego M = 62%, *SEM* = 8%) in contrast to Allo males who traveled less distance and spent more time in the correct quadrant than Ego males (Distance: Allo: M = 181, *SEM* = 50, Ego: M = 210, *SEM* = 61, Dwell: Allo: M = 62%, *SEM* = 6%, Ego M = 74%, *SEM* = 8%) (see Fig 7 b and c). However, the interaction between strategy and gender was not significant ($F(47) = .093$, $p < 0.76$. This was possibly due to high intersubject variability, especially in the male Allo group, and small n for both genders in the Ego group. Adoption as indicated by performance was similar between gender and strategy groups however Ego females did seem to reach asymptote later than the other groups (see Figure 12). This was not reflected in overall performance due to variability of performance in the other groups in later trials.

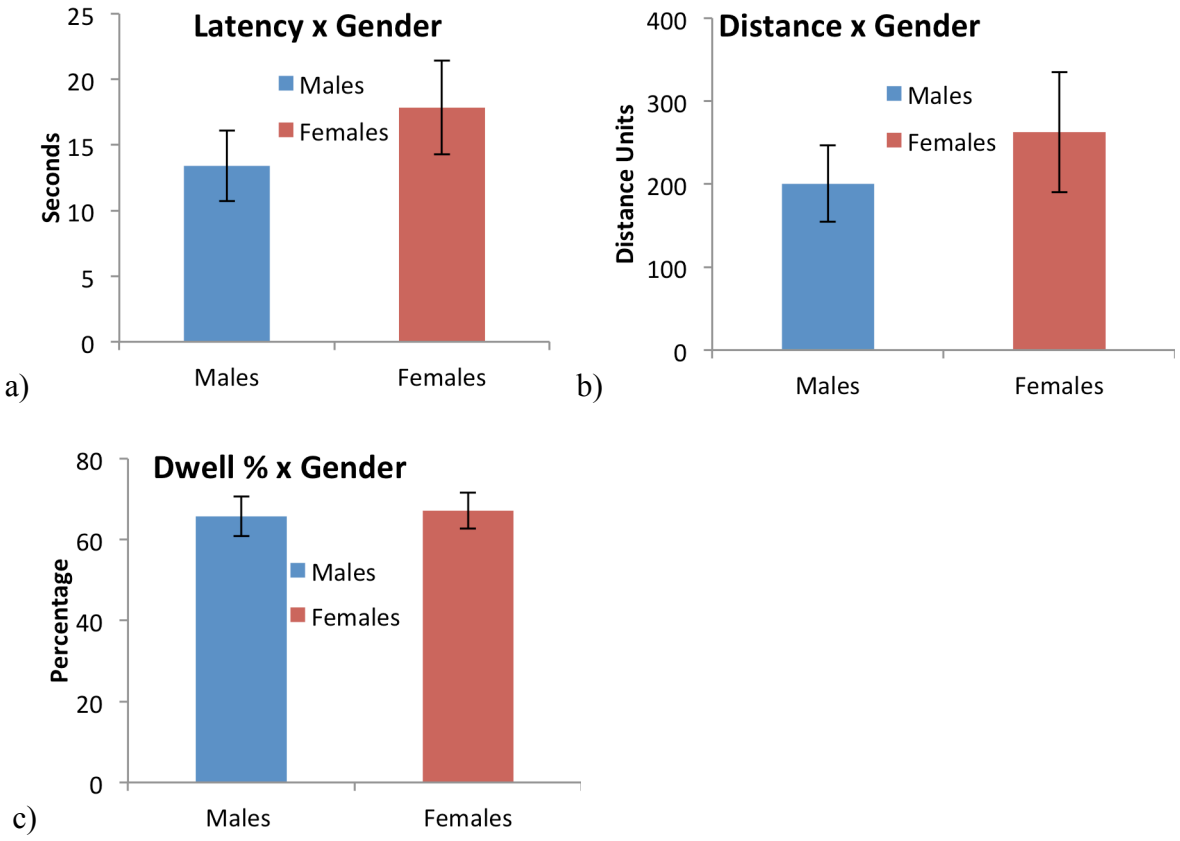


Figure 9. Performance by Gender.

Performance grouped by gender. There are no significant differences between latency (a), distance (b), or dwell percentage (c) by gender.

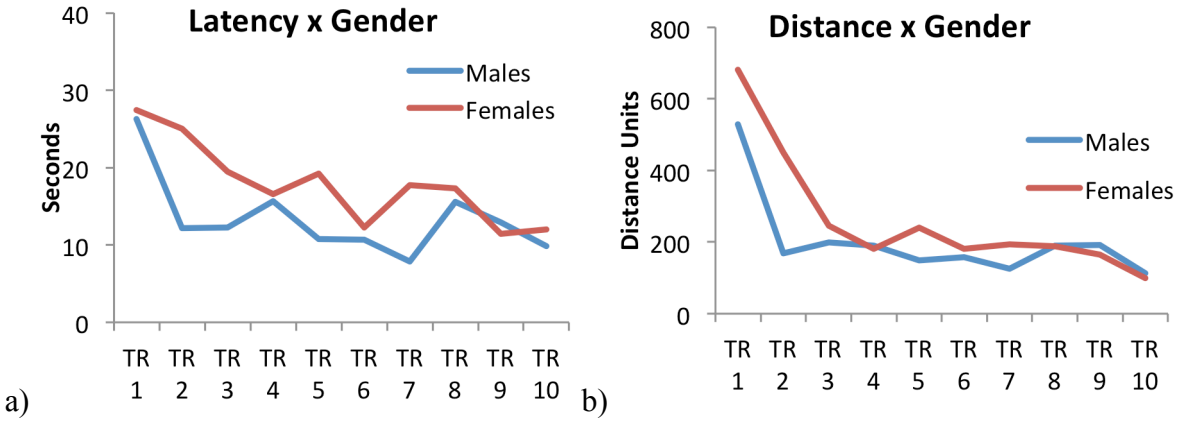


Figure 10. Behavioural Adoption by Gender Performance

Both males and females show similar decreases in both latency and distance to reach the platform. Females take a little longer to reach asymptotic performance, but both genders are arguably asymptotic by trials 5-7

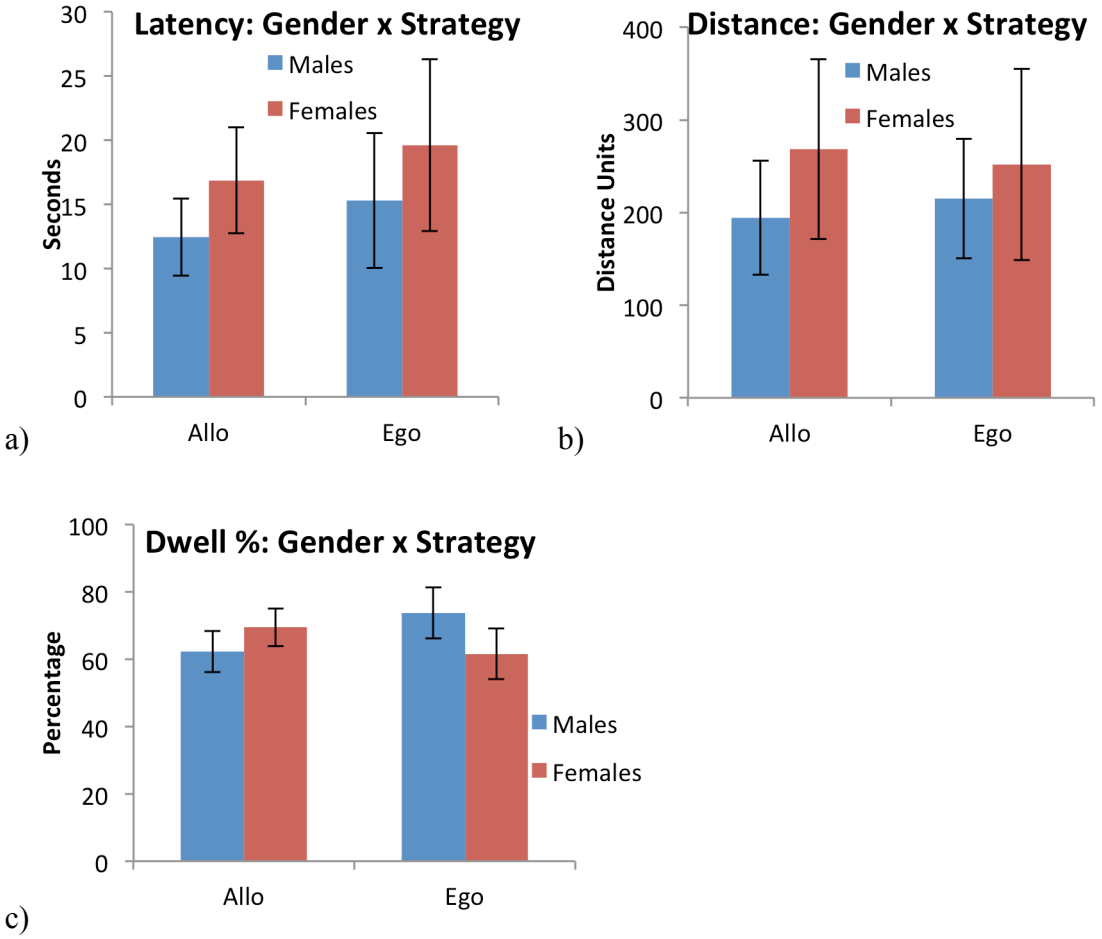


Figure 11. Behavioural Performance, Strategy by Gender.

Performance difference grouped by gender and strategy. Note the significant differences in latency (a) between males and females in the Allo group and between males in the Allo group and females in the Ego group as well as the significant difference in distance (b) traveled between males and females in the Allo group but no significant differences in dwell percentage (ns p=.07).

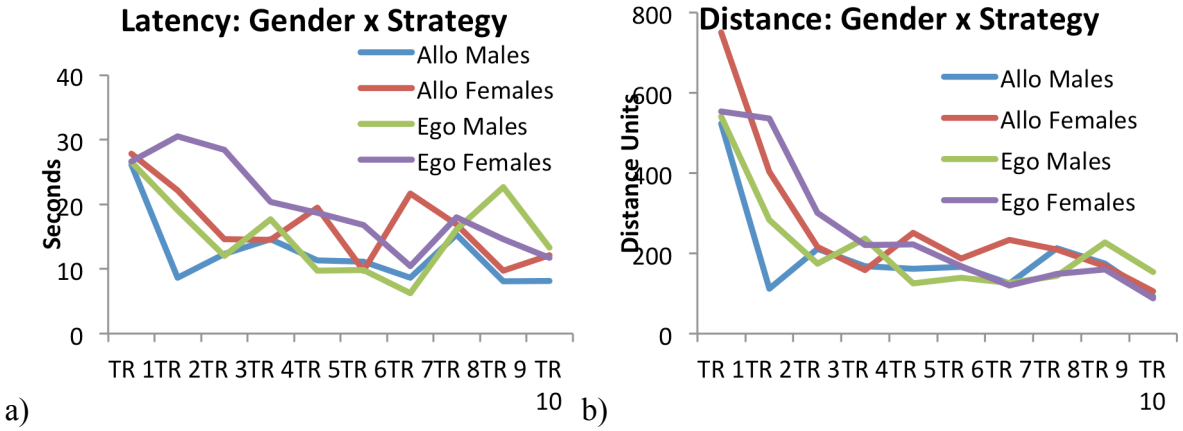


Figure 12. Behavioural Adoption, Strategy by Gender.

Acquisition curves grouped by strategy and gender in the Ambig maze. Notice the similarities in latency (a) and distance (b) when grouped by strategy and gender. The one group that looks slower than the others is Ego-Females (n=7).

Strategy was not a factor in place maze performance which was expected since it was completed as a comparison maze and forced the use of an allocentric navigation strategy in all participants. There were no differences between strategy groups in either latency ($t(47)$ = .1.04, p < 0.30) or distance ($t(47)$ = .68, p < 0.50). Based on previous work we expected gender to be a factor in the place maze however performance was not significantly different between males and females in either latency ($t(47)$ = 0.54, p < 0.58) or distance ($t(47)$ = 0.43, p < 0.67).

Eye movement results

Overall Navigational Strategy

Participants gathered task relevant information during the early stages of the trial. This was confirmed by a slight upward trend in vertical gaze position at the beginning and a downward trend at the end of the first second especially in the Place maze (see Figure 13). This was similar to previous results that also found that the first second was most indicative of strategy specific gaze (Livingstone-Lee et al., 2011). The shift in gaze from low to high and then back to low indicated that participants needed only a second or less to gather information regarding environmental feature location in order to find the hidden platform. This validates the decision to confine analysis of gaze position to the 1st second.

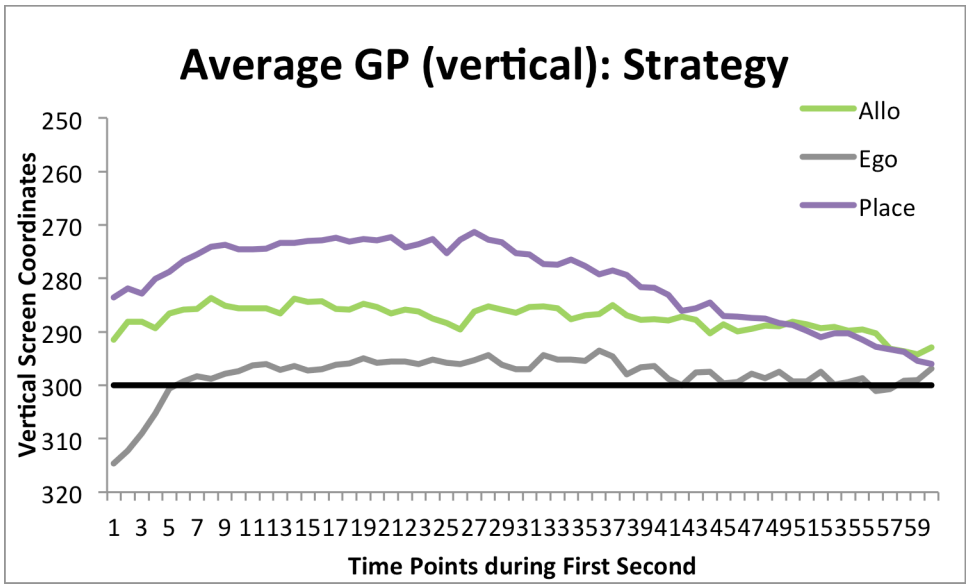


Figure 13. Average Vertical Gaze Position

This figure shows the average gaze positions across all trials between the strategy groups as well as the average gaze position for all participants in the forced allocentric strategy place maze. The allocentric gaze is well above the horizon similar to average gaze in the place maze while egocentric gaze remains near the horizon.

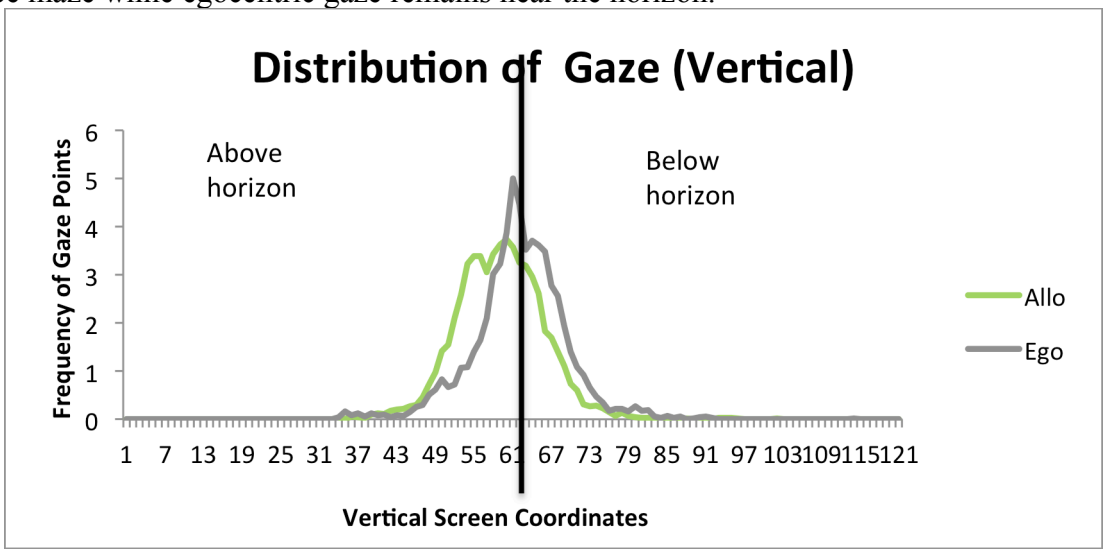


Figure 14. Average Frequency Distribution above the Horizon.

Average frequency distribution of gaze positions above or below the horizon for Ego and Allo groups. Gaze position for the allo participants is distributed higher (i.e., more above the horizon) than that of the Ego group. The Allo group looks above the horizon more often than the Ego group.

Heat maps give a qualitative illustration (see Figure 15) of how gaze was distributed during the initial (orientation) second of each trial (see Figure 14). These indicate that gaze position was affected by strategy. The Allo group appeared to have a higher central gaze concentration in contrast to a low multimodal distribution for the Ego group. The heat maps showed that gaze corresponded to high central gaze that gave a view of the outside environment whereas a lower multimodal gaze distribution gave a view of the objects perched on the arena wall.

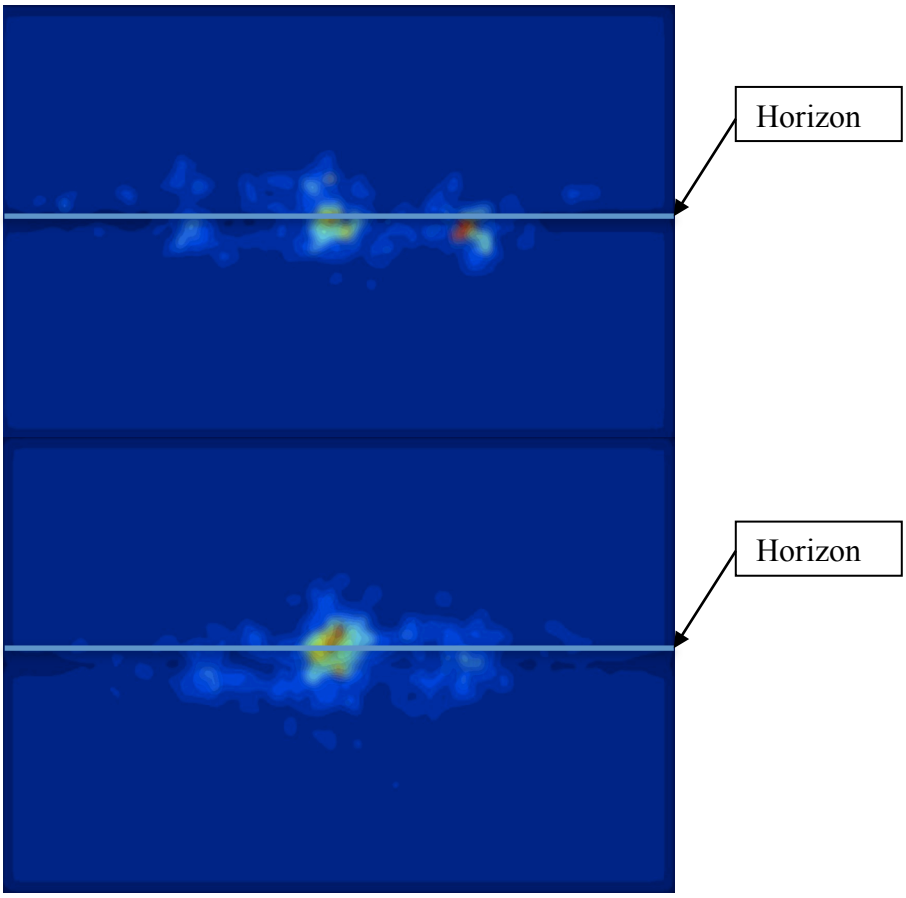


Figure 15. Heatmaps by Strategy Group.
Heatmaps of gaze during the first orienting second. The Ego group (top figure) has low and dispersed gaze during trials 7-11 whereas the Allo group has high central gaze during trials 7-11.

Gender

There were small but non-significant gender differences in gaze position. Females seemed to gaze slightly higher (M = 297, *SEM* = 7.75) than males (M = 311, *SEM* = 6.40) (*t(47)* = 1.53, p < 0.13). The current study did not analyze gender as a main factor in gaze position, see appendix B.

Strategy

The Allo group looked at the external landscape above the horizon more often while the Ego group looked at the object cues below the horizon more frequently (see Fig 16). The Allo group had a higher average gaze position (M = 289, *SEM* = 4.82) and a higher frequency of gaze above the horizon (M = 65%, *SEM* = 6.08%) compared to the Ego group who had a lower average gaze position (M = 300, *SEM* = 7.35) ($t(47) = 1.67$, $p < 0.10$), and lower frequency of gaze above the horizon (M = 49%, *SEM* = 9.01%) (*t(47)* = 5.08, $p < 0.03$) (see Figure 16). This difference suggested the use of strategy specific cues since allocentric environmental features were located above the horizon while egocentric environmental features were located below the horizon.

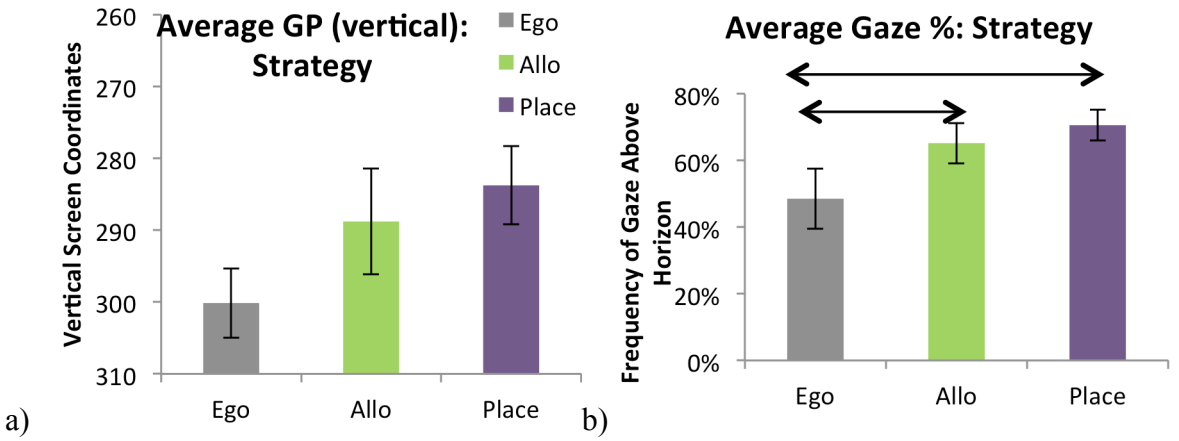


Figure 16. Average Vertical Gaze Position.
Average gaze position and average gaze percent for trials 2-10. The differences are statistically significant, Allo gaze above and Ego gaze being below the horizon ($p < .05$ ↔).

The place maze comparison only presented allocentric environmental features thereby forcing allocentric gaze patterns (see Figure 16). The Allo group showed a vertical gaze pattern that was similar to all participants gaze in the place maze (Gaze average: M = 281, *SEM* = 7.1, gaze %: M = 71%, *SEM* = 5%) (Gaze average: $t(47) = 1.18$, $p < 0.24$, Gaze %: $t(47) = 0.97$, $p < 0.34$). In contrast, the Ego group had a very different vertical gaze pattern than all participants in the place maze ($t(47) = 3.1$, $p < 0.004$). This suggests that feature use between the Allo group and all participants in the place maze was more similar than between the Ego group and all participants in the place maze. This also suggests that the Allo group is using allocentric features.

Horizontal gaze position

Due to the difference in location of strategy specific environmental features at the beginning of each trial, landscape visible in the center of the screen and objects located in three different points evenly distributed across the horizon, horizontal gaze position was compared between the groups. However, the difference in horizontal gaze distribution was not significantly different between the strategy groups, see appendix A.

Regions of Interest (ROI)

In order to compare overall strategy choice, a new technique was designed that allowed the analysis of gaze within particular regions of the screen. To do this, the display was divided into 6 regions of interest, see methods section for more detailed explanation (see Figure 5). Given that the distal environment was located above the horizon, and meaningful information could be gained centrally, the hi-center was chosen to represent the allocentric region of interest. In contrast, the proximal objects were located below the horizon, and meaningful information could be gained in the off center regions, the low off-center was chosen to represent the egocentric region of interest.

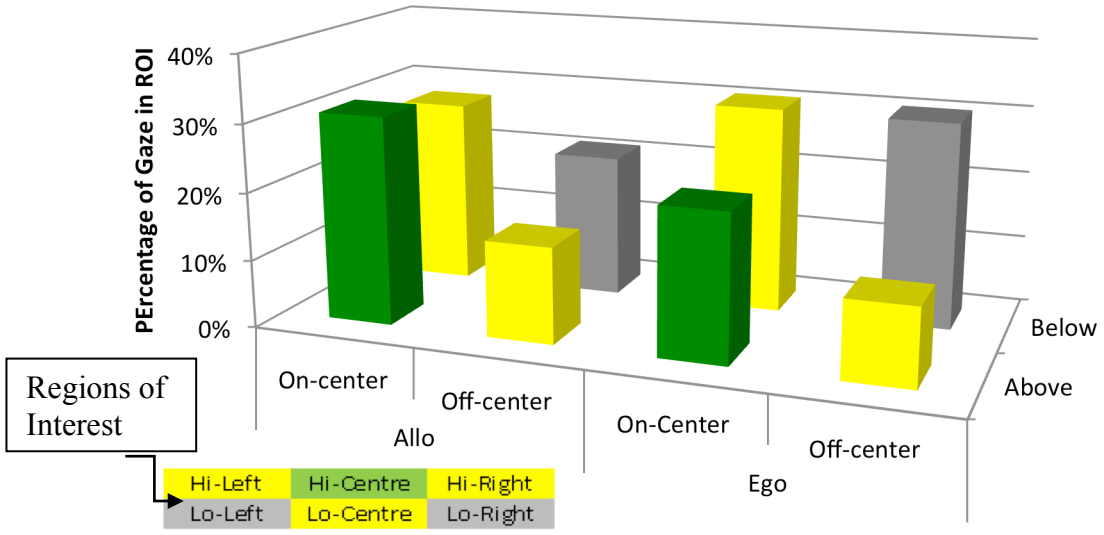


Figure 17. Proportion of Gaze within Regions of Interest
The Allo group spent the most gaze time in the hi on-center region while the Ego group spent the most gaze time in the low off center region.

The Allo group spent the most time gazing at the landscape visible in the hi central region of the screen (green rectangle in figure 17 screen diagram) while the Ego group gazed most often at the object cues located below the horizon and nearer the edges of the screen (grey regions in figure 17 screen diagram) (see Figure 17). This data gives a more clear picture of the groups'

gaze distribution differences and is consistent with the heat maps (see Figure 15) which showed a highly central and above horizon distribution of gaze for the Allo group whereas a low multi modal distribution for the Ego group. These differences were not statistically different between the strategy groups; however, these regions do provide a method of analyzing strategy adoption as a discriminate ratio of gaze time spent in each region over trials.

Strategy adoption

Strategy grouped by dDTS

Adoption of strategy was first examined by grouping participants according to navigational strategy determined by strategy probe (dDTS trial). Adoption was defined as participants increasing gaze spent on environmental features relevant to completing the task. On the first trial, both groups had a gaze position below the horizon. By trial two, both groups showed significantly higher gaze positions (Allo: $t(31) = 3.36$, $p < 0.05$) (Ego $t(16) = 2.98$, $p < 0.05$) (see Fig 18) meaning they realized that in order to finish the trial quickly, they had to use environmental features to navigate by. The Allo group continued to increase their vertical gaze position until peaking at trial five and maintained a similar vertical gaze position for the remaining trials. Similarly, the Ego group fluctuates in vertical gaze position until trial 5 at which point gaze position stabilizes at an average slightly below the horizon for remaining trials. However the Ego group continues to fluctuate in time spent above the horizon over trials. This could possibly be due to the close proximity of the object cues to the horizon, this will be considered in more detail in the discussion section.

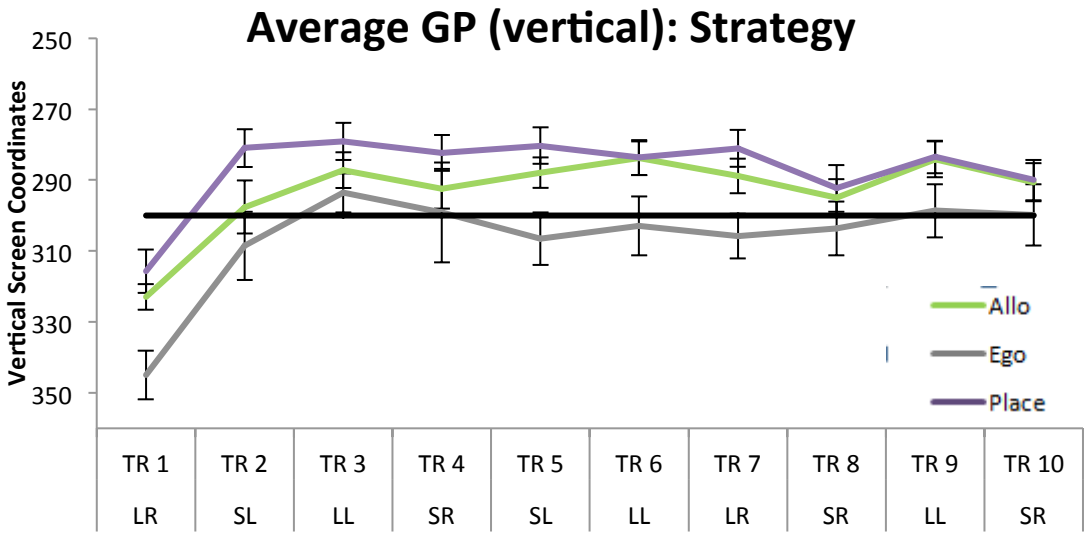


Figure 18. Average Vertical Gaze Position Over Trials

Average vertical gaze position over trials. Both strategy groups begin to show strategy specific gaze early on in trials. Average vertical gaze in the place maze is well above the horizon from trial two. The Allo group shows a gaze pattern that is more similar to gaze in the place maze than the Ego group.

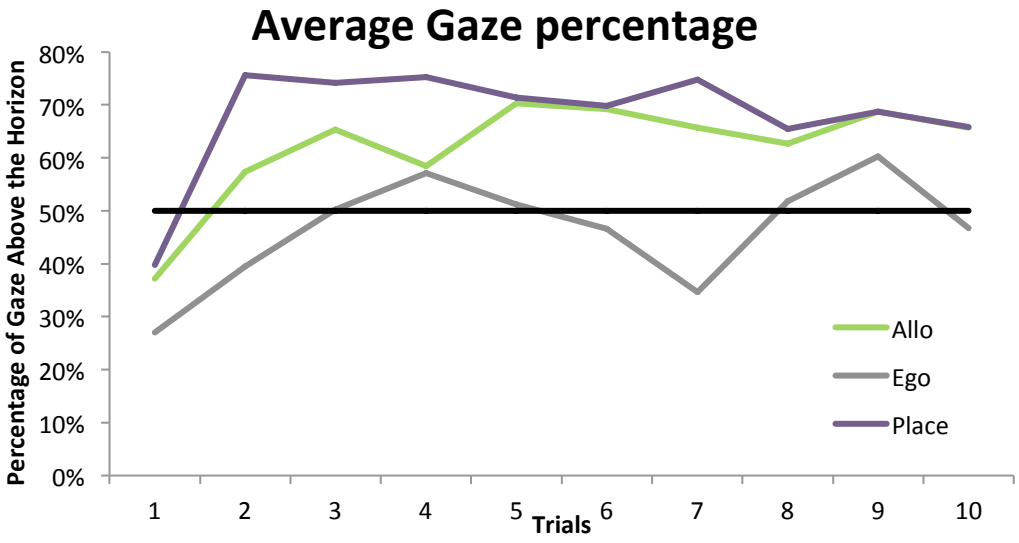


Figure 19. Average Frequency of Gaze Above the Horizon

Average gaze percentage over trials. Both strategy groups begin to show differences in frequency of gaze spent above the horizon early in trials. The Allo group shows a fairly consistent proportion of time spent looking above the horizon however the Ego group tends to fluctuate between above and below the horizon. This may be a result of close proximity of objects to the horizon. Also, gaze in the place maze was mostly above the horizon from trial two and the Allo group shows similar tendencies in comparison to the Ego group.

Strategy group differences in adoption rate cannot be compared using vertical gaze due to the difference in proximity of strategy specific environmental features to the horizon (allocentric features are well above the horizon while the egocentric features are below the horizon however not by a great margin). Both strategy groups begin trials low however on subsequent trials strategy specific changes are evident. With visual inspection we can see that early in trials the Allo group begins to look at the landscape and continue to look at the landscape whereas the Ego group begins to look at the objects early in trials and continue to look at the objects however we cannot quantitatively determine adoption rate since the Allo groups gaze changes more than the Ego group as a function of environmental feature location. This may be due to the difference in vertical location, statistical analyses will show differences inherently as a result of the design of the maze not necessarily because of differences in adoption per say. As such, a different measure of gaze was used to compare strategy adoption.

Horizontal gaze distribution has been shown to be useful in a paradigm where participants are trained in a specific strategy before entering the dual strategy maze. However, in our paradigm where there is no training before participants entered the dual strategy maze, horizontal gaze distribution was very similar between the two groups. For a detailed description and analysis, see appendix A.

ROI

Gaze in regions of interest allowed quantitative analysis of the increasing amount of gaze spent looking at strategy specific environmental features over trials, which allowed us to determine that both participants using an allocentric and an egocentric strategy adopted their strategy at a similar rate. Figure 20 shows that both the Allo and Ego groups quickly increase in amount of time spent in the ROIs looking at the landscape and object features. By trial two both

Allo and Ego groups spend 46% and 52% of gaze respectively within the ROIs. On subsequent trials, percentage of gaze within these regions increases but only slowly until peaking in mid trials. This suggests that both strategy groups learn what features to orient to very early in trials and that they both acquire this knowledge at a similar rate.

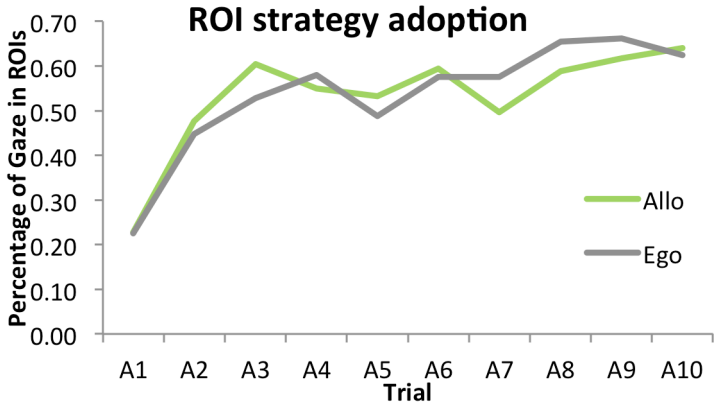


Figure 20. Proportion of Gaze Spent in Regions of Interest Over Trials
Discriminant ratio of time spent in ROIs reaches close to asymptote early in trials and increases throughout the task at a similar rate for both the Allo and Ego groups.

Allo and Ego groups both adopt their chosen strategy early in trials as analyzed by trials to criterion. In order to determine the trial at which a strategy is adopted we determined a criterion (80% of asymptote) and took the average trial during which the criteria was met. Figure 21 shows that, both Allo and Ego groups adopted their chosen strategy by trials 2.7 and 2.8 respectively. The second method of finding the trial during which acquisition has reached asymptote was to take the second consecutive trials at 80% of asymptotic gaze percentage within the ROIs. According to this method Allo and Ego strategy groups generally reach asymptote by trial 6.52 and 6.81 respectively (see Figure 22). These results suggest that both strategies are acquired at the same rate.

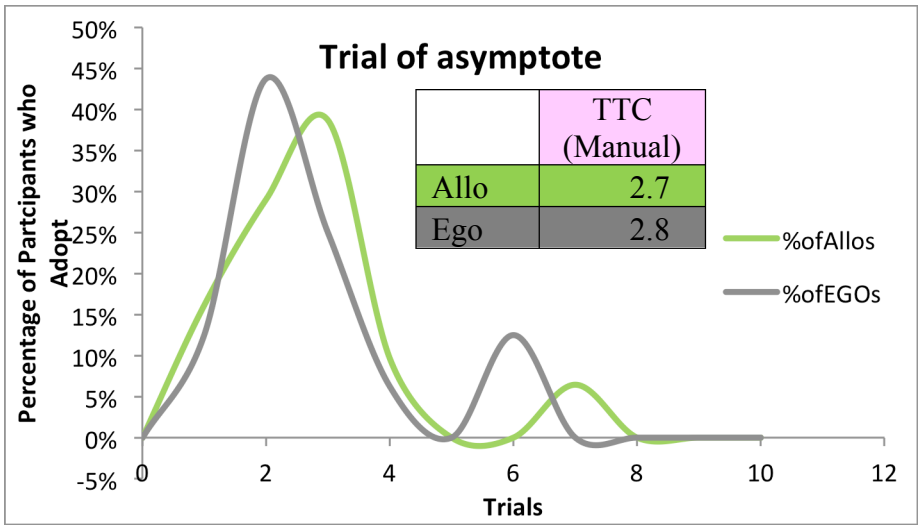


Figure 21. Trial of First Asymptote

Both strategy groups reach their maximum amount of gaze within the ROI's (strategy adoptions) by trial 2.74 for the Allo group and 2.75 for the Ego group.

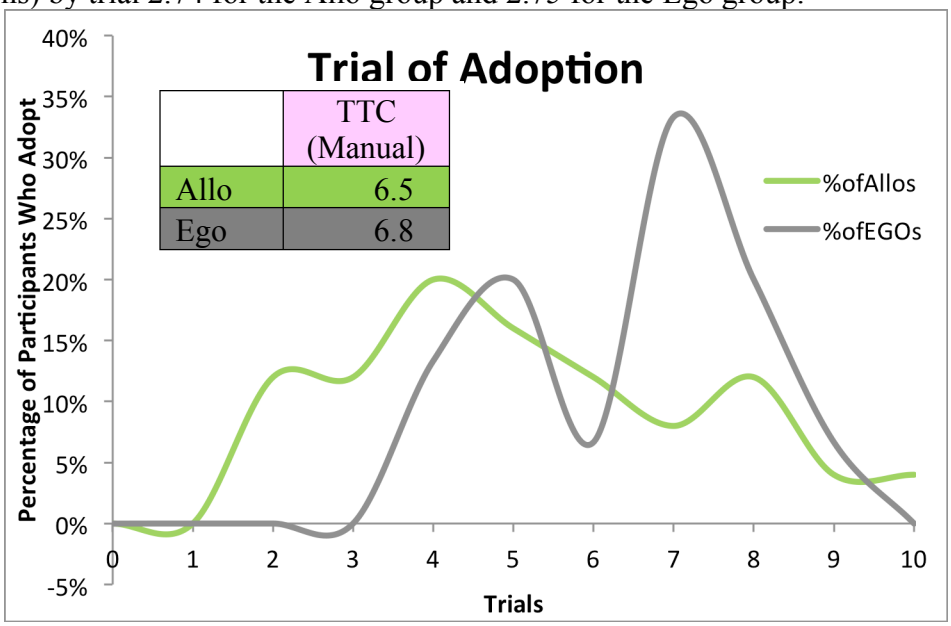


Figure 22. Trial of Second Consecutive Asymptote.

Asymptote was reached and maintained (2 consecutive trials of asymptotic gaze) at a similar time between the Allo and Ego group. The Allo group maintains asymptotic gaze by trial 6.52 and the Ego group maintains asymptotic gaze by trial 6.81.

The concordance between strategies indicated by the strategy probe trial and by average gaze position during trials 2-10. At the start of the experiment it was expected that strategy according to the strategy probe and strategy according to gaze position would be the same (table

A). However, the concordance between the two measures was not high (table B), meaning that some participants used an egocentric strategy according to the strategy probe but gazed high indicating an allocentric strategy. This discordance led to the analysis of groups by strategy determined by vertical gaze position. According to the strategy probe, 31 participants chose to navigate allocentrically whereas 16 chose to navigate egocentrically. However, according to gaze, of the 31 participants who chose an allocentric strategy, 24 had above 50% of their gaze above the horizon and seven had gaze less than 50% above the horizon (see Figure 23). Also, of the 16 participants who chose an egocentric strategy, nine had less than 50% of gaze below the horizon but seven had more than 50% gaze above the horizon.

A)Expected		**dDTS**	
		Allo	Ego
GP	Allo	31	0
	Ego	0	16
B) Actual		**dDTS**	
		Allo	Ego
GP	Allo	25	7
	Ego	6	9

Separation of participants by vertical GP

Analysis of gaze position adoption did not produce as clear differentiation between navigational strategy groups as expected. We wondered whether we had overestimated how tight

the coupling was between navigational strategy, and navigation strategy – that is the strategy (and subsequent environmental features) by which participants navigated (located the goal location) versus orientation strategy – that is the strategy by which people oriented themselves during the first second of the trial, when we were measuring gaze position. We felt that grouping by orientation strategy might give us a better picture of how the ultimate orientation strategy (as shown by gaze position) was adopted. Therefore, we re-examined the data based on what environmental features were being attended to during the first second of each trial late in the session (trials 9-11). To do so, we divided the participants into only Hi-Lookers (above horizon gaze on trials 9-11), only Lo-Lookers (below horizon gaze on trials 9-11) and Switchers (variation in gaze above and below the horizon between trials 9-11).

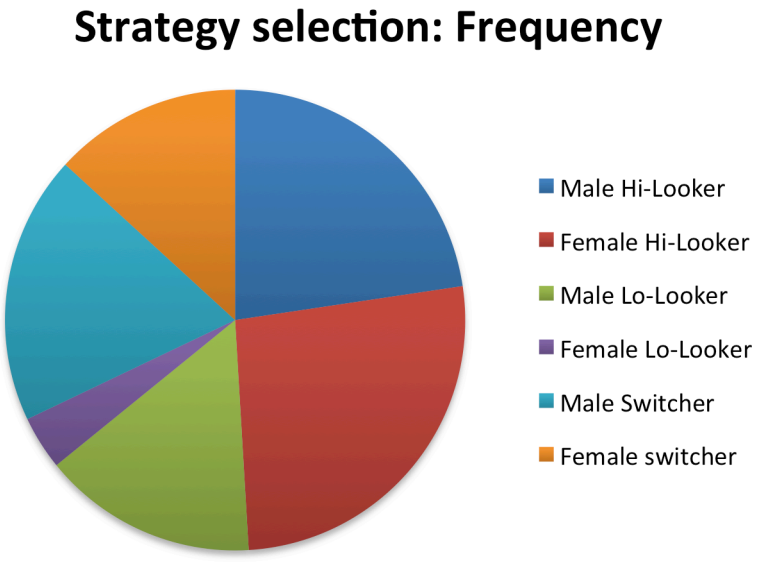


Figure 23. Strategy Selection by Orientation Strategy.
Almost half of the participants used only the landscape features to orient to. Approximately a third used both the landscape and objects and a small number of participants used only the objects to orient.

Participants, when grouped by gaze, were found to begin the task with a bias towards one strategy or the other. Figure 23 shows that the Lo and switcher group both start at similarly low

points (Lo-looker: M = 357, *SEM* = 3.61, Switcher: M = 343, *SEM* = 5.0) however the hi-looker group begins trials with an already hi bias (M = 323, *SEM* = 6.47). All groups quickly increase gaze to a consistent average position, above the horizon for the hi-lookers and below the horizon for both the lo-lookers and switchers.

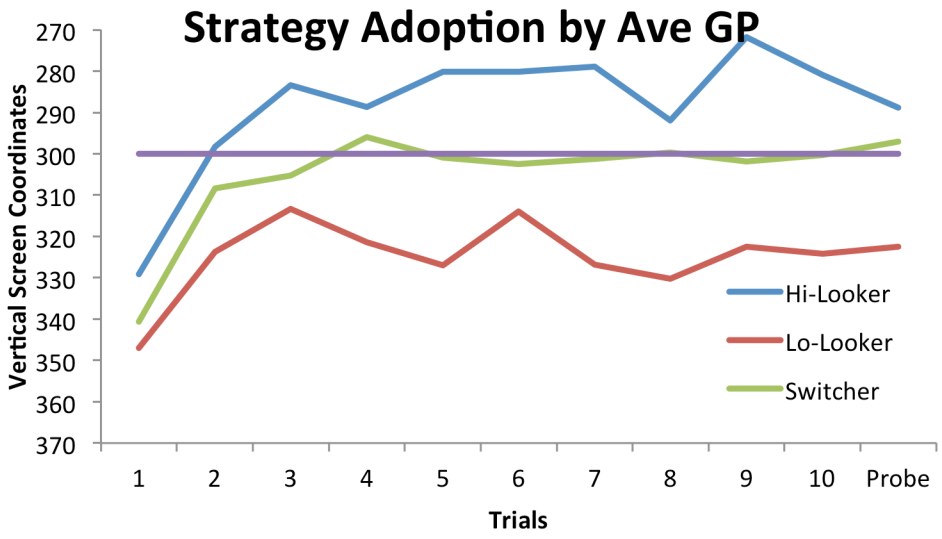


Figure 24. Average gaze between orientation strategy groups
Hi lookers begin the trials with a high gaze bias. The hi-lookers maintain an average gaze position above the horizon whereas the switcher and lo-looker groups maintain gaze below the horizon throughout trials.

Frequency of gaze time spent above and below the horizon increases for the Hi-Looker and Lo-Looker groups respectively whereas the switcher group remains near 50% above and below (see Figure 25). The hi-lookers again begin with slightly more gaze spent below the horizon (41%) and quickly increase to most gaze (77%) above the horizon by trial 3. In contrast, the lo-looker group begins with most gaze below the horizon (25%) and quickly increases to most gaze below the horizon by trial 3 (20%). The switcher group begins with most gaze below the horizon (17%) but does not show a clear preference for gaze above or below the horizon. This is likely due to using both allocentric and egocentric features to orient by.

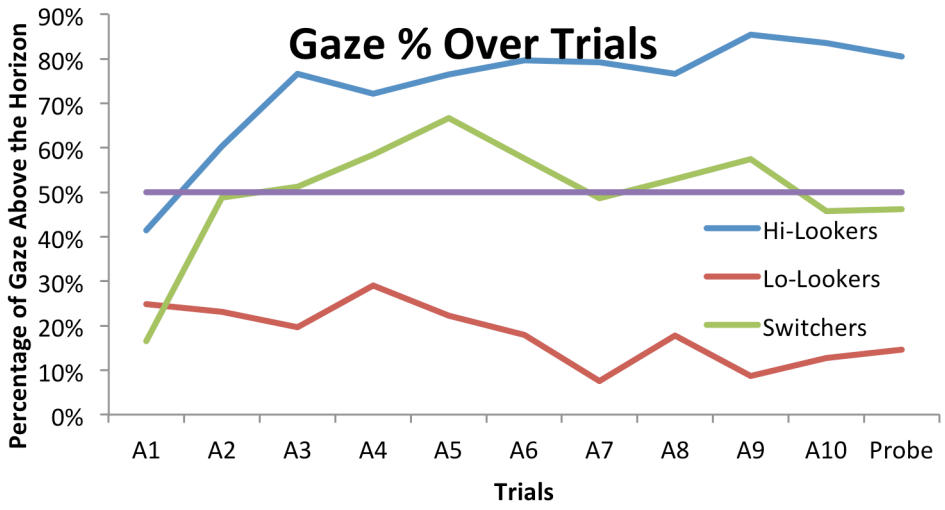


Figure 25. Average frequency of gaze above the horizon.
The hi-lookers increase their gaze frequency above the horizon very quickly (by trial 3). The lo-looker group increases gaze spent looking below the horizon. The switchers maintain gaze near 50% above the horizon. Group differentiation by orientation strategy gives a clearer picture of strategy acquisition than differentiation by navigation strategy.

ROI Strategy Adoption

When participants were grouped by which strategy they used to orient themselves in the environment, adoption rate was shown to be very similar between groups and to occur very early in trials (see Figure 26). The Hi-Lookers adopted their strategy by trial 5.2, the Lo-Looker group adopted their strategy by trial 5.1 and the switcher strategy group adopted their strategy by trial 5.7 (see Figure 27).

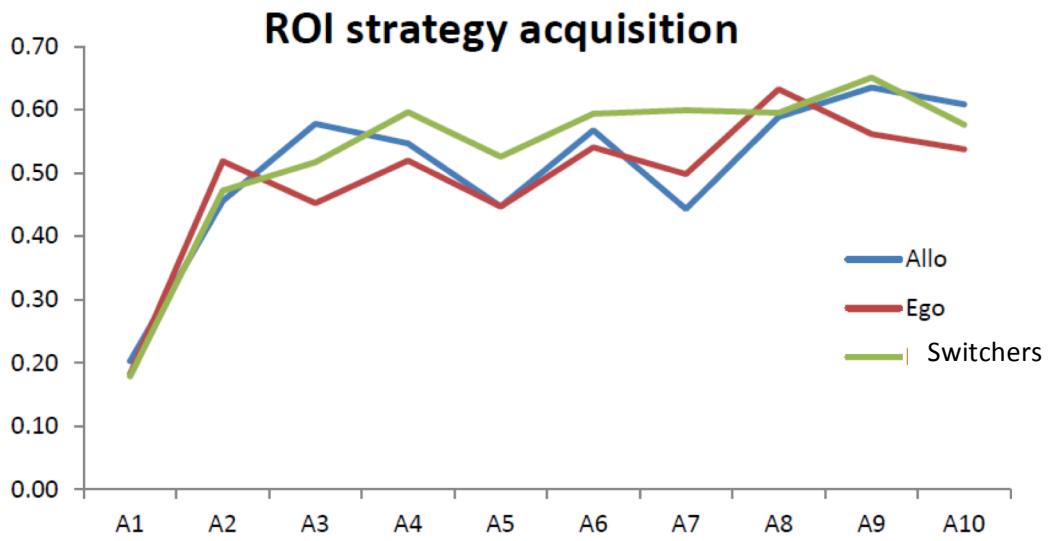


Figure 27. Percentage of Gaze Spent in Regions of Interest

Differential ratios of time spent in regions of interest (ROI) were similar between groups. All strategy groups seem to reach asymptote gaze within ROIS early in trials and to maintain a similar proportion of time in ROIs till the end of trials

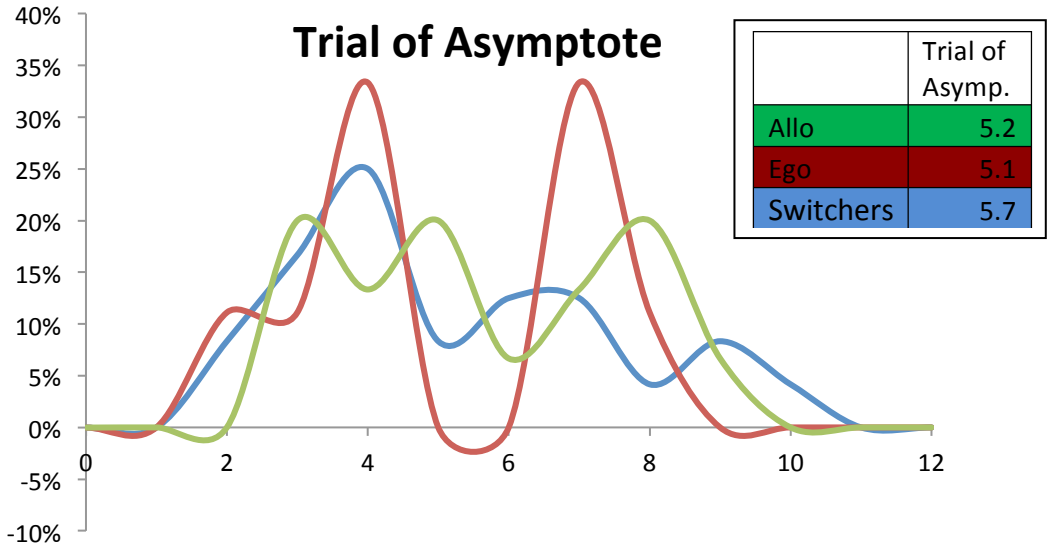


Figure 27. Trial of adoption after grouping by orientation strategy

All orientation strategy groups adopted a strategy early in trials, however, the Switcher group seemed to adopt slightly later than the Hi-Lookers or Lo-Lookers.

Interestingly, there were no performance differences when participants were grouped by navigation strategy, but when they were grouped by orientation strategy, there were differences in efficiency of behavioural performance (see Figure 29). Hi-lookers took more time (M = 18, *SEM* = 1.6) than both the Lo-lookers (M = 14, *SEM* = 1.6) and Switcher groups (M = 13, *SEM* = 1.1) although the difference was only significant between the Hi-looker and Switcher groups ($t(55) = 2.54$, $p < 0.01$). Distance showed a similar trend although the differences were not significant. This data suggests that the most efficient way to navigate in our maze is by switching environmental feature use and subsequent strategy choice depending on the trial demands.

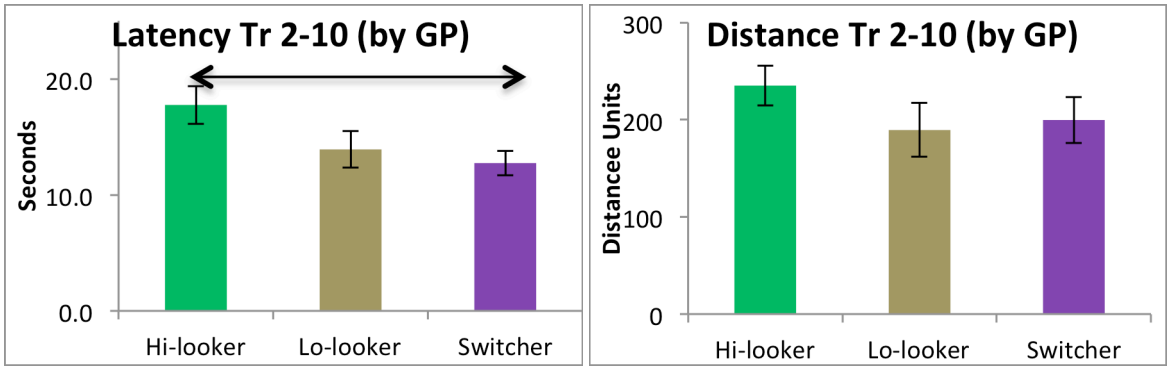


Figure 28. Performance between groups by gaze position

After participants were grouped by gaze position, behavioural analysis revealed that the switchers were the best navigators, having faster latencies and shorter distances than the Hi-looker group. ($p < .05$ ⟷)

Discussion

The present study investigated the relative rate of adoption of allocentric and egocentric strategies in an environment that allowed individuals to adopt one or the other, or switch between them. Results indicated that by the end of testing nearly all participants had adopted one strategy or the other. Also, more participants used an allocentric strategy than an egocentric strategy.

However strategy selection was not related to gender, or the relative efficiency of the two strategies. Analysis of gaze position at the start of trials showed that those who adopted an allocentric strategy tended to focus their attention on the distal (landscape) features of the environment whereas those who adopted an egocentric strategy tended to focus their attention on the proximal object features. Unfortunately, vertical gaze position could not be used to reveal the rate of adoption of an egocentric strategy, because this did not vary over trials. Analysis of gaze position using "regions of interest" overcame this problem and showed that both strategies are adopted at a similar rate and early in trials. Comparison of strategy by gaze position and strategy by navigation probe indicated that these two metrics were measuring two different stages of navigation. Finally, analysis of the navigational efficiency of different orientation strategies indicated that the best navigators were those who used both strategies.

In this study we employed a method for differentiating navigational strategy choice in a maze supporting both allocentric and egocentric strategies, the dDTS or strategy probe trial. In this trial, the proximal objects on the arena wall that supported egocentric navigation are dissociated from the distal landscape features that support allocentric navigation. During this trial participants had to choose, and non-verbally reveal, which environmental features they used to complete the dual strategy maze and which strategy had been dominant in immediately preceding trials. This method is novel because it dissociates strategy use by allowing the participant to non-verbally choose which features they had been using in preceding trials, in effect explicitly demonstrating their strategy choice.

Most participants accurately identified the quadrant that the invisible platform (goal) was in during the strategy probe trial, indicating that nearly all participants had selected an allocentric or an egocentric strategy by which to find the platform. Of the 55 participants, 47 participants

knew the quadrant that the platform was in and were fairly accurate at knowing the platform location within that quadrant as well. Seven participants knew which quadrant the platform was located in but did not have a clear idea of the platform location within the quadrant. Also, one participant was unable to identify the quadrant containing the platform. Participants who located the quadrant and the platform within it were most likely using one strategy or the other since, if they had not been using a strategy, they likely would not have been able to locate the correct platform location without it rising out of the floor when walked over. Only the 47 participants who had a clear idea of the platform location within the correct quadrant, and were concluded to have selected a strategy, were included in subsequent analyses.

Of the participants that knew the platform location, more chose to navigate allocentrically than egocentrically which was interpreted as due to a bias of the environment. The larger proportion of participants navigating allocentric was initially a concern as the participants may have entered the experiment already biased towards an allocentric strategy. However, we concluded that this was not the case because unpublished data from this lab has found that when participants were presented with larger object cues than were presented in the current study, they were more likely to navigate egocentrically than allocentrically (Ghandi, 2007). The difference in proportion of participants choosing each strategy when the object size changes suggests that the design of the environment can influence which strategy participants tend to choose, perhaps as a result of feature saliency. Therefore, it is safe to conclude that more participants chose to navigate allocentrically because the maze was biased towards allocentric navigation and not because the participants were.

Navigation performance was similar for all participants despite navigation strategy selected indicating that strategy was not determined solely on navigational efficiency. Non-

significantly different performances (distances and latencies) to reach the platform indicated similar navigational efficiency between the allocentric and egocentric groups. This similarity was expected since the maze was designed to support both allocentric and egocentric strategies despite the necessary engagement of different cognitive processes in order to find the platform. Similar navigational performance confirms that strategy selection was not based on how efficient a strategy was in completing the task and instead was based on factors yet to be determined.

Self report information indicating which features participants had been using to complete the task was collected on a questionnaire at the end of the study however this information was not helpful in differentiating strategy use. Self report's tended to indicate a list of environmental features used to solve the task making it difficult to distinguish those who had navigated allocentrically from those who had navigated egocentrically based solely on this information. The difficulty in using self-report could have stemmed from the fact that participants were more likely to have used multiple features in the environment and self-report is not sensitive enough to determine which features were used predominantly. Due to these limitations, self-report was not included in determining strategy choice.

Contrary to what would be expected from previous literature on strategy use and preferences, gender did not seem to be a factor in strategy selection since both males and females chose strategies in similar proportions. Our results show that 53% of males and 52% of females chose to navigate allocentrically and 30% of males and 28% of females chose to navigate egocentrically. These results are not consistent with previous literature examining gender differences in spatial navigation which have suggested that males are better at spatial tasks and therefore will have a propensity for choosing an allocentric strategy (Saucier et al., 2002; Astur, Ortiz, & Sutherland, 1998). In contrast, due to lesser spatial abilities, it is thought that females

will tend to choose an egocentric strategy (Lawton, 1994). In contrast, our results suggest that gender may not be as important in strategy selection as previously believed and in fact may not influence strategy selection at all.

The lack of gender differences or an interaction between gender and strategy in the current study was surprising given the strong body of research that has found differences in navigation performance strategy selection as a result of gender. There are several possible reasons for the lack of differences. The first is that our paradigm provided equal opportunity for navigation using either strategy unlike previous studies that forced the use of one strategy separate from the other. It could be argued that perhaps even though equal proportions of participants located the platform using both sets of features, these features were used in a different manner by females than by males, but no evidence directly supports this theory. A second reason why no gender differences were seen possibly stems from the hypothesis that suggests that because male and female children have been exposed to increasingly similar activities and toys over the past 20 years, gender differences in spatial cognition among undergraduates may be less pronounced now than previous reported (Casey, 2002). However, this hypothesis and the previous data relate to spatial cognition in the form of mental rotation and pencil paper and therefore may not be valid when applied to spatial navigation. Finally, the lack of statistical interaction between gender and strategy (i.e., that neither males nor females performed significantly better using one or the other strategy) may have been due to the very small number in the statistical test, which was in turn due to the small number of individuals who chose to navigate egocentrically. With a larger number of participants, this interaction may have reached significance. Although we did not find gender differences in the current study, the present results provide little support for the idea that there is any difference between the

cognitive means by which males and females navigate. Nevertheless, gender differences will always remain controversial and warrants further investigation.

The absence of difference in navigational cognition between males and females leads to several conclusions. First, results indicated no gender bias towards choosing one strategy over the other, meaning that navigational strategy selection is not gender specific. This leads to the second conclusion, that differences in navigational performance are not due to differences in the strategies selected by males or females. This paired with close-to-significant male advantage when navigating allocentrically suggests that although males and females choose strategies similarly, males may be better at using an allocentric strategy. Finally, a third possible conclusion drawn from the lack of gender difference in strategy selection is that selection and adoption are due to a combination of intrinsic and extrinsic factors. That is, a combination of intrinsic factors such as gender or the increased ability to learn and use one over the other and extrinsic factors such as tasks demands and the environment.

Attentional Focus and Navigational Strategy

A key aspect to this study was that it confirmed the ability of gaze position to determine strategy use in an environment supporting either an allocentric or an egocentric strategy. In order to be able to differentiate strategy by gaze, environmental features supporting one strategy or the other were dissociated by vertical separation above and below the horizon. Despite the vertical separation of features it was not clear whether gaze would be different between groups since both allocentric and egocentric features were present within the same environment. This ensured that strategy choice was spontaneous and more similar to a real world situation but also made it more difficult to elicit differential gaze patterns typical of one strategy or the other. However vertical gaze, after participants were grouped by strategy choice according to the strategy probe,

was significantly higher (where the landscape features were located) for the group navigating allocentrically compared to egocentrically. This allowed us to infer strategy selection by determining environmental feature use and confirmed that gaze position could be used to determine strategy use.

The average vertical gaze position for the allocentric group was more similar to gaze within the place maze, where allocentric gaze was forced, than the egocentric group, supporting the inference that the gaze pattern of the allocentric group was indeed that of participants who were using an allocentric navigation strategy. When gaze from both strategy groups in the dual-strategy maze was compared to gaze in the place maze it was clear that the allocentric group had similar gaze patterns to participants in the place maze (forced allocentric strategy) but that the egocentric group did not. This suggests that the allocentric group is using landscape features similar to how landscape features are used within the place maze whereas the egocentric group is not using landscape features. Because gaze is similar between the allocentric group and participants navigating allocentrically within the place maze, we infer that the allocentric group is using allocentric features in a similar way, in order to navigate to the platform

Attentional Focus and Adoption of Navigational Strategy

Strategy adoption as indicated by vertical gaze position showed an early adoption for the allocentric group however adoption rate was unclear for the egocentric group. Gaze position for both strategy groups began very low on the screen but it quickly began to differentiate, the allocentric group increasing gaze spent above the horizon and the egocentric group increasing to an average position directly below the horizon. Strategy adoption for the allocentric group is clear since the landscape features were well above the horizon. In contrast, strategy adoption for the egocentric group was unclear because the object features were located just below the horizon

and only slightly above the average starting gaze position. As a result the allocentric group showed large changes in average gaze position over trials whereas the egocentric group maintained very similar gaze positions over trials. As such statistical comparison was impossible between the two groups.

In order to analyze strategy adoption, a new analysis technique was developed based on determining the percentage of gaze spent within regions of interest (ROI) during the first second of each trial. We defined ROIs as specific regions of the screen where strategy specific features were located; above the horizon in the center of the screen for the landscape allocentric features, and below the horizon off-center for the object egocentric features. The analysis of ROI was more indicative of adoption because, as participants adopted a strategy, they were learning where in the environment to look for cues to guide their navigation. Improvement in navigation is expected to be a result of looking at strategy specific features more often in order to navigate with more efficiency. Gaze within ROIs was also a relatively easy way to condense the data and index the changes on a trial-by-trial basis allowing us to make inferences as to the rate of adoption between strategy groups.

Adoption rate, indicated by proportion of gaze spent in ROIs between trials, is similar between the two groups suggesting that there is no early allocentric bias. During the first trial both groups focused very little on strategy specific features within the ROIs. By trial two both groups greatly increased focus on strategy specific features and by trial three they had reached close to asymptotic proportions of gaze spent focused on strategy specific features. These results demonstrate that both strategy groups chose a set of features by which to navigate (adopt) very early in trials and quickly learned that using these features led to successful navigation to the task. Adoption rate could have been similar because the environment equally supported both

strategies, meaning that one was not more efficient than the other. It also implies that there are more similarities in how the two navigation systems encode information and adopt a navigation strategy than previously believed.

In the current study, strategy adoption occurred by trial three for both groups, confirming the hypothesis that information for both strategies is encoded at a similar rate and suggests the possibility that strategies are adopted equally as efficiently. In order to determine the trial during which a strategy was adopted, we used a trials to criterion method whereby trials were marked if 80% of their total asymptotic gaze was reached during the trial. Strategy was adopted during the second consecutive trial during which 80% of asymptotic gaze within the region of interest was reached. According to this analysis technique, those who navigated allocentrically adopted their strategy by trial 2.7 and those who navigated egocentrically adopted their strategy by trial 2.8. The similarity in adoption rate could mean that the cognitive mechanisms that contribute to the formation of both strategies encode information in a similar way and that contrary to previous theory, an egocentric strategy is equally as easy to adopt early in trials as an allocentric strategy.

One of the key aspects of this study was to confirm that the analysis of gaze position could indeed differentiate strategy use in the same way that the strategy probe could, i.e. by identifying the features that participants used to find the goal location. Gaze position was thought to be similar to the strategy probe trial because vertical gaze position was significantly different between groups determined by the strategy probe. We continued the study with the assumption that feature use during the strategy probe (finding the platform location at the end of trials) was very similar to gaze position at the beginning of trials. However, we did not find good concordance between strategy use determined by strategy probe compared to strategy use

according to vertical gaze position suggesting that the two metrics were measuring different constructs.

Emergent construct: Multiple strategies during single trials

The distinction between strategy use according to the strategy probe (navigation strategy) versus strategy use according to gaze position (orientation strategy) suggests that our two metrics determining strategy use are actually measuring two different processes, perhaps even two different stages of navigation. The strategy probe trial is completed after all training trials and it allows participants to make a choice between which features have been predominantly used. There are two important aspects to this task, first, it measures which features participants are using to localize the goal within the environment and second, it is administered after the training trials, meaning that we infer that participants have been using a similar strategy in preceding trials. In contrast, gaze position data is collected during the first second of each trial and measures attentional focus, indicating which environmental features (and so, which strategy) participants used to localize themselves at the start of each trial. More specifically, gaze identified the features participants used in order to localize themselves in the environment, and the strategy probe identified the predominantly used features that participants used in order to localize the goal location within the environment.

The hypothesized distinction in strategy use while localizing oneself and localizing the goal location within the environment is a new and very interesting finding that could spark a whole new area of research looking at the stages of the navigation process. Currently, navigation research is occupied with the search for factors that influence navigation (Maguire, Burgess, & O'Keefe, 1999), with identifying the neuroanatomical correlates (Maguire, Burgess, Donnett, Frackowiak, Frith & O'Keefe, 1998) and is just recently beginning to assess strategy adoption in

humans (Igloi et al., 2009). However, no current studies have been able to analyze the fundamental process of how humans navigate to this depth, i.e. differentiating between strategy used at the beginning versus the end of trials. The present results suggest that perhaps navigation has multiple stages during which different strategies can be used. Also, that these strategies vary between individuals but also within individuals, some maintaining consistent strategies during both stages and between tasks and some fluctuating between stages and tasks.

Attentional Focus and Adoption of Orientation Strategy

The difference in navigational strategy and orientation strategy suggestions that there may be a subtle difference in the cognitive mechanisms that individual's engage in when locating themselves within an environment versus when locating a goal within an environment. Therefore we also grouped participants by orientation strategy and again assessed adoption rate and behavioural performance. Participants engaged in three types of orientation strategies, further supporting the hypothesis that orientation strategy and navigational strategy were two aspects of the navigation process that may be related but not equivalent. Participants were grouped by feature use during the last three trials; only oriented to the landscape (Hi-Lookers), only oriented to the objects (Lo-Lookers) and switched orientation between the landscape and the objects between trials (Switchers). The participants in the hi-looking orientation group began trials at a (close to) significantly higher gaze position than both the Lo-looker and switcher groups. The early difference between groups was initially a concern since it could have been due to a pre-existing bias. However, after further consideration, even if groups had been previously biased towards orienting to certain features, this could be an important distinction that warrants further investigation.

Participants in the switcher group, those able to switch between orienting to allocentric or egocentric features, were the best navigators suggesting that an integration of two strategies led to the most advantageous use of environmental features and most efficient navigation. The switcher group had a significantly shorter latency to the platform when compared to the hi-looker group and also traveled less distance, although not significantly so. We infer that this group is most efficient at reaching the platform because they encode information for both an allocentric and an egocentric strategy, which allows them to use either or both sets of features depending on the task demands. This is consistent with previous work that found that in a virtual task involving a 4-on-8 virtual maze and a virtual town, successful navigation was correlated with the ability to switch strategies based on the virtual environment. For example, an allocentric strategy was more efficient within the virtual maze whereas an egocentric strategy was more efficient within the virtual town (Etchamendy, & Bohbot, 2007). Most participants maintained one strategy throughout both the virtual maze and town; however, some were able to switch from an allocentric strategy within a virtual maze to an egocentric strategy in the virtual town. The group who was able to switch between strategies completed the task fastest much like our study where people who used both types of environmental features to navigate by, were the best navigators.

Theoretical implications

The present study suggests that both egocentric and allocentric strategies may be encoded at similar rates and that strategy selection may be based more on the environment than on organismic factors. Previous authors have often proposed, concluded, or implied that individuals use navigational strategies based on organismic factors such as gender or the cognitive mechanisms governing the formation of each strategy. For example, males and females have been said to navigate differently, or at least have different preferences for navigational strategies

(Levy, Astur, & Frick, 2005). This implies that a given individual only has a single strategy at their disposal at any given time. However, those who have studied strategy selection have found that many individuals are able to switch from one strategy to another. Indeed, in the study by Iaria et al. (2003), at the outset of learning in a virtual radial arm maze, half of the participants chose an allocentric strategy and half chose an egocentric strategy. Later in training, approximately 40% of those choosing an allocentric strategy switched to an egocentric strategy, whereas none who chose an egocentric strategy switched to an allocentric strategy. These authors suggested that strategy selection is based on intrinsic characteristics of the cognitive systems that govern each strategy, and that the cognitive system for an allocentric strategy is more easily activated in early trials. In contrast, Igloi et al. (2009) found that participants adopted either an egocentric or allocentric strategy early in training and often switched to the other strategy as training progressed, and sometimes switched back and forth for no apparent reason. When the environment was changed to preferentially support one strategy or the other, participants easily switched strategies, in either direction. The authors suggested that the two strategies are adopted in parallel and that task demands and the environment determine which one is going to be adopted.

In contrast to both of these previous studies, the current study found that both strategies are adopted at a very similar rate and early in training, and that a sizable proportion of participants switch from one trial to another throughout training. The present results suggest that selection is governed by external factors rather than internal ones. This interpretation is supported by the finding that participants were biased towards choosing an allocentric strategy by the stimulus features of the virtual environment rather than the navigational advantage of one over the other. The finding that some participants used both strategies, switching back and forth

between trials clearly indicated that at least a third of the participants not only were capable allocentric and egocentric strategies, but were comfortable using either in a given task. The participants who switched from one strategy to the other took slightly longer to adopt a strategy however they were the most efficient at navigating to the goal location. This suggests that the strategies work cooperatively based on which strategy is most advantageous in a given situation. This finding is similar to that of Etchamendy and Bohbot (2007) who presented two consecutive tasks, a virtual town and a virtual maze, and found that the most successful navigators switched from an egocentric strategy in the virtual town to an allocentric strategy in the virtual maze. The ability to switch strategies based on the task led to the most successful performance compared to participants who only used one strategy throughout both tasks.

Another key aspect of this study was the discovery that participants may use different strategies at different stages within a given trial. The current study is the first to make the distinction between the strategies that participants use to localize themselves in the environment and the strategy that they use to localize the goal location. The theoretical implications of this finding are that participants may not tend to prefer one strategy instead of the other even within a single task; they may use a combination of strategies both between tasks but also within a singular task. This result also contributes support to the hypothesis that strategy selection occurs at a similar rate and selection does not entirely depend on organismic factors but more on environmental and task demands. This means that strategy is used based on whether it will lead to the most efficient navigation in a given environment. This finding could be integral in understand the process of navigation, and the factors that influence it, future research will focus on replicating these results.

The possibility that we select a strategy based on extrinsic factors and perceived efficiency of one strategy or the other suggests that perhaps there is some higher level executive control over which strategy we ultimately select. This top-down control mechanism could be as a result of connections between the hippocampus, caudate and prefrontal cortex. Previous research has found that the prefrontal cortex works in concert with the temporal lobe to encode spatial information (Mitchell, & Laiacona, 1998) and also to plan specific navigation behaviour (Granon, 1995). It has also been suggested that there is a prefrontal-striatal-hippocampal circuit that interconnects and influences spatial cognition and memory (Floresco, Seamans, & Phillips, 1997). It may be that the prefrontal-striatal-hippocampal circuit is more involved in behavioural flexibility and determining which cognitive mechanism associated with a specific strategy should be engaged. For example, lesions to the prefrontal cortex caused impairments when performing navigational reversal tasks, when a behavioural strategy shift was necessary, but no impairments when during a spatial learning task, when a behavioural strategy shift was not necessary (de Bruin,Sanchez-Santed, Heinsbroek, Donker, & Postmes, 2003). Our results showing that some participants are able to switch strategy use also suggests some executive mechanism allowing participants to flexibly shift between strategies depending on the task demands and possibly the environment. In human spatial navigation, the connections between the prefrontal cortex, striatum and hippocampus may be particularly useful when behavioural flexibility and a switch in strategy use could lead to more efficient navigation.

Future applications

The ability to know what features a person is focusing on and therefore which strategy they are using has great potential for future studies relating neural activity to specific types of navigational cognition. Brain imaging, specifically fMRI, has been successfully used to identify

the neural correlates of specific navigational strategies (Iaria et al., 2003) however fMRI does not have the temporal resolution necessary to capture strategy adoption on a trial-by-trial basis. However, electrophysiological recording has the necessary temporal resolution to capture changes in brain physiology associated with navigational strategy adoption. The addition of EEG to the current eye tracking technique could represent a significant advance in the ability to associate behavioural strategy adoption with changes in brain physiology. This combination has the potential to determine how the brain adopts a navigational strategy.

We also plan to replicate the current study in order to confirm the distinction between orientation and navigational strategy. First, with a larger sample size, we will be able to discriminate whether there are indeed three types of orientation strategy, one being able to use both allocentric and egocentric strategies, and whether being able to use allocentric and egocentric features is the most efficient way to navigate. Second, we will be able to confirm the difference between orientation and navigation strategies as separate stages during the navigation process. If we can confirm that the best navigators are those that can use both strategies we may also be able to infer that the two strategy systems can be adopted and work in parallel and cooperatively. Also, if we can replicate the difference in orientation and navigational strategy then we can make further inferences regarding whether there are different stages while navigating, including locating oneself in the environment and then locating the goal within the environment.

Conclusions

An important novel finding of this study was that spatial navigation strategy adoption occurs at the same rate for both egocentric and allocentric strategies, in no particular sequence. This result was contrary to some previous research (Iaria et al., 2003), that suggested an

allocentric strategy is adopted first because it is easier to learn and use. Instead the present results showed participants adopting strategies at similar rates, in no sequence and also indicated that participants switched between strategies from one trial to another. These results indicate that people can use either strategy and engage them flexibly as a result of task demands and the extrinsic environment.

In conclusion, the results of this study reveal similarities, not differences, in the rate of strategy adoption between those navigating allocentrically and egocentrically. While the strategy probe trial showed that more participants chose to navigate allocentrically, this bias was not as a result of an allocentric navigation strategy being easier to adopt, as previous studies have suggested. In other words, both strategies were equally as efficient (similar navigational performance) and equally as easy to adopt early in trials suggesting that the maze itself was influencing strategy selection. Our results highlight the importance of trial-by-trial analysis to accurately measure strategy adoption directly, rather than indirectly inferring adoption from verbal reports and or intermittent strategy probe trials. An important distinction that emerged from the data was the difference between navigational strategy and orientation at different stages in the navigational process. Our results indicate that participants may not maintain a dominant strategy consistently between trials or even within a single trial. Rather, it seems that approximately a third of participants switch between using the landscaping or the objects to orient themselves to the surrounding environment before proceeding with navigation. Further, some participants orient to the landscape or the objects but locate the goal location using features for the opposite strategy than the one they started most trials using. Finally, the finding that strategy adoption occurs at a similar rate and that there is a distinction between orientation and navigational strategy both have important implications for further experimentation assessing the

cooperative and integrated nature of allocentric and egocentric strategy systems in the process of spatial navigation.

References

Andersen, G. J., & Enriquez, A. (2006). Use of landmarks and allocentric reference frames for the control of locomotion. *Visual Cognition, 13(1),* 119-128.

Aslin, R. N., & McMurray, B. (2004). Automated corneal-reflection eye tracking in infancy: Methodological developments and applications to cognition. *Infancy, 6(2*), 155–163.

Astur, R. S., Ortiz, M. L., & Sutherland, R. J. (1998). A characterization of performance by men and women in a virtual Morris water task: A large and reliable sex difference. *Behavioural Brain Research, 93(1-2*), 185–190.

Astur, R. N., Tropp, J., Sava, S., Constable, R. T., & Markus, E. J. (2004). Sex differences and correlations in a virtual Morris water task, a virtual radial arm maze, and mental rotation. *Behavioural Brain Research, 151(1-2),* 103-115.

Baenninger, M., Newcombe, N. (1989). The role of experience in spatial test performance: A meta-analysis. *Sex Roles, 20(5-6),* 327-344.

Blodgett, H. C., McCutchan, K., & Mathews, R., (1949). Spatial learning in the T-maze: the influence of direction, turn, and food location. *Journal of Experimental Psychology, 29(6),* 800-809.

Brandeis,R.,Brandys, Y., & Yehuda, S. (1989). The use of the Morris water maze in the study of memory and learning. *International Journal of Neuroscience, 48,* 29-69.

Burgess, N., Becker, S., King, J. A., & O'Keefe, J. (2001). Memory for events and their spatial context: models and experiments. *Philosophical Transactions B, 356(1413*), 1493.

Cantlon, J. F., Brannon. E. M., Carter, E. J., & Pelphrey, K. A., (2006). Functional imaging of numberical processing in adults and 4-y-old children. *PLOS Biology, 4(5),* 125-130.

Chang, Q., & Gold, P. E., (2003). Switching memory systems during learning: Changes in patterns of brain acetylcholine release in the hippocampus and striatum in rats. *The Journal of Neuroscience, 23(7),* 3001-3005.

Crider, B. (1944). A battery of tests for the dominant eye. Journal of General Psychology.

Committeri, G., Galati, G., Paradis, A., Pizzamiglio, L., Berthoz, A., & LeBihan, D. (2004). Reference grames for spatial cognition: Different brain areas are involved in viewer-, object-, and landmark centered judgments about object location. *Journal of Cognitive Neuroscience, 16(9),* 1517-1535.

Cutmore, T. R. H., Hine, T. J., Maberly, K. J., Langford, N. M., Hawgood, G. (2000), Cognitive and gender factors influencing navigation in a virtual environment, *International Journal of Human-Computer Studies, 53(2),* 223-249.

Dabbs, J. M., Chang, E. L., Strong, R. A., & Milun, R. (1998). Spatial ability, navigation strategy, and geographical knowledge among men and women. *Evoluation an dHuman Behaviour, 19,* 89-98.

Droll, J. A., Hayhoe, M. M., Triesch, J., & Sullivan, B. T. (2005). Task demands control acquisition and storage of visual information. Journal of Experimental Psychology, 31(6), 1416–1438.

Etchamendy, N., & Bohbot, V. D. (2007). Spontaneous navigational strategies and performance in the virtual town. *Hippocampus, 17*, 595-599.

Evans, K. K., Cohen, M. A., Tambouret, R., Horowitz, T., Kreindel, E., & Wolfe, J. M. (n.d.). Does visual expertise improve visual recognition memory? Attention, Perception, & Psychophysics, 1–6.

Feigenbaum, J. D., & Morris, R. G. (2004). Allocentric versus egocentric spatial memory after unilateral temporal lobectomy in humans. *Neuropsychology, 18(3),* 462-472.

Fletcher-Watson, S., Leekam, S. R., Benson, V., Frank, M. C., & Findlay, J. M. (2009). Eye-movements reveal attention to social information in autism spectrum disorder. Neuropsychologia, 47(1), 248–257.

Floresco, S. B., Seamns, J. K., & Phillips, A. G. (1997). Selective roles for hippocampal, prefrontal cortical, and ventral striatal circuits in radial-arm maze tasks with or without a delay. *The Journal of Neuroscience, 17(5),* 1880-1890.

Goodrich-Hunsaker, N. J., Livingstone, S. A., Skelton, R. W., & Hopkins, R. O. (2010). Spatial deficits in a virtual water maze in amnesic participants with hippocampal damage. Hippocampus, 20(4), 481–491.

Gramann, K., Muller, H. J., Schonebeck, B., & Debus, G. (2006). The neural basis of ego- and allocentric reference grames in spatial navigation: Evidence from spatio-temporal coupled current density reconstruction. *Brain Research, 118,* 116-129.

Gramann, K., Onton, J., Riccobon, D., Mueller, H. J., Bardins, S., & Makeig, S. (2010). Human brain dynamics accompanying use of egocentric and allocentric reference frames during navigation. *Journal of Cognitive Neuroscience, 22(12),* 2836-2849.

Gr\ön, G., Wunderlich, A. P., Spitzer, M., Tomczak, R., & Riepe, M. W. (2000). Brain activation during human navigation: gender-different neural networks as substrate of performance. Nature Neuroscience, 3(4), 404–408.

Hamilton,D. A., Driscoll, I., & Sutherland, R. J. (2002). Human place learning in a virtual Morris water task: some important constraints on the flexibility of place navigation. *Behavioural Brain Research, 129(1-2),* 159-170.

Holdstock, J. S., Mayes, A. R., Cezayirli, E., Isaac, C. L., Aggleton, J. P., & Roberts, N. (2000). A comparison of egocentric and allocentric spatial memory in a patient with selective hippocampal damage. Neuropsychologia, 38(4), 410–425.

Holmqvist, K., Holsanova, J., Barthelson, M., & Lundqvist, D. (2003). Reading or scanning? A study of newspaper and net paper reading. *Mind, 2,* 657-670.

Humphreys,G. W. (1998). Neural representation of objects in space: a dual coding account. *Philosophical Transactions of the Royal Society, 353(1373),* 1341-1351.

Iaria, G., Lanyon, L. J., Fox, C. J., Giaschi, D., & Barton, J. J. (2008). Navigational skills correlate with hippocampal fractional anisotropy in humans. Hippocampus, 18(4), 335–339.

Iaria, G., Petrides, M., Dagher, A., Pike, B., & Bohbot, V. D. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: variability and change with practice. Journal of Neuroscience, 23(13), 5945.

Iaria, G., Chen, J., Guariglia, C., Ptito, A., & Petrides, M. (2007). Retrosplenial and hippocampal brain regions in human navigation: complementary functional contributions to the formation and use of cognitive maps. *European Journal of Neuroscience, 25(3),* 890-899.

Igloi, K., Zaoui, M., Berthoz, A., & Rondi-Reig, L. (2009). Sequential egocentric strategy is acquired as early as allocentric strategy: Parallel acquisition of these two navigation strategies. *Hippocampus, 19(12),* 1199-1211.

Jacobs, W. J., Thomas, K. G., Laurance, H. E., & Nadel, L. (1998). Place learning in virtual space: II. Topographical relations as one dimension of stimulus control. *Learning and Motivation, 29(3),* 288-308.

Jordan, K., Schadow, J., Wuestenberg, T., Heinze, H. J., & J\äncke, L. (2004). Different cortical activations for subjects using allocentric or egocentric strategies in a virtual navigation task. Neuroreport, 15(1), 135.

Klatzky, R. L. (1998). Allocentric and egocentric spatial representations: Definiations, Distinctions and Interconnections, *Lecture Notes in Computer Science, 1404,* 1-17.

Knauff, M., Rauhm R., & Renz, J. (1997). A cognitive assessment of topological spatial relations: Results from an empirical investigation. *Lecture Notes in Computer Science, 1329,* 193-206.

Kosslyn, S. M., Koenig, O., Barrett, A., Cave, C. B., Tang, J., & Gabrieli, J. D. E. (1989). Evidence for two types of spatial representations: Hemispheric specialization for categorical and coordinate relations.

Kraemer, S. (2000). The fragile male. British Medical Journal, 321(7276), 1609.

Levy, L., Astur, R. S., Frick, K. M. (2005). Men and women differ in object memory but not performance of a virtual radial maze. *Behavioural Neuroscience, 119(4),* 853-862.

Livingstone, S. A., & Skelton, R. W. (2007). Virtual environment navigation tasks and the assessment of cognitive deficits in individuals with brain injury. *Behavioural Brain Research, 185,* 21-31.

Livingston-Lee, S. A., Murchison, S., Zeman, P. M., Gandhi, M., van Gerven, D., Stewart, L., Livingston, N. J., & Skelton, R. W. (2011). Simple gaze analysis and special design of a virtual Morris water maze provides a new method for differentiating egocentric and allocentric navigational strategy choice. *Behavioural Brain Research 225,* 117-125.

Lawton, C. A. (1994). Gender differences in way-finding strategies: Relationship to spatial ability and spatial anxiety. Sex Roles, 30(11), 765–779.

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, 122,* 73-91.

Maguire, E. A., Burgess, N., Donnet, J. G., Frackowiak, F. S. J., Frith, C. D., & O'Keefe, J. (1998). Knowing where and getting there: A human navigation network. *Science, 280,* 921-924.

Maguire, E. A., Burgess, N., & O'Keefe, J. (1999). Human spatial navigation: cognitive maps, sexual dimorphism, and neural substrates. Current Opinion in Neurobiology, 9(2), 171–177.

Maguire, E. A., Gadian, D. G., Johnsrude, I. S., Good, C. D., Ashburner, J., Frackowiak, R. S. J., & Frith, C. D.,(1999). Navigation-related structural change in the hippocampi of taxi drivers. *Proceedings of the National Academy of Sciences of the United States of America, 97(8),* 4398-4403.

Maguire, E. A., Burgess, N., & O'Keefe, J. (1999). Human spatial navigation: cognitive maps, sexual dimorphism, and neural substrates. Current Opinion in Neurobiology, 9(2), 171-177.

Miles, W. R., (1930). Ocular dominance in human adults, *Journal of General Psychology, 3,* 412-430.

Moffat, S. D., & Resnick, S. M. (2002a). Effects of age on virtual environment place navigation and allocentric cognitive mapping. Behavioral Neuroscience, 116(5), 851–858.

Moffat, S. D., & Resnick, S. M. (2002b). Effects of age on virtual environment place navigation and allocentric cognitive mapping. Behavioral Neuroscience, 116(5), 851–858.

Moffat, S. D., Zonderman, A. B., & Resnick, S. M. (2001). Age differences in spatial memory in a virtual environment navigation task. Neurobiology of Aging, 22(5), 787–796.

Moghaddam, M., & Bures, J. (1996). Contribution of egocentric spatial memory to place navigation of rats in the Morris water maze. Behavioural brain research, 78(2), 121–129.

Morris, R. (1984). Developments of a water-maze procedure for studying spatial learning in the rat. Journal of Neuroscience Methods, 11(1), 47–60.

Mueller, S. C., Jackson, C. P. T., & Skelton, R. W. (2008). Sex differences in a virtual water maze: An eye tracking and pupillometry study. *Behavioural Brain Research, 193(2),* 209-215.

Newcombe, N., Bandura, M., & Taylor, D. (1983). Sex differences in spatial ability and spatial activities. *Sex Roles, 9,* 377-386.

O'Keefe, J., & Nadel, L. (1978). *The Hippocampus as a Cognitive Map.* Clarendon Press: Oxford.

Ortner, T. M., & Sierverding, M. (2008). Where are the gender differences? Male priming boosts spatial skills in women. *Sex Roles, 59(3-4),* 274-281.

Packard, M. G., & McGaugh, J. L. (1996). Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place and response learning. Neurobiology of Learning and Memory, 65(1), 65–72.

Rapp, P. R., Rosenberg, R. A., & Gallagher, M. (1987). An evaluation of spatial information processing in aged rats. *Behavioural Neuroscience, 101,* 3-12.

Roof, N. (1993). Neonatal exogenous testosterone modifies sex differences in radial arm and Morris water maze performance in prepubescent and adult rats. *Behavioural Brain Research, 53,* 1-10.

Rosenthal, R., & Rubin, D. B. (1982). Further meta-analytic procedures for assessing cognitive gender differences. *Journal of Educational Psychology, 74,* 708-712.

Ruddle, R. A., & Péruch, P. (2004). Effects of proprioceptive feedback and environmental characteristics on spatial learning in virtual environments. International Journal of Human-Computer Studies, 60(3), 299–326.

Sandstrom, N. J., Kaufman, J., & Huettel, S. A., (1998). Males and females use different distal cues in a virtual environment navigation task. *Cognitive Brain Research, 6(4),* 351-360.

Schneider, A., & Witchiuk, D. (2009, May). *Gender differences in spontaneous selection of navigational strategy: A study in virtual space.* Poster session presented at the North Western Cognition and Memory conference, Bellingham, Washington.

Shagass, C., Roemer, R. A., & Amadeo, M. (1976). Eye-tracking performance and engagement of attention. Archives of General Psychiatry, 33(1), 121.

Sherman, J. A. (1974). Field articulation, sex, spatial visualization, dependence, practice, laterality of the brain and birth order. *Perceptual and Motor Skills, 38,* 1223-1235.

Skelton, R. W., Bukach, C. M., Laurance, H. E., Thomas, K. G. F., & Jacobs, W. J. (2000). Humans with traumatic brain injuries show place-learning deficits in computer-generated virtual space. *Journal of Clinical and Experimental Neuropsychology, 22(2),* 157-175.

Skelton, R. W., Ross, S. P., Nerad, L., & Livingstone, S. A. (2006). Human spatial navigation deficits after traumatic brain injury shown in the arena maze, a virtual Morris water maze. *Brain Injury, 20(2),* 189-203.

Skinner, D. M., Etchegary, C. M., Ekert-Maret, E. C., Baker, C. J., Harley, C. W., Evans, J. H., & Martin, G. M. (2003). An analysis of response, direction, and place learning in an open field and T maze. *Journal of Experimental Psychology, 29(1),* 3-13.

Sutherland, R. J., & Dyck, R. H. (198). Place navigation by rats in a swimming pool. *Canadian Journal of Psychology, 38,*322-347.

Tatler, B. W., & Vincent, B. T. (2009). The prominence of behavioural biases in eye guidance. Visual Cognition, 17(6), 1029–1054.

Tlauka, M., Brolese, A., Pomeroy, D., & Hobbs, W. (2005). Gender differences in spatial knowledge acquired through simulated exploration of a virtual shopping centre. Journal of Environmental Psychology, 25(1), 111–118.

Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature, 428 (6984),* 751-754.

Tolman, E. C., Ritchie, B. F., & Kalish, D. (1946). Studies in spatial learning. II. Place learning versus response learning. *Journal of Experimental Psychology, 36(3),* 221-229.

Tolman, E. C. (1948). Cognitive maps in rats and men. *The Psychological Review, 55(4),* 189-209.

Touretzky, D. S., & Redish, A. D. (1996). Theory of rodent navigation based on interacting representations of space. Hippocampus, 6, 247-270.

Trullier, O., Wiener, S. I., Berthoz, A., & Meyer, J. (1997). Biologically based artificial navigation systems: Review and prospects. *Progress in Neurobiology, 51,* 483- 544.

Waller, D., Hunt, E., & Knapp, D. (1998). The transfer of spatial knowledge in virtual environment training. Presence, 7(2), 129–143.

Wang, R. F., & Spelke, E. (2002). Human spatial representation Insight from animals, *Trends in Cognitive Sciences, 6,* 376-382.

Appendix A: X data

X data- overall strategy

Assessing eye movements and gaze is a well-established method of determining attention allocation and inferring cognitive process in psychological research. Research using eye movements began with simple studies recording visual attention (Yarbus, 1967) however new technology has enabled the use of eye tracking in studies of spatial navigation (Mueller et al., 2008). One difficult aspect of using eye movements in research is the volume of data that can be collected during the task, often upwards of 30 frames/s. As such we analyze gaze during the first second of every trial as separate vertical and horizontal gaze points before continuing with more complex analysis.

Previous study within this lab has found significant differences in the horizontal distribution of gaze during mazes that require an allocentric or an egocentric strategy (Livingstone-Lee et al., 2011). When participants were required to complete a Place maze where only allocentric cues were useful to completion of the task, participants' gaze was above the horizon and centrally distributed. In contrast, in a cue maze where only egocentric cues were useful to completion, participants' gaze was below the horizon and multimodally distributed. Given these results it was expected that there would be a difference in horizontal gaze distribution in the current study. However, given the availability of both allocentric and egocentric cues and that participants could choose to use either, these results were relatively insignificant and are thus discussed in the appendices.

Methods

Horizontal gaze position was determined first by finding the average horizontal gaze position and then by analyzing the frequency of gaze points spent in each of five regions across

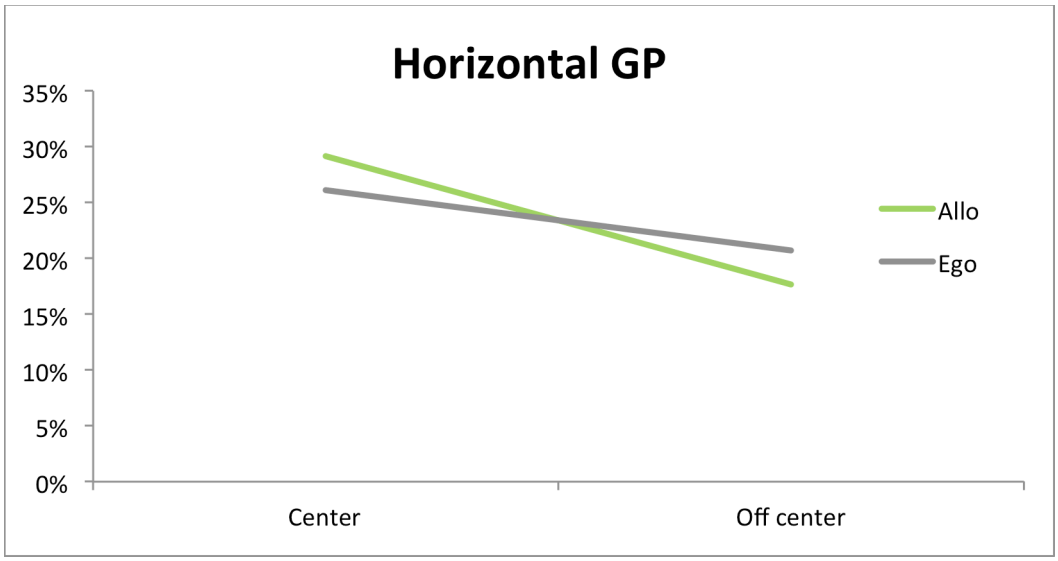


Figure 29. Horizontal Gaze by Strategy

Both the Allocentric and Egocentric strategy groups spend more time looking in the central section of the screen and less time looking at the off-center section; although, the Allo group spends slightly more time looking at the center than the Ego group.

the screen (far left, left, center, right and far right), each horizontal region being 160 pixels across. Following binning, data was condensed into on and off-center sections by comparing frequency of gaze points spent in left and right sections against frequency in the center. This data was compared using an independent samples t-test. Strategy adoption using horizontal gaze was also analyzed as the difference in on and off-center gaze between trials.

Results

Overall strategy: Horizontal distribution

Strategy may have weakly influenced horizontal gaze distribution (see Figure 30). The Allo group showed a slightly larger proportion of central gaze (where allocentric cues were located) (On-center: 29%, Off-center: 18%) while the Ego group seemed to have a larger proportion of gaze off-center (where egocentric cues were located) (One-center: 26%, Off-center: 21%). However, these differences were non-significantly different (On-Center: $t(47) = 0.27$, $p < 0.79$, Off-center: $t(47) = 1.54$, $p < 0.13$).

Strategy adoption: Horizontal gaze

The horizontal GP when participants were separated by strategy group yielded slightly more interesting results. Figure 31. shows a trend in proportion of time spent on and off-center for the Ego group. The Ego group begins with very little gaze spent off-center however this quickly changes with more GP spent in the off-center section. The Allo group also begins trials with almost all GP in the on-center section with a shift towards more dispersed gaze during trial two. However they maintain a high proportion of GP in the on-center section throughout trials.

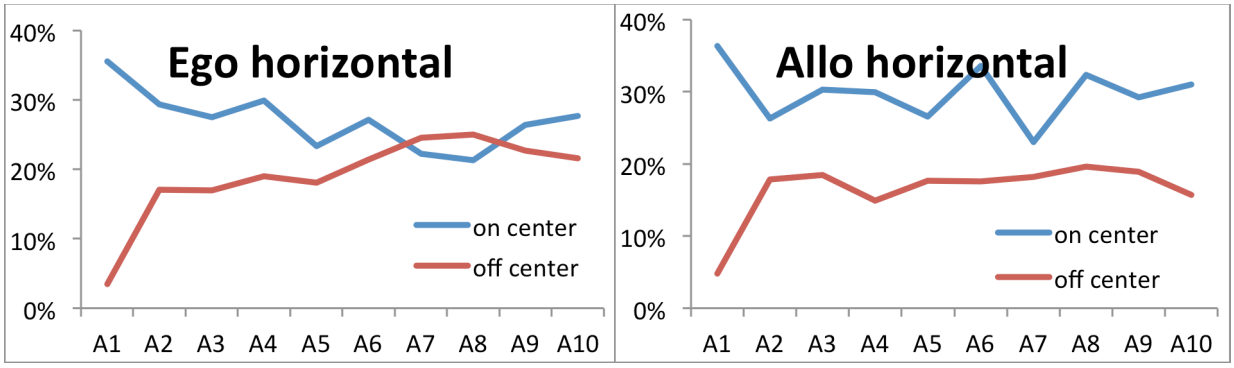


Figure 30. Strategy Adoption According to Horizontal Gaze

Both the Ego and Allo groups spend most of their time gaze at the center of the screen during the first trial. The Ego group increases the amount of gaze in the off-center region and finally spent an equal amount of time on and off-center at the end of trials. The Allo group increases their gaze on off-center regions but maintains more gaze on-center till the end of trials.

Appendix B: Gender

Substantial evidence indicates that males may have better spatial abilities and therefore may navigate in both real and virtual environments better than females (Saucier et al., 2002; Astur, Ortiz & Sutherland, 1998). These abilities are suggested to be the result of males' propensity for using an allocentric (cognitive map) navigational strategy, in contrast to females' tendency to use an egocentric navigation strategy (Igloi, Zaoui, Berthoz, & Rondi-Reig, 2009). Differences in navigational ability and strategy selection are shown by evidence from several types of study. Self-report studies show that males report using an allocentric strategy while females are more likely to report using egocentric strategies (Lawton, 1994). Also, when asked to give directions, males are more likely to provide instructions using allocentric referents in contrast to females using egocentric referents (Dabbs, Chang, Strong, & Milun, 1998). Although, eye tracking studies show that both males and females use similar features despite providing different directions (MacFadden, Elias, & Saucier, 2003). This suggests that gender differences may be due to utilization of different cognitive strategies with similar environmental cues or that the difference may not be related to spatial perception but instead to verbal expression. The final piece of evidence contributing to the assumption that males are better at navigation due to strategy is that when both genders are required to complete an allocentric or egocentric task, males perform significantly better than females when navigating allocentrically however there are no gender differences when navigating egocentrically (Astur et al., 1998).

The predisposition for males to be better at allocentric navigation suggests that males may also prefer to use an allocentric strategy (Woolley et al., 2009). This preference may underlie the advantage males seem to have in spatial navigation tasks. However, there has been

only one study outside of this lab to assess strategy preference between genders and in this study, no gender difference in strategy choice was apparent (Levy et al., 2005).

Eye tracking has been added to the methods of examining gender differences in environmental feature use during navigation in an attempt to elucidate the underlying cognitive differences in navigation. Using eye tracking during a navigation task to asses location of fixation, duration of fixation, and visual spread, researchers have been able to determine that females fixate for longer durations and scan less of the environment than men do (Mueller et al., 2008). This difference was similar to differences in experts compared to novices, novices spending more time fixating on fewer features. However, in a study that presented a navigation task on a larger display allowing a wide field of view, females were shown to take a wider view which was correlated with a decrease in the gender difference in performance (Czerwinski, Tan, & Robertson, 2002). Therefore, gender differences in gaze position remain contentious.

Given the well-known differences in performance and the new findings that gender may also play a role in guidance of eye movements, the current study did analyze the data for gender differences. However, gender differences were secondary and as such are listed in the appendices.

Methods: data analysis

Behavioural

Gender was analyzed as a factor influencing performance. The simple main effect between males and females was analyzed by independents samples t-tests. The interaction between gender and strategy was also analyzed using a 2x2 ANOVA.

Gaze position

Gender was analyzed as a factor in gaze position. Comparisons between genders were conducted on horizontal, vertical and gaze in regions of interest using independent samples t-tests. Data was again compared to determine overall differences (tr 2-10) as well as to determine differences in adoption (over trials). The interaction between gender and strategy on overall gaze was also analyzed using an ANOVA.

Results

Overall strategy: Gender

During orientation, females tended to look at the landscape (above the horizon) more than males did. The average vertical GP from the first second of invisible trials 2-10 were slightly higher for females (M = 297.5, SEM = 7.8) than for males (M = 311.1, SEM = 1.0) (Figure 29). The percentage of time spent above horizon was also higher for females (M = 66.0%, SEM = 4.9%) than for males (M = 50.0%, SEM = 6.0%) (Figure 29). However, these differences were not statistically significant (Ave Gaze Position: $t(47) = 1.53$, $p < 0.13$, Gaze %: $t(47) = 1.39$, $p < 0.28$). Despite the non significant difference there is still a trend that should be considered in further analysis and gaze differences.

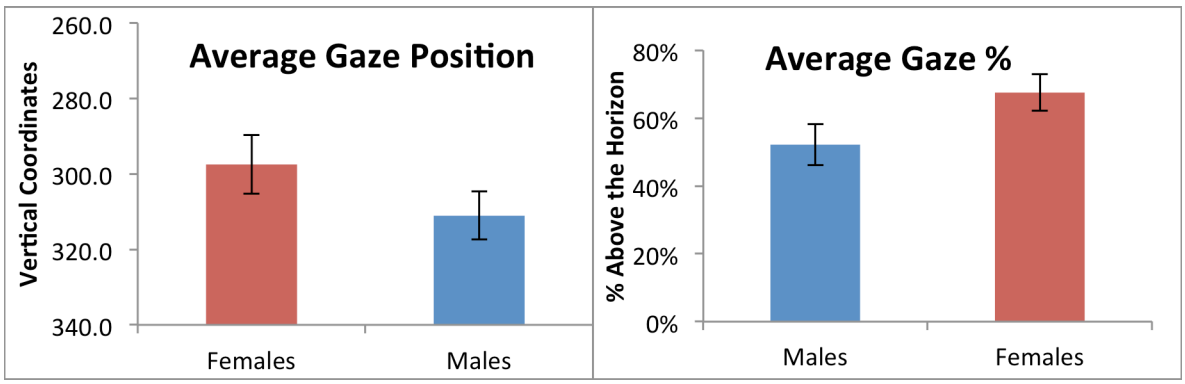


Figure 31. Average gaze position and percentage by gender

Females had a slightly higher average gaze position than males. They also spent more time above the horizon, however, neither of these differences were significantly different.

Gender did not seem to be a factor in horizontal data which was only marginally different between males and females. As fig 33 shows both males and females have a multimodal horizontal gaze distribution with most gaze falling in the central region. Figure 30 shows that, proportions of gaze spent on and off center between males (% on: M = 27%, SEM = 3% and off: M = 20%, SEM = 3%) and females (% on: M = 29%, SEM = 4%, and off: M = 18%, SEM = 4%) was very similar (Off center: $t(47) = 0.44$, $p < 0.66$, Off center: $t(47) = 1.09$, $p < 0.28$).

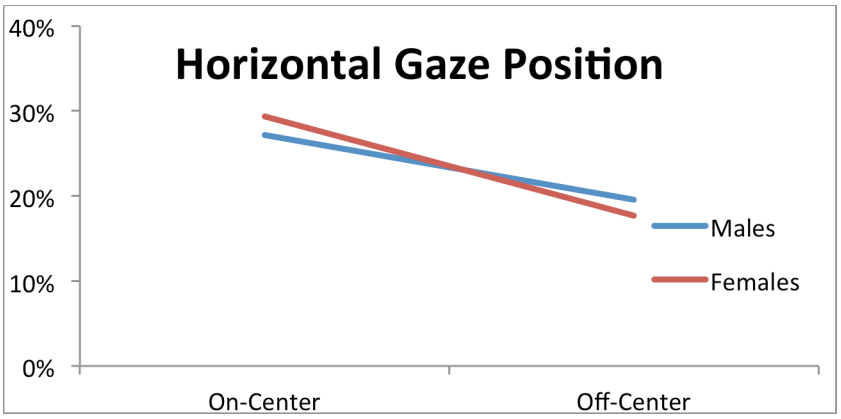


Figure 32. Horizontal Gaze Position by Gender

Both males and females spent more time in the on-center section of the screen, although, females spent slightly more time on-center and less time off-center than males. Males and females were the most variable in gaze spent in particular regions of interest, females spending more time in the high central region (M = 29%, SEM = 4.5%), males spending more time in low off center regions (M = 20%, SEM = 3.2%) (see Figure 34). These areas are important because strategy specific cues are located in specific regions of the screen as previously discussed. These differences were close to statistically significant which suggests that there may be an effect of gender influencing our GP data in addition to the effect of strategy. choice.

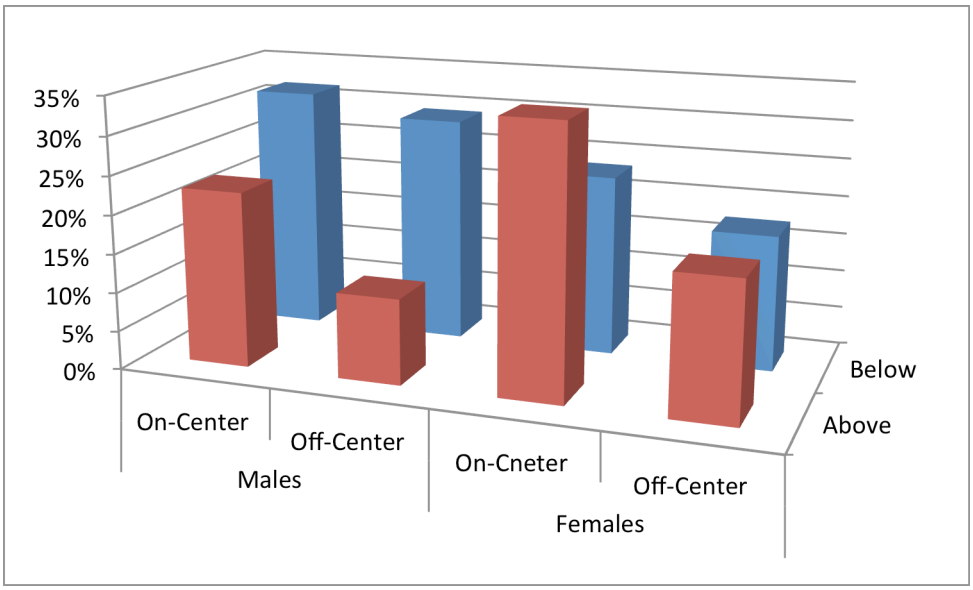


Figure 33. Gaze Spent in Regions of Interest by Gender

Females spent more time in the high on-center region compared to males and males spent more time below on and off-center than the females.

Adoption: Gender

Both males and females showed early acquisition of a navigation strategy. Males and females exhibited low average vertical gaze position at the beginning of trials but quickly increased to near or above the horizon (see Figure 35). Average GP for females stabilized by trial four above the level of the horizon. In contrast, average GP for males plateaued during trial 3 at an average GP closer to the horizon. Average time spent above the horizon showed similar differences with males and females quickly learning where to look for certain cues within the environment.

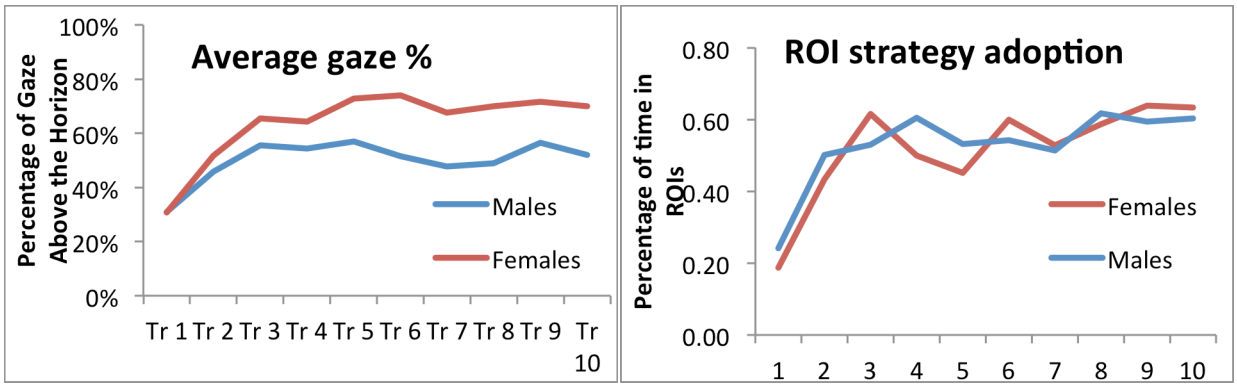


Figure 34. Strategy Adoption by Gender

Both males and females increase their time spent above the horizon however females spend increase to a higher amount of gaze above the horizon compared to the males. Both males and females increase the amount of gaze spent in regions of interest in similar proportions.

Gender was not a factor in strategy acquisition as indicated by gaze spent looking at strategy specific environmental features Indeed we found that both males and females increase in gaze time spent in the hi on-center and low off-center regions very early in trials (see Figure 36). After determining the asymptote discrimination ratio for each participant we were able to determine the average trial during which participants reached maximum gaze time spent in the strategy specific ROIs. For both males and females, strategy was acquired early in trials, trial 2.7 for males and trial 2.8 for females.

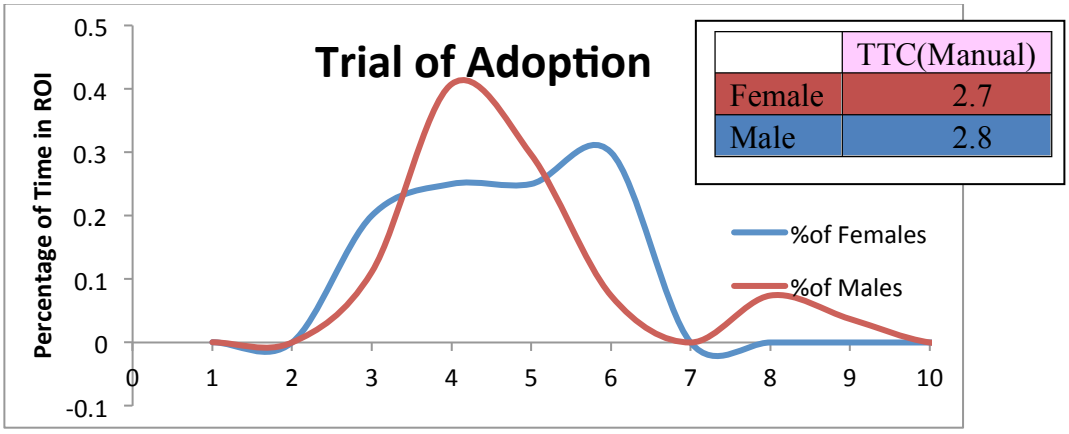


Figure 35. Trial of Adoption by Gender

Strategy adoption occurs in mid trials for both males (trial 2.8) and females (2.7).