Environmental and Experiential Determinants of Human Allocentric and Egocentric Navigation Systems

by

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B.A, Malaspina University-College, 2002
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Abstract

The research program described in this dissertation updates the knowledge base concerning human navigation and presents new methods for investigating selection and use of cognitive navigational strategies. Four experiments were designed to answer questions about the effects of environmental and experiential factors on cognitive mapping and selection of navigation strategies. Humans are thought to navigate using two different reference frames often referred to as "world based" and "person based". These reference frames correspond to two probable cognitive/memory systems respectively labelled "allocentric" for the formation and use of cognitive maps of the environment, and "egocentric" for navigation by stimulus response or guidance. Different navigational strategies are associated with the two systems. Allocentric strategies rely on the presence of a stable environmental structure containing a number of more distal, relational stimuli whereas egocentric strategies rely only on the presence of simple, local cues (cue-based egocentric) or on body movements (response-based egocentric). The experiments tested navigation behaviour and strategy selection using virtual environment

analogues of an animal model, the Morris water maze. Adaptations included, 1) the Place maze biasing participants toward the use of an allocentric strategy, 2) the Cue maze (and Floor Cue maze) biasing participants toward the use of an egocentric strategy, and 3) the Dual-strategy maze that has no bias because participants can choose to utilize either an allocentric or egocentric strategy. Experiment 1 was a behavioural study testing 101 university students in the Place maze and Floor Cue maze, with and without the opportunity to explore the environment before testing. The experiment showed for the first time that exploration is necessary for allocentric but not for egocentric navigation, suggesting that prior exploration is important for cognitive mapping. Experiment 2 outlined a novel and reliable eye tracking method for differentiating strategy use in the Place and Cue mazes. Eye movements were measured during the first orientation second of behavioural trials to differentiate allocentric from egocentric strategy use. Experiment 3 employed the established eye tracking method to test the effects of experience on strategy selection. Participants were trained in either the Place maze or the Cue maze and then tested in the Dual-strategy maze. A strategy probe trial was introduced at the end of testing to indicate whether participants had selected an allocentric or an egocentric strategy. Training experience had a strong behavioural effect on later strategy selection at the end of testing. Furthermore the effect of experience occurred independently of the gender of participants. However, the experience effect was only briefly shown using eye tracking measures. Experiment 4 was a successful feasibility study showing that eye tracking measures can be utilized to measure navigational strategy use in survivors of traumatic brain injury. Together these experiments may indicate that strategies are not innate or within the person but rather are interactions of the person with the environment.

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For my children, Angela, Heather and Ian... thank you for your remarkable support of a Mum on a different path.

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Preface

The format of this dissertation is unconventional but approved by the supervisor and committee members. The dissertation consists of six chapters: an introductory (literature review) chapter, three independent manuscripts, one feasibility study and a concluding (general discussion) chapter. This dissertation is formatted primarily according to APA (sixth edition) style with some exceptions to allow for key chapters to be presented as draft manuscripts. Each chapter begins with a short summary describing its purpose and linking it to previous sections. These chapter summaries are not formatted in APA style but rather follow general university formatting guidelines. Chapters Two to Five are presented as self-contained APA style manuscripts with the exception that all references are presented in one list at the conclusion of the document. Appendices are presented at the end of each chapter.

Chapter One

This chapter consists of a literature review and outline of the problems to be addressed by this dissertation. It provides the background and rationale for the four manuscript-style chapters that follow.

Introduction

The ability to navigate the environment is a basic process (much like memory or language) that most of us engage in without giving very much thought to the complexity of brain activity, cognition and behaviour necessary to perform even the simplest of navigation tasks. To get from one place to another in our environment we have to select a goal location, select strategies by which to navigate and then move safely through the environment to our destination. Further, we must be able to adapt flexibly if our goal location changes, if our strategies don't work or if we encounter obstacles along our path. Accomplishing all of this is no mean feat and is dependent on complex activity in multiple brain areas necessary for sensation and perception of the environment, cognitive computations and locomotion toward the goal.

The research described in this dissertation examined specific behavioural aspects of spatial navigation with the goal of improving understanding of how humans find their way around in the world. Figure 1.1 shows the general outline of the dissertation. The present introductory chapter includes an introduction to navigation terminology, the definitions utilized in the proposal, a literature review and overall rationale for the research program. The body of the dissertation consists of three experiments and a feasibility study.

Defining Wayfinding and Spatial Navigation

To start, a definition of spatial navigation is required in order to place navigation within the larger "way-finding" context. Way-finding is understood as the overall process of finding one's way from one place to another in both familiar and unfamiliar environments (Aguirre & D'Esposito, 1999; Barrash, 1998). Spatial navigation is the

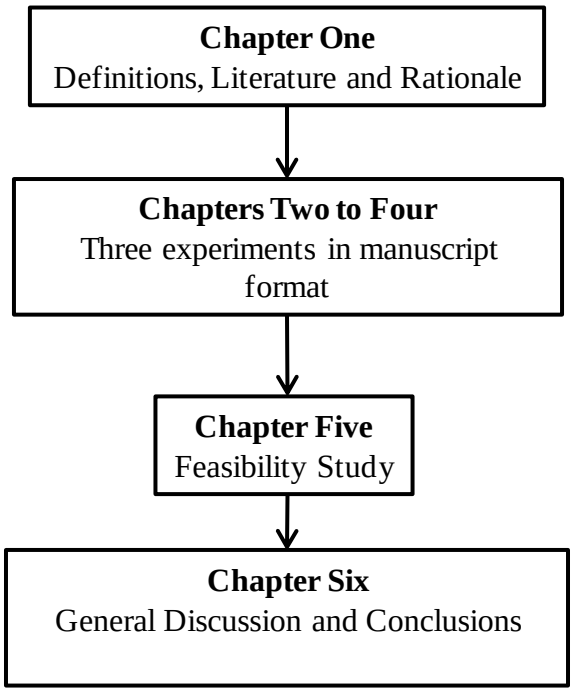

Figure 1.1. Structure of the dissertation entitled "Environmental and experiential determinants of human allocentric and egocentric navigation systems".

means by which navigators[1] are able to get from one place to another in the environment. It does not include way-finding processes like decision making about where to travel or the formation and maintenance of the intent to travel. Spatial navigation also includes locomotor processes necessary for moving the organism through the environment. For example, the spatial navigation processes involved in traveling to the local shopping mall include the navigator deciding where they are and where to go next but do not include the decision to go to the mall in the first place or the maintenance of the intent to travel to the mall. Locomotor processes of navigation would include those necessary for driving or getting on the bus. At the most basic level, spatial navigation can be understood simply as

[1] The term navigator generally refers to *any* navigating organism or even machine. The current research concerns human navigators and is based animal models and cognitive models.

the goal-directed movement of the navigator through the environment toward a target location. It includes all sensory, perceptual, cognitive and motor mechanisms that enable the navigator to get to the target location. The working definition that will be adopted for this proposal is that spatial navigation is the mechanism by which way-finding is carried out and that it consists of processes including sensation, perception, cognitive computations and motor functions that are specific to carrying out the intentions and decisions of the navigator. A map of way-finding and navigation terminology is shown in Appendix 1-A.

Modeling Spatial Navigation

Computer Vision and Robot navigation. The field of study known as computer vision overlaps with the study of human navigation through its modeling systems, particularly in the area of robot navigation. The core of computer vision research is concerned with sensory/perceptual and computational processing for the purpose of acting in the environment. In order to overcome problems such as how to provide the navigating robot with an updated map of the environment or how the robot computes a navigational path, computational and computer models are constructed and tested (Elfes, 1989). An example of how computer vision solves navigation problems is provided in Turek (2011) who described the stages involved in "programming" a robot to find and pick up an object in the environment. The necessary steps are that the robot must acquire an image (usually by means of a camera), locate the object, determine the object's position and orientation, send this information to the robot's computational system, and then send the information back to the robot so that it can move toward the object and grasp it. Thus the robot is able to find its way to a target in the environment, the main

goal in any navigation task.

Much like a human navigator, the navigating robot is likely to encounter obstacles to finding the target location. These may include changes to the terrain, unexpected events or having to locate targets in unfamiliar environments (Elfes, 1989). In order to overcome some of these problems, researchers have employed what is known are known as "sense-decide-act" models. In these models, "sense" refers to information received on the sensors of the robot, "decide" refers to computations within the robot, and "act" refers to its mechanics of movement and its observed actions (see for example, Goodwin & Winfield, 2008; Elfes, 1989). These models also emphasize a loop in which the sense-decide-act process can be repeated to perform successive tasks or to adapt to new circumstances in the environment.

A key problem for robots (as it can be for humans) is to have a map of the environment that is sufficient for navigating (Thrun, 2002). The mapping problem has been central to the robot navigation field because pre-programmed maps frequently become outdated or may contain errors. Thus the ideal is to design a robot that can construct maps of the environment via its own sensors, much as navigating animals appear to do. A key solution has been to develop algorithms that map the environment in three dimensions (Elfes, 1989) and allow for the robot both to estimate its position and to adapt when its location is not exactly as predicted (due to mechanical problems or changes in the environment) (Thrun, 2002). Work in this field is ongoing and in short, the mapping problem mirrors the problem of trying to understand how humans and other animals manage to compute their own location with respect to the environment and then navigate efficiently to a desired target. Thus robot navigation models can inform

cognitive models of human navigation and at the same time animal navigation may provide clues as to how these models can be formulated (e.g., Trullier, Wiener, Berthoz, & Meyer, 1997).

Cognitive-behavioural modeling. The current research program is based in part on a new cognitive-behavioural model of wayfinding. This model has its roots in "sense-decide-act" models and describes spatial navigation as a dynamic loop of this type that exists within a larger way-finding loop (Figure 1.2 & Appendix 1-B). Once the navigator has decided when and where to go, the navigator first scans (senses and perceives) the environment and then combines this information with prior knowledge to compute a path of travel (navigational cognition). The navigator then engages the motor system and locomotes toward the target location. Along the way, the navigator receives a continuous flow of new input scanned from the environment. This information is integrated with existing knowledge of the environment and used to compute necessary changes to the current navigational travel path. The navigation loop is thought to be flexible to newly received information on the order of several times per second whereas the way-finding loop is thought to be slower, with decisions and intentions changing on the order of a few times a minute to a few times an hour. The area of focus for the proposed research is the cognitive mechanisms and systems that are at the centre of the spatial navigation loop (Figure 1.2). These systems are proposed to allow for two types of navigation known as "allocentric" and "egocentric" that will be described below. Current theory and experimental findings suggest that brain activity in the allocentric and egocentric systems determines the selection of either an allocentric or egocentric strategy during spatial navigation. The overall objective of the research reported in the following experiments is

to better understand the cognitive mechanisms underlying spatial navigation and the conditions that lead to the selection of different navigational strategies.

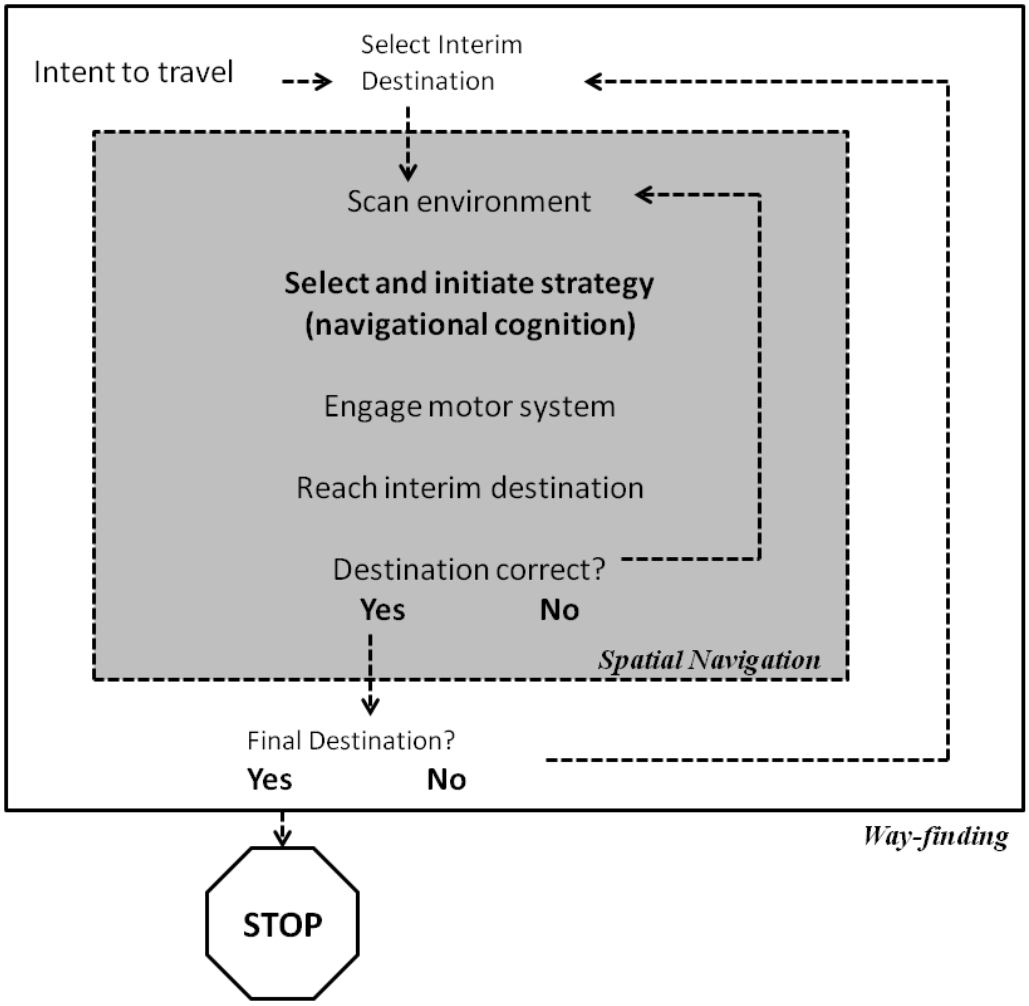

Figure 1.2. A brief schematic showing spatial navigation as a sub-process of way-finding. Spatial navigation (grey box) encompasses scanning, strategy selection and engagement of the motor system. Decision making about when and where to travel is included in the larger way-finding context. Note that the navigation loop can occur many times per second whereas the way-finding loop is more infrequent, occurring anywhere from a few times a minute to a few times an hour. The focus of the proposed research is on navigational cognition.

Navigation and Cognition

The cognitive computations associated with spatial navigation can be considered separately from the general concept of spatial cognition that includes some "non-navigational" processes. Specifically, navigational cognition is a component of way-finding and can be conceptualized as consisting of some basic processes of spatial cognition along with additional processes that are unique to navigation. Navigational cognition consists of the learning, memory and computations that are necessary for locomotion of the navigator toward a target location in the environment. Put another way, navigational cognition is the thinking component of navigation rather than the intent to navigate or the locomotor processes that occur during travel to a destination. Consequently it has two key features: 1) it occurs *while* the navigator is moving and 2) it occurs for the purpose of reaching a particular target location in the environment.

It has long been understood among navigation researchers that a key function of spatial navigation is to provide for movement of the navigator in the correct direction (with respect to the target). Over thirty years ago Kaplan (1973) described the information necessary for mapping space by assuming that action relative to the environment was one of the key psychological processes and Ittelson (1973) pointed out that perception of the environment is necessarily for the purpose of action. O'Keefe & Nadel (1978) also noted that organisms (navigators) map space for the purpose of moving through it (p.2). However, the importance of movement is not always emphasized and although considerable progress has been made it is still true that "in the history of experimental psychology, the overwhelming bulk of perception research has been carried out in the context of object perception rather than environment perception with the

findings of the former providing the basis for understanding the latter" (Ittelson, 1973, p.3). In other words, there is a tendency to design experiments that emphasize the perception of objects and/or the perception of static scenes and to generalize findings to situations where the environment is perceived and navigated in three dimensions. This approach is limited because it does not take into account the dynamic nature of three dimensional real world environments (Tatler, 2009) and therefore cannot encompass real world navigational situations that researchers are presumably hoping to explain. For this reason it is important to distinguish navigational cognition (for navigating in three dimensions) from general spatial cognition (for spatial understanding of objects and static scenes).

Built in to the definition of navigational cognition are several assumptions that underlie the present research. These assumptions with explanations are given below (for a full description of assumed aspects of spatial processing see Appendix 1-C):

1. *Spatial cognition includes both navigational and "non-navigational" processes.* Spatial cognition requires basic sensory and perceptual processing that may or may not underlie navigational processing.

2. *"Non-navigational" processes include a) basic sensory and perceptual processes, b) spatial cognitions computed from a fixed perspective, and c) spatial perceptions that are computed from a fixed perspective but may be shared by navigational systems.* Basic sensory and perceptual processing includes aspects of vision, audition, olfaction and touch. Spatial cognitions computed from a fixed perspective (and not forming part of navigational cognitive processing) include face recognition, object manipulation and mental rotation. Spatial perceptions that may be

necessary for navigation include the perception of objects, scenes and locations of objects within scenes.

3. *Navigational cognition includes the cognitions specific to navigation and computed while the navigator is moving.* Specifically, navigational cognition includes the perception of objects configurations and routes in walking space and guidance toward landmarks. Navigational cognition also includes the choice of which path to take and the coordination of body movements with distal objects to maintain the correct trajectory.

4. Navigational cognition does not include non-cognitive locomotor processes. Therefore, navigational cognition does not include proprioceptive feedback or integration of movements within the proximal environment (to avoid collisions or falls). However, it is clear that locomotion is a necessary aspect of successful navigation.

Animal Models of Navigation (Theory and Brain Bases)

The primary foundation for human studies of navigation is consistent and reliable findings from animal models. These models are currently being applied to the study of human navigation with considerable success. This section describes the history of animal navigation research by linking cognitive map theory, anatomical findings (for example place and head direction cells) and the proposition that there are two memory systems contributing to navigation in mammals. Specifically, it shows that animal models have identified mechanisms of learning and memory (Brandeis, Brandys, & Yehuda, 1989) and cognition (D'Hooge & De Deyn, 2001) often in the context of spatial navigation tasks like the Morris water maze (MWM, described below)(Morris, 1981). Such models

have not only provided a basic understanding of mammalian navigation behaviour but have also allowed for the study of its functional anatomy and physiology.

The Theoretical Cognitive Map

The influential cognitive map theory has driven much of the brain and behaviour research concerning spatial navigation in animals and continues to influence thinking about the cognitions underlying spatial navigation. Tolman (1948) was among the first to suggest that rats use some sort of internal representation or "field" map of the environment in order to navigate and he coined the term "cognitive map" to describe this representation. He then described some basic features of the map, asserting that it is often broad and comprehensive and contains all of the "routes, paths and environmental relationships" (p. 192) necessary for navigation. The cognitive map construct flew in the face of theories suggesting that animals navigated mostly by associating body movements with rewards (for example food) in the environment. That is Tolman (1948) proposed that animals did not navigate only by simple stimulus-response mechanisms but were able to learn in the absence of reward. The empirical work of Tolman (1948) and his colleagues demonstrated that in some experimental situations animal navigation behaviours could be better explained by cognitive mapping than by stimulus response. O'Keefe & Nadel (1978) later developed an expanded cognitive map theory and described the cognitive map as a "non-centred stationary framework" (p.2), that is, a representation of the environment that is not dependent on the position of the organism (navigator). They defined the map as being Euclidean (p.6), that is following the angle/distance laws of three dimensional geometry, and as a "schemata" (rather than a picture) of the environment (footnote, p.30).

Evidence for the Role of the Hippocampus in Cognitive Mapping

Place and head direction cells.

The discovery of functionally specific neurons for identifying the position and head direction of the rat in its environment suggests that information from multiple areas is combined to form the cognitive map. However, the hippocampus appears to be the central structure for cognitive mapping. The first evidence of this was the recording of place cells (O'Keefe & Dostrovsky, 1971) in the rat hippocampus, a first step toward understanding of the functional anatomy of spatial navigation in animals. These specialized place cells are active when rats are freely moving and within the vicinity of a goal location (location of reward) in the environment. Place cells were taken to be key contributors to the formation of cognitive maps in the rat brain (Burgess, Jeffery, & O'Keefe, 1999; J. O'Keefe & Nadel, 1978) because their activity corresponds to the position of the rat in the environment. As well, single cell recording has revealed similar head direction cells in the dorsal pre-subiculum and the anterior thalamic nucleus of the rat (Taube, Muller, & Ranck, 1990). These cells fire in response to head direction rather than body position or location of the animal in the environment. Although the discovery of place and head direction cells and their links to behaviour is important, perhaps the most crucial development in animal navigation research was the MWM.

The Morris water maze and lesion studies. Around the time of the discovery of hippocampal place cells and formulation of cognitive map theory, Richard Morris developed the MWM task (Morris, 1981) for the purpose of studying spatial learning and memory in rats. The MWM requires rats to swim to an invisible platform (the goal location) in a pool of milky water. The rat completes this task from a variety of starting

positions around the wall of the pool, and thus has to learn the location of the platform using available visual cues that include only the wall of the pool (which is a uniform texture and colour) and distal stimuli outside the maze pool. The ability of the rat to directly return to the same location in the pool from different start points strongly suggests that the rat has formed a representation (or cognitive map) of the environment external to the pool. There were two main advantages of the MWM over other mazes (spatial apparatuses) in use at the time. First, the MWM allowed for the study of navigation behaviour in the absence of scent trails so that it could be shown that the animal was not navigating by simple stimulus response (i.e., the animal was not simply smelling the its way to a food reward in the maze environment (Brandeis et al., 1989). Second, the MWM allowed for much more rapid learning than occurred in other paradigms and was therefore a more expedient test of spatial navigation (Morris, 1984).

Lesion studies employing the MWM have shown that damage to various brain areas impairs different aspects of maze performance and have provided important insight into the neural basis of navigation. More importantly, they have delineated the multiple cognitive processes involved in spatial navigation. Lesions to areas including the striatum, basal forebrain, cerebellum and frontal cortex and parietal cortex and especially the hippocampus have been shown to impair performance in the MWM (for review see D'Hooge & De Deyn, 2001) showing that spatial navigation is indeed a complex function that employs multiple brain areas/systems. For example, lesions to the striatum may interfere with consolidation of the procedural aspects of the MWM (Setlow & McGaugh, 1999). Lesions of the basal forebrain region also impair MWM performance at least in part because this region contains important cholinergic nuclei that

innervate cortex and the hippocampus (Brandeis et al., 1989). Lesions of the cerebellum likely interfere with control of the procedural aspects of spatial tasks (Mandolesi, Leggio, Spirito, & Petrosini, 2003) and exploratory behaviour (Petrosini, Leggio, & Molinari, 1998) whereas lesions of parietal cortex probably interfere with perception of object location in the environment and the consequent integration of incoming information with information from the hippocampus (Arbib, Erdi, & Szentagothai, 1998, p.170). Lesions of prefrontal cortex appear to impair water maze performance by causing deficits in the planning processes necessary to form representations of movements (Redish & Touretzky, 1998) or by disrupting the connections between the hippocampus and prefrontal cortex that promote actions based on information about the environment (White & McDonald, 2002; Yong et al., 2007). However, the most notable and studied structure in the context of the MWM is the hippocampus. When the MWM was applied in lesion studies of navigation behaviour it became apparent that the hippocampus is a key structure involved in the ability of an animal to find target locations indicated only by the presence of distal (extra-maze), visual cues. Lesions to the hippocampus or hippocampal formation profoundly impaired performance in early testing with the MWM (Morris, Garrud, Rawlins, & O'Keefe, 1982) and this finding has been replicated consistently (Brandeis et al., 1989; D'Hooge & De Deyn, 2001) demonstrating that the hippocampus is important for spatial navigation.

Contributions of the Hippocampus to the Cognitive Map

The hippocampus is a crucial structure for cognitive mapping in the rat brain (White & McDonald, 2002). As noted above, animal lesion models of navigation behaviour have demonstrated the importance of the hippocampus for spatial

learning/memory and single cell recordings have isolated specialized place cells in the rat hippocampus. Behaviourally, the hippocampus seems to be important in situations where a) the task requires the navigator to make representations (maps) based on the spatial relationships among multiple cues rather than single cues, and/or b) the task requires the flexible use of relational information that has already been acquired i.e., the hippocampus allows for the solving of new navigation tasks using previously acquired cognitive maps (Eichenbaum, Stewart, & Morris, 1990). The functional anatomy of the hippocampal formation provides further clues as to how cognitive maps might be formed. The hippocampus proper appears to receive spatial information from the entorhinal cortex (Fyhn, Molden, Witter, Moser, & Moser, 2004; Quirk, Muller, Kubie, & Ranck, 1992), a major input that in turn receives multimodal information from all of the association areas of neocortex (Arbib et al., 1998, p. 145; Fitzgerald & Folan-Curran, 2001, p. 279; White & McDonald, 2002). Performance in the MWM is impaired by lesions to entorhinal cortex or to the perforant path which is the main input from entorhinal cortex to the hippocampus and this behavioural impairment is accompanied by disruptions in the activity of hippocampal place cells (Miller & Best, 1980). This finding suggests to researchers that the hippocampus translates multimodal information into a representation (cognitive map) of the environment that allows place cells to fire when the animal is in a particular location (Burgess et al., 1999). More recently, Fyhn et al. (2004) identified "grid cells" in the dorsocaudal medial entorhinal cortex of the rat. The activity of these cells (like hippocampal place cells) also corresponds to the position of the rat in the environment and appears to roughly map the environment before passing information to the hippocampus for further processing. Fhyn et al. (2004) have suggested that

information from both grid and head direction cells is probably combined in the entorhinal cortex before being made available to the hippocampus for the purpose of integrated encoding (and construction of a cognitive map). Thus the hippocampus is the brain structure central to a rat cognitive mapping system.

Systems of Navigation in Animals

Behavioural Systems. Researchers have described three behavioural systems of navigation in animals, each responding to environmental stimuli in different ways. O'Keefe & Nadel (1978) proposed two systems associated with two behaviours: 1) navigating toward a target place (location) in the environment or, 2) navigating toward a particular (visible) cue in the environment. They described two types of space perception corresponding to these behaviours and labelled these "locale" and "taxon", respectively. Locale space reflects the relationships of environmental stimuli to each other, regardless of the perspective of the organism. By contrast, taxon space includes the sensory and motor systems that reflect the accumulated experience of space from the perspective of the organism itself. Therefore, locale space supports navigation using places or configurations of more distal cues whereas taxon space supports navigation using local, proximal cues. A third behavioural system, the "praxis" system, supports navigation based on sequences of body movements (Sutherland & Dyck, 1984). The basic distinction among these three types of navigation behaviour is still acknowledged today and forms the foundation for many animal and human studies of spatial navigation.

Memory Systems. White & MacDonald (2002) modelled three memory systems in the rat and two of these appear to be important for processing spatial information and engaging particular navigation behaviours. These are the hippocampus system and the

dorsal striatum (caudate/basal ganglia) system. White & MacDonald (2002) proposed that each of the rat memory systems consists of a set of interconnected neural structures with one of the structures central to each. For example, the hippocampus is at the centre of a system responsible for obtaining information about the relations between stimuli for the purpose of cognitive mapping. However, the basal ganglia (and especially the caudate nuclei) are at the centre of a system that is implicated in stimulus response behaviour. There is general agreement about the existence of the two memory systems in animals (Poldrack & Packard, 2003; White & McDonald, 2002) and possibly in humans (Doeller, King, & Burgess, 2008) and they are studied in terms of their functional neuroanatomy, associated cognitive mechanisms, navigational strategies and resulting behavioural output.

The two animal memory systems are thought to act in parallel and to both cooperate and compete with each other to cause behaviours depending on the nature of the behavioural task (Poldrack & Packard, 2003; White & McDonald, 2002). For example, in tasks where either the hippocampal or striatal system can lead to successful learning, both systems can be activated simultaneously and in a cooperative way (McDonald & White, 1994). Further, in some cognitive mapping tasks early learning employs the hippocampal system but with extensive training the basal ganglia appear to guide behaviour (Packard & McGaugh, 1996; Poldrack & Packard, 2003). Also, Poldrack & Packard (2003) suggested that the two systems may directly compete with each other. Evidence for this comes from studies where a lesion to one or the other system (before task training) leads to enhanced performance in lesioned compared to the non-lesioned animals (McDonald & White, 1993; Mitchell & Hall, 1988; Packard, Hirsch & White,

1989). Further, as a direct consequence of the different memory systems there are thought to be two sets of strategies available for navigation. However, the precise mechanisms of cooperation and competition among systems are unknown, and therefore it can be difficult to predict which system (and corresponding strategy) an animal will select to solve a particular task. Better understanding of the mechanisms involved and their timing is the key to understanding how animals (including humans) navigate space.

Summary. Animal models of navigation have identified the hippocampus as being important for tasks like the MWM which is thought to require cognitive mapping. Single cell recordings have identified place cells in the hippocampus and grid cells in the entorhinal cortex. These cells are considered to be contributors to the cognitive map that is ultimately formed by the hippocampus. Animal research further implies that there are two navigational memory systems in the brain, 1) a hippocampus system for cognitive mapping and 2) a striatal (caudate) system for stimulus response. The systems act in parallel and the observed navigational behaviours likely reflect the preferential action of one of these systems, either by cooperation or competition. It remains to be seen how the systems interact and how this might translate to the study of human navigation.

Human Spatial Navigation

During the last decade or so evidence has been accumulating that there are at least two functional systems underlying human spatial navigation and that these may mirror the systems proposed in other mammalian species. However, the connection to animal systems of navigation was not made until much more recently and nearly a century after human navigation deficits and topographical disorientation was first reported in the psychological literature. Initial reports of human navigation deficits came from case

studies showing that damage to visual association and parietal areas was associated with way-finding problems. The nature of these deficits was not well understood and key structures like the hippocampus were not initially recognized as being important for navigation. However, modern brain imaging techniques, especially in combination with virtual navigation tasks, have shown that the hippocampus and caudate appear to be central structures in two distinct human navigation systems. This research is ongoing and is demonstrating that when it comes to cognitive mapping and allocentric/egocentric systems, humans may have much in common with other mammals.

Allocentric and Egocentric Cognitive Systems and Terminology

The cognitive/memory systems of human navigation are frequently referred to as either "allocentric" for cognitive mapping or "egocentric" for stimulus response (Antonova et al., 2005; Burgess, 2006; Maguire et al., 1998; Parslow et al., 2004; Pine et al., 2002; Pizzamiglio, Guariglia, & Cosentino, 1998; Amy L. Shelton & Gabrieli, 2004). These cognitive systems are proposed to underlie spatial navigation and correspond to the two navigational memory systems identified in rodents (Doeller et al., 2008; O'Keefe, 1999; Yaski, Portugali, & Eilam, 2009). It is important to note that there are a number of pairs of terms used to describe these two navigational cognitive systems and Table 1.1 gives just a few of the more commonly used. For the purposes of the present research cognitive systems will be referred to as either allocentric or egocentric mainly because these terms are commonly recognized in the human spatial navigation literature. However, reference will sometimes be made to cognitive mapping or to place-based and cue-based tasks.

Case studies of topographic disorientation

Older case studies concerning way-finding problems have collectively identified several

Table 1.1

Corresponding terms (in no particular order) used to describe allocentric and egocentric systems, strategies and behaviours.

Allocentric	Egocentric
Cognitive mapping	Stimulus response
Place based	Cue based
Locale	Taxon and guidance, and praxis - response
World based	Person based
Viewer independent	Viewer dependent
Spatial	Non-spatial
Holistic	Analytic

tasks and corresponding cortical brain areas implicated for human navigation. In the late nineteenth century clinicians began to describe a condition known as "topographical disorientation" characterized by patients not being able to find their way around in either familiar or unfamiliar environments. By the mid-twentieth century several different brain lesions had been associated with topographical disorientation and interest has focused on the right hemisphere. For example, Paterson & Zangwill (1944, 1945) identified several cases of brain injured individuals who had difficulty orienting in space and they suggested that this deficit was associated with damage to the right hemisphere. A more consistent picture of topographical disorientation emerged when researchers of human memory and navigation began to take a meta-analytic approach to older case reports (Aguirre & D'Esposito, 1999; Barrash, 1998; Grusser & Landis, 1991). Barrash (1998) concluded that the inability to navigate in unfamiliar environments was associated with

damage to the medial temporal lobe whereas the inability to navigate in familiar environments was associated with damage to visual association areas. Grusser & Landis (1991) found that the ability to learn a new route was disrupted mainly by damage to parietal and occipito-temporal areas and a general inability to orient to a new environment appears to be associated in part with damage to the parahippocampal gyrus (Aguirre & D'Esposito, 1999). However, the link to sub-cortical and limbic regions was not made until recently and there could be two reasons for this. First, most of the damage noted in human case studies was to cortex and therefore it would have been difficult to make the links to animal studies. Second, most of the research efforts into topographical disorientation in the early half of the last century were focused on phenomena of interest at the time, for example visual agnosia, apraxia, and aphasia (Barrash, 1998).

Links to the Hippocampus and "Lesion" Studies

In the mid-twentieth century, the human hippocampus became a structure of interest to researchers. This was primarily because of H.M., the famous patient who, after removal of significant portions of his medial temporal lobes, was unable to form new memories (Scoville & Milner, 1957). The areas of damage included the hippocampus and amygdala and the researchers proposed that the formation of new episodic memories requires the hippocampus. Smith & Milner (1981) went on to show that the ability to recall a location was most impaired in patients (including H.M.) who had a right temporal lobectomy rather than a left lobectomy or no brain damage at all. However, evidence for the specific involvement of the hippocampus in spatial memory and human navigation was not acquired until the advent of imaging methods including Computerized Axial Tomograhy (CAT), structural Magnetic Resonance Imaging (MRI) and Positron Emission

Tomography (PET). This evidence came from lesion type studies of brain damage as well as structural analyses of healthy hippocampi. For example, Barrash, Damasio, Adolphs & Tranel (2000) correlated brain lesions with behaviour by having participants with stable focal lesions complete a complex indoor route learning task. Analysis of structural images (MRI) of participant brains revealed that poor route learning and memory was associated with damage to medial occipital cortex, posterior parahippocampal cortex, right inferior temporal cortex and notably, the right hippocampus. In a study with healthy participants, Maguire et al. (2000) found that the hippocampal structure of experienced navigators (taxi drivers) differed from that of comparison participants such that taxi drivers had larger posterior hippocampi (and smaller anterior hippocampi) than comparison participants. Together, these studies demonstrate via real-world testing that structural change in the hippocampus is correlated with navigation behaviour.

Real World and Virtual Environments

Real world environments. Real world tests of human spatial navigation were important for developing paradigms to test behavioural differences and for rehabilitation purposes. Researchers have tested navigation behaviour in both outdoor and indoor environments and have developed both individualized and standardized clinical tests of navigation deficits. Real world tests have also been used to identify gender differences in map use (Schmitz, 1999) and route learning (Ross, Skelton, & Mueller, 2006; Silverman et al., 2000). Using an indoor standardized test (The Route Learning Test), Barrash (1994) demonstrated that route learning becomes increasingly difficult with age. In another more individualized approach, researchers have used real world environments to

rehabilitate navigation performance in people with developmental topographical disorientation (Iaria, Bogod, Fox, & Barton, 2009; Incoccia, Magnotti, Iaria, Piccardi, & Guariglia, 2009). However, real world tests are difficult to control and therefore don't always allow for the systematic study of navigation. For these reasons researchers have increasingly turned to virtual environments for testing human spatial navigation abilities and deficits.

Virtual environments. Desktop computerized virtual environments have recently (within the past fifteen years or so) become well established as tools for investigating spatial navigation behaviour in humans. These environments have been found to be ecologically valid (Jacobs, Thomas, Laurance, & Nadel, 1998; Rizzo, Buckwalter, & Neumann, 1997) and to generate navigation data that is similar to that obtained from real world environments (Ross et al., 2006) and from studies with animals (Jacobs et al., 1998). Sutherland (2010) recently commented on the utility of human virtual navigation analogues of animal models of spatial memory and how they suggest that the profusion of information about the neurobiology of rat spatial memory may well apply to humans. Further, virtual environments also have several distinct advantages over real world environments when applied to the study of human navigation:

1. They are safer than real world environments, especially for participants who have navigation deficits.
2. They allow for creation of almost any type of environment through exacting control over environmental features, e.g. geometry of space, size of space, and location of objects in space.

3. They allow for improved analysis of navigational cognition because spatial stimuli and environmental contingencies can be varied systematically (Rizzo, Schultheis, Kerns, & Mateer, 2004).
4. They are portable, and therefore can be transported to other labs or to rehabilitation, hospital or home settings.
5. They can be created and readily shared with other researchers for replication or new applications whereas real world environments cannot be replicated by other laboratories.

For these reasons, virtual environments were key methods applied in the present research. Specifically, a virtual analogue of the MWM will be used as a behavioural test of navigation. Virtual MWM tasks are sensitive to a number of important group differences including gender differences in navigation (Astur, Ortiz, & Sutherland, 1998; Moffat, Hampson, & Hatzipantelis, 1998; Ross et al., 2006), age differences (Moffat & Resnick, 2002) and differences due to traumatic brain injury (Livingstone & Skelton, 2007; Skelton, Ross, Nerad, & Livingstone, 2006). Virtual MWM tasks have also begun to test for differences in allocentric and egocentric navigation as will be described below. Given that virtual environments are becoming the standard for testing human spatial navigation ability the virtual MWM tasks used in the present research program were considered to be methodologically appropriate.

Combining Virtual Environments and Functional Brain Imaging

Virtual environments have already proven useful for testing allocentric and egocentric systems and strategies when combined with PET and functional magnetic resonance imaging (fMRI). In a landmark PET study, Maguire, Frackowiak & Frith

(1997) showed that when experienced navigators (London taxi drivers) recalled familiar routes there was increased activation of the hippocampus when compared to activation on baseline tasks. As well, a series of studies employing virtual environments have shown that the hippocampus is a key structure for allocentric navigation, that is, for navigating by distal stimuli and making short-cuts/detours (Doeller et al., 2008; Grön, Wunderlich, Spitzer, Tomczak, & Riepe, 2000; Hartley, Maguire, Spiers, & Burgess, 2003; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Maguire et al., 1998). However, spatial navigation in virtual environments activates many areas other than the hippocampus (Grön et al., 2000; Hartley et al., 2003; Spiers & Maguire, 2006). Spiers & Maguire (2006) noted that several dynamic brain systems likely underlie the way-finding process in real environments and concluded that the role of the hippocampus is to facilitate the planning of routes to targets in the environment.

The presence of allocentric and egocentric brain systems for navigation is indicated by the results of several recent studies. Hartley et al. (2003) found that when good navigators navigated in a virtual town, the anterior hippocampus was activated during "wayfinding" navigation and the head of the caudate during route following. In a similar study Maguire et al. (1998) found that the right hippocampus was activated when participants accurately navigated between places whereas the right caudate was activated when participants went to places quickly and this caudate activity was not related to simple motor control but rather appeared to be a higher level aspect of movement planning. In a human lesion-type study, Voermans et al. (2004) showed that during route recognition there was significantly more activity in the right caudate in healthy participants than in participants with caudate dysfunction (early Huntington's disease).

More importantly, these researchers were able to show that in participants with caudate dysfunction the hippocampal system compensated for low activity in the caudate during route recognition tasks. The authors proposed that two human memory systems cooperate during navigation and attempt to compensate when one or the other is damaged.

Spatial Navigation and Traumatic Brain Injury

Traumatic brain injury survivors are a population of interest in navigation studies because they frequently report being lost (Lezak, 1995, p. 348). Furthermore, TBI survivors are very likely to have hippocampal damage (Bigler, 2001) and to experience spatial deficits (Bigler, 2001; Tate & Bigler, 2000) and problems forming new memories, including spatial memory (Barrash, 1998). Deficits in navigation in a virtual MWM allocentric task have already been reported in TBI survivors (Livingstone & Skelton, 2007; Skelton et al., 2006) and it has been suggested that these deficits are related to the inability of TBI survivors to form or use a cognitive map. Interestingly, TBI survivors were able to navigate using a single cue placed near the target location and were also able to navigate to this cue when it was surrounded by a number of other similar proximal cues (Livingstone & Skelton, 2007). This would suggest that TBI survivors are able to solve navigation tasks using egocentric but not allocentric strategies. The fourth experiment in this dissertation will consider the feasibility of testing strategy selection in survivors of TBI.

Eye Movements and Navigation

This section examines the recent use of eye movements as indicators of cognition and the feasibility of applying eye movements to the study of navigational cognition and human navigation systems.

Historical development. The tracking of eye movements is by no means a new approach to studying psychological states. The earliest tracking systems were developed mainly to ascertain how the experiences of the person might reflect where they look in a given two dimensional scene. For example, Buswell (1935) was especially interested in the perceptual aspects of gaze and how people might direct their gaze at artwork according to their personal experiences. He used a sophisticated eye tracking camera system to record the eye movements of 200 individuals while they looked at photographs of art pieces. He also commented on the instability and rapid movements of the human eye and noted different types of saccadic movements as well as occasional "drifting" of the eye from one side to another. Later on, Yarbus (1967) published research with one participant that clearly indicated a cognitive influence on eye movements. In other words, eye movements were discovered to be not only "stimulus driven" (bottom-up) but also affected by previous experience with the environment and the task demands (top-down). This effect has recently been replicated using a head mounted eye tracking system and a plasma screen display (DeAngelus & Pelz, 2009) although not with such a large effect size. However, many researchers have found differing patterns of brain activity associated with eye movements that are driven either by exogenous or endogenous stimuli (for review see McDowell, Dyckman, Austin, & Clementz, 2008). This finding is important for the measurement of eye movements during navigation because it implies that experience with different types of navigational stimuli and with the immediate task at hand may both be reflected in the choice of where participants look during navigation tasks.

Contemporary applications. Eye movement tracking can be applied in many

research contexts, but for the purposes of navigation research the point of interest is that eye movements are both stimulus driven and task dependent (DeAngelus & Pelz, 2009; Yarbus, 1967) and therefore are likely to reflect cognitive processing. However, psychological investigations are only one application of eye movement tracking and an informal search of more recent literature (2000 to 2010) shows that eye movements are measured consistently and reliably in several different contexts which can be roughly divided as follows:

1. Examination of basic processes of eye movement (types of saccades and fixations; associated neuroanatomy):
2. Clinical interventions such as training individuals to operate computer interfaces using eye movements.
3. Clinical Assessment of abnormal eye movements associated with psychiatric conditions.
4. Commercial applications such as tracking eye movements during internet viewing to improve advertising design.
5. Studies of eye movements as indicators of perception and cognition.

For the purposes of the present research program the approach was to examine eye movements as behavioural correlates of particular cognitive processes, in this case allocentric or egocentric type processing (c.f. #5 above). Eye movements were recorded during virtual navigation tasks and analyzed according to where participants look early in the navigation process. These eye movements were analyzed to show which environmental stimuli were significant under what task conditions. Gaze patterns are also discussed in terms of whether or not top down processing (or prior experience) affects

eye movements while navigating and whether gaze patterns are correlated with behavioural performance.

How eye movements are tracked. This section provides a brief explanation of eye movement types, pointing out their relevance to the present experiments. There are five different subsystems of eye movements (Gilman & Newman, 2003) that allow for the interaction of the human visual system with the environment. The eye movements of interest in cognitive research tend to be saccades and pursuit movements. Saccadic movements are fast, occurring typically in 100 ms or less (Fischer & Ramsperger, 1984; McDowell et al., 2008) and can be either volitional (internally guided) in response to remembered locations or reflexive (externally guided) in response to new or non-visual stimuli (Gilman & Newman, 2003, p. 169). Saccades can also be either vertical or horizontal. Slower pursuit movements are used to maintain fixation on moving targets, however if the targets move too quickly then saccades are required (Gilman & Newman, 2003, p. 171). The net effect of these movements in to produce periods of fixation or dwell that indicate the stimuli which are capturing the participant's attention at that point in time (Duchowski et al., 2002). In other words, it is the position of the gaze which is most important. The present experiments incorporate measures of both vertical and horizontal gaze positions.

One of the most common ways to track eye movements in relation to a screen display is to establish a region (or regions) of interest and then measure the fixation time or percentage of trial gaze in that region by using pupil detection methods (Duchowski et al., 2002; Smyrnis, 2008). This method assumes that the head is relatively still (often in a chin rest) and that visual angle of the display remains constant (Duchowski et al., 2002).

The eye tracking experiments reported in this dissertation took this approach and regions of interest were defined for both vertical and horizontal gaze.

Applications in spatial cognition studies. Eye movements have frequently been used as correlates of spatial cognition using two dimensional computer screen presentations (for example of static scenes). However less work has been done with three dimensional presentations or presentations where the participant is moving through a virtual environment (Tatler, 2009). In general, this probably reflects the problem of analyzing the substantial amount of data that is generated when multiple frames (images) are presented to participants. Having said this, recent research is validating eye movement tracking during real world exploration (Hart et al., 2009) and eye movement measures are being used to improve presentation of stimuli (Hillaire, Lecuyer, Cozot, & Casiez, 2008) and measurement techniques (Duchowski et al., 2002) in virtual environments. Researchers have also compared eye movements in real and virtual environments and found subtle differences in gaze such that in virtual environments participants tend to look down more (Schoch, Gillner, & Mallot, 2005). However, studies of eye movements in three-dimensional environments are still few in number when compared to studies of two-dimensional scenes.

Eye tracking and navigation studies. There have been very few specific applications of eye movement tracking to the study of human navigation although some researchers have used eye movements as correlates of brain activations in fMRI studies of navigation (Mikropoulos, 2001; Spiers & Maguire, 2006). In a way-finding study, Okazaki, Kitahama, Miura, & Shinohara (2000) demonstrated changes in eye movements (in relation to head and body movements) during navigation in a real-world maze task but

did not link this to cognitive strategies. Mueller, Jackson & Skelton (2008) developed a paradigm which linked vertical gaze positions to specific navigational strategies and showed gender differences in vertical gaze during navigation in a virtual MWM task. The inference from this work is that eye movements indicate differing strategies utilized by males and females during spatial navigation. Gramann, Sharkawy & Deubel (2009) also used a virtual environment task with allocentric and egocentric biases and claimed that eye movements did not differ for the two different strategies. However, their virtual environment was extremely sparse, consisting only of tunnels and turns with no landmarks other than arrows at choice points. Consequently the two "strategies" identified in their study may have both relied on allocentric processing. The present research program addressed this problem by using more visually realistic displays and by creating a strong bias in the egocentric and allocentric tasks which were expected to drive eye movements in different ways.

Research Program Rationale

Theory

The experiments described in the current research program are based on cognitive map theory and on more recent interpretations of this theory. For example, the definitions of allocentric and egocentric are based on the mapping and taxis distinction proposed by O'Keefe & Nadel. However, a third praxis strategy has been noted in the animal research and might be considered purely egocentric because it pertains to body movements and not the relationship of the body to an external stimulus (e.g. Kolb, Sutherland & Whishaw, 1983). In the strictest sense this would imply that taxis (or cue-based) strategies are not egocentric. However, Trullier et al. (1997) argued that navigation is

hierarchical and that guidance (maintenance of a relationship of the body to one particular cue) is an egocentric strategy. That is, the task of reaching a goal can be accomplished by memorizing sensory information and without the need to form a spatial representation, as long as the target can be found using a single landmark. This definition of egocentric navigation was adopted during the design of the experiments reported here and thus the place-based virtual environment was considered allocentric and the cue-based environments were considered to be egocentric.

Purpose

The overall purpose of the research program reported in this dissertation was to address gaps in knowledge regarding how people form cognitive maps and how the information they gather from the environment influences their choice of navigational strategy. Figure 1.3 gives the structure of the present dissertation including details of study type, basic question and study population of interest. The research addresses the following general questions:

1. What is the influence of exploration of an environment on the formation of the cognitive map and on the ability to navigate?
2. How quickly can humans acquire a useful cognitive map?
3. How do different types of environmental stimuli influence strategy use/selection?
4. Are eye movements reliable indicators of navigational strategy use?
5. What is the influence of navigational experience on later strategy selection and navigation performance?

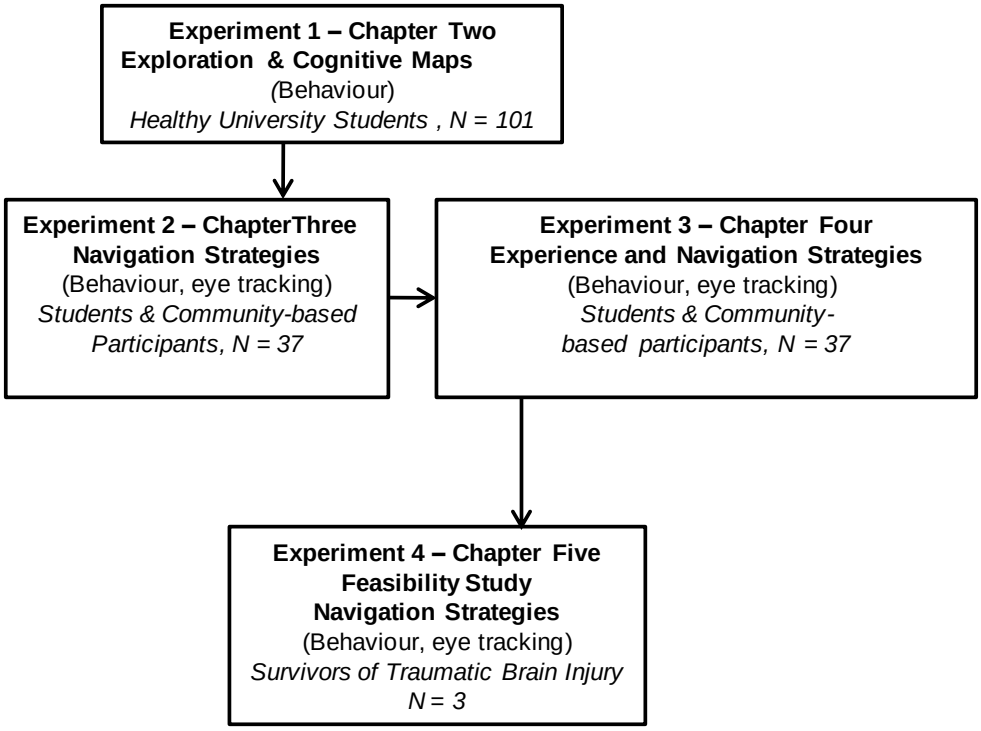

Figure 1.3. Chart showing experiments and flow of the research program for the dissertation entitled "Environmental and experiential determinants of human allocentric and egocentric navigation systems". .

6. How does brain injury affect navigational strategy use/selection?

Experiments

The importance of exploration for cognitive map formation was investigated in Experiment 1 by testing university students in a behavioural study of the effects of exploration on cognitive mapping and navigation in place-based and cue-based virtual environments. The reliability of eye tracking as a measure of strategy use was addressed in Experiment 2. Eye movements were recorded while participants navigated in either place-based or cue-based virtual environments. The influence of environmental experience on strategy selection was the subject of investigation in Experiment 3. Participants were trained to utilize either an allocentric or an egocentric strategy and then tested in an environment where either strategy would lead to successful navigation. Eye

movements were tracked during testing and compared to the behavioural strategies participants selected at the end of testing. Experiment 4 outlined the feasibility of employing the eye tracking method to differentiate strategy use in survivors of TBI. The foundation for Experiment 4 was an earlier study (Livingstone & Skelton, 2007) showing that survivors of traumatic brain injury have very particular navigational deficits and preserved abilities. The data analyzed in these experiments was collected within the context of a collaborative study with Dr. Philip Zeman (recently graduated from the University of Victoria) whose interest was the investigation of brain activity during specific cognitive tasks using a new electroencephalography (EEG) analysis technique.

Appendix 1-A

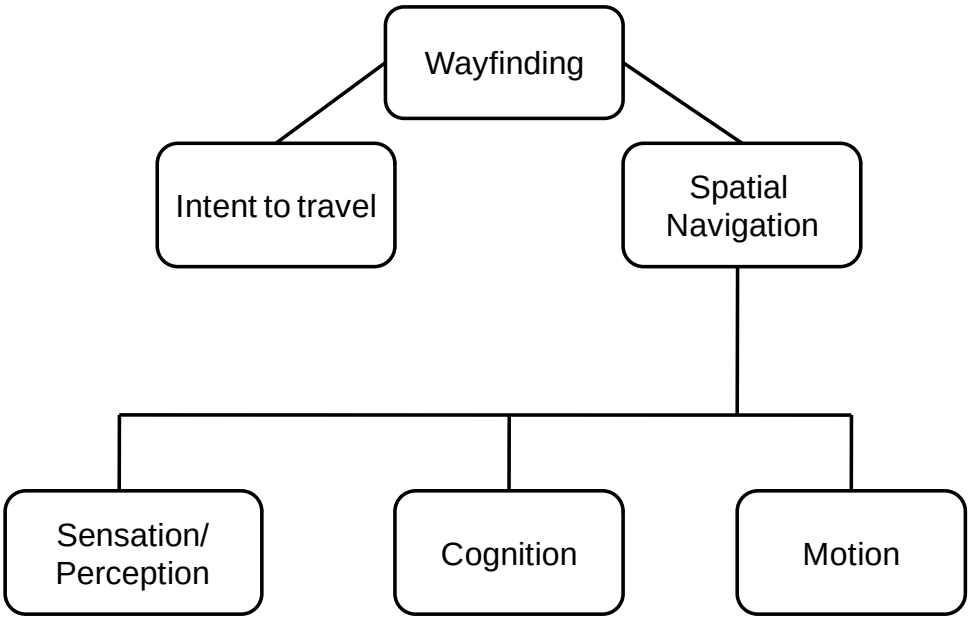

Figure 1-A.1. A map of terminology used to categorize wayfinding and its sub-processes, showing that spatial navigation occurs via the multiple processes of sensation, perception, cognition and motion. Note. From "Spatial navigation: Distinguishing navigational cognition and corresponding functional anatomy (candidacy exam)", by Sharon (Livingstone) Lee, 2008.

Appendix 1-B
Cognitive-Behavioural Model of Navigation

"At the heart of navigational cognition then, is a process (see the oval component in Figure 1-B.1) whereby strategies can be initiated via either system depending upon the

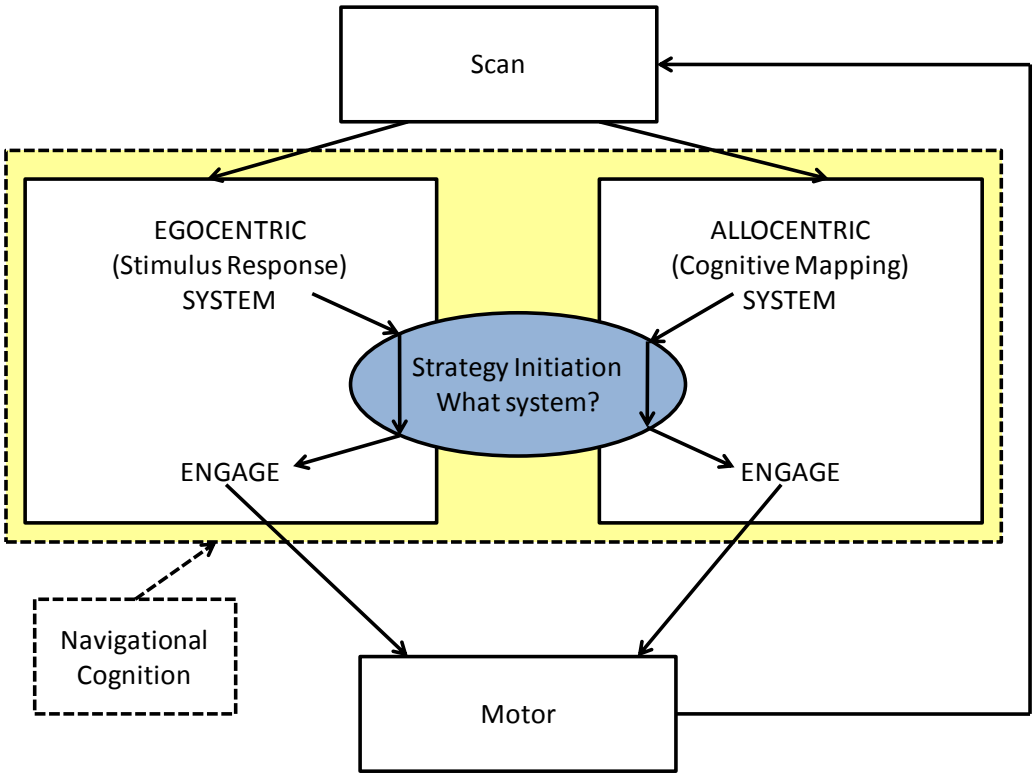

Figure 1-B.1: A model of navigational cognition showing two navigational systems and the strategy selection process. The basic navigation loop of scan, select (make behavioural decision) and move is shown. The large dashed box represents navigational cognition. The (blue) oval represents the relationship between the two cognitive systems.

strength of activity. For modeling purposes, strategies are reflected in subsequent navigational behaviour so that behaviours like navigating to invisible target locations or making detours are indicative of allocentric strategies whereas as simple guidance and route following result from egocentric strategies (Figure 1-B.1). Once the selection of strategy has taken place it is engaged by the system (either egocentric or allocentric) and

Appendix 1-B (continued)
Cognitive-Behavioural Model of Navigation

leads to corresponding activity in the motor system for locomotion toward the target location in the environment.

A second important aspect of the model is the emphasis on rapid selection of strategies. This rapid selection occurs via two circumstances: 1) both systems are activated by incoming stimulus information and therefore both systems are 'prepared' to respond and 2) the movement of the navigator through the environment supplies a continuous stream of ever-changing stimuli. The model proposes that the 'scan-select-move' loop can occur many times per second (Figure 1-B.2) accounting for the observation that healthy individuals usually navigate smoothly through the environment. It is also important to note that although there is a place in the model for navigating to 'interim destinations', the updating that is implied is done so rapidly that interim destinations can be any location on the path to the ultimate target. Thus this model takes both movement and time into account. The speed of the navigation loop is also important because the navigator must be able to avoid obstacles while maintaining a course toward the target location. In order to accomplish this, the navigator's motor and locomotor systems must receive frequent updates from the navigational systems allowing for quick and subtle responses while locomoting.

Note. Excerpt from "Spatial Navigation: A new model of navigational cognition (candidacy exam)", by Sharon (Livingstone) Lee, 2009, p. 17.

Appendix 1-B (continued)
Cognitive-Behavioural Model of Navigation

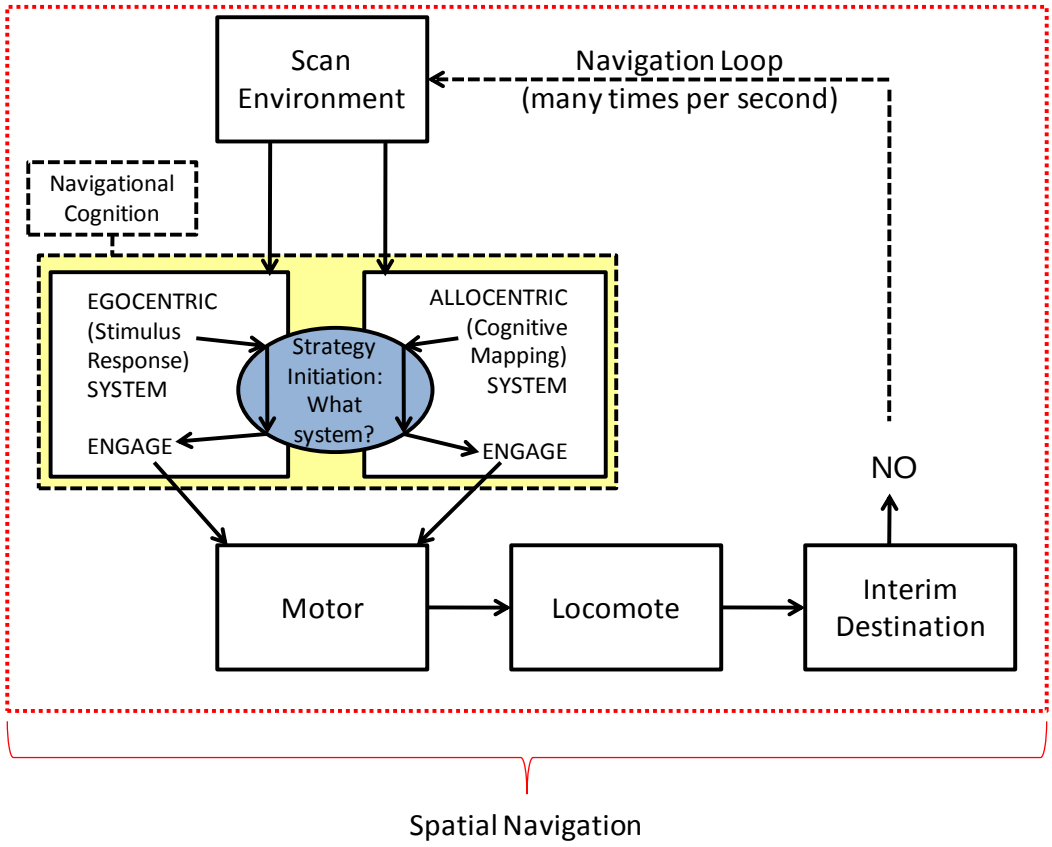

Figure 1-B.2: A model of spatial navigation showing that the process of scanning for stimuli, processing stimuli and responding to them can occur rapidly (many times per second). Note that navigational cognitive mechanisms allow for the flexible selection of strategies in response to new or changing stimuli in the environment.

Appendix 1-C
Navigational Spatial Processes

Navigational cognition includes the learning, memory and computation necessary for locomotion toward a target location in the environment. As such, the types of spatial cognition related to navigation are those processes necessary *for* movement or *during* movement. These include the perception and processing of environmental stimuli before navigating begins or, as the navigator is moving through the environment. As well, navigational cognition includes those processes involved in integrating currently available stimuli with remembered stimuli and computing routes while in the process of navigating or locomoting. It is important to note that locomotion is a separate process necessary for the navigator to coordinate their movement through the environment in the context of potential obstacles or changes to the terrain. Logically, the locomotor system must receive input from stimuli in the environment so it can move the navigator over rough terrain, maintain balance, and keep to a path or track if available.

As previously stated, the important cognitive (navigational) mechanisms are those necessary to locomote toward a goal in space rather than the (non-navigational) processes underlying the manipulation of objects near to the body or the sensory/perceptual (pre-navigational) processes that feed into spatial cognition **(**Table 1-C.1). Navigational processes include stimulus-response processes such as guidance toward a single landmark goal in the environment, the making of routes, and the choice of immediate path. Navigational processes also include the important ability to perceive configurations of objects in walking space i.e., during locomotion. These configurations of objects are acquired specifically for the purpose of navigation.

Note. Excerpt from "Spatial navigation: Distinguishing navigational cognition and corresponding functional anatomy (candidacy exam)", by Sharon (Livingstone) Lee, 2008, p. 12

Appendix 1-C
(continued)

Table 1-C.1: *The division of spatial processes according to their association with sensory, motor or cognitive processes. These processes are further classified according to whether there is a navigational component.*

Non-navigational spatial processes	
Process	Examples
Pre-navigational information processing (sensory and perceptual)	• Vision – optic flow, object motion perception • Audition, olfaction and touch
Non-navigational spatial cognition (computed from a fixed perspective)	• Mental rotation • Face recognition • Object manipulation • Configurations of objects in grasping space (e.g., on a tabletop)
Shared pre-navigational perceptual information (necessary for navigation but may be shared by other spatial cognition processes; computed from a fixed perspective)	• Perception of objects, scenes, objects within scenes, locations of objects in a scene • All of the above using other sensory modalities
Navigational spatial processes	
Process	Examples
Non-cognitive movement processes (locomotor processes)	• Sensory-motor integration of movements with proximal objects in the environment (for impact avoidance) • Proprioceptive information for self-locomotion
Navigational Cognition (cognitions specific to navigation; computed for movement or while moving)	• Perception of routes, landmark guidance and configurations of objects in walking space • Choice of immediate path • Coordination of movements with distal objects in the environment (for guidance and approach)

Note. Adapted from "Spatial navigation: Distinguishing navigational cognition and corresponding functional anatomy (candidacy exam)", by Sharon (Livingstone) Lee, 2008, p. 10.

Chapter Two

This chapter consists of a manuscript describing the relationship of exploration to two types of navigation (allocentric and egocentric) in virtual environment navigation tasks. The study investigated the effects of exploration on navigation performance in a sample of university students. The main objective was to determine whether pre-trial exploration was necessary for allocentric navigation, but not for egocentric navigation.

Exploration and cognitive maps are required for optimal allocentric navigation in a virtual Morris water maze.

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Abstract

The effect of exploration on human navigation has not been directly tested. The objectives of the present experiment were to show that the opportunity to explore improves allocentric navigation and that exploration is not required for egocentric navigation. University students (N = 101) were tested either in an allocentrically biased "Place" maze or an egocentrically biased "Floor Cue" maze, versions of a virtual Morris water maze (vMWM). The Place maze required participants to repeatedly find a target platform hidden under the floor of the arena and from differing start positions around the arena wall. The Floor Cue maze had two objects on the floor of the arena, with one marking the location of the platform. Participants learned which object marked the platform location and traveled to the platform from differing start positions. Half of participants were permitted to explore the environment before testing and to scan the environment from the perspective of the platform at the end of each trial. Exploration was associated with improved performance in the Place maze but not in the Cue maze. Thus exploration selectively improved performance in an allocentric, place-based navigation task. Without exploration participants in the Place maze had impaired scores on cognitive map tests whereas Floor Cue maze participants did not. These findings highlight the importance of exploration for human spatial navigation and have implications for the ecologically valid design of vMWM tasks as well as their application in brain imaging studies. The results are especially important for the study of navigation deficits because limiting exploration may have more profound effects on performance in clinical populations.

Exploration and Cognitive Maps

Cognitive maps have long been considered the cornerstone of mental representations of large-scale space (O'Keefe & Nadel, 1978; Tolman, 1948) and a key component in the cognitive mechanisms of spatial navigation (O'Keefe & Nadel, 1978). Cognitive maps allow navigators (birds and mammals) to make detours or shortcuts to goal locations (Gallistel, 2009; Jacobs & Schenk, 2003; O'Keefe & Nadel, 1978; Trullier, Wiener, Berthoz, & Meyer, 1997). Although it is generally proposed that such maps are not "pictures" of the environment (O'Keefe & Nadel, 1978), their contents are still being debated (Hamilton, Akers, Weisend, & Sutherland, 2007; Jacobs & Schenk, 2003). Consequently, it has not been determined what processes are necessary for the acquisition of cognitive maps.

Cognitive Map Acquisition

The cognitive map theory of navigation proposes that maps are acquired via the navigator's interaction with (experience with) the environment (O'Keefe & Nadel, 1978). The theory also suggests that such experience leads to automatic updating of the cognitive map to incorporate new environmental information. In research with non-human animals, one important source of environmental experience is assumed to be exploration (O'Keefe & Nadel, 1978, p.263). In spite of this, the contribution of environmental experience (and therefore exploration) to human cognitive map acquisition is a relatively recent subject of study. Some research has demonstrated that during acquisition of a cognitive map humans automatically update the developing map (Yaski et al., 2009) and that exploration is linked to map acquisition (Hamilton, Driscoll, & Sutherland, 2002; Hardt, Hupback, & Nadel, 2009; Iaria, Palermo, Committeri, & Barton,

2009; Yaski, Portugali, & Eilam, 2009). However, it has also been shown that in familiar environments for which a cognitive map already exists, the introduction of new stimuli does not necessarily lead to automatic updating of the map (Hardt et al., 2009). This finding may be linked to changes in exploratory behaviour, but the links between exploration and cognitive map acquisition have not been fully tested in human studies.

If exploration is important for map acquisition and updating, there are implications not only for the quality of the cognitive map but also for navigational performance. This issue is becoming increasingly important because researchers are putting more time and effort into understanding the neural basis of navigation and spatial cognition, particularly with respect to navigation that requires a cognitive map. Additionally, not all types of navigation may require a cognitive map and therefore exploration may not be necessary for navigation in all cases. Thus, to properly investigate the neural basis of navigation, it is important to clarify under what circumstances exploration is required (or not) for best performance.

Cognitive Mechanisms of Navigation

Research with animals has identified at least two distinct types of navigation associated with two separate cognitive navigational systems (Morris, Hagan, & Rawlins, 1986; for reviews see, Nadel & Hardt, 2004; Poldrack & Packard, 2003). These systems are frequently referred to as "allocentric" and "egocentric" and they provide the computations necessary for optimal performance under differing navigational circumstances. The allocentric system was labelled the 'locale' or cognitive mapping system by O'Keefe & Nadel (1978) and is also referred to as "place-based" because it allows for navigation to a place by the use of configurations of stimuli. The egocentric or

"taxon" system (O'Keefe & Nadel, 1978) is sometimes referred to as "cue-based" because it allows for navigation toward stimuli that are visible in the immediate environment. Thus the egocentric system was initially described as pertaining to landmarks or routes based on series of landmarks. A third "praxis" system (Sutherland & Dyck, 1984) has been described as relying on body-based responses (for example, left or right turns) and is also considered egocentric.

The two navigation systems allow animals to navigate space from two perspectives, one from the immediate viewpoint of the animal (egocentric) and another from an imagined perspective (allocentric). Most importantly, the allocentric system allows the animal to navigate to places in the environment that are not marked by a proximal stimulus but rather are marked by configurations of stimuli. The allocentric system is therefore considered to be flexible (Jacobs & Schenk, 2003; O'Keefe & Nadel, 1978; Trullier et al., 1997) because it allows animals to take detours and create new routes once they are familiar with the environment (i.e., have acquired a cognitive map). Further, as long as a number of related distal stimuli are present, no particular one is necessary for allocentric navigation (Schenk, 1998, p. 145) to be successful.

The presence of the two navigation systems in animals is supported by research into the functional anatomy of navigation mainly in rodents (e.g., Poldrack & Packard, 2003; White & McDonald, 2002). The central structure of the allocentric system is the hippocampus whereas the central structure of the egocentric system is the striatum, specifically the caudate nucleus. In humans, convergent evidence for the two systems is accumulating through combined behavioural and brain imaging studies (Doeller, King, & Burgess, 2008; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Maguire, Frith, Burgess,

Donnett, & O'Keefe, 1998; Pizzamiglio, Guariglia, & Cosentino, 1998). In the current context (i.e., the study of exploration effects), one of the most important distinctions between allocentric and egocentric navigational systems is that while the egocentric system is thought to require only the acquisition of simple stimulus-response associations, the allocentric system is proposed to require exploration and the acquisition of a cognitive map.

Exploration and Cognitive Map Acquisition

Exploration of an environment is assumed to be a sensory-motor (or cognitive) process and can be accomplished in different ways. Kuipers (1983) identified four of these that can be measured in an experimental context: 1) free exploration, 2) naive search, 3) observation of others, and 4) route following. Kallai, Makany, Karadi & Jacobs (2005) identified a fifth category, exploration by visual scan. Free exploration of the environment is simply movement through the environment in the absence of a defined task goal. Darken & Sibert (1996) define it as a "wayfinding task in which there is no target" (p. 143) and as "the basic task of spatial comprehension" (p.143) implying that it contributes basic understanding of the layout of an environment (and thus the cognitive map). Free exploration may occur when participants in an experiment are given the opportunity to familiarize themselves with an environment prior to testing. Exploration might also occur during naive search, that is, when participants are initially searching for a particular target whose location is unknown. Participants may also explore and acquire a cognitive map of the environment by observing the behaviour of another participant as they navigate in the same environment. Both rats (Leggio et al., 2003) and humans (Thomas, Hsu, Laurance, Nadel, & Jacobs, 2001) appear to be able to do this.

Exploration can also be accomplished via visual scan when the participant is in a fixed position (Kallai et al., 2005). This can occur during initial orientation to the environment or during pauses in movement. Although various methods of exploration have been identified, their efficacy in contributing to cognitive mapping and optimal navigation has not been fully tested. The focus of the present experiment was on free exploration (before training trials) and exploration by visual scan from a fixed location.

Animal exploration. Exploration is thought to be an important factor in the ability of rats to acquire cognitive maps (Nadel, 1991; O'Keefe & Nadel, 1978) although empirical evidence for this is somewhat sparse. In rats exploration is a natural behaviour that tends to occur spontaneously in new (unfamiliar) environments (Leggio et al., 2003; Renner & Pierre, 1998). It is proposed to allow the animal to gather information from the environment (for review see, Renner, 1990) and therefore to provide the foundation for learning including spatial learning. However, the behaviour itself has sometimes been considered a 'nuisance variable' (Renner, 1990, p. 16) and is therefore downplayed in many studies. Exceptions are those directed at the relationship between exploration and cognitive mapping. For example, by measuring velocity, distance and angle of rat exploration trajectories, Tchernicovski & Golani (1995) showed the changes associated with a place becoming familiar to the rat. The authors interpreted this as evidence for a system that in early exploration allows rats to construct several spatial representations that may combine to form the cognitive map.

The opportunity to explore (and presumably form a cognitive map) may further be associated with better performance on place-based tasks. Experimental manipulation of the opportunity to explore has been shown to influence allocentric performance. For

example, Ellen, Parko, Wages, Doherty, & Herrmann (1982) demonstrated better performance in a place-based task (Maier's 3-table spatial problem solving task) when rats were given the opportunity to explore all features of the testing environment as opposed to being given the opportunity to explore only one part of the environment. A similar result has been reported for navigation in the Morris water maze (MWM) task (Sutherland, Chew, Baker, & Linggard, 1987).

Human exploration. Because cognitive map theory predicts that exploration should be linked to mapping, it seems likely that if healthy human navigators are restricted in their opportunity to learn the configurations of environmental stimuli the result should be that they acquire insufficient cognitive maps (Jacobs & Schenk, 2003). However, the contribution of exploration to the effective acquisition and use of cognitive maps is not well understood in humans. Exploration is not generally quantified in human navigation research (Jacobs, Thomas, Laurance, & Nadel, 1998) although the ability to engage in real world exploration might be very important under certain navigational conditions, for example where the environment is unusual or may be dangerous (Wu, Zhang, & Zhang, 2009). A small number of experiments have demonstrated the importance of exploration for cognitive mapping and potentially for allocentric navigation performance. Yaski et al. (2009) showed that exploration is a sequential process that appears to stabilise once a cognitive map is acquired. In their study participants were blindfolded but were able to gradually acquire cognitive maps as evidenced by the use of detours to find target locations in the room environment.

Exploration and Egocentric Navigation

Because research has mainly been directed toward understanding allocentric

navigation, there is no study of the effects of exploration on egocentric navigation in humans. It is simply assumed that exploration would not be required. Some animal studies have examined the exploration of objects in the environment, although this work tends to focus on exploration for the purpose of acquiring or updating a cognitive map (e.g., Galani, Weiss, Cassel, & Kelche, 1998) rather than cue-response navigation. One study did show that allocentric cues are probably more dominant for animals than are single cues/landmarks (Kealy et al., 2008). Further, overtraining in an allocentric maze does not lead to the use of egocentric learning strategy as might be expected when the animal becomes more familiar with the environment. It is not known whether exploration is necessary for egocentric navigation, especially within the context of an environment where many proximal cues are available to the navigator.

The Morris Water Maze

In animal research, the gold standard for measurement of allocentric navigation is the MWM (Brandeis et al., 1989; D'Hooge & De Deyn, 2001). This task (Morris, 1981) requires rats to swim to an invisible platform placed just below the surface in a round pool of milky water. The rat completes a number of trials from different start positions around the wall of the pool, and thus has to learn the location of the platform using available cues that include the arena wall (which is a uniform texture and colour) and distal room cues located outside of the pool. The ability of the rat to directly return to the platform regardless of start position is taken to mean that the rat has formed a representation (or cognitive map) of the environment (Morris, 1981; Morris, Garrud, Rawlins, & O'Keefe, 1982) and uses an allocentric system to navigate. The MWM task has also shown that the hippocampus is a structure important for allocentric navigation (J.

O'Keefe & Dostrovsky, 1971). Damage to this structure has repeatedly been associated with impaired water maze performance in animals (for review see D'Hooge & De Deyn, 2001, p.67) and more recently in humans by using virtual MWM (vMWM) tasks (Astur, Taylor, Mamelak, Philpott, & Sutherland, 2002; Barrash et al., 2000; Goodrich-Hunsaker, Livingstone, Skelton, & Hopkins, 2010).

Exploration and the Morris water maze. If the amount of exploration seems to be an important factor in determining navigational performance, and the MWM is the gold standard for investigating navigational cognition, then it makes sense to examine more closely the effect of exploration on performance in the MWM. This examination will consider the previously mentioned studies of exploration in the MWM in the context of other exploration-MWM investigations.

In animal studies employing the MWM explicit exploration trials are not generally provided. Rats are usually given invisible platform trials sometimes followed by visible platform trials (e.g., Hannesson & Skelton, 1998). However, during the inter-trial intervals, rats are often kept in a holding cage in the room containing the maze, thereby providing an experience containing some of the elements of exploration, i.e., via visual scan. Such incidental experience could potentially influence performance in the maze task. In studies where the links between environmental experience and navigation performance are the subject of interest, aspects of the animals' exploratory behaviours are measured or manipulated. An example is the study of behaviours on the water maze platform, presuming that animals explore (i.e., scan) the environment during their time on the platform at the end of behavioural trials. Sutherland et al. (1987) reported that rats can benefit from exploring while on the platform but only when they have already had

some experience of navigating in the environment. A more direct study of the behaviour of rats on the platform in a MWM has shown that a reduction in turning or rearing behaviour is associated with impaired navigation performance (Schulz, Kouri, & Huston, 2007). One interpretation of this finding is that turning and rearing represent exploratory behaviours that when reduced, interrupt cognitive mapping and thus impair navigation performance. Exploration behaviour can also be directly manipulated by limiting and varying exposure to the environment during training trials. For example, Sutherland et al. (1987) demonstrated that rats performed significantly better in transfer trials of the MWM if they had the opportunity to navigate the entire pool during training as opposed to conditions where they were only free to navigate half of the pool. This result occurred despite the fact that the animals whose exploration was restricted were still able to view the entire maze environment through a Plexiglas™ barrier. Thus to locate the platform quickly, simply viewing the environment was not as effective as moving through the environment while searching for the platform.

Virtual Morris water maze tasks. Recently, researchers have developed virtual versions of the MWM task for testing human allocentric navigation (e.g., Astur, Ortiz, & Sutherland, 1998; Jacobs, Laurance, & Thomas, 1997). These computer-based tasks are translations of animal paradigms and provide measures of cognitive mapping and allocentric navigation. They are also thought to be ecologically valid tools for measuring navigation performance (Jacobs et al., 1998; Rizzo, Buckwalter, & Neumann, 1997; Ross, Skelton, & Mueller, 2006; Waller, Hunt, & Knapp, 1998).

In general, vMWM tasks require participants to learn the location of a spot in a virtual pool located within a room that has distal stimuli in the form of windows, pictures

or other objects located on its walls. Participants must search for the platform and once they find it, successive trials require them to find it from different starting points around the edge of the pool. The main advantages of these virtual tasks are that they are safe for participants, easily replicated, and that they allow for exacting control and systematic variation of the features of the environment. In the current context these manipulations included variations in the amount of free exploration and the amount of time permitted on the maze platform at the end of each behavioural trial.

Virtual MWM tasks have only rarely highlighted or tested exploration behaviour. In a replication of an earlier animal study (Sutherland et al., 1987), Hamilton, Driscoll &Sutherland (2002) showed that when participants were able to navigate only half of the virtual environment, they were behaviourally impaired on later transfer trials that allowed navigation of the whole environment. This effect occurred even when participants were given the opportunity to explore the previously hidden half of the maze at the end of each trial block and even though they were able to view the whole maze environment at all times. The authors speculated that locomotion to the target on training trials constituted exploration and caused participants to acquire and update a cognitive map of only half of the MWM and that this map was insufficient for transfer of spatial knowledge. In another exploration study, Hardt, Hupback & Nadel (2009) showed that when participants were encouraged to explore the environment they were able to overcome the effects of blocking in a vMWM task. The authors concluded that human cognitive maps (based on visual stimuli) are automatically updated by exploration, suggesting that without exploration updating of the cognitive map will not occur and performance will be impaired as a result. However this hypothesis has not been directly tested.

There is considerable variability in performance in different vMWMs as measured by differences in conventional maze variables such as latency and distance to the platform or learning rate. This variability may relate to whether or not participants are allowed to explore the environment before testing or from the vantage point of the platform. Some vMWM tasks appear to be learned in only 2 or 3 trials when free exploration is allowed, whereas learning may take as long as 12 trials when exploration is not permitted (Astur, Tropp, Sava, Constable, & Markus, 2004; Driscoll, Hamilton, Yeo, Brooks, & Sutherland, 2005; Hamilton et al., 2002). An informal review of 30 vMWM studies showed that free exploration (or practice with the environment before testing) was provided in only about a third of studies (Table 2.1). Further, where latency and distance measures were provided, there appear to be large differences such that participants who were given the opportunity to explore the environment before testing located the hidden platform more quickly and by taking shorter paths (as measured on the 10^{th} performance trial). These differing learning rates suggest that exploration may be an important factor in the acquisition of a high quality cognitive map that allows for optimal place navigation. However, these observations are correlational and there has been no systematic test of allocentric navigational performance based upon whether or not exploration was permitted.

Summary

Research to date on the role of exploration in the acquisition of cognitive maps would suggest that exploration is an important factor in navigational performance. Two distinct navigational cognitive systems (allocentric and egocentric) have been identified in animals and their central structures are the hippocampus and the striatum (caudate),

Table 2.1

An informal comparison of vMWM studies where exploration of the environment was or was not permitted prior to testing. Latency and distance to the platform are both reduced when exploration is allowed.

Measure	No Exploration	Exploration
Mean Latency to platform on search trial (Trial 1)	65s	33s
Mean Latency to platform on Trial 10	34s	10s
Mean Distance to platform on search trial (Trial 1)	3pd	3pd
Mean Distance to platform Trial 10	1.5pd	.7pd

Authors

Astur et al., 1998
Astur et al., 2002
Astur et al., 2004
Bartsch et al., 2010
Burkitt et al., 2007
Chamizo et al., 2003
Cornwell et al., 2010
Driscoll et al., 2005
Hamilton & Sutherland 1999
Hamilton et al., 2002
Hamilton et al., 2003
Hanlon et al. 2006
Hardt, Hupbach & Nadel, 2009[a]
Jacobs et al., 1997
Jacobs et al., 1998
Kallai et al., 2005
Chai et al., 2010
Goodrich-Hunsaker et al., 2010
Hardt, Hupbach & Nadel, 2009[a]
Livingstone & Skelton, 2007
Skelton et al., 2006
Mueller et al., 2009
Mueller Jackson Skelton 2008
Ross Skelton Mueller 2006
Sandstrom et al., 1998
Shipman & Astur, 2008
Thomas et al., 1999[a]

Table 2.1. *An informal comparison of vMWM Studies(continued)*

Exploration	No Exploration
Authors	
Nadel et al. 1998	
Newhouse et al., 2007	
Rahman & Koerting, 2008	
Thomas et al., 1999 [a]	
Woolley et al., 2010	

Note1. Latency measured in seconds(s) and all distance measures converted to pool diameters (pd).
Note 2. vMWM = virtual Morris water maze.
[a] Studies include both an 'explore' and 'no explore' condition.

respectively. Damage to the hippocampus causes impaired navigation performance in MWM tasks (both real and virtual). In animals, exploration is thought to be important for the development of a cognitive map and therefore for allocentric navigation. When animals are denied the opportunity to explore the entire environment before navigation testing, their performance is impaired. Further, reduced exploration behaviour has been correlated with poor allocentric navigation. In humans, maps appear to be developed sequentially and to be updated by exploration. Exploration may also lead to improved performance in vMWM tasks. However, the nature of the relationship of exploration to navigational performance (both allocentric and egocentric) has not been directly tested.

Investigations to date have not determined whether humans need to engage in exploratory behaviour to achieve optimal performance on navigation tasks. Consequently, research has not clarified how navigational performance is affected by the quality of the cognitive map or how much exploration is needed for an adequate map to be acquired. Indeed the quality of human cognitive maps has not been the focus of research. Further, research has not clarified the conditions under which exploration may

or may not be required. For example, it has not been demonstrated that exploration is needed for tasks which can be solved using egocentric navigation. Because egocentric navigation relies on simple stimulus-response associations and not cognitive maps, presumably tasks which can be solved using egocentric navigation would not need or benefit from exploration prior to the onset of learning trials.

Research Questions and Hypotheses

The research presented below considers two main questions. First, is (pre-trial) exploration required for the formation of a cognitive map and does it improve place (allocentric) navigation in humans? And second, is (pre-trial) exploration required for cue-response (egocentric) navigation? To answer these questions the amount of pre-trial exploration was manipulated before testing in either an allocentrically or egocentrically biased vMWM task. The "Place" maze tested allocentric navigation with and without exploration of the virtual environment prior to testing. The present study investigated whether exploration *selectively* affects allocentric navigation. To do this the "Floor Cue" maze was used to test egocentric navigation with and without exploration of the virtual environment before testing. In conditions where exploration was allowed participants were also able to visually scan the environment from the vantage point of the platform at the end of each behavioural trial. It was hypothesized that without the opportunity to explore the environment before testing (or at the end of trials) performance in the allocentric Place maze would be significantly impaired compared to when exploration was possible before testing and after each trial. It was also hypothesized that the absence of exploration opportunity would not impair performance in the egocentric Floor Cue maze.

Methods

Participants

Participants were 101 healthy adults (Male = 61, Female = 40) recruited from the introductory psychology class at the University of Victoria. They met the following inclusion criteria: a) male or female between the ages of 19 and 60, b) English first language, c) no history of brain injury or neurological disorder. Participants were asked to read and fill out a background information questionnaire (Appendix 2-A) providing demographic information as well as information about computer game experience (Appendix 2-A). They also gave informed consent and the research was approved by the Human Research Ethics Committee at the University of Victoria.

Maze Apparatus

Spatial navigation was tested using three vMWM tasks: the Place maze, the Floor Cue maze and the "Visible Platform" maze. These are adaptations of the Arena maze task (Livingstone & Skelton, 2007; Skelton, Bukach, Laurance, Thomas, & Jacobs, 2000; Skelton et al., 2006). These desktop virtual environments were developed using a commercially available video game editor, Unreal® (Epic Megagames), and were displayed on a 19 inch LCD monitor at a resolution of 800 x 600. Participants navigated through the trials using a typical "game pad" that is held in two hands. The game pad features were modified so that participants could move forward, left and right, but not in reverse.

The Place maze environment consisted of a large circular arena bordered by a low wall and situated in a large square room .The room had large windows in all four walls, providing panoramic views of an outdoor landscape (Figure 2.1). The four walls of the

room were arbitrarily assigned cardinal directions of North, South, East and West and the room lacked any distinctive features other than the environment outside the windows. There was a large window on each of the north and south walls and three windows on each of the east and west walls. The views looking out each side of the room were distinct. Mountains were visible through the north window and hills sloped down to a sandy beach outside both the east and west windows. A body of water with a small island could be viewed through the south window. The outdoor landscape provided distal stimuli to aid in navigation to a hidden platform and therefore the Place maze biased participants toward the use of an allocentric strategy.

The Floor Cue maze (Figure 2.1) was identical to the Place maze except for the addition of two cue objects situated on the floor of the arena, each in the centre of adjacent quadrants. The location of the target platform was changed on each trial, but the same object (a red flare) always indicated the correct location. A distracter object (a flashlight) was always located at the same distance from the start position as the cue object (the flare) in the centre of the adjacent quadrant. This Floor Cue maze promoted the use of egocentric strategies because the platform was easily located using a single proximal cue.

The Visible Platform maze utilized the same virtual environment as the Place maze. The platform was always visible on the floor of the arena but its location changed on each trial.

Procedures

Design. The main question addressed by this research concerns differences in performance based on whether or not participants were allowed to freely explore the

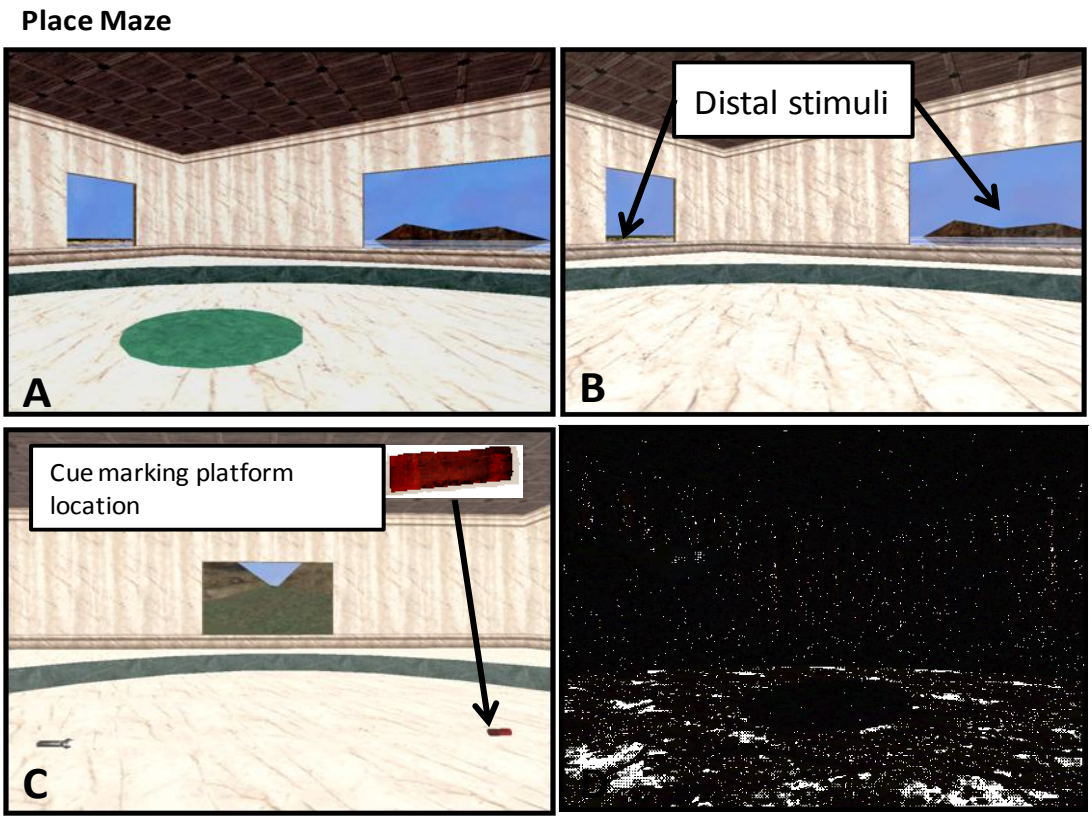


Figure 2.1. Views of the Place maze and the Floor Cue maze from inside the virtual arena. The two virtual environments appear identical to the participant except for the addition of two proximal cue objects (a red flare and a grey flashlight) on the arena floor in the Floor Cue maze. **A.** The Place maze showing the target platform after it has been found by the participant. **B.** The location of the platform on all trials of the Place maze and the distal cues available for navigating. **C.** The Floor Cue maze environment showing two proximal objects on the floor. The platform is always located under the red flare but participants have to select between the flare and a distracter cue (the grey flashlight) that appears either to the left or to the right of the flare. **D.** A view of the Floor Cue maze showing an example of the platform in the northeast quadrant of the arena (the platform location changes from trial to trial). Note. In both mazes, the platform is always invisible until the participant steps on it.

virtual environment before completing the navigation tasks. Therefore, a 2 x 2 between subjects design was implemented with 2 levels of exploration (explore and no-explore) and 2 levels of navigation (place and cue). Thus there were four experimental conditions: 1) place-explore, 2) cue-explore, 3) place-no-explore and 4) cue-no-explore. Participants were randomly assigned to one of these four conditions. Table 2.2 describes the

operational definitions for each experimental condition and descriptions of the individual trials are presented below.

Explore Condition. The order of presentation of trials in the explore condition was: exploration, visible platform, invisible platform (place or floor cue), probe, Drop-the-seed (DTS) (Table 2.3). The purpose of each trial is given in Table 2.4 and the trials are described below.

Table 2.2

Design and operational definitions for explore and no-explore conditions and the two mazes (Place and Floor Cue).

Exploration Definitions	
Explore	No-explore
Free exploration of room	No free exploration
Visible platform training pre-test Time on platforms *ad libitum*	Visible platform training post-test Time on platform limited (6 s)
Maze Definitions	
Place maze	Floor Cue maze
Platform invisible but always in one place in room, in the centre of a quadrant.	Platform in the centre of one of four quadrants in the arena, marked by cue on floor at the centre of the invisible platform.

Room Exploration trial. The purpose of this trial was to allow participants to become familiar with the environment and to practice using the game pad. The trial began with participants situated at the centre of the east wall, outside of the arena and looking toward the middle of the room. Participants were told that they could explore the

Table 2.3

Order of trials for the four experimental conditions. There were two levels (Place and Cue) of maze type and two levels (explore and no-explore) of exploration type.

Test phase	Place-explore	Cue-explore	Place-no-explore	Cue-no-explore
Pre	Room explore	Room explore		
	VP maze	VP maze		
	RR map test			
Testing	Place maze	Floor Cue maze	Place maze	Floor Cue maze
	Probe	Probe	Probe	Probe
	DTS	DTS	DTS	DTS
Post	WTWT	WTWT	WTWT	WTWT
	RRT	RRT	RRT	RRT
			VP maze	VP maze

Note. VP = Visible Platform, WTWT = Where's the Water Task, RRT = Room Reconstruction Task, DTS = Drop-the-seed.

room for as long as they liked. The exploration trial ended when the participant indicated comfort with the video game pad and satisfaction with their exploration of the virtual environment.

Visible platform maze trials. The purpose of these four trials was to confirm that participants could navigate to a single visible target in the environment and to allow participants to become familiar with the environment. During the trials a large, green, circular platform was visible on the floor of the arena in the centre of a different quadrant for each trial. The start position for each trial was different, with all start positions being inside the arena wall and at a cardinal point. Participants were instructed to walk to

Table 2.4

Number (how many) of trials, trial types and trial purpose. The order of the trials depends upon the experimental condition.

Trial type	Purpose	Number of
Room Exploration	To allow participants in explore condition to become familiar with the environment and to practice using the game pad.	1
Visible Platform	To confirm that participants are able to navigate to a single target in the environment and to allow participants in the explore condition to become familiar with the environment	4
Invisible Platform	To test participants' ability to navigate to a location in the room	10
Probe Trial	To implicitly test how well participants learned the platform location.	1
DTS trial	To explicitly test how well participants could recall the platform location.	1

the platform as quickly and directly as possible. When they stepped on the platform it made a sound like a bell ringing and four low walls rose up to surround the platform so that the participant could not move any further. Participants were then given the opportunity to look around the room (while remaining confined to the platform). When the participant was ready they were "jumped" to the beginning of the next trial, the start of which was indicated by a short high-pitched beep.

Invisible platform trials. The purpose of these 10 trials was to test participant ability to navigate to a location in the room. Start positions were always just inside the arena wall, at one of the four cardinal points and varied in a fixed, pseudo-random order. Start positions were also balanced according to whether the participant should make a left

or right turn and according to the distance from the start position to the target location. The platform remained invisible until the participant stepped on it, at which point it rose up making a sound like a bell ringing. As in the visible trials, four low walls rose up to surround the platform at the end of each trial and a high-pitched beep indicated the beginning of each new trial. While on the platform, participants were able to look around the room as much as they liked before proceeding to the next trial.

For the Place maze, the invisible platform was in a fixed location in the centre of the southeast quadrant. Participants were informed that the platform would always be in the same place and that they should go to the platform as quickly and directly as possible.

For the Floor Cue maze, the platform was located in different quadrants but was always marked by the red flare on the floor of the arena. It remained invisible until the participant stepped on it. Participants were informed that the platform would not always be in the same place but that there would always be a clue as to its location.

Probe trial. The purpose of this trial was to test how well the participants learned the platform location. Prior to testing, participants were informed that on one trial the platform would be very difficult to find but that they should continue to search for it anyway. During this probe trial, the platform remained hidden for 50s and the end of the trial was indicated by the usual bell ringing sound.

Drop-the-seed (DTS). The purpose of this trial was to test the explicit knowledge of participants with respect to the platform location. Participants were instructed to go to the spot where they thought the platform should be (based on the trials they were just completing) and once there the experimenter dropped a virtual seed to mark the location. The virtual seed grew into a virtual plant that marked the spot for later

scoring. For scoring, a ringed "bull's eye" target was placed over the quadrant where the platform was located during the invisible platform trials, with the centre of the target matched in size to the platform (Figure 2.2). Scores from 0 to 7 were assigned based on the location of the participant's marker to the centre of the target (or bull's eye). A score of 0 indicated that the marker was not on the target rings whereas a score of 7 indicated that the marker was placed on the bull's eye (i.e., on the platform location). Participants did not observe the scoring procedure.

No-explore conditions. The trials in the no-explore conditions were as described in the explore conditions however the order of presentation differed such that participants in the no-explore conditions were not given the opportunity to explore the environment prior to testing. The order of trials was: invisible platform (Place or Floor Cue maze), probe, DTS, visible platform. Time on the platform on all maze trials was limited to 6s, at which point participants were automatically moved to the next trial. Therefore there was very little time available to participants for the formation and/or improvement of a cognitive map either before or during testing.

Cognitive Map Tasks

Where's the Water Task (WTWT). The purpose of this test was first to ascertain that participants felt "embedded" or felt a sense of "presence" in the virtual environment. Second, the test was a measure of how well the participants understood the locations of the important distal features in the environment. At the completion of the computer tasks, participants were moved to a trial where they faced the north window, through which they could view the mountains. Participants were then asked to indicate, by pointing, where the water was located in the virtual environment. If participants

Figure 2.2. Scoring for the DTS trial. The plant marks the spot where the participant dropped a virtual "seed". The task is scored using target rings with the center "bull's eye" matching the size and location of the platform in the maze. Scores range from 0 for placement outside the target rings (and outside the correct quadrant) to 7 for placement on the bull's eye. The placement shown would receive a perfect score of 7.

pointed away from the computer screen (i.e., either beside or behind themselves) they were judged to have perceived the virtual environment as a three dimensional space and to have made a cognitive map. The task was scored on a 3-point scale (for details see Appendix 2-B).

Room Reconstruction Task (RRT). The purpose of this task was to directly assess the degree to which participants formed a cognitive map. Participants were asked to reconstruct the room using two dimensional pictures of the four room walls, the room floor (showing the arena) and the four window views of the landscape. Participants were first given the picture of the room floor and asked to place each of the four walls in the correct location according to the maze task they had just completed. They were then

asked to locate the landscape views according to their orientation outside of the room during the maze tasks. Participants in the Place maze conditions (with and without exploration) were then given a small green disc (designed to represent the platform) and asked to place it on the floor of the arena where they thought the platform was located in the Place maze. Participants in the Floor Cue maze conditions were given an additional, separate picture of the room floor with the two cues (the flashlight and the red flare) clearly visible in the arena. Their task was to place the green disc where they thought the platform was located in the Floor Cue maze. In addition, participants who completed the "exploration" Place maze were presented with an earlier RRT immediately after the fourth visible platform trial. This early task was identical in all respects to the usual Place maze room reconstruction except that participants were not asked to indicate a platform location.

Appendix 2-C provides scoring for the RRT. For the Place maze room reconstruction participants received a maximum score of 8 for correctly placing the walls (1) and landscapes (4), for orienting walls to landscapes (1) and for platform placement in correct hemisphere (1) and quadrant (1) of the arena. For the early RRT given in the place-explore condition only, scoring was to a maximum of 6 for placement and orientation of walls and landscapes. A score could not be given for platform placement since participants had not yet completed the first behavioural trial. For the Floor Cue maze room reconstruction, scoring took place in two stages. First, participants received a maximum score of 6 for placement and orientation of the walls and landscapes. Secondly, they received a separate sheet which showed the floor of the arena with the two objects (the red flare and the grey flashlight) and they received two additional points for

placement of the platform in the correct hemisphere and quadrant of the arena based on orientation to the important cue object (the red flare).

Computer Game Experience

Because the experiment concerned the effects of training in a virtual environment, participants were asked about their computer gaming experience. They were asked whether they play two and/or three dimensional games, how often they play (now and as children) and about their experience with game controllers/joysticks. Participants responded on a Likert type scale by circling one of the following responses: “never”, “occasionally”, “monthly”, “weekly”, “every few days”, or “daily”. Results were tabulated first by examining each question separately and then by calculating a combined score.

Demographic Variables

Demographic variables were recorded from a background information questionnaire and included age, gender and education level. These variables were recorded for later comparison of experimental groups and to assure that there were no confounds of age, sex, education or computer experience with the maze variables. The medical variables were recorded for screening purposes. The data of participants who indicated medical problems were generally excluded from analysis if the problem in question was known to affect the ability to navigate.

Analysis

All data were summarized using Excel® and inferential statistics computed using SPSS®. The maze data were analyzed using three conventional measures of performance: 1) latency (time in seconds) to reach the platform, 2) distance (in pool

diameters) travelled to the platform, and 3) dwell time or percentage of time spent searching in the correct quadrant of the arena on maze probe trials. For latency and distance variables only the data from trials 2 to 10 were analyzed. Trial 1 is considered to be a search trial and was thus excluded from the behavioural analysis. The data was converted and analyzed using TRAM®, a locally developed software program that is designed to extract latency, distance and probe variables from computer game files recorded while participants navigate in the maze environments. An omnibus spatial score (SS) was calculated for each participant by computing z scores and then combining the three measures of performance using the following formula:

SS = (0.5 x dwell time maze probe z-score) – ((0.25 x latency z-score) + (0.25 x distance z-score))

This omnibus score has been employed in previous studies (Skelton et al., 2006; Livingstone & Skelton, 2007) and was used here to confirm navigation performance in the four experimental conditions.

Results

Visible Platform Trials

All participants were able to navigate to the visible platform equally well. There were no differences in latency or distance to the platform among the four participant groups (place-explore, place-no-explore, cue-explore, cue-no-explore) (Figure 2.3). Descriptive statistics for all experimental conditions are reported in Table 2.5. It should also be noted that there were no differences based on whether participants received visible platform trials either before or after invisible platform testing. These visible platform results indicate that all participants were able to use the game controller and understood the task instructions.

Invisible Platform Trials and Probe Trial

In all four experimental conditions (place-explore, place-no-explore, cue-explore, cue-no-explore) learning was evident across invisible platform trials (Figure 2.3). However, learning rate and trials to asymptote differed. Performance in the place-no-explore condition was worst, with participants in this group exhibiting the slowest learning rate and the greatest number of trials to reach asymptote, especially on the distance measure.

Exploration affected all maze performance measures (spatial score, distance, latency, probe trial) in the Place maze but not the Floor Cue maze (Figure 2.4). ANOVA results are reported in Table 2.6. The omnibus spatial score depended on both exploration and maze type and there was a significant interaction effect, $F(1, 93) = 18.49$, $p<.001$, $\omega^2 = .001$. In order to examine the source of the interaction, simple main effects were analyzed using planned comparisons (independent t-tests) with equal variance not assumed. Exploration was important in the Place maze where spatial scores were worse in the no-explore group ($M = -.71$, $SEM = .17$) than in the explore group ($M = .36$, $SEM = .17$) that was allowed to explore the environment before testing, $t(47) = -4.39$, $p = .0001$, $d = 1.25$. In the absence of exploration, maze type was more important and in the no-explore condition, spatial scores were worse in the Place maze ($M = .71$, $SEM = .17$) than in the Floor Cue maze ($M = .20$, $SEM = .09$), $t(36) = -4.69$, $p = .000$, $d = 1.33$ (Figure 2.4). It should be noted that main effects of maze type and exploration are reported in Table 2.6, but since the differences between groups were largely within one level of maze (place) and one level of exploration (no-explore), these main effects were not considered meaningful and therefore are not discussed.

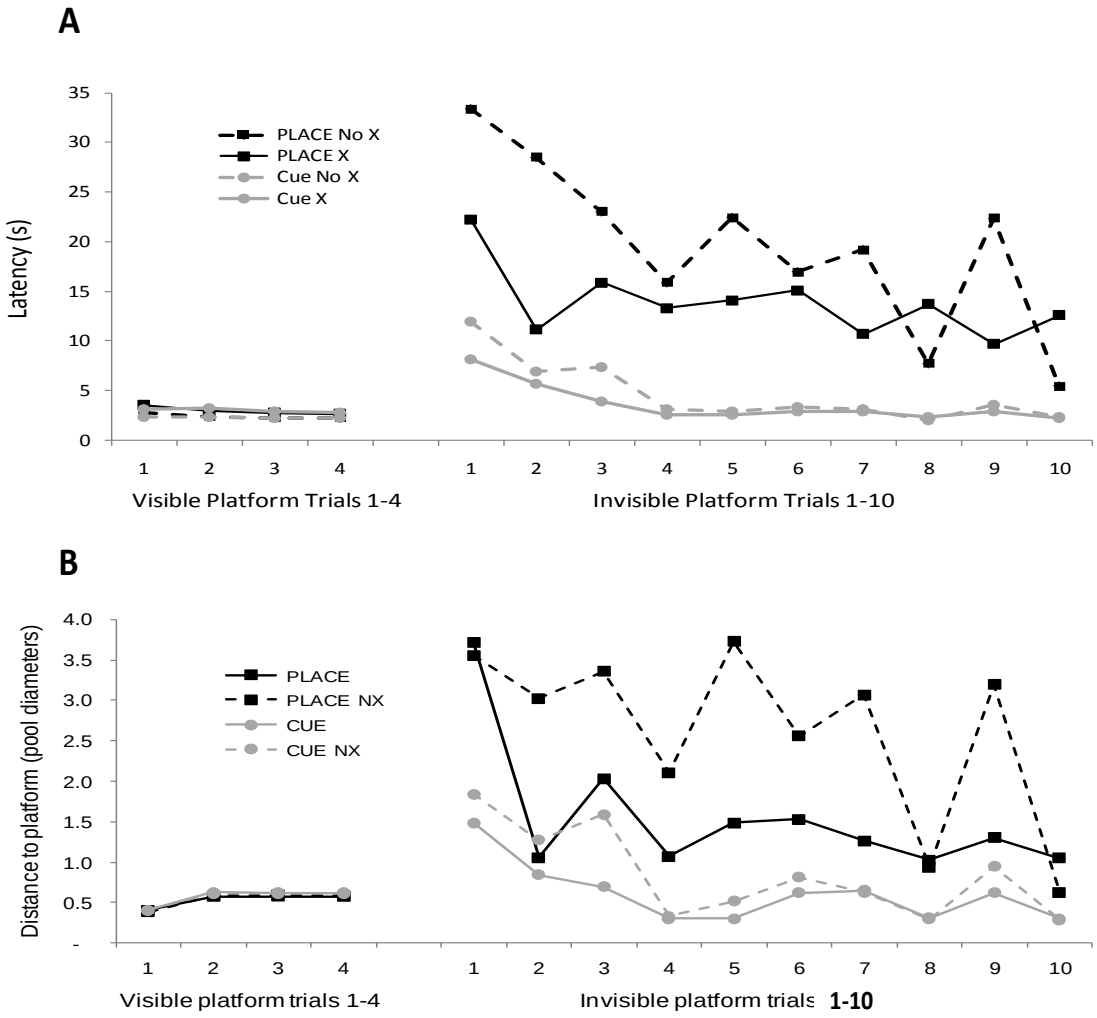


Figure 2.3. Latency (A) and Distance (B) to find the platform for visible and invisible platform trials. The four conditions were: Place = Place maze with exploration, Place NX = Place maze without exploration, Cue = Floor Cue maze with exploration, Cue NX = Floor Cue maze without exploration. Performance was similar for all groups in the visible platform trials. In the Place maze, latency and distance were significantly greater when participants were not given the opportunity to explore. In the Floor Cue maze, there were no detectable differences in performance.

Not surprisingly, the pattern of results shown for the spatial scores was repeated in the maze performance variables, latency and distance (Figure 2.4, Table 2.6). Overall, latency on invisible platform trials depended on both exploration and maze type, $F(1,93) = 7.45$, $p = .008$, $\omega^2 = .02$. Planned comparisons showed that in the Place maze,

Table 2.5

Descriptive statistics for the four experimental conditions (place-explore, place-no-explore, cue-explore, cue-no-explore.

	Place-explore (n = 24)	Place-no-explore (n = 25)	Cue-explore (n = 26)	Cue-no-explore (n = 26)
Variable	Mean (*SEM)*	Mean (*SEM)*	Mean (*SEM)*	Mean (*SEM)*
Spatial score	0.4 (0.20)	-0.8 (0.19)	0.2 (0.07)	0.3 (0.12)
Latency (s)	13.3 (1.56)	19.7 (2.59)	3.2 (0.27)	4.3 (1.18)
Distance (pd)	1.3 (0.19)	2.2 (0.28)	0.5 (0.02)	0.7 (0.13)
Probe percent dwell	60.1 (5.51)	33.0 (3.61)	37.5 (2.42)	43.4 (2.66)
DTS	5.21 (0.46)	2.6 (0.47)	6.42 (0.30)	6.27 (0.39)
RRT	7.2 (0.41)	5.1 (0.58)	7.3 (0.19)	6.2 (0.40)
WTWT	1.83 (0.08)	1.25 (0.13)	1.62 (0.10)	1.00 (0.12)

Note. pd = pool diameters, DTS = Drop-the-seed, RRT = Room Reconstruction Task, WTWT = Where's the Water Task.

latencies were worse (i.e., greater) in the no-explore group (M = 23s, SEM = 2.57) than in the explore group (M = 14s, SEM = 1.42) that was allowed to explore the environment before testing, t(37) = 3.06, p = .004, d = 0.86. In the absence of exploration maze type was important such that latencies were worse in the Place maze (M = 23s, SEM = 2.57) than in the Floor Cue maze (M = 4s, SEM = .50), t(26) = 6.91, p = .000, d = 1.97 (Figure 2.4). Similar results were found for distance (an indication of directness of the path). Like latency, the distance travelled to the platform depended on both exploration and maze type and there was a significant interaction effect of the two, $F(1,93) = 4.74$, p = .03, $\omega^2 = .01$. In the Place maze, distances were worse (i.e., longer) in the no-explore

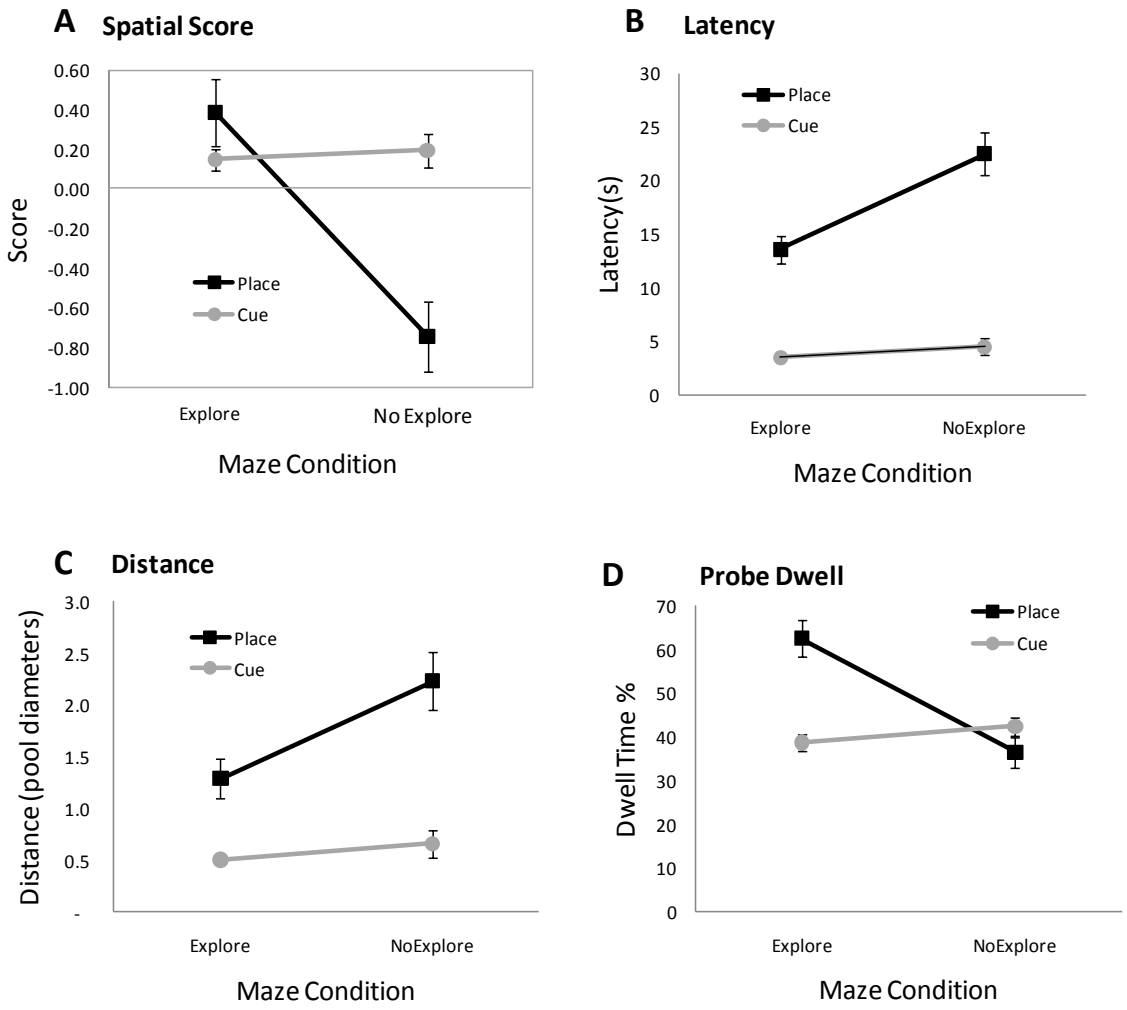


Figure 2.4. Significant interactions for omnibus spatial score and maze variables latency, distance and probe dwell in correct quadrant. Exploration led to improved performance (shorter latency, shorter distance and longer probe dwell) in the Place maze but not in the Floor Cue maze. Bars indicate standard error of the mean.

group (*M* = 2.2pd, *SEM* = .28) than in the explore group (*M* = 1.3pd, *SEM* = .19) that was allowed to explore the environment before testing, t(42) = 2.74, p = .009, *d* = 0.78. In the absence of exploration, distances were worse in the Place maze (*M* = 2.2pd, *SEM* = .28) than in the Floor Cue maze (*M* = .7pd, *SEM* = .13), t(34) = 5.04, p = .000, *d* = 1.43 (Figure 2.4).

Table 2.6

Results of 2 x 2 (Maze x Explore) ANOVA tests. Results are reported for the five maze variables (spatial score, latency, distance, probe dwell time, and DTS score) and two cognitive map tests (WTWT and RRT scores).

Tests of between subjects effects					
Measure	Source	*df*	*F*	ω^2	*p*=
Spatial Score	Maze (M)	1	**7.61****	.87	**.007**
	Explore (E)	1	**15.46*****	.11	**.0002**
	M x E	1	**18.49*****	.001	**.0000**
	Error	93	(0.42)		
Latency	Maze (M)	1	**91.42*****	.29	**.0000**
	Explore (E)	1	**11.45*****	.03	**.001**
	M x E	1	**7.45****	.02	**.008**
	Error	93	(54)		
Distance	Maze (M)	1	**42.05*****	.16	**.0000**
	Explore (E)	1	**9.02****	.03	**.003**
	M x E	1	**4.74***	.01	**.03**
	Error	93	(18780)		
Probe (% dwell)	Maze (M)	1	**8.37****	.03	**.005**
	Explore (E)	1	**13.27*****	.00	**.0004**
	M x E	1	**23.76*****	.10	**.0000**
	Error	93	(236)		
DTS	Maze (M)	1	**35.99*****	.14	**.0000**
	Explore (E)	1	**11.51****	.04	**.001**
	M x E	1	**9.01****	.03	**.003**
	Error	93	(4.18)		
WTWT	Maze (M)	1	**4.65***	.02	**.04**
	Explore (E)	1	**28.76*****	.12	**.0000**
	M x E	1	.04	.004	**.09**
	Error	93	(0.31)		

Table 2.6. *Results of 2 x 2 (Maze x Explore) ANOVA tests (continued).*

Measure	Source	*df*	*F*	ω²	*p*=
RRT	Explore (E)	1	**18.59*** **	.08	**.0000**
	M x E	1	**10.29** **	.04	**0.002**
	Error	93	(3.06)		

Note. Values in parentheses represent mean square errors.
Note. DTS = Drop-the-seed, WTWT = Where's the Water Task, RRT = Room Reconstruction Task.
***p < .05, **p < .01, ***p < .001**

Results for the probe trial mirrored those found for the other maze variables (Figure 2.4). For the probe trial measure (percentage dwell time in the correct quadrant), there was a significant interaction effect of exploration and maze type, $F(1,93) = 23.76$, $p<.001$, $\omega^2 = .10$. In the Place maze, dwell times were worse (i.e., lower) in the no-explore group (M = 36%, SEM = 3.56) than in the explore group (M = 62%, SEM = 4.22) that was allowed to explore the environment before testing $t(46) = -4.72$, $p = .000$, d = 1.35. However, unlike the result for other maze variables, in the absence of exploration performance in the Place and Floor Cue mazes was not significantly different.

Drop-the-seed (DTS) Trials

As with other measures of navigational performance, exploration was necessary for good performance in the DTS trial (Figure 2.5) in the Place maze but not in the Floor Cue maze. For DTS scores, there was a significant interaction effect of exploration and maze type, $F(1,93) = 9.09$, $p = .003$, $\omega^2 = .03$. In the Place maze, scores were worse for the no-explore group (M = 2.6, SEM = .47) than for the explore group (M = 5.21, SEM = .46) that was allowed to explore the environment before testing, $t(47) = -3.96$, $p = .0003$, d = 1.13. More than half of participants in the explore group had scores of 6 or 7 whereas in the no-explore condition no participant had a score higher than 5. In the absence of

exploration, scores were worse in the Place maze (*M* = 2.6, *SEM* = .47) than in the Floor Cue maze (*M* = 6.27, *SEM* = .39), t(47) = -5.96, p = .000, *d* = 1.68.

Cognitive Map Tests (WTWT and RRT)

Exploration was associated with how well participants were able to indicate their knowledge of the important features of the virtual environment on the WTWT (Figure 2.6). In this task, conducted at the end of behavioural trials, participants had to point to an environmental feature (the body of water outside one of the windows) that was not visible on the display. A loglinear analysis compared frequencies of association for three variables, exploration (explore or no-explore), maze type (place or cue), and WTWT score (low, medium or high). For this last variable, expected frequencies for the score of 0 were not great enough to justify the analysis. Therefore the data were collapsed across scores of 0 and 1 to create a dichotomous WTWT variable consisting of two levels, high score (indicated by a score of 2) and low/medium score (indicated by a score of either 0 or 1). The three-way association (explore x maze x WTWT score) was not significant and there was no interaction of maze type with WTWT score. However, there was a significant association between exploration (explore or no-explore) and how well participants were able to identify the location of the water on the WTWT, $\chi^2(2) = 11.97$, $p<.0001$. In the explore groups (both place and cue) the modal response was to accurately point in the direction of the water (Figure 2.6), whereas in the no-explore groups (both place and cue) the modal response was to point at the sloping hills (forward and to the left or right) rather than the water (straight behind). Put another way, odds ratios showed that if participants explored the environment they were 6.8 times more likely to have good knowledge of the location of the water.

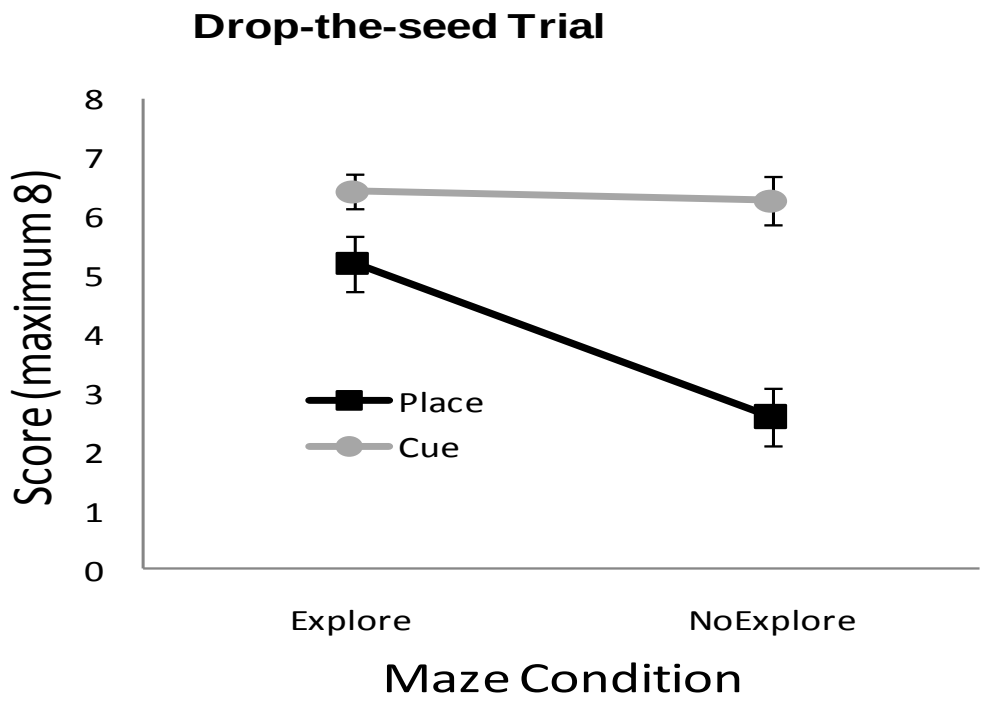


Figure 2.5. Significant interaction for the Drop-the-seed trial. Participants dropped a marker to indicate their knowledge of the platform location. Exploration led to greater accuracy of marker placement after the Place maze but not the Floor Cue maze. Bars indicate standard error of the mean.

Exploration was also important for reconstruction of the environment (landscapes, room walls, platform location) at the end of behavioural testing (Figure 2.7). A loglinear analysis was used to assess frequencies of association for three variables, exploration (explore or no-explore), maze (place or cue) and RRT score (low or high). For the RRT variable scores were collapsed in order to create two categories thought to represent either limited or very good knowledge of the locations of important features of the environment and based on the hierarchical nature of the RRT. The low score category had a range of 0 to 5 and represented understanding of the locations of the landscapes and walls. The high score had a range of 6 to 8 and represented additional understanding of the proper orientation of the walls to the landscapes and the location of the platform in

relation to the other environmental features. The three-way association (explore x maze x RRT score) was not significant and there was no interaction of maze type with RRT score. However, there was a significant association between exploration (explore or no-explore) and how well participants were able to reconstruct the room $\chi^2(2) = 6.76$, $p < .01$. Odds ratios indicated that when participants explored the environment they were 3.7 times more likely to have a high RRT score. Although, there was no significant association between the type of maze (place or cue) and RRT scores, there were some interesting results related especially to the Place maze. Notably, 90% of participants in the place-explore condition had high scores of 6 to 8, whereas in the place-no-explore condition only half of participants had high scores. This effect was not observed for the Floor Cue maze where three quarters of participants had high scores regardless of whether they had explored.

Participants in the place-explore group also did surprisingly well on the early RRT. Most were able to reconstruct the room after only limited exposure to the environment, i.e., one exploration trial and four visible platform trials. More than half (57%) of participants had a perfect score of 6, showing that they knew the locations and correct orientations of the room walls and landscapes. Only two participants had scores of 4 or less.

Although the pattern of results was similar for the two cognitive map tests, there were some interesting relationships noted both between the tests themselves and with other navigational measures. Correlations were initially conducted for all groups (i.e., by combining both mazes and both explore conditions). However, because cognitive maps only had utility in the Place maze, the correlation analysis was focused on the two

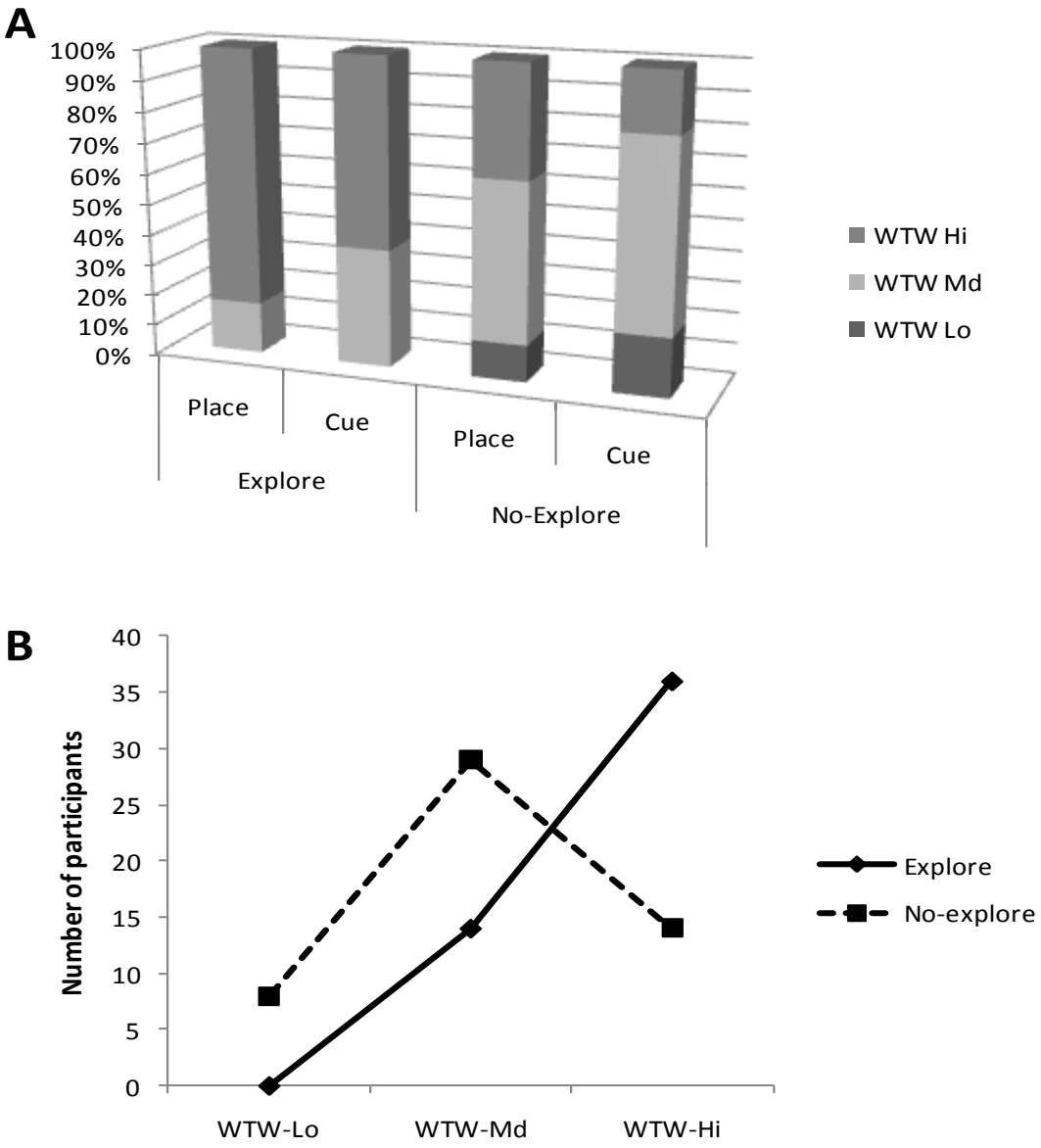


Figure 2.6. Results for the Where's the Water cognitive mapping test. **A.** There was a significant association of exploration with score (Lo/Md = low score of 0 or medium score of 1, Hi = high score of 2) such that participants who explored tended to have high scores rather than medium or low scores, regardless of which maze (Place or Cue) they completed. **B.** The modal score was high when participants explored and medium when exploration was not permitted. Low scores were recorded only in the no-explore conditions.

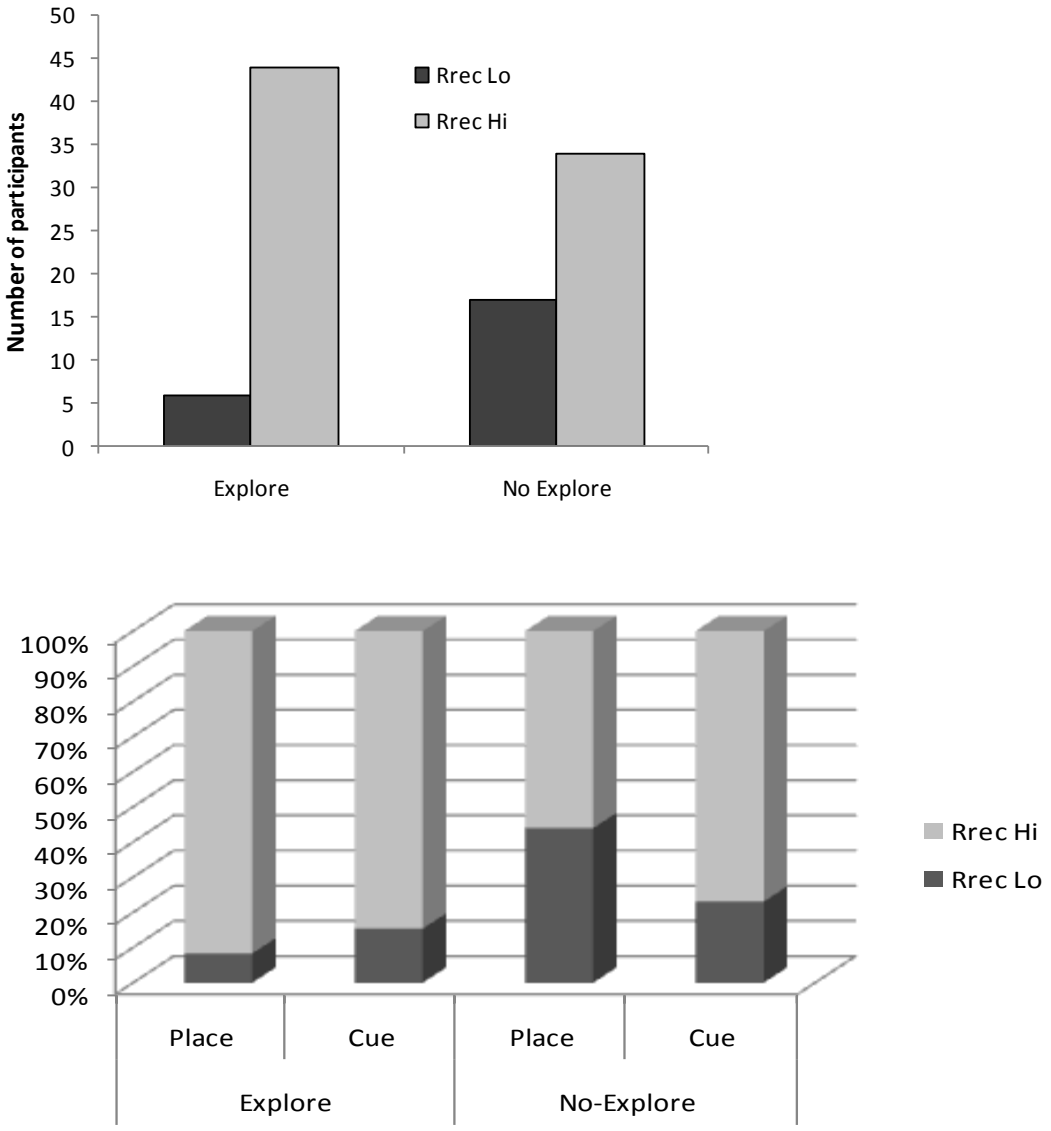


Figure 2.7. Results for the Room Reconstruction cognitive mapping test. **A.** There was a significant association of exploration with score (High score above 6 = Hi, Low score below 6 = Lo) such that participants who explored tended to have high scores regardless of which maze (Place or Cue) they completed. **B.** Exploration mattered more in the Place Maze where 90% of participants in the explore condition had high scores and only about half of participants in the no-explore condition had high scores.

conditions, place-explore and place-no-explore (Table 2.7). One unexpected result was that scores for the two mapping tasks were not related to one another ($r = .12$, $p = .41$) although both sets of scores were related to the overall spatial score measure. Further, results for the two cognitive mapping tests were correlated with different sets of maze

Table 2.7

Correlations between maze and cognitive mapping variables for participants in the Place Maze.

Variable	Exploration	Spatial Score	Latency	Distance	Probe	DTS	WTWT	RRT
Exploration	1							
Spatial Score	0.54**	1						
Latency	(0.40)**	(0.76)**	1					
Distance	(0.37)**	(0.86)**	0.84**	1				
Probe	0.57**	0.90**	(0.45)**	(0.57)**	1			
DTS	0.50**	0.48**	(0.31)*	(0.39)**	0.49**	1		
WTWT	0.47**	0.35*	(0.52)**	(0.34)*	0.24	0.24	1	
RRT	0.56**	0.40**	(0.25)	(0.24)	0.44**	0.37**	0.12	1

Note. WTWT = Where's the Water Task, RRT = Room Reconstruction Task, DTS = Drop-the-seed.
Note. Parentheses indicate negative correlations.
*p < .05, **p < .01

variables. The ability to point toward a feature in the environment not visible on the screen display was significantly related to navigational performance in the Place maze; higher scores on the WTWT were associated with better spatial scores ($r = .35$, $p < .05$), reduced latencies ($r = .52$, $p < .001$), and shorter distances to the platform ($r = .34$, $p < .05$). However, the ability to reconstruct the features of the room after testing was significantly related to both overall navigational performance and to performance on probe trials. Higher RRT scores were associated with better spatial scores ($r = .40$, $p < .01$), greater dwell time in the correct quadrant on the probe trial ($r = .44$, $p < .01$), and more accurate placement of the marker in the DTS trial ($r = .37$, $p < .01$). Taken together, these results suggest that although both mapping tests are measures of spatial knowledge, they may represent independent cognitive processes.

Gender Comparisons

There were no gender differences in navigational performance in any of the four experimental conditions. However, there was a slight male advantage in both Place and Floor Cue tasks when exploration was not permitted.

Latency. When exploration was permitted, there was no significant difference between males and females in latency to the platform in the Place maze (Males, *M* = 13.3 s, *SEM* = .2; Females, *M* = 12.4 s, *SEM* = 1.7) or in the Floor Cue maze (Males, *M* = 3.0 s, *SEM* = .2; Females, *M* = 3.3 s, *SEM* = .3). When exploration was not permitted males traveled to the platform slightly more quickly than females in both the Place maze (Males, *M* = 16.5 s, *SEM* = 2.4; Females, *M* = 20.1 s, *SEM* = 3.5) and the Floor Cue maze (Males, *M* = 2.7 s, *SEM* = .3; Females, *M* = 5.7 s, *SEM* = 1.9). However, the differences noted were not significant (Place maze, t = .85, p = .40; Floor Cue maze, t = 1.45, p = .16).

Distance. When exploration was permitted, there was no significant difference between males and females in distance traveled to the platform in the Place maze (Males, *M* = 1.5 pd, *SEM* = .3; Females, *M* = 1.1 pd, *SEM* = .2) or in the Floor Cue maze (Males, *M* = .5 pd, *SEM* = .04; Females, *M* = .5 pd, *SEM* = .03). When exploration was not permitted males took slightly more direct paths to the platform than did females in both the Place maze (Males, *M* = 2.1 pd, *SEM* = .4; Females, *M* = 2.5 pd, *SEM* = .4) and the Floor Cue maze (Males, *M* = .5 pd, *SEM* = .02; Females, *M* = .9 pd, *SEM* = .3). However, as per latency, these differences were not significant (Place maze, t = .65, p = .52; Cue maze, t = 1.1, p = .27).

Discussion

Healthy, young adults had no difficulty with simple guidance navigation to the visible platform, regardless of whether they were given the opportunity to explore the environment. Participants navigated to the visible platform quickly and directly, showing that they were competent in the procedural aspects of the maze tasks including using the game controller and understanding the task instructions.

Learning was evident in all four experimental conditions, as shown by the latency and distance measures across trials, but performance was better in some conditions than in others. In the Place maze performance was impaired when participants were not permitted to explore the environment either before testing or while on the platform at the end of trials. Participants who were not permitted to explore took longer and more circuitous paths to the platform than participants who explored. They also spent less time searching in the correct quadrant on the probe trial and had significant difficulty in showing their knowledge of the platform location on the DTS trial. In the Floor Cue maze performance was not impaired by the absence of exploration and participants navigated to the platform equally well regardless of how much or how little time was spent exploring. They also demonstrated good knowledge of the platform location on probe trials and the DTS trial. Overall, these results show that a lack of exploration selectively impairs place (allocentric) navigation but spares cue (egocentric) navigation at least in the case where egocentric navigation involves selecting which of two possible cues to go to.

Group differences in cognitive map test scores indicate that exploration improved the formation of cognitive maps. The opportunity to explore was associated with better room reconstruction and better accuracy of pointing in the WTWT, regardless of which

maze participants completed. Further, the early cognitive map test indicated that participants who explored before testing in the Place maze were able to reconstruct key features of the environment after completing only one exploration trial and the four visible platform trials.

Although there have been procedures similar to the RRT (Livingstone & Skelton, 2007; Nadel et al., 1998; Skelton et al., 2000) and WTWT (Wilson, 1999) these two measures are still relatively new. Both are ways of assessing cognitive maps, but it is not clear that they are assessing the same (or the same aspects of) cognitive maps. In the current study cognitive mapping was associated with navigational performance as indicated by significant positive correlations with spatial scores. However, results for the two cognitive map tests were not correlated with one another, suggesting that they measure distinct aspects of mapping. The ability to reconstruct the room was correlated with probe trial measures whereas the ability to point in the direction of an important environmental feature was correlated with latency and distance measures.

Taken together, the present data suggest that exploration improves navigation in allocentrically but not egocentrically biased environments and that the effect of exploration on allocentric navigation is mediated by cognitive map formation. The improved performance in the Place maze after exploration is likely due to the acquisition of better cognitive maps as confirmed by the two map tests. It might be argued that the observed differences in Place maze performance were due to other factors such as computer gaming experience of the participants, idiosyncratic behaviour in the virtual environment or to organismic variables. However, participants in all four experimental conditions had equivalent prior experience with computer gamepads and with computer

games including three-dimensional games. Furthermore, computer experience has been found to have only small effects on the acquisition of spatial knowledge in virtual environments (Waller, 2000). Also, the virtual nature of the Place maze task probably did not contribute to behavioural differences between the explore and no-explore groups. This is because the ability to acquire spatial information (and presumably a cognitive map) in a virtual environment corresponds to the ability to transfer this knowledge to real world environments (Waller, 2000). That is, when people explore virtual environments, they are capable of transferring this learning to similar real world exploration tasks, suggesting that virtual environments are valid measures of exploration behaviour (Jacobs et al., 1998; Rizzo et al., 1997; Ross et al., 2006; Waller, 2000).

The design of the experiment should rule out any influence of organismic variables such as gender, verbal ability, or spatial ability, variables shown to be important for the acquisition of spatial knowledge in virtual environments (Waller, 2000). Each of the four experimental groups had equal numbers of males and females, thus any gender differences should not have affected the group measures. Similarly the random assignment of participants to each of the experimental conditions should have prevented any influence of differences in verbal or spatial ability. Furthermore, the participant sample was comprised mainly of healthy, young university students who are a fairly homogeneous population in terms of intelligence and language ability.

Most previous studies of human spatial navigation have been concerned with allocentric rather than egocentric navigation and the two types of navigation are rarely compared, at least in MWM tasks. Researchers do sometimes examine the circumstances under which animals navigate either egocentrically and allocentrically. Tamara, Leffel, &

Timberlake (2010) demonstrated that when animals are trained to travel relatively long distances to reach the platform they will use distal stimuli (an allocentric approach) rather than egocentric body turns when required to navigate from a new start location on later trials. Hamilton, Rosenfelt, & Whishaw (2004) showed that animals utilize both egocentric and allocentric navigational behaviour within visible platform trials when the visible platform remains in the same location. Their study demonstrated that, with training, rats navigate to a visible target in the MWM initially by orienting toward distal, directional beacons (as evidenced by head scanning while swimming) and later in the trial by using local (taxon) stimuli (in this case the visible platform). In other words, the animals may have been acquiring cognitive maps while navigating to the visible platform in an essentially cue-based task. Interestingly, in the absence of exploration, participants in the Floor Cue maze were still able to reconstruct the features of the room relatively well (even though the platform location was moved on every trial). This suggests that, like rats, they were also orienting toward the distal features of the environment either at the start of trials or from the perspective of the platform. However, this finding did not extend to the Place maze where the acquisition of a cognitive map appeared to be disrupted by a lack of exploration.

Comparisons of allocentric and egocentric navigation are more frequently made in studies using the radial arm maze task (RAM) (e.g., Pothuizen, Aggleton, & Vann, 2008; Steckler, Weis, Sauvage, Mederer, & Holsboer, 1999). However it is possible that the RAM may be solved simply by egocentrically navigating toward a distal "guidance" stimulus (O'Keefe & Nadel, 1978; Trullier et al., 1997) that marks the target arm of the maze, rather than necessarily by knowing the exact location of the food source in relation

to a configuration of the distal stimuli. It is therefore uncertain whether performance in a RAM interpreted as allocentric (using configurations of distal stimuli) might really be a form of distal beacon guidance or directionality rather than cognitive mapping. Researchers disagree as to whether directionality is 1) a form of navigation that is separate from place (allocentric) navigation (Hamilton et al., 2007) or 2) a component of allocentric navigation (Jacobs & Schenk, 2003) that may combine with positional information to provide a complete cognitive map. In short, navigation toward distal beacons in the environment does not necessarily demonstrate that the navigator has formed a complete or integrated cognitive map (Jacobs & Schenk, 2003) because the navigator may be using only one component of mapping (i.e., directionality) in order to solve the task. For this reason it is difficult to compare egocentric and allocentric navigation in the RAM.

The two measures of cognitive mapping, the RRT and the WTWT, produced some unexpected and interesting results. Given the priorities of this study, the cognitive map tests were intended as auxiliary measures. However, there were indications in the data that the two tests may provide important information about different aspects of mapping. Other researchers have proposed that different neural systems may be activated depending upon whether an environment is encoded (i.e., mapped) from either a survey (aerial) or route (ground level) perspective (Blanch, Brennan, Condon, Santosh, & Hadley, 2004; A. L Shelton & Gabrieli, 2002). However, survey encoding is not the usual means of acquiring spatial knowledge, since people more frequently navigate from a ground level perspective. Therefore it is not clear whether the survey and route encoding constructs are mutually exclusive mechanisms for encoding the environment.

The current data do suggest that there are survey (aerial) and route maps, but that both are developed during ground level navigation. It is proposed that the aerial map is useful for mentally placing oneself in the environment and is a mental translocation to a top-down or bird's eye view of the environment. The presence of this map was likely demonstrated when participants successfully reconstructed the room using a top-down paper representation of the environment. However, the survey/route distinction may not capture all aspects of cognitive map acquisition because it does not include the case where the two could be acquired simultaneously (Maguire, Burke, Phillips, & Staunton, 1996; Moar & Carleton, 1982). An alternative view of the cognitive map is that it is acquired by "through the wall imagining" of the environment. In this way the cognitive map can be viewed as a sort of "x-ray" map that allows the individual to mentally see through structures to the position of a distal location in the map (e.g., another building, or destination). The key to this type of mapping is that the individual acquires spatial knowledge from the ground level perspective without necessarily imagining the environment from an aerial perspective, although translocation of ground level maps may occur (Moar & Carleton, 1982; Maguire et al., 1996). The WTWT may assess the x-ray map because participants point toward a feature outside the walls (and currently not in view) while viewing the environment from the ground level perspective. Interestingly, the Shelton & Gabrieli (2002) study found that information encoded from the ground level perspective involved brain activations in the medial temporal regions (including the hippocampus) whereas survey/aerial type encoding did not.

An important limitation of the current study was that it did not differentiate types of exploration behaviour, for example free exploration (before testing) and visual scan

from the perspective of the platform. It is probable that these exploration types contribute differently to map acquisition and therefore it would be useful to study their effects on navigational performance. Further, the current paradigm was unable to test the degree of exploration that might take place during movement toward the platform. At least one animal study suggests that cognitive maps are formed partly through locomotion toward the target and partly by visual scan from the perspective of the platform (Harvey et al., 2008). These limitations are currently being addressed by comparing different exploration types as well as examining eye movements during visual scan within trials.

The omission of an exploration component from human studies is somewhat surprising. Many studies of allocentric navigation using vMWM tasks have provided little or no opportunity for participants to explore (and presumably form a cognitive map) *before* they are tested (e.g., Astur et al., 2004; Burkitt, Widman, & Saucier, 2007; Driscoll et al., 2005; Hamilton & Sutherland, 1999; Hardt, Hupback, & Nadel, 2009; Jacobs et al., 1997). Participants were immediately presented with testing trials without previous exposure to the environment. Thus, in order to navigate, they must have acquired a cognitive map while simultaneously searching for the platform. Further, participants were sometimes permitted very little time (10s or less) to scan or search the environment after finding the platform (e.g., Astur et al., 1998, 2004; Burkitt et al., 2007; Driscoll et al., 2005; Hamilton & Sutherland, 1999). The current findings suggest that limiting exploration in this way leads to less than optimal allocentric navigation. Further, if participants have not had the opportunity to explore and acquire a good cognitive map, then it is possible that they may invoke egocentric strategies in an attempt to solve place-based vMWM tasks. While this certainly seems a logical conclusion, a future research

question is whether or not egocentric strategies dominate when allocentric strategies are not available to the navigator.

The study of exploration behaviour may contribute to improvements in the validity of vMWM tasks. To be valid, a vMWM should measure optimal navigation performance so that participants are able to navigate to the best of their ability and without barriers to performance. At least one study has demonstrated that verbal instructions to explore the environment remove the effects of blocking in a vMWM task and may improve the quality of the cognitive map (Hardt et al., 2009). The current findings show that allocentric navigation is improved with exploration and suggest that an exploration component is important for vMWM paradigms. Further, if exploration is not permitted, there is always the possibility of a bias toward the utilization of egocentric strategies in the maze. In other words, if participants have not formed sufficient cognitive maps they may attempt to solve place tasks using available egocentric strategies like circling or orienting toward one guidance landmark. In vMWM tasks, such behaviour could lead to apparently impaired navigation performance. For example, it may be that in the place-no-explore condition participants simply used egocentric strategies that were available to them and that these were not very helpful for solving the task. It is reasonable to suspect that poor performance in a vMWM might not be so much due to the quality of a person's allocentric ability as to a misapplication of an egocentric strategy in a situation better suited to an allocentric solution. The study of navigation deficits could benefit from an understanding of this possibility.

The present study provides new evidence about cognitive map formation and new insight into cognitive map theory. Our results show that exploration is important both for

the quality of the cognitive map and for navigational performance in allocentric tasks and that one mediates the other. Although the necessity of exploration for acquiring cognitive maps was axiomatic in the original theory (O'Keefe & Nadel, 1978), we could find no direct test of this in human or animal research. Previous studies on the effect of pre-exposing animals to the environment prior to testing in the MWM (i.e., latent learning) found conflicting results. In general, pre-exposure facilitated subsequent learning (e.g., Whishaw, Pellis, Gorny & Pellis, 1991; Sutherland & Linggard, 1982) but at least one study reported inhibition (Prados, Chamizo & MacKintosh.,1999) and in no case was the benefit of pre-exposure on subsequent learning as great as the benefit of even a single learning trial. However, in these studies, the rat was put in a single location, usually the goal platform, and not given the opportunity to actively explore the environment. The strictest interpretation of cognitive map theory would posit that maps are formed almost instantly, and should be very good even when the environment is viewed from a single point in space. However, the studies that failed to find instantaneous and perfect transfer from pre-exposure to the platform position were conducted with rats, which have very limited binocular vision and therefore require movement in space to properly appreciate relative distances between objects in the environment. Although the findings of latent learning studies were interpreted as supporting associative learning rather than cognitive mapping theory (Whishaw et al., 1991), it is hard to see how this could be true of the present findings, where the facilitative effects of exploration applied to allocentric, but not egocentric, navigation.

Our findings also provide converging evidence for the existence of two separate

cognitive navigational systems. Exploration was only important in the place-based task and not in the cue-based task. Participants performed the cue-based task equally well regardless of whether they were given the opportunity to explore the environment. This is interpreted as support for two systems, an allocentric system that relies on cognitive mapping and an egocentric system that does not. Interestingly, participants in the cue-based task had very good scores on the cognitive mapping tests (WTWT and RRT). This suggests that cognitive maps are developed effortlessly as opposed to being driven by the requirement to utilize a map to solve the task. In the cue-based task the platform location changes on every trial and therefore the surrounding features of the environment (windows and landscapes) are not consistently related to the platform location. A cognitive map is not useful for solving such a task yet participants formed cognitive maps as evidenced by their knowledge of the location of features outside the room and their ability to reconstruct the room correctly. This suggests that humans form cognitive maps regardless of their utility for the task at hand and that the quality of the map only becomes relevant when attempting to solve an allocentric task.

The study of exploration has several implications for testing in vMWM tasks especially in the context of brain imaging. It is becoming common practice to combine a vMWM with functional brain imaging to make statements about navigational ability as well as the particulars of cognitive map acquisition and utilization. The present study demonstrates that variability in exploration duration or environmental exposure could have significant effects on later navigation performance. This could in turn lead to problems with interpretation of which brain areas are activated or important for allocentric navigation. An added complication is that it is not always clear what

strategies, egocentric or allocentric, people use to solve the navigation task at hand (Iaria et al., 2003). It makes sense that if the goal is to test allocentric navigation it is best to design tasks that maximize the likelihood of participants using allocentric strategies. Given the possibility that navigation is hierarchical (i.e., egocentric precedes allocentric) (Maguire et al., 1996), sufficient exploration may be crucial in this context. Further, the subtractive nature of brain imaging requires that baseline tasks be designed for comparison to the activity of interest. In the case of testing allocentric navigation this usually means removal of activity related either to basic visual perception or to egocentric type processing (e.g., Maguire et al., 1998). Greater understanding of how people explore in virtual environments should support the development of improved baseline tasks and better interpretation of new and existing virtual navigation tasks.

The opportunity to explore may be especially important for studies concerning deficits in allocentric navigation performance. Virtual MWM tasks are routinely used to identify navigation differences based on gender (Astur et al., 1998; Ross et al., 2006; Sandstrom, Kaufman, & Huettel, 1998; Woolley et al., 2009) and age (e.g., Driscoll et al., 2005; Moffat & Resnick, 2002). In the present study, there were no gender differences in either latency or distance to the platform in the allocentric task (the Place maze) however there was a slight male advantage in both latency and distance when exploration was not permitted. This suggests that exploration could be a contributing factor in determining gender differences in allocentric navigation but the effect appears small. Interestingly, the same slight male advantage was observed for the egocentric (Floor Cue maze) task.

Virtual MWM tasks are also applied in the study of a wide variety of clinical conditions such as schizophrenia (Hanlon et al., 2006) transient global amnesia (Bartsch

et al., 2010), fibromyalgia (Canovas, Leon, Roldan, Astur, & Cimadevilla, 2009), anxiety (Mueller et al., 2009), depression (Cornwell et al., 2010), anoxia (Goodrich-Hunsaker et al., 2010), fetal alcohol syndrome (Hamilton, Kodituwakku, Sutherland, & Savage, 2003) and traumatic brain injury (Skelton et al., 2000; Livingstone & Skelton, 2007). In some of these populations the degree of familiarity (or not) and practice (i.e., exploration) with the environment may have a substantial effect on allocentric navigation. Adequate exploration may maximise navigational performance and therefore avoid overstatement of deficits in navigational ability.

Conclusion

In conclusion, exploration is an important aspect of spatial navigation probably mediated by cognitive mapping. Exploration is crucial for mapping and for navigational performance on place-based tasks. However, exploration does not matter for cue-based or simple stimulus-response tasks. The degree of exploration may be directly reflected in the quality of the cognitive map acquired and in the type of navigational strategy people select. Further, cognitive maps may be acquired incidentally whether or not they are required for the navigation task. The current findings suggest that exploration should be included as an important component of all allocentric vMWM paradigms. Understanding the effects of exploration on cognitive mapping and navigation performance will improve vMWM task design and ultimately contribute to improved navigation measures important for brain imaging studies and for research with clinical populations.

Appendix 2-A
Background Information Questionnaire

1. Date of Birth (day, month, year): _____ 2. Sex (M/F): _____

3. Education: (Last Grade or Year of University Completed, please specify which)
_____

4. Handedness (Right/Left): _____ 5. First language:_____

6. Do you have any problems with dizziness? (Yes/No) _____

7. Have you ever sustained a brain injury (i.e. been hospitalized overnight for a head injury)? (Yes/No)_____

If yes, please explain:_____

8. Do you suffer from any neurological disorders (eg. epilepsy, MS)?

(Yes/No) _____

If yes, which disorder? _____

9. Do you suffer from any psychiatric disorders (eg. depression, schizophrenia)?

(Yes/No)_____If yes, which disorder? _____

10. Are you currently taking any medications? (Yes/No)_____

If yes, please specify: _____

For the following questions, please circle the answer that best describes you:

How often did you play computer or video games as a child/youth?

Never -Occasionally -Monthly -Weekly -Every few days -Daily

How often have you played computer or video games in the last year?

Never -Occasionally -Monthly -Weekly -Every few days -Daily

How often do you play 3D computer games (e.g. Halo, James Bond)?

Never -Occasionally -Monthly -Weekly -Every few days -Daily

How often do you play 2D computer games (e.g. Super Mario, Solitaire)?

Never -Occasionally -Monthly -Weekly -Every few days -Daily

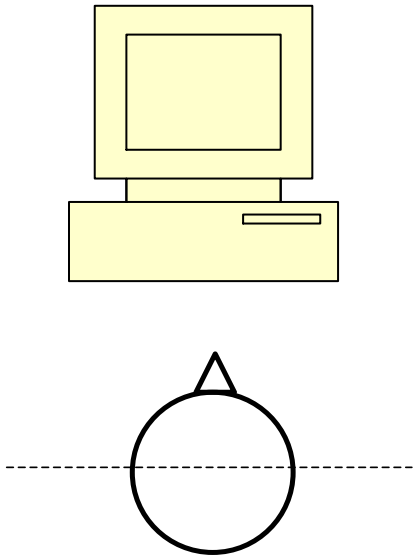
How often have you used a joystick similar to the one in front of you on the computer desk?

Never -Occasionally -Monthly -Weekly -Every few days -Daily

Appendix 2-B
Where's the Water Task

Instructions:
Curtain up after probe trial. Place participant on platform and facing **Northwest** corner of the room.

Then ask, "From here, where is the water? You can show me by pointing."
Record (1) Direction of pointing by drawing an arrow on the diagram below (2) Any comments by the participant with regard to whether he/she felt embedded in the space.



Scoring: 0=point at screen, 1=point in front of midline (dotted line), 2=point behind midline.

Comments:_____

_____

_____

Appendix 2-C
Room Reconstruction Task

Place Maze Room Reconstruction (after invisible platform trials and probe)
Total Score: _____ (max 8) **Code#: _____**

Room Reconstruction Test Instructions:

Presentation: Lay out the laminated floor of the room and explain that this represents the room and that the circle represents the arena. Give the participant the four laminated walls and then ask, "Based on what you were just doing could you place these walls where you think they were?" Give the participant the four laminated landscapes and then ask, "Based on what you were just doing can you place the landscapes where you think they were?" Give the participant the laminated green platform and then ask, "Based on the maze could you put the green platform where you think it was?"

Recording: On the data sheet record the position of 2 large windows. Indicate the placement of the landscapes, by drawing the water, slopes, the island, and the mountains. If you have time, note the order in which the walls were placed (i.e., which one was placed first) in the little boxes. After the participant has placed the platform, place the grid over the arena and use this as a guide to draw the location of the platform on the data sheet.

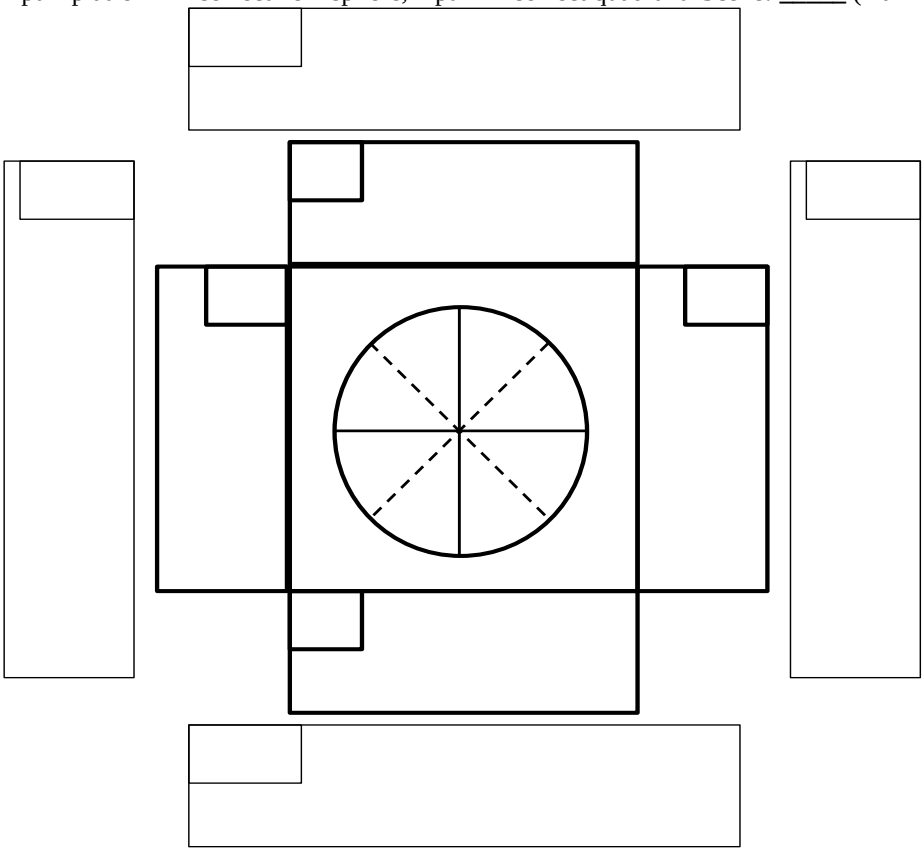
Scoring:

Walls : 1 pt if correct, 0 pts if incorrect **Score: _____** (max 1)

Landscape: 1 pt for each adjacent pair and 1 pt for each opposite pair **Score: _____** (max 4)

Walls to Landscape: 1 pt if landscape matches walls **Score: _____** (max 1)

Platform: 1 pt if platform in correct hemisphere, 1 pt if in correct quadrant **Score: _____** (max 2)



Appendix 2-C (continued)
Room Reconstruction Task

Place Maze Early Room Reconstruction (after exploration)
Total Score: _____ (max 6) **Code#: _____**

Room Reconstruction Test Instructions:

Presentation: Lay out the laminated floor of the room and explain that this represents the room and that the circle represents the arena. Give the participant the four laminated walls and then ask, "Based on what you were just doing could you place these walls where you think they were?" Give the participant the four laminated landscapes and then ask, "Based on what you were just doing can you place the landscapes where you think they were?"

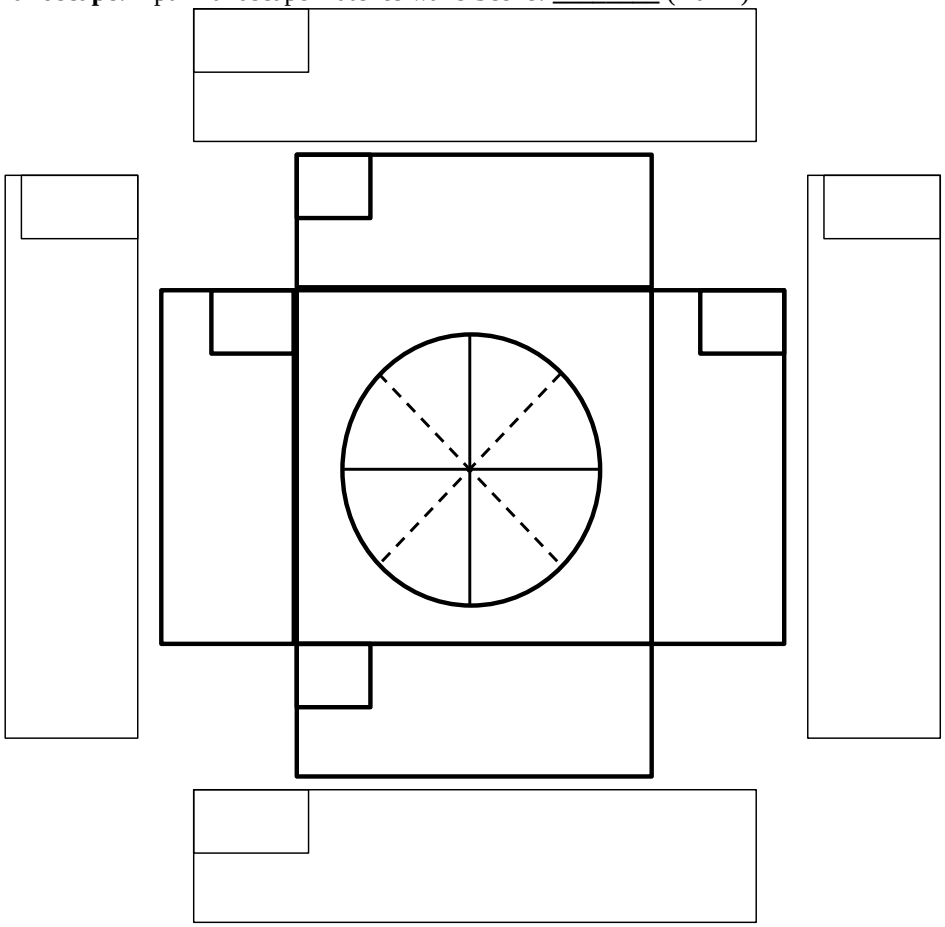
Recording: On the data sheet record the position of 2 large windows. Indicate the placement of the landscapes, by drawing the water, slopes, the island, and the mountains. If you have time, note the order in which the walls were placed (i.e., which one was placed first) in the little boxes.

Scoring:

Walls: 1 pt if correct, 0 pts if incorrect **Score: _____** (max 1)

Landscape: 1 pt for each adjacent pair and 1 pt for each opposite pair **Score: _____** (max 4)

Walls to Landscape: 1 pt if landscape matches walls **Score: _____** (max 1)



Appendix 2-C (continued)
Room Reconstruction Task

Floor Cue Maze Room Reconstruction (no arena)

Total Score: _____ (max 6) **Code#: _____**

Room Reconstruction Test Instructions:

Presentation: Lay out the laminated floor of the room and explain that this represents the room and that the circle represents the arena. Give the participant the four laminated walls and then ask, "Based on what you were just doing could you place these walls where you think they were?" Give the participant the four laminated landscapes and then ask, "Based on what you were just doing can you place the landscapes where you think they were?"

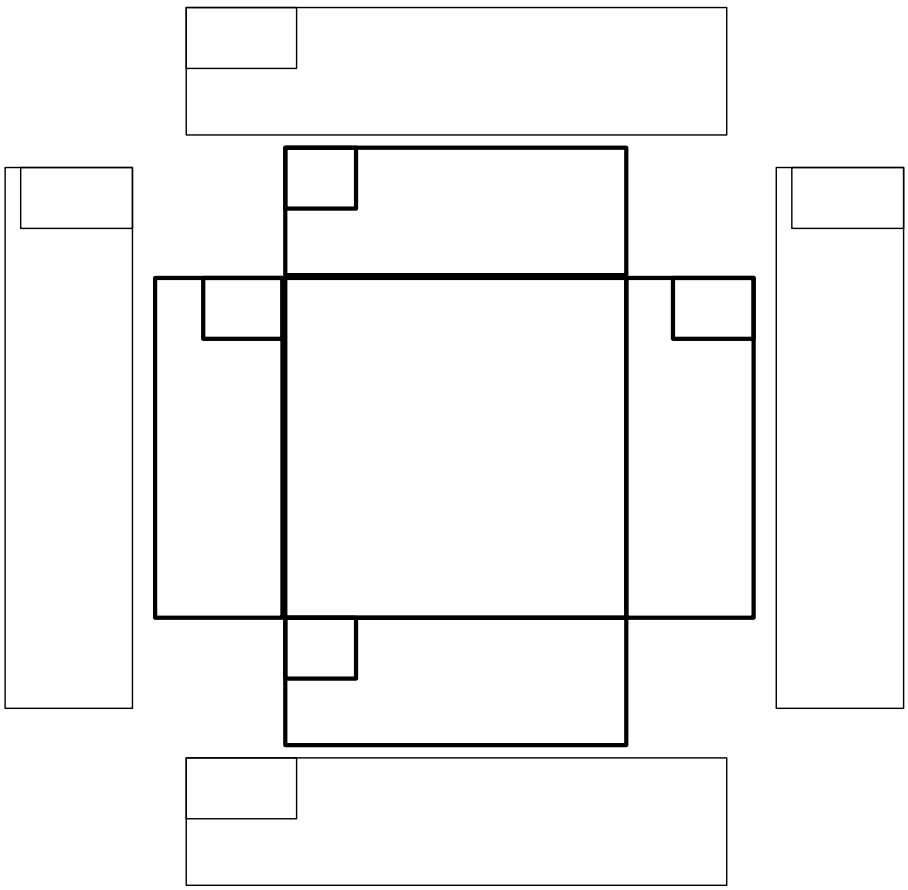
Recording: On the data sheet record the position of 2 large windows. Indicate the placement of the landscapes, by drawing the water, slopes, the island, and the mountains. If you have time, note the order in which the walls were placed (i.e., which one was placed first) in the little boxes.

Scoring:

Walls : 1 pt if correct, 0 pts if incorrect **Score: _____** (max 1)

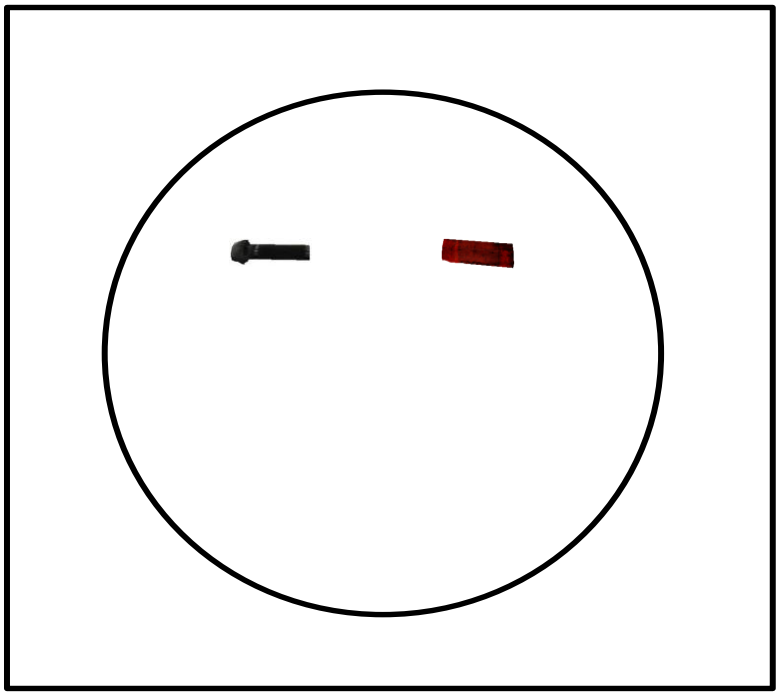
Landscape: 1 pt for each adjacent pair and 1 pt for each opposite pair **Score: _____** (max 4)

Walls to Landscape: 1 pt if landscape matches walls **Score: _____** (max 1)



Appendix 2-C (continued)
Room Reconstruction Task

Floor Cue Maze Platform Placement:



Chapter Three

This chapter consists of a manuscript describing the relationship of eye movements to strategy use in virtual environment navigation tasks. The study is a partial replication of previous work showing that people look in different regions of the screen display depending on which strategy type they employ. The present study examined strategy effects in a combined sample of university students and participants who volunteered from within the local community. The first objective was to examine differences in gaze position based on differing navigational task demands. Other objectives were to examine the reliability of the eye-tracking measures and to examine the time course of gaze acquisition in the different navigational tasks.

Simple gaze position analysis reliably differentiates allocentric and egocentric strategy use in a virtual Morris water maze

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Abstract

Wayfinding in the real world is an everyday task for most people, but there is considerable controversy over how many strategies people use, and what factors determine which strategy a person will use. Allocentric strategies rely on the presence of distal, relational stimuli whereas egocentric strategies rely on the presence of proximal or simple guidance stimuli. The current study replicates and examines the reliability of a new method combining eye tracking with specially designed virtual environments to provide objective evidence of navigational strategy use. A simple, inexpensive video camera with an infrared LED array was used to capture eye movements at 60 Hz and simple algorithms were used to analyze gaze position at the start of each virtual maze trial. Participants were tested either in an allocentrically biased "Place" maze or an egocentrically biased "Cue" maze, versions of a virtual Morris water maze (vMWM). Because the environmental features for allocentric and egocentric navigation were clustered in different regions of the environment (and the video display), a simple analysis of gaze-position during the first (i.e., orienting) second of each trial revealed which features were being attended to, and therefore, which navigational strategy was about to be employed on the upcoming trial. Results showed that during the first second of orientation gaze in the allocentrically biased Place maze participants attended more to distal room features whereas in the egocentrically biased Cue maze they attended more to proximal cue objects. Overall, gaze position was established early in the trial sequence (by the third trial) in both maze tasks. Results also showed reliable differences in gaze position in the two virtual navigation tasks for 75% of participants. These results suggest that eye tracking measures are useful for demonstrating differences in strategy use in

virtual environment navigation tasks and may be applied to the examination of experience effects on strategy selection. This research has applications for understanding the cognitive basis of spatial navigation and for the development of brain imaging studies of navigation including studies of navigation deficits.

Differentiating Navigation Strategies

Navigating from place to place in the real world is an everyday task for most people. Differentiating which navigational strategies people use and under what circumstances they use them is important for understanding how people execute this everyday task and find their way in the world. The development of reliable measures of navigation strategy would also contribute to accurate testing of navigational ability and the design of rehabilitation tools for individuals with navigation deficits. The aim of the experiment presented here was to confirm a reliable and objective method for differentiating human navigational strategies. The method was applied to the study of a combined group of university students and community-based participants.

Cognitive Map Theory

Much of current navigation research (including investigations into navigational strategy) is grounded in the concept of the cognitive map first proposed by Tolman (1948) and later enlarged upon by O'Keefe & Nadel (1978). O'Keefe & Nadel (1978) proposed that animals can navigate either by the use of a cognitive map or by making simple stimulus response behaviours. The cognitive map is thought to represent the spatial relationships among environmental stimuli and allows the navigating animal to travel to a goal by relating it to the locations of other stimuli in the environment. In contrast, navigation by stimulus response would consist of simply traveling to a visible target or following a route from one landmark to the next where the next landmark is always in sight. Yet another way of navigating by stimulus response is to use body responses, e.g., turn right, then turn left. Navigation that employs a cognitive map is often referred to as "allocentric" (for short review see, Nadel & Hardt, 2004)(for short review

see, Nadel & Hardt, 2004) because it is ‘world based’, that is it allows the navigator to imagine the spatial relationships of environmental stimuli and to make novel routes to navigational targets. Further, these routes can be made even when the target is not visible from the start position. Navigation by stimulus response is referred to as “egocentric” because navigating to visible targets or by simple body turns is accomplished from the perspective of the navigator and without the necessity for understanding the relationships among stimuli in the environment.

Two Cognitive Systems

The current study was based on research suggesting that there are at least two navigation systems (allocentric and egocentric) in animal and human brains and that these systems facilitate allocentric and egocentric navigation. In animals (mainly rats) two memory systems have been associated with the two types of navigation (White & McDonald, 2002). Lesion studies have identified central structures of these systems, with the hippocampus being important for allocentric navigation and the caudate for egocentric (specifically stimulus response) navigation (Poldrack & Packard, 2003; White & McDonald, 2002). In humans, converging evidence from behavioural and brain imaging studies point to the presence of the same two systems (for review, see N. Burgess, 2006). For example, Doeller & Burgess (2008) demonstrated two types of learning (reinforcement and incidental) associated with egocentric and allocentric tasks, respectively. They interpreted this finding to mean that stimulus response learning is associated with an egocentric system (probably centered on the caudate) whereas a cognitive mapping system is associated with a separate allocentric system centered on the hippocampus. Other researchers have combined brain imaging with virtual environment

navigation tasks to differentiate brain activity associated with different navigation tasks, allocentric or egocentric (Hartley et al., 2003; Iaria et al., 2003). The findings from these studies also suggest that there are two systems underlying the two types of navigation.

The Morris Water Maze

In animals, the standard for testing spatial navigation is the Morris water maze (MWM) (Brandeis, Brandys, & Yehuda, 1989; D'Hooge & De Deyn, 2001; Morris, 1981). The original version of the task (Morris, 1981; Morris, Garrud, Rawlins, & O'Keefe, 1982) required animals to swim to a Plexiglas™ (invisible) platform submerged in a pool of milky water and to do this on multiple trials beginning from different positions around the edge of the pool. The wall of the pool was of uniform colour and texture and the only stimuli available for navigating were distal room features located outside of the pool. After several trials, rats were able to take direct paths to the platform, regardless of start position, thus indicating that they had formed a spatial representation (cognitive map) of the surrounding environment. More recently, the task has been used to identify place-based (allocentric) vs. cue-based (egocentric) behaviours in animals (e.g., Hamilton, Rosenfelt, & Whishaw, 2004; McGregor, Good, & Pearce, 2004). Virtual versions of the MWM are also becoming standard in human navigation testing with both healthy (e.g., Astur, Tropp, Sava, Constable, & Markus, 2004; Hardt, Hupback, & Nadel, 2009; Woolley et al., 2009) and brain injured (e.g., Goodrich-Hunsaker, Livingstone, Skelton, & Hopkins, 2010; Livingstone & Skelton, 2007) participants. However, there are only a few direct tests of strategy type and utilization (e.g., Hartley et al., 2003).

Measuring Navigational Strategy

A main goal of the current study was to demonstrate an objective measure of

navigational strategy that does not rely on verbal report and has the potential to be applied in brain imaging studies. Several researchers have proposed that the best navigators (those who take the quickest and most direct paths) are those who possess a full repertoire of navigational strategies and who are able to select and utilize the most efficient strategy when navigational task demands change (e.g., Etchamendy & Bohbot, 2007; Gluck & Fitting, 2003; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003). However, there are only a few direct studies of this premise (e.g., Etchamendy & Bohbot, 2007; Hartley et al., 2003). It would be helpful to develop reliable methods for measuring navigational strategies so that individual differences in strategy selection and utilization could be better clarified. Current findings from studies where strategies are reported, tend to use verbal report either to establish the type of strategy being utilized (Etchamendy & Bohbot, 2007; Hartley et al., 2003) or as a correlate of navigational behaviour (e.g., Spiers & Maguire, 2006). While verbal and self report may be useful correlates, relying on these as valid measures of cognition may not be advisable because verbal and self-report are not always reliable (e.g., Nisbett & Wilson, 1977). This may be especially true in the case of spatial cognition where much of the cognitive processing is likely unavailable to consciousness (Gluck & Fitting, 2003).

Identifying the strategy being used is also particularly important for imaging studies using virtual navigation paradigms. If people are navigating by two different strategies, and the two strategies have different anatomical bases, then this could impede the development of a clear understanding of the anatomical basis of navigation. In other words, some individuals may use different strategies than anticipated by experimenters and this could lead to problems with interpretations of brain activity. Indeed, if a method

can be developed to identify strategy use on a moment-by-moment basis, then it would be possible to improve understanding of the anatomical basis of navigation by capturing the functional anatomy of cognitive strategies and strategy switching. A first step toward this is to identify what strategies people are using and when they are using them.

Eye Movement Tracking

Eye movement measures were employed in the current study for several reasons. First, there is a long history of research suggesting that there is a strong relationship between eye movements (and more specifically, gaze position) and cognitions within the context of viewing scenes (e.g., Buswell, 1935; DeAngelus & Pelz, 2009; Yarbus, 1967). Second, eye movements likely reflect cognitions that are both stimulus driven and task dependent (DeAngelus & Pelz, 2009). This suggests that gaze position defines attentional focus and is related to cognitive processing for the task at hand. In the case of navigation this is important because gaze position should then be related to the cognitions (and strategies) utilized to navigate. Third, the application of gaze position analysis to study navigation in three dimensional virtual environments is a relatively new (Tatler, 2009) but promising approach to studying spatial ability and navigational strategies. Virtual navigation tasks can be specially designed and in combination with gaze position analysis, may reveal different associated cognitive strategies. Investigations of this type have already shown that gaze position differs depending on the nature of the navigation task (Gramman, Sharkawy, & Deubel, 2009; Hamilton, Johnson, Redhead, & Verney, 2009; Livingstone-Lee et al., 2011) and that there are gender differences in gaze position during navigation (Andersen, Dahmani, Konishi, & Bohbot, 2011; Mueller, Jackson, & Skelton, 2008).

Eye-tracking methods are frequently applied to the study of spatial cognition, but to date, most researchers have made inferences about spatial ability by testing participants using static two-dimensional images presented on a computer screen (e.g., Albert et al., 2005; MacFadden, Elias, & Saucier, 2003; Schmidt et al., 2007). While this may be appropriate in many circumstances, static displays do not capture the full navigational experience that requires the navigator to perceive the environment and navigate through it while moving toward a target location. This is important because as the navigator moves within the environment the stimuli which can be perceived change: they may appear or disappear, or change their relation to one another. This is an important point given that Hart et al. (2009) compared eye movements while participants viewed static versus dynamic (real-world or video) scenes and found significant differences in gaze. These authors also found that gaze allocation while viewing a first person navigation video was predictive of gaze allocation on a real world exploration task, but that this result depended upon how the stimuli were presented in the virtual environment. Further, Hahm et al. (2007) demonstrated that participants are significantly better at a post-hoc object recognition task after active navigation of a virtual environment compared to when they passively viewed the environment. Together these findings suggest that active navigation influences the way in which environmental stimuli are attended to and perceived. Thus, there is a need to investigate navigation using eye tracking while the participant is moving through space.

A relatively new development in navigation research is to apply eye tracking measures to analyze which navigational stimuli (distal or proximal) hold the attention of participants most during tasks that require active navigation (Gramann, Muller, Eick, &

Schonebeck, 2005; Hamilton et al., 2009; Jin, Gillner, & Mallot, 2004; Spiers & Maguire, 2006). However, the analysis of eye movement data is often a complex process because of the large volume of data generated when presentations are dynamic, i.e., either real world or virtual environment tasks where participants are actively navigating. For example, Andersen, Dahmani, Konishi, & Bohbot (2011, in press) used a relatively laborious procedure that limited their study to a small sample size of seven. One possible solution to this problem is to isolate regions of interest by measuring average gaze position in select areas of a visual display (Holmqvist, Holsanova, Barthelson, & Lundqvist, 2003; Livingstone-Lee et al., 2011; Mueller et al., 2008). This method greatly reduces the volume of data to be analyzed and has the advantage of being an 'a priori' approach in that it allows for planned comparisons.

Research Approach

The current study examined gaze position in several specially-designed virtual environments. The Place maze was a human analogue of the MWM was therefore designed to be biased toward the use of allocentric strategies. A second task, the Cue maze, was an adaptation of the Place maze and designed to be biased toward the use of egocentric strategies. This task differed from the Place maze because there were objects (proximal stimuli) situated on the arena wall. One of these objects always marked the location of the platform but its position changed from trial to trial. A crucial design feature of both virtual environments was that the locations of important proximal and distal stimuli were separated on the screen display. The distal features of the environment (the landscapes) useful for allocentric navigation in the Place maze were always located vertically above a horizon (the vertical midline of the display). The proximal features of

the environment (the objects on the arena wall) useful for egocentric navigation in the Cue maze were always located below the horizon. Thus it was possible to identify which type of stimuli (allocentric or egocentric) participants were attending to while navigating.

Objectives

The main objective of the current study was to confirm findings from feasibility work and a recently published manuscript (Livingstone-Lee et al., 2011) proving an eye tracking method for use in a population of university students. Specifically, the goal was to confirm that gaze position during orientation in the navigation tasks could successfully capture differences between behavioural conditions and thus indicate strategy use. However, by studying a larger sample size, this experiment sought to extend the analysis of Livingstone-Lee et al. (2011) by introducing a new gaze position analysis method and by examining acquisition of gaze position to reveal the time course of strategy acquisition. A secondary objective of the present study was to test whether findings with university students could be extended to community-based participants.

Research Questions and Hypotheses

The current study addressed three specific research questions as follows:

1. Will the difference in the navigational task demands of Place and Cue mazes lead to a difference in gaze position?
2. With what reliability will gaze positions differ? That is, in the Place maze how many participants will look up (above the horizon) and in the Cue maze how many will look down (below the horizon or at the objects)?
3. What is the time course of gaze position acquisition?

The main hypothesis was that in the Place maze vertical gaze position would be higher than in the Cue Maze. It was also expected that most participants would have average gaze positions that were higher (directed toward the outdoor landscapes) in the Place maze than in the Cue maze, where they were expected to direct their gaze downward toward the objects or the arena floor. It was further hypothesized that differences in gaze position (both vertical and horizontal) would be observable very early (within the first second) in behavioural trials and that differences in gaze would be acquired quickly (by the second or third trial). Given the findings of Hamilton, Johnson, Redhead & Verney (2009) it was also expected that a proportion of gaze would be directed toward the floor during orientation in both maze conditions.

Methods

Participants

Participants were 52 individuals from two source populations, first year Psychology students at the University of Victoria (n = 33) and volunteer participants from the local Victoria community (n = 19). The data from these two sources was combined because there were no interactions between sources and key navigational and eye movement variables (Appendix 3-A). Participants met the following inclusion criteria: a) male or female between the ages of 19 and 60, b) English first language, c) no history of brain injury or neurological disorder, d) normal vision or vision corrected by contact lenses, i.e., no eye glasses. Participants were excluded from the study if 1) a data set (EEG, eye movement or behaviour) was missing or incomplete due to technical problems, or 2) if participants had experienced a brain injury in the past. Brain injury was defined as having received an injury to the head that required an overnight stay in the hospital. Participants

were also asked to provide demographic information, medical history and information about computer game experience. The data from 37 participants (students, n = 23; community volunteers, n = 14) was included in the analysis. Of these 37 participants, 16 were male and 21 female. The mean age of participants in the sample was 25 years (student mean = 22 years; community volunteer mean = 30 years). All participants gave informed consent and the study was approved by the Human Research Ethics Board at the University of Victoria. This study formed part of a collaboration with an engineering student (Dr. Phil Zeman, recently graduated) who was interested in investigating the effects of the maze tasks on brain activity using a new electroencephalography (EEG) analysis technique. Therefore participants were wearing an electrode cap for the duration of the behavioural tasks.

Apparatus

Virtual maze environments. Spatial navigation was tested using three versions of a virtual Morris water maze (vMWM) task; the "Place Maze", the "Cue Maze", and the "Visible Platform Maze". These desktop virtual environments were created using the commercially available video game editor, Unreal® (Epic Megagames), and were displayed on a 19 inch LCD monitor at a resolution of 800 x 600. Participants navigated through the trials using a typical gaming joystick that was stable on the desk in front of them. The joystick features were modified so that participants could move forward, left and right, but not in reverse.

The Place Maze environment was an adaptation of the Arena Maze environment (Skelton, Bukach, Laurance, Thomas, & Jacobs, 2000; Skelton, Ross, Nerad, & Livingstone, 2006) and consisted of a large circular arena bordered by a low wall and

situated in a large square room .The room had large windows in all four walls, providing panoramic views of an outdoor landscape (Figure 3.1). The four walls of the room were arbitrarily assigned cardinal directions of North, South, East and West and the room lacked any distinctive features other than the environment outside the windows. There was a large window on each of the north and south walls and three windows on each of the east and west walls. The views looking out each side of the room were distinct. Mountains were visible through the north window and hills sloped down to a sandy beach outside both the east and west windows. A body of water with a small island could be viewed through the south window. The outdoor landscape provided distal stimuli to aid in navigation to a hidden platform and therefore the Place Maze was designed to bias participants toward the use of an allocentric strategy. The Cue Maze (Figure 3.1) was identical to the Place Maze except that there were eight objects evenly spaced around the low rising arena wall at cardinal points. These objects served as proximal stimuli (or local cues) that the participant could use to navigate to the hidden platform. Therefore the Cue maze was designed to bias participants toward using an egocentric strategy. The Visible Platform Maze utilized the same virtual environment as the Place Maze. The platform was always visible on the floor of the arena but its location changed on each trial.

Eye movement tracking. Participant's gaze positions were recorded using a remote eye tracking system consisting of an LED-infrared lighting system (Hamamatsu Corporation) and a Flea Firewire Camera (Point Grey Research). The technology for the tracking device was developed by CanAssist, (Canadian Institute for Accessibility and Inclusion at the University of Victoria). Participants supported their heads in a chin rest

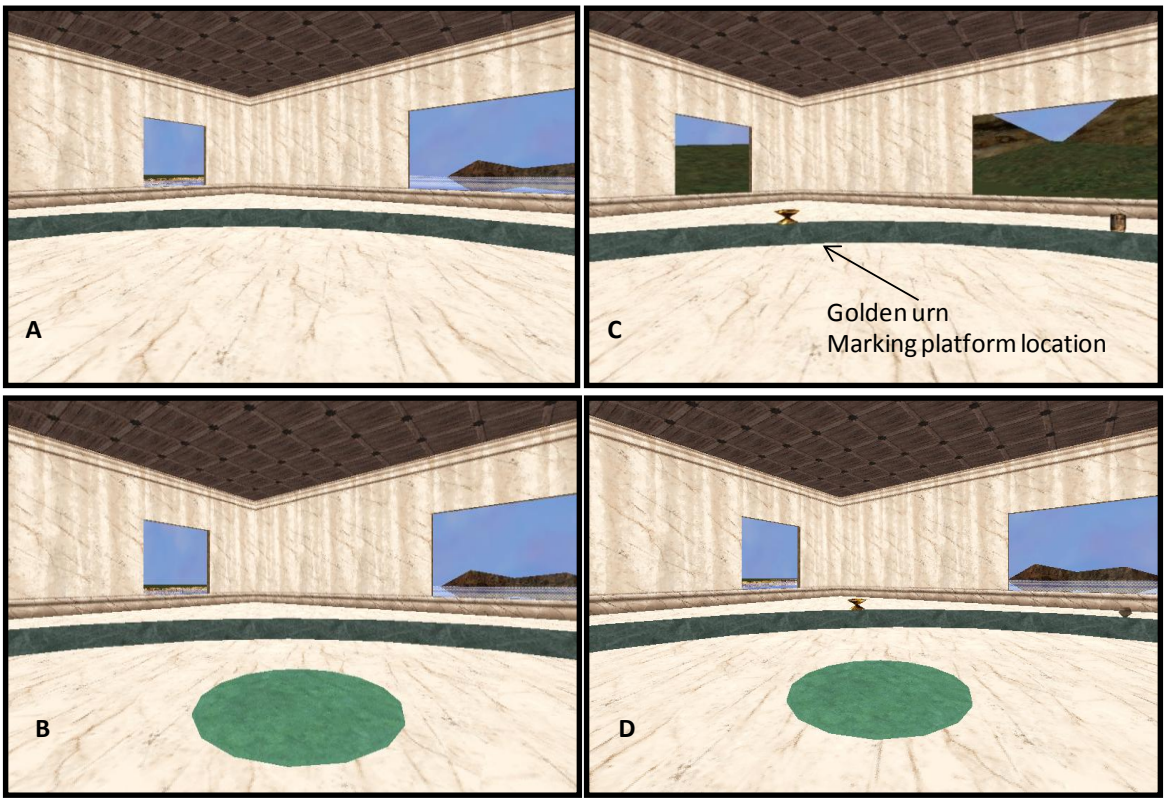


Figure 3.1. The virtual environments. **A**. The Place maze, a vMWM. **B.** The Place maze with the platform visible in its fixed location (i.e., after the participant has stepped on it). Note that during trials, the platform's location can be identified only by a constellation of distal landmarks, biasing participants to use allocentric strategies. **C.** The Cue maze, a virtual landmark maze. **D.** The Cue maze with the platform visible (coincidentally) in the southeast quadrant, marked by the golden urn. Because the platform (and urn) change quadrants each trial, this proximal object provides the only means of identifying the platform location, biasing participants to use an egocentric strategy.

throughout the experiment while the eye tracking system recorded monocular positional coordinates at a rate of 60 samples per second. A 9-point calibration was performed for each participant before testing began and participants completed a "baseline" task in which they were instructed to follow the movement of the tip of a pen horizontally across the entire width of the display at the vertical midline. Two computers were set up to simultaneously present the virtual mazes and to log the eye movement data. A television and digital video disk (DVD) player (hidden to the participant) recorded the screen output

overlaid with the gaze position. In this manner, the experimenters could directly view the eye movements of participants as they navigated the virtual environment.

Procedures

A summary of the experiment protocol is given in Appendix 3-B and Table 3.1 gives a brief summary of maze trials and their purpose. Note that for this experiment an arena exploration trial was added prior to each block of invisible platform trials. The following sections describe each trial type. Figure 3.2 gives schematic aerial views of all maze trials showing their number, platform locations and trial start positions while Table 3.2 shows the order of presentation of trials for the two experimental conditions.

Table 3.1

Description of maze trials, the number of them presented and their purpose. The order of presentation of the trials depended upon the experimental condition.

Trial type	Purpose	Number
Room Exploration	To familiarize participants with the environment and using the game pad	1
Arena Exploration	To familiarize participants with the environment from inside the arena	1
Visible Platform	To familiarize participants with procedural aspects of the task and confirm their mastery	4
Invisible Platform	To test participants' ability to navigate to a location in the room	10
Probe	An implicit test of the participants' knowledge of the platform location	1
DTS	An explicit test of the participants' knowledge of the platform location	1

Room exploration trial. The purpose of this trial was to familiarize the participant with movement using the gamepad/joystick and to provide them with a good

view of the outdoor landscape. The trial began with participants situated at the centre of the east wall, outside of the arena and looking toward the middle of the room. Participants were told that they could explore the room for as long as they liked and they were asked to look at the landscape outside each of the windows. The exploration trial ended when the participant indicated comfort with the video game pad and satisfaction with their exploration of the virtual environment.

Visible platform trial. The purpose of these four trials was to confirm that participants were able to navigate to a single visible target in the environment. A large, green, circular platform was visible on the floor of the arena in the centre of a different quadrant for each trial. The start position for each trial was different, with all start positions being just inside the arena wall and at a cardinal point (Figure 3.2). When the participant "stepped" on the platform it made a sound like a bell ringing. Participants were informed that they should stay on the platform until they were ready to proceed to the next trial, the start of which was indicated by a short, high pitched beep.

Arena exploration trial. The purpose of this trial was to allow participants to become familiar with the environment from the perspective of the arena. The start position was just inside the arena wall at the north cardinal point with the participant facing inward toward the centre of the arena. Participants were informed that they could explore inside the arena for as long as they liked, but that they could not pass beyond the arena wall. The trial ended when the participant indicated satisfaction with their exploration of the arena.

Place maze invisible platform trial. The purpose of these ten trials was to test the ability of participants to navigate to a location in the room when the location was

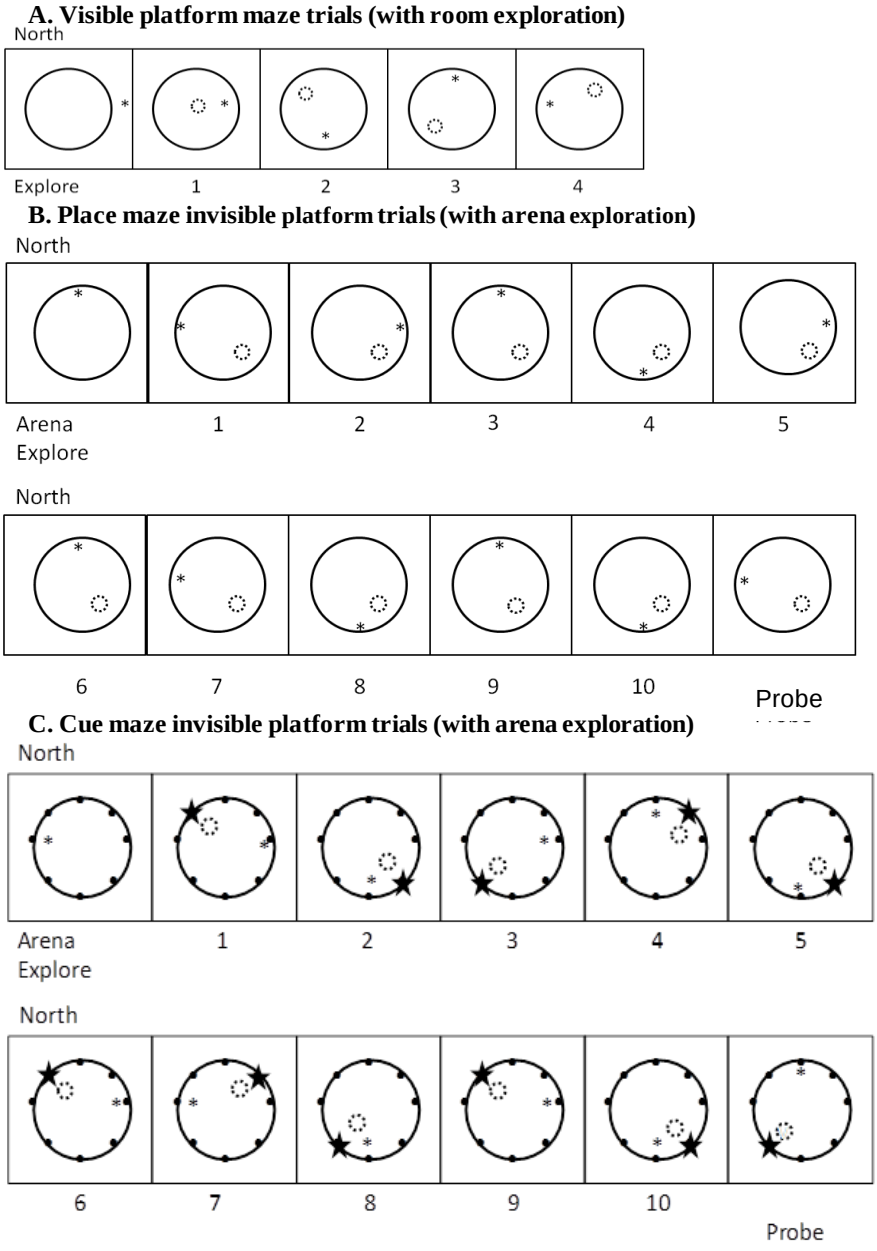


Figure 3.2. Aerial schematic of the virtual maze trials. The arbitrary cardinal 'north' wall of the room is shown. The dotted circle marks the invisible platform location and the asterisk (*) marks the start position of the participant. **A.** Location of visible platform changed on each trial. **B**. In the Place maze, the platform was always in the same location. Note that for the probe trial, the platform was not present but the dotted circle marks its location on previous trials. **C.** In the Cue maze, the platform changed location on each trial but was always located in front of the golden urn cue object (represented by a black star). The other objects perched on the wall are represented by small black dots. On the probe trial the dotted circle marks the location of the platform on previous trials (in front of the cue object).

Table 3.2

Experimental design. The order of maze testing trials and post tests is given according to the two experimental conditions, place- first and cue- first.

Test Phase	Experimental Condition	
	Place-first	Cue-first
Explore/Visible	Room explore Visible Platform maze DTS	Room explore Visible Platform maze DTS
Place or Cue	Arena explore Place maze Probe DTS	Arena explore Cue maze Probe DTS
Spatial task	Described and reported in a later experiment	Described and reported in a later experiment
Cue or Place	Arena explore (with objects) Cue maze Probe DTS	Arena explore (with objects) Place maze Probe DTS
Post test	WTWT RRT	WTWT RRT

Note. DTS = Drop-the-seed, WTWT = Where's the Water Task, RRT = Room Reconstruction Task.

found most easily by using features like the outdoor landscapes visible through the windows. The invisible platform was in a fixed location in the centre of the southeast quadrant of the arena. Participants were informed that the platform would always be in the same place and that they should go to the platform as quickly and directly as possible. Start positions were always just inside the arena wall, at one of the four cardinal points and varied in a fixed, pseudo-random order. Start positions were also balanced according to whether the participant should make a left or right turn and according to the distance

from the start position to the target location (Figure 3.2). The platform remained invisible until the participant stepped on it, at which point it rose up making a sound like a bell ringing. While on the platform, participants were able to look around the room (while remaining on the platform) as much as they liked before proceeding to the next trial, the start of which was indicated by a high pitched beep.

Probe trial. The purpose of this trial was to test how well the participants learned the platform location. Prior to testing, participants were informed that on one trial (the probe) the platform would be very difficult to find but that they should continue to search for it anyway. During this probe trial, the platform remained hidden for 50s and the end of the trial was indicated by the usual bell ringing sound.

Drop-the-seed (DTS) trial. The purpose of this trial was to test the explicit knowledge of participants with respect to the platform location. Participants were instructed to go to the spot where they thought the platform should be (based on the trials they were just completing) and once there the experimenter dropped a virtual seed to mark the location. The virtual seed grew into a virtual plant that marked the spot for later scoring on a 0-7 scale. For scoring the DTS trial, a ringed "bull's eye" target was placed over the quadrant where the platform was located during the invisible platform trials, with the centre of the target matched in size to the platform (Figure 3.3). Scores from 0 to 7 were assigned based on the location of the participant's marker to the centre of the target (or bull's eye). A score of 0 indicated that the marker was not on the target rings whereas a score of 7 indicated that the marker was placed on the bull's eye (i.e., on the platform location). Participants did not observe the scoring procedure.

Figure 3.3. Scoring for the "Drop-the-Seed" trial. The plant marks the spot where the participant dropped a virtual seed. The task is scored using target rings with the center "bull's eye" matching the size and location of the platform in the maze. Scores range from 0 for placement outside the target rings (and outside the correct quadrant) to 7 for placement on the bull's eye. The placement shown would receive a perfect score of 7.

Cue arena exploration trial. The purpose of this trial was to allow participants to become familiar with the environment when objects were added to the arena wall. This trial was identical to the Place arena exploration trial except for the addition of an object to each of the 8 cardinal points of the arena wall.

Cue maze invisible platform trials. The purpose of these ten trials was to test the ability of participants to navigate to a location in the room marked by a nearby (proximal) cue object. Invisible platform testing in the Cue Maze followed the same procedures as for the Place Maze invisible platform trials described above. The platform changed location (from quadrant to quadrant) but was always located in front of the same object, a "golden urn" (Figure 3.1). Participants were told that the platform would not

always be in the same location, but that there would always be a clue to its whereabouts. The probe trial and DTS trial were as described for the Place maze.

Ancillary tasks

Where's the Water Task (WTWT). The purpose of this test was to ascertain that participants felt "embedded" or felt a three dimensional sense of "presence" in the virtual environment. At the completion of the computer tasks, participants were moved to a trial where they faced the north window, through which they could view the mountains. Participants were then asked to indicate, by pointing, where the water was located in the virtual environment. If participants pointed away from the computer screen (i.e., either beside or behind themselves) they were judged to have perceived the virtual environment as a three dimensional space and to have made a cognitive map. Therefore the test was another measure of how well the participants understood the locations of the important distal features in the environment. The task was scored on a 3-point scale (Appendix 2-B).

Room Reconstruction Task (RRT). The purpose of the RRT is to assess the degree to which participants formed a cognitive map. Participants were asked to reconstruct the room using two dimensional pictures (screen shots) of the four room walls (showing windows that included landscape views) and the room floor (showing the arena). Participants were first given the picture of the room floor and asked to place each of the four walls in the correct location according to the maze task they had just completed. They were then given a small green disc (designed to represent the platform) and asked to place it on the floor of the arena where they thought the platform was located in the Place Maze, that is, in the maze with no objects. The task was scored on a

4-point scale (Appendix 3-C).

Computer Gaming Experience

Because the experiment concerned the effects of training in a virtual environment, participants were asked about their computer gaming experience. They were asked whether they play two and/or three dimensional games, how often they play (now and as children) and about their experience with game controllers/joysticks. Participants responded on a 6-point Likert-type scale (Appendix 2-A) by circling one of the following responses: “never”, “occasionally”, “monthly”, “weekly”, “every few days”, or “daily”. Results were tabulated first by examining each question separately and then by calculating a combined score.

Demographic Variables

Demographic variables were recorded from a background information questionnaire (Appendix 2-A) and included age, gender and education level. These variables were analyzed to assure that there were no confounds of age, sex, education or computer experience with the maze or gaze position variables. The medical variables were recorded for screening purposes. The data of participants who indicated medical problems were generally excluded from analysis if the problem in question was known to affect the ability to navigate.

Analysis

Behavioural and gaze position data were summarized using Excel and inferential statistics were computed using SPSS® (Statistical Package for the Social Sciences). Raw eye tracking data and heat map illustrations were generated using MATLAB® (Matrix Laboratory).

Maze variables and scoring. The maze data were analyzed using the three conventional dependent measures of performance: 1) latency (time in seconds) to reach the platform, 2) distance (in pool diameters) travelled to the platform, and 3) dwell time or percentage of time spent searching in the correct quadrant of the arena on probe trials. Latency and distance variables were analyzed for trials 2 to 10, excluding the first trial because it is considered to be a search trial. The data collected in Unreal® were converted and analyzed using TRAM®, a locally developed software program.

Gaze position variables. The behavioural conditions were designed to validate the gaze position analysis and the primary interest of the study was differences in gaze position according to the use of the different environmental stimuli. For this experiment both vertical and horizontal gaze positions were examined. For the purpose of analyzing vertical (or y-axis) gaze position, the size of the objects in the Cue Maze was modified so that they always appeared below a horizon that divided the screen display into upper and lower halves (Figure 3.4). The Place Maze was designed to bias participants toward using the outdoor landscapes (distal stimuli) that always appeared above this horizon. Conversely, the Cue Maze was designed to bias participants toward using objects (proximal stimuli) that always appeared just below the horizon. To quantify vertical gaze position, the uppermost point of the screen display was assigned a value of 0 and the lowermost point a value of -600 with the horizon having a value of -300 (Figure 3.4). The two variables of interest were vertical gaze position (as defined by position on the y-axis) and the percentage of trial gaze above the horizon. These measures were analyzed for the first second (60 samples) of trial data based on findings from the feasibility work and a recent study (Livingstone-Lee et al., 2011) showing that spatial orientation to the relevant

Figure 3.4. Definition of the vertical horizon on the display. During navigation and from all viewpoints in the arena the objects (proximal stimuli) in the Cue Maze appeared below a horizon (marked here by the black line) that split the screen display in half. All of the outdoor landscapes (distal stimuli) were located above this horizon. The horizon (at a value of -300) was located at the vertical midline of the display.

stimuli occurs within this time frame. Horizontal (or x-axis) gaze position was quantified in a similar way to vertical gaze position, by splitting the screen display at the horizontal midline (Figure 3.5). The far left point of the screen display was assigned a value of 0 and the far right a value of 800, with the midpoint of the display having a value of 400. The display was divided into five equal sections (of 160 units each) with the middle section centred at 400 on the x-axis (Figure 3.5). The sections were labelled far left (0-160), left (160-320), centre (320-480), right (480-640), and far right (640-800). The two variables of interest were horizontal gaze position (defined by position on the x-axis) and the percentage of trial gaze in each of the five sections of the screen. For ease of analysis

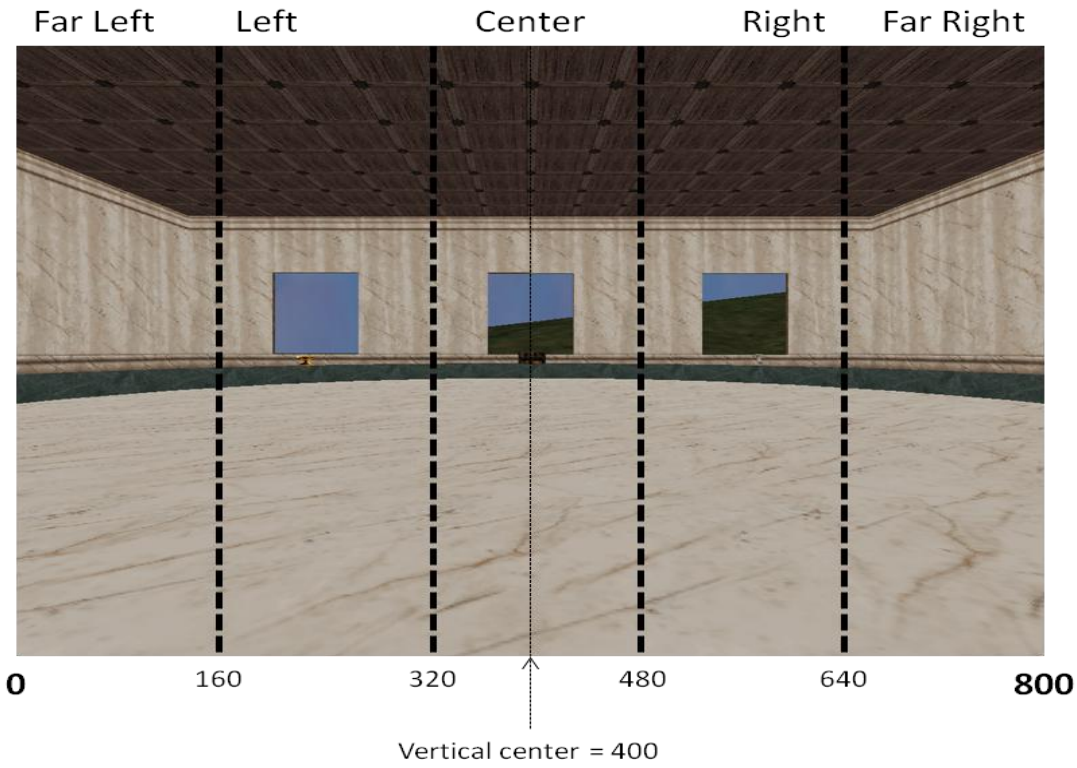


Figure 3.5. Definition of "on-centre" horizontal gaze position. Screen segments are shown for one Cue maze start position. For analysis the screen display was divided into 5 equal segments with the middle segment defining "on-centre" gaze with a central value of 400. The display was 800 units (pixels) wide and therefore each segment was 160 units wide. Note that the cue objects appeared in the left, center and right segments but not in the far left or far right segments.

data from the "off-centre" sections (left, far left, right, far right) were collapsed so that the gaze position variable had two categories, "percentage off-centre" and "percentage on-centre". Because these two categories are percentages and sum to 100%, only the on-centre data were analyzed.

Combining horizontal and vertical gaze positions. To analyze horizontal and vertical gaze positions combined, 10 regions of interest were defined (Figure 3.6). These regions were then collapsed into four regions selected to exclude areas of the display where there was little or no participant gaze and to include areas where participants looked most frequently. They captured over 90% of gaze for both the Place and Cue

mazes. They four regions were defined as 1) on-centre and above the horizon, 2) on-centre and below the horizon, 3) off-centre and above the horizon, and 4) on-centre and below the horizon.

Data Analysis.

Behavioural navigational data. The main behavioural analyses were as follows:

1. For the Place and Cue mazes, group differences in the behavioural maze dependent variables (latency, distance, and probe dwell time) will be compared using t-tests.
2. To ensure that there was no confound based on whether participants were in the place-first or cue-first groups a 2 x 2 repeated measures Analysis of Variance (ANOVA) was conducted on the latency data.

Gaze position data. The main analyses were as follows:

1. For the Place and Cue mazes, group differences in the two variables "vertical gaze position," "percentage of trial gaze above horizon" and "on-centre (horizontal) gaze position" will be compared using t-tests.
2. To ensure that there is no confound based on whether participants were in the place-first or cue-first groups a 2 x 2 repeated measures ANOVA was conducted on the vertical gaze position data.
3. For the first maze presentation (either Place or Cue) a 2 x 2 repeated measures ANOVA was conducted on data for the percentage of trial gaze above the horizon in Trials 1 and 3. The purpose was to test acquisition of vertical gaze position differences.

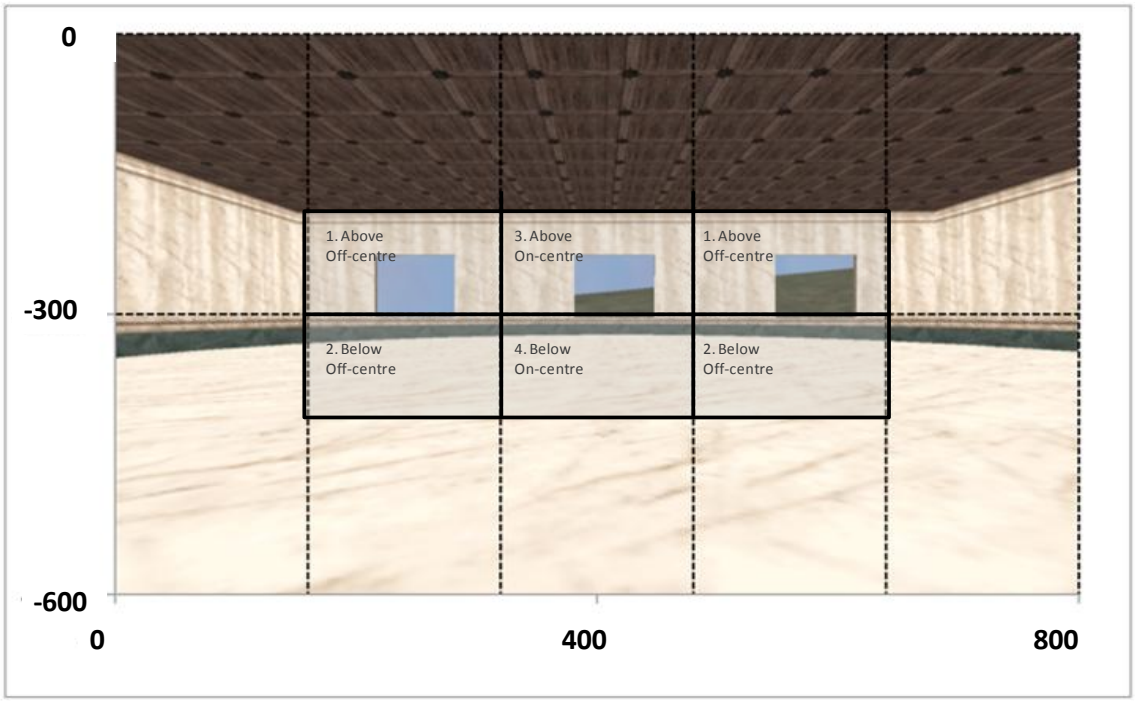


Figure 3.6. Regions of interest combining vertical and horizontal gaze position. View of the Place maze from one of four start positions. The display was divided vertically into two segments (above and below the horizon) and horizontally into five segments. Dotted lines indicate the resulting ten regions of interest. For analysis regions of interest were selected because they incorporated the majority of participant gaze in the mazes. The resulting regions compared were 1) Above and off-centre, 2) Below and off-centre, 3) Above and on-centre, and 4) Below and on-centre.

4. For the Place and Cue mazes a preliminary 2 x 2 x 2 repeated measures ANOVA was conducted on vertical and horizontal gaze position data.

Results

Navigation Results

Latency and distance variables. Participants mastered the use of the joystick and other procedural aspects of the behavioural tasks. This was indicated by their performance on the visible platform trials (Figure 3.7). They were able to find the platform quickly and efficiently (Latency, M = 3.8s, SEM = 0.18; Distance, M = 0.55pd, SEM = 0.02) and in a manner similar to that of healthy participants in previous studies (e.g., Livingstone & Skelton, 2007). Overall, participants took less time to find the

platform when its location was marked by a proximal cue than when they had to navigate using only the distal stimuli (room and landscape features) presented above the horizon (Figure 3.8). Latency to the platform was significantly shorter in the Cue maze (*M* = 10.7s, *SEM* = 1.08) than in the Place maze (*M* = 16.8s, *SEM* = 2.7), t(36) = 2.42, p = .02, d = .49. For this analysis, latencies were compared for trials 2 to 10. Trial 1 was excluded because it was considered to be a search trial in which participants had not yet seen the platform location and therefore could not be expected to demonstrate their learning of its location. Participants traveled a somewhat shorter distance to the platform when its location was marked by a proximal cue than when only the distal stimuli were available for navigation (Figure 3.8). However, there was no significant difference in the distance

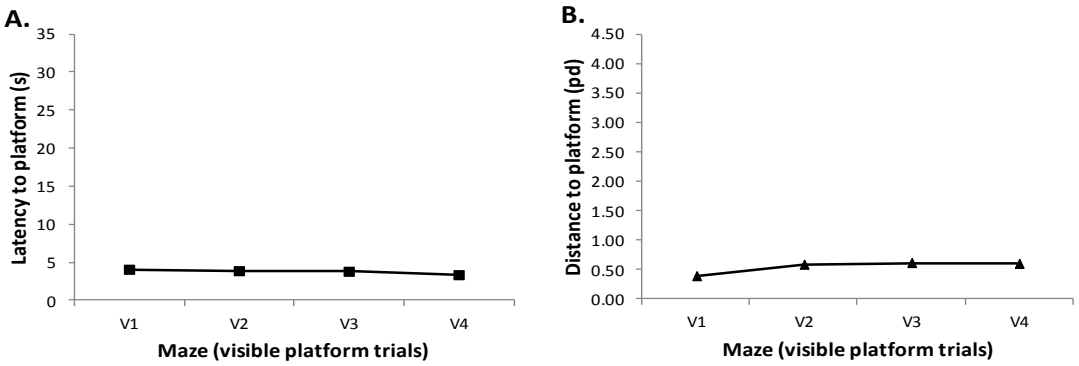


Figure 3.7. Latency and distance to the platform in visible platform trials. Mean latency **(A)** was below 4.5s. Distance traveled **(B)** to the platform was consistent with the physical distance from the start position to the platform location. Note: pd = pool diameters.

traveled in the Place (*M* = 1.08pd, *SEM* = 0.10) and Cue (*M* = 0.96pd, *SEM* = 0.10) mazes.

Probe trial. As expected, participants demonstrated good knowledge of the platform location after completion of either the Place or Cue maze (Figure 3.8). Time spent searching in the correct quadrant of the arena was well above chance performance

(25%) for both probe trials. Participants spent slightly more time in the correct quadrant in the Place maze than in the Cue maze but there was no significant difference between the mazes in the percentage of time spent searching in the correct quadrant (Place, *M* = 57%, *SEM* = 3%; Cue, *M* = 62%, *SEM* = 4%). Participants' understanding of the whereabouts of the platform was consistent with findings for healthy participants in previous work using similar experimental paradigms (e.g., Livingstone & Skelton, 2007; Mueller et al., 2008).

Drop-the-seed trial. Results for the DTS trial were similar to those for the probe trial (Figure 3.8). Participants demonstrated relatively accurate knowledge of the platform location by dropping a 'seed' marker as close as possible to where they thought the platform was located during behavioural trials. Accuracy was slightly greater in the Cue maze (*M* = 5.6, *SEM* = 0.36) than in the Place maze (*M* = 5.1, *SEM* = .37) but this difference was not significant. In the Cue maze 69% of participants had high scores of 6 or 7 indicating very good knowledge of the platform location and in the Place maze 54% of participants had high scores. Most importantly, in both mazes over 90% of participants dropped the seed marker in the correct quadrant of the arena.

Acquisition. Participants learned to find the platform equally well in the Place and Cue mazes. Acquisition rates for the two mazes were similar (Figure 3.9). For both latency and distance measures, visual inspection shows that performance reached asymptote on about the 5^{th} or 6^{th} trial. In both mazes, latency showed slightly more variability than distance and in the Cue maze latencies were shorter than in the Place maze. This pattern of results was consistent regardless of order of maze presentation, place-first or cue-first (data not shown).

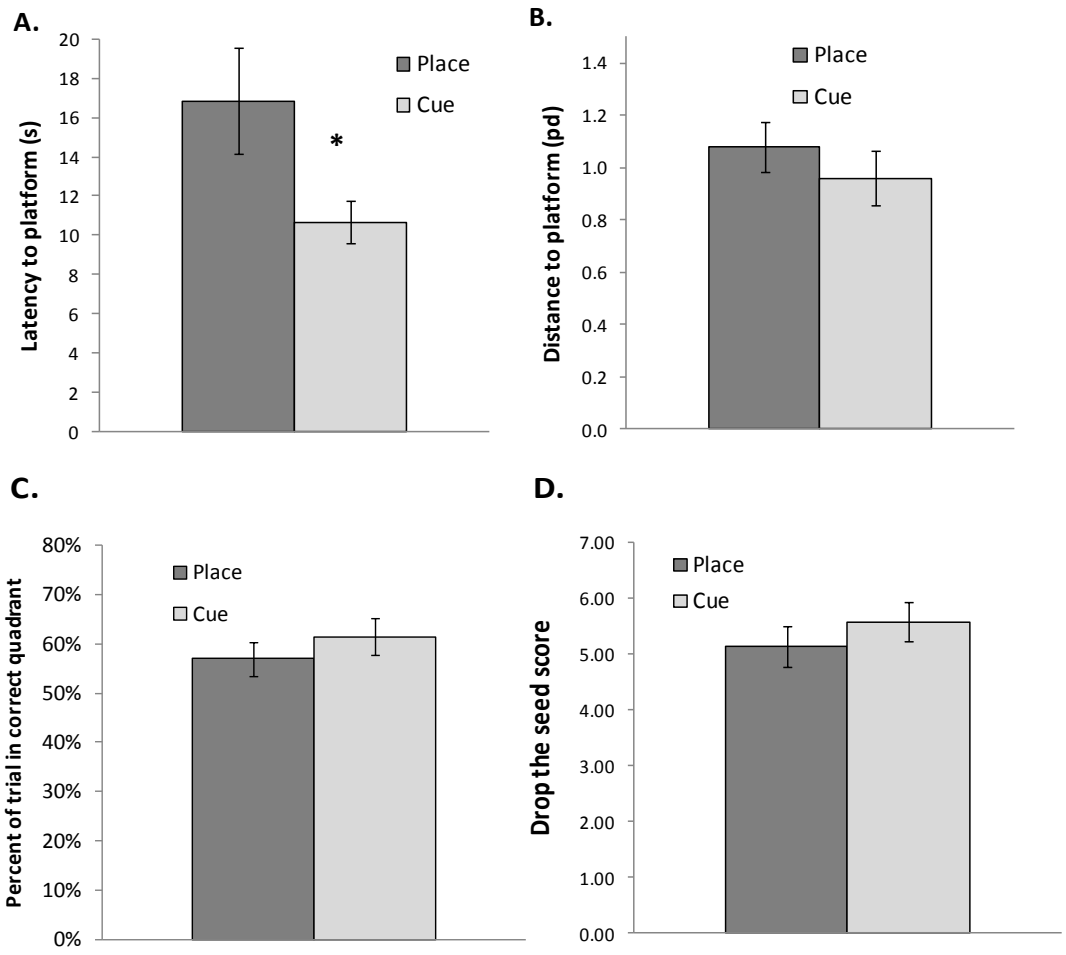


Figure 3.8. Navigation behaviour measures for Trials 2 to 10 in Place and Cue mazes. With the exception of the latency variable, there were no detectable differences in performance in the two mazes. **A.** There was a significant difference between mazes in latency to the platform. **B.** Distance traveled was somewhat greater in the Place maze than in the Cue maze. **C.** Time spent searching in the correct quadrant on the probe trial was slightly greater in the Cue maze than in the Place maze. **D.** Drop-the-seed scores were slightly higher in the Cue maze than in the Place maze. Bars indicate standard error of the mean.

Order effects on navigation variables. Appendix 3-D outlines tests of the navigation variables (latency, distance, probe and DTS trial) for order effects related to which maze was presented first, i.e. Place maze first or Cue maze first. There were no order effects identified for probe or DTS trial variables. One effect on latency and distance was discovered for the order of Cue maze presentation. Participants who received the Cue maze second traveled to the platform more quickly and directly than

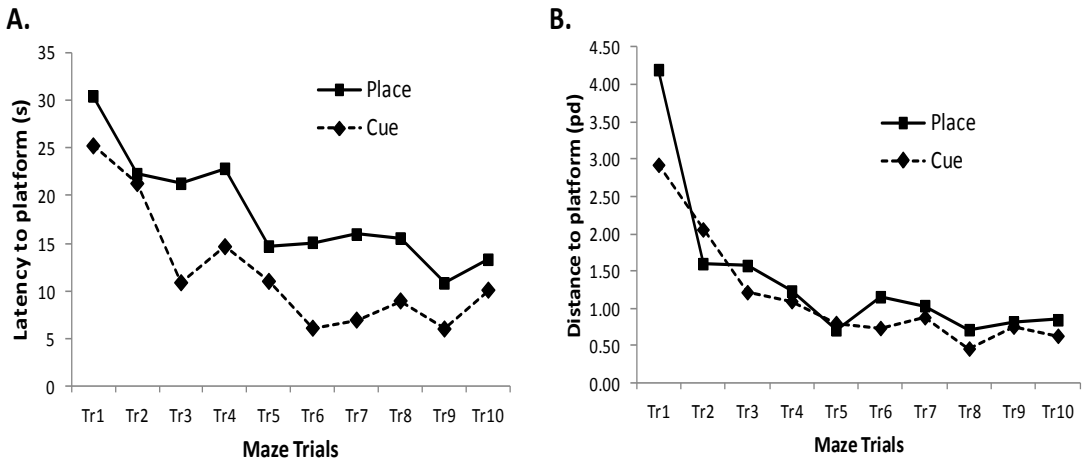


Figure 3.9. Acquisition curves for latency and distance in the Place and Cue mazes. Latency **(A)** and distance **(B)** curves were comparable for the two mazes. Latency to the platform was greater in the Place maze than in the Cue maze.

participants who received the Cue maze first. However, this effect was limited to early trials.

Individual performance. For both mazes, most participant scores were within one standard deviation of the centre of the group distribution and all were well within two standard deviations. In the Place maze 92% (n= 34) of participants had scores within one standard deviation of the center of the distribution and in the Cue maze 89% (n = 33) of participants had scores within one standard deviation.

Gender Comparisons. Overall, there were no gender differences in navigational performance. There were no significant differences between males and females in latency to the platform in either the Place maze (Males, *M* = 12.0 s, *SEM* = 1.8; Females, *M* = 20.1 s, *SEM* = 4.5) or in the Cue maze (Males, *M* = 10.4 s, *SEM* = 1.9; Females, *M* = 11.2 s, *SEM* = 1.2). Similarly, there were no significant differences between males and females in distance traveled to the platform in either the Place (Males, *M* = .96 pd, *SEM* = .14; Females, *M* = 1.16 pd, *SEM* = .15) or Cue maze (Males, *M* = .86, *SEM* = .14;

Females, *M* = 1.03, *SEM* = .10). There was a slight male advantage demonstrated by shorter latencies (t = 1.73, p = .09) in the Place maze but this difference was not present (t = 1.03, p = .31) when males and females were compared on the distance variable. Furthermore, there were no significant differences in the ability of participants to search for the platform in the correct quadrant on probe trials in either the Place maze (Males, *M* = 61%, *SEM* = 7%; Females, *M* = 54%, *SEM* = 3%) or the Cue maze (Males, *M* = 67%, *SEM* = 5%; Females, *M* = 57%, *SEM* = 5%).

Vertical Gaze Position

Average vertical gaze position. Overall, average vertical gaze position first rose and then fell slightly during the first second of Trials 2 to 10 in both the Place and Cue mazes (Figure 3.10). Trial 1 was excluded from the analysis for reasons analogous to those given previously in the navigation results section, that is, that Trial 1 is a search trial in which participants are ignorant as to the relevance of different environmental stimuli whereas subsequent trials reflect their gaze after at least some maze learning. Average gaze position for Trials 2 to 10 was always higher in the Place maze than in the Cue maze. Further, average gaze position in the Place maze was mainly above the defined horizon whereas gaze in the Cue maze was mainly below this horizon. This suggests that participants more frequently looked upward in the direction of distal room features at the start of the Place maze trials than at the start of the Cue maze trials and that they looked downward in the direction of the proximal cue objects at the start of Cue maze trials. As noted in previous research (e.g., Livingstone-Lee et al., 2011) orientation to environmental stimuli appears to take place very early in trials, in this case by about 300ms or just under 20 samples. This pattern of results was obtained regardless of

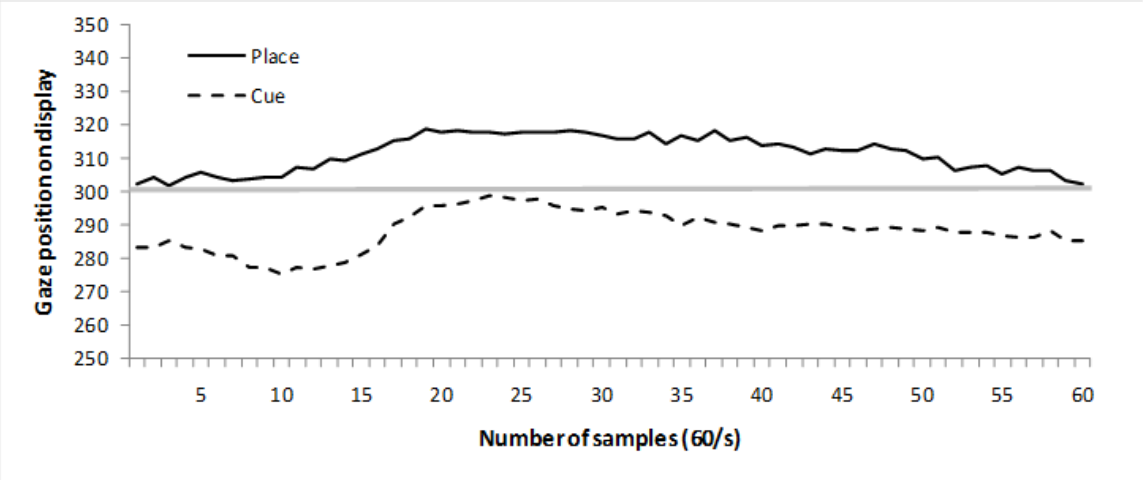


Figure 3.10. Average vertical gaze position in Place and Cue mazes in the first second of trials. Sampling rate was 60 samples per second. The grey line indicates the horizon defined at the vertical midline on the screen display.

whether the participants were tested in the Place maze first or the Cue maze first (data not shown). Further, when vertical gaze position on Trials 2 to 10 was compared for the two mazes (Figure 3.11) there was a significant difference, with gaze position in the Place maze *(M* = 313, *SEM* = 5.4) being higher overall than gaze position in the Cue maze (*M* = 286, *SEM* = 3.8), $t(36) = 6.31$, $p < .001$, $d = .93$. This difference in vertical gaze position suggests that in the Place maze participants may have been looking more at the upper area of the screen containing the outdoor landscapes, whereas in the Cue maze they may have looked more at the lower area of the screen containing the objects on the arena wall. Indeed, when vertical gaze was measured as a proportion of total gaze (Figure 3.11), the percentage of gaze above the horizon was significantly greater in the Place maze (*M* = 67%, *SEM* = 5%) than in the Cue maze (*M* = 38%, *SEM* = 4%), $t(36) = 6.73$, $p < .001$, $d = 1.08$.

Acquisition of vertical gaze position. When gaze position was averaged trial by trial and compared for the two mazes, a clear separation in vertical gaze position was

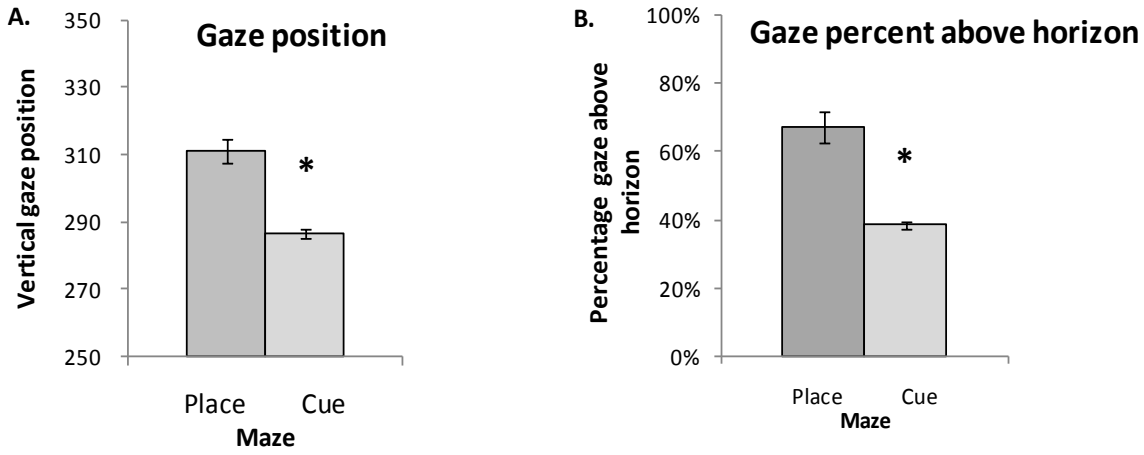


Figure 3.11. Comparing vertical gaze position in the Place and Cue mazes. **A.** The position of gaze was significantly higher in the Place maze than in the Cue maze on Trials 2 to 10. **B.** The percentage of trial gaze above the horizon was significantly higher in the Place maze than in the Cue maze on Trials 2 to 10. Bars indicate standard error of the mean.

observed between the Place and Cue mazes (Figure 3.12) such that by Trial 3 participants looked above the horizon in the Place maze and below the horizon in the Cue maze. After Trial 3 this separation of gaze position around the horizon was observed across all subsequent trials (4 to 10). Participants tended to look below the horizon on the first 'search' trial but thereafter began to direct their gaze gradually upward.

A comparison of change in gaze position from Trial 1 to Trial 3 showed that participants looked up proportionately more often in Trial 3 than in Trial 1 and that this effect was stronger in the Place maze than in the Cue maze (Figure 3.13). This effect was examined for those participants who received the mazes (Place or Cue) first and therefore had not had any prior experience with the maze tasks. A repeated measures ANOVA with two factors, maze type (Place vs. Cue) and trial order 1 (Trial 1 vs. Trial 3 of first maze presentation) was conducted for the dependent variable, percentage of trial gaze

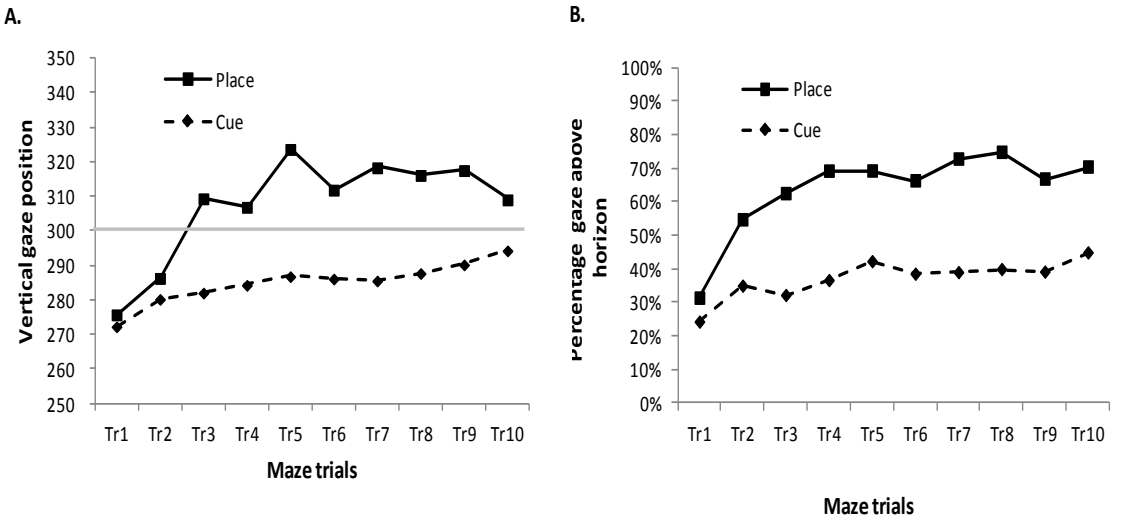


Figure 3.12. Vertical gaze trial by trial in Place and Cue mazes. In both mazes vertical gaze position **(A)** was low (below the horizon) on the first trial. By Trial 3 gaze position was above the horizon in the Place maze but remained below the horizon in the Cue maze. The grey line indicates the horizon. In both mazes percentage of vertical gaze above the horizon **(B)** was small (approximately 30% or less) on the first trial. Thereafter, gaze position gradually increased but to a much greater degree in the Place maze than in the Cue maze.

above the horizon. There was a significant main effect of trial order such that, overall, participants looked above the horizon more often in Trial 3 than in Trial 1, $F(1,35) = 13.54$, $p < .001$, $r = .53$. Most importantly, there was a significant interaction between maze type and trial order such that the change in gaze position from Trial 1 to Trial 3 differed for the two mazes $F(1,35) = 4.44$, $p = .04$, $r = .36$. In the Place maze there was a sharp increase in gaze above the horizon from Trial 1 to Trial 3 whereas in the Cue maze the proportionate increase in vertical gaze was less pronounced. These changes in gaze position from Trial 1 to Trial 3 suggest that during this interval participants learned

where to look (either above or below the horizon) for useful stimuli in each maze environment. Visual inspection of the data revealed that when participants encountered their second maze task (either Place or Cue) the pattern of results was similar to those for the first maze task (Figure 3.13). Gaze was first directed down and then rose by the third

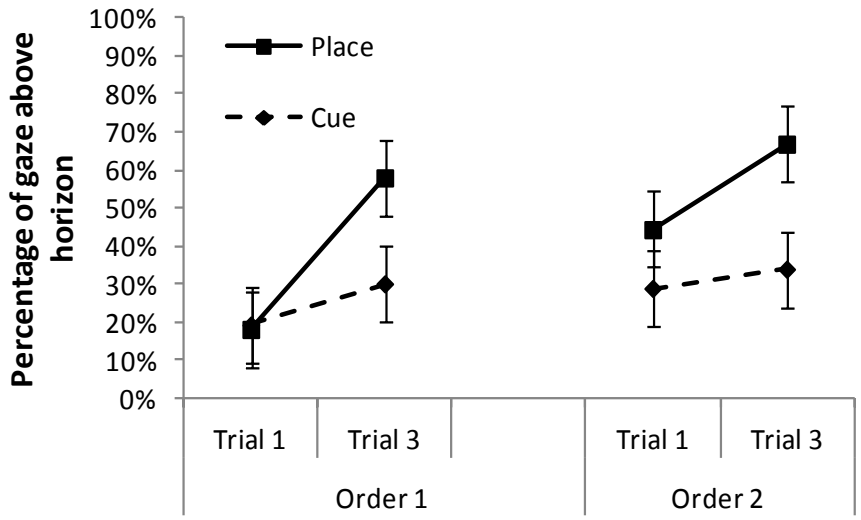


Figure 3.13. Vertical gaze position in Place and Cue mazes by order of maze presentation. Order 1 refers to the first presentation of the mazes (either Place or Cue). Order 2 refers to the presentation of the second maze, either the Cue maze (for the place-first group) or the Place maze (for the cue-first group). Participants looked up more in Trial 3 than in Trial 1. Bars indicate standard error of the mean.

trial, with gaze rising above the horizon in the Place maze and remaining below the horizon in the Cue maze. However, gaze position on Trial 1 was slightly higher in the second maze, suggesting that there was a small effect of experience.

Individual vertical gaze position. In Trials 2 to 10, in both Place and Cue mazes, the majority of participants looked up in the Place maze (78%) and down in Cue maze (68%). When maze order was taken into account these proportions did not change significantly (data not shown) indicating that most participants responded differently to

the two different maze environments rather than continuing to look in the direction they had done in a previous maze. In other words, the vertical gaze position of most participants was affected by changes to the available environmental stimuli.

Combining Horizontal and Vertical Gaze Positions

During early orientation participants looked in very different places on the screen display depending on whether they were navigating in the Place maze or the Cue maze. Heat maps of averaged gaze position data were created in order to qualitatively show gaze position (both vertical and horizontal) during the first second of invisible platform Trials 2 to 10 (Figure 3.14). Regions where the number of gaze position coordinates was more concentrated indicated areas of the screen that were looked at most frequently. In the Place maze, participants looked more at the center of the display and in the region above the horizon. In the Cue maze, participants looked more frequently below the horizon and had gaze position coordinates concentrated on three regions of the screen that corresponded to the locations of the three objects that were always visible from the start position of each trial. These qualitative effects were observed regardless of the order of presentation of the mazes.

Horizontal gaze position. Figure 3.15 shows the frequency distributions (in 5-pixel bins) of both vertical and horizontal gaze positions in Trials 2 to 10 in the Place and Cue mazes. The vertical distributions confirm that participant gaze was proportionately higher in the Place maze than in the Cue maze and that in the Cue maze, participants tended to focus their gaze around and just below the horizon. The horizontal distributions also illustrate differences in looking in the Place maze when compared to the Cue maze. In the Place maze, gaze tended to be central whereas in the Cue maze it was distributed

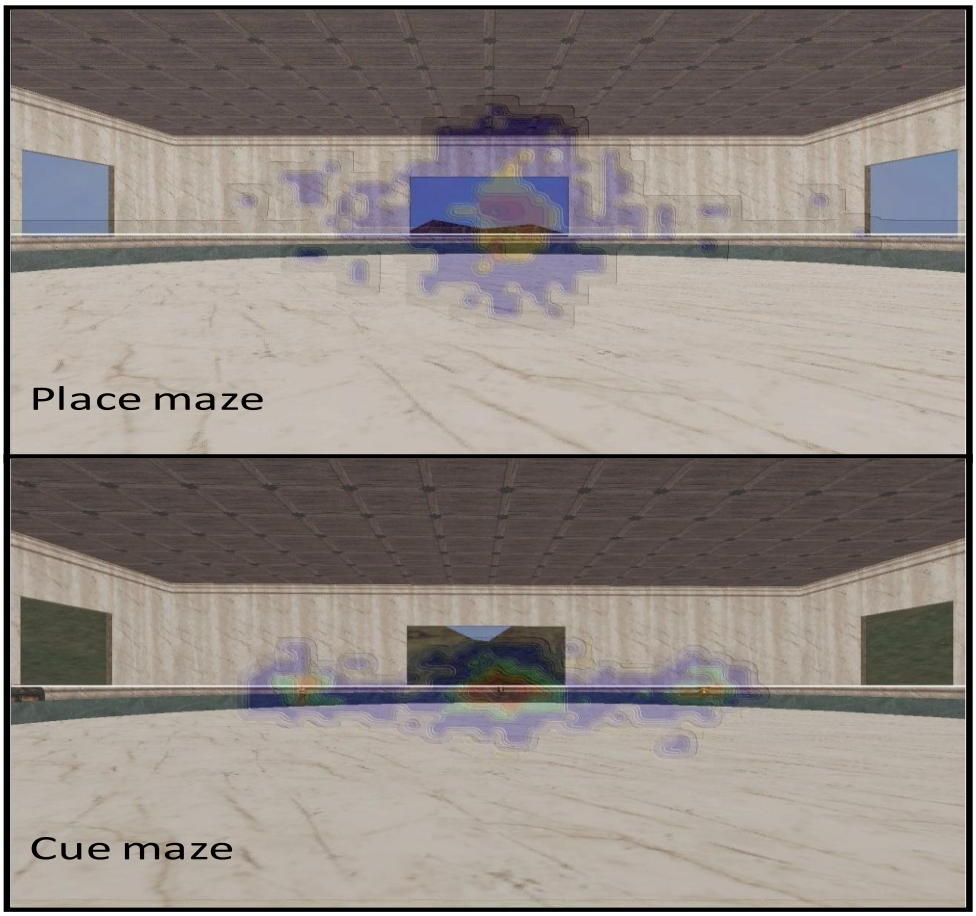


Figure 3.14. Heat maps of vertical gaze position in the Place and Cue mazes. In the Place maze participant gaze was directed more frequently above the horizon. In the Cue maze participant gaze was directed more below the horizon and at the objects on the arena wall. The white line represents the vertical horizon.

more broadly across the display. The Place maze distribution has one distinct central peak whereas the Cue maze distribution contains three distinct peaks corresponding roughly to the horizontal locations of the objects on the arena wall (Figure 3.15). When central ('on-center') gaze position on Trials 2 to 10 was compared (Figure 3.16) for the two mazes there was a significant difference, with looking in the Place maze (M = 69%, SEM = 2%) being more central than looking in the Cue maze (M = 48%, SEM = 2%), $t(36) = 7.77$, $p < .001$, $d = 1.67$. This difference in horizontal gaze position along with the locations of

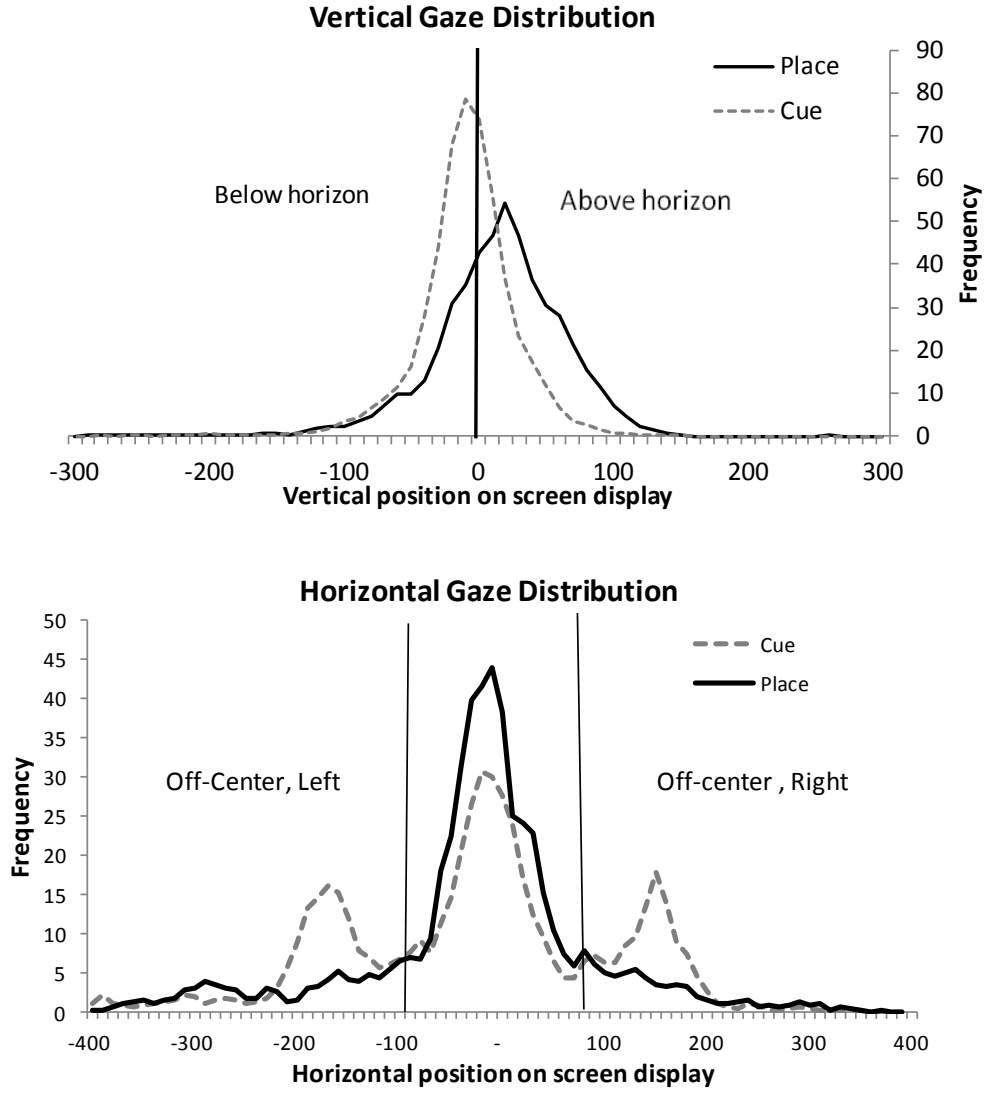


Figure 3.15. Frequency histograms of vertical and horizontal gaze (in 5-pixel bins). A higher proportion (area under curve) of vertical gaze is directed above the horizon in the Place maze than in the Cue maze. Horizontal gaze is proportionately more central in the Place maze and more distributed in the Cue maze. For the vertical gaze distribution the horizon is indicated by the vertical line at '0'. For the horizontal gaze distribution the vertical lines distinguish regions of 'on-center' and 'off-center' gaze.

peaks in the horizontal gaze distributions suggests that participants looked left and right toward the objects when orienting in the Cue maze but oriented by gazing more centrally in the Place maze where there were no objects.

Analyzing regions of interest. To investigate the relative importance of

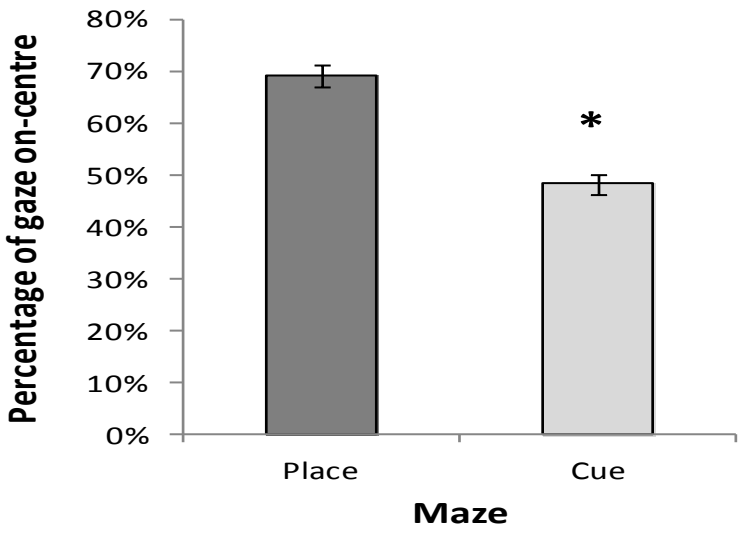


Figure 3.16. Horizontal gaze position in the Place and Cue mazes. In the Place maze looking was significantly more central than in the Cue maze. Bars indicate standard error of the mean.

horizontal and vertical gaze positions a preliminary 'region of interest' analysis was conducted. Frequency data (percentage of gaze) from the 4 regions was entered into a 2 x 2 x 2 repeated measures ANOVA with 3 factors: 1) Maze (Place or Cue), 2) Vertical gaze position (above or below), 3) Horizontal gaze position (centre or off-centre). Figure 3.17 illustrates the proportion of gaze in the four regions for both Place and Cue mazes. As expected participants looked up more in the Place maze than in the Cue maze and looked more centrally in the Place maze than in the Cue maze. There were significant interactions of maze type with both vertical gaze position, $F(1,36) = 81.02$, $p < .001$, and horizontal gaze position, $F(1,36) = 38.36$, $p < .001$. More importantly, the pattern of gaze in the Place maze was significantly different from the pattern in the Cue maze when vertical and horizontal gaze positions were combined. There was a significant 3-way interaction of maze type (Place or Cue) with vertical (above or below) and horizontal (centre or off-centre) gaze positions in the regions of interest, $F(1,36) = 16.05$, $p < .001$.

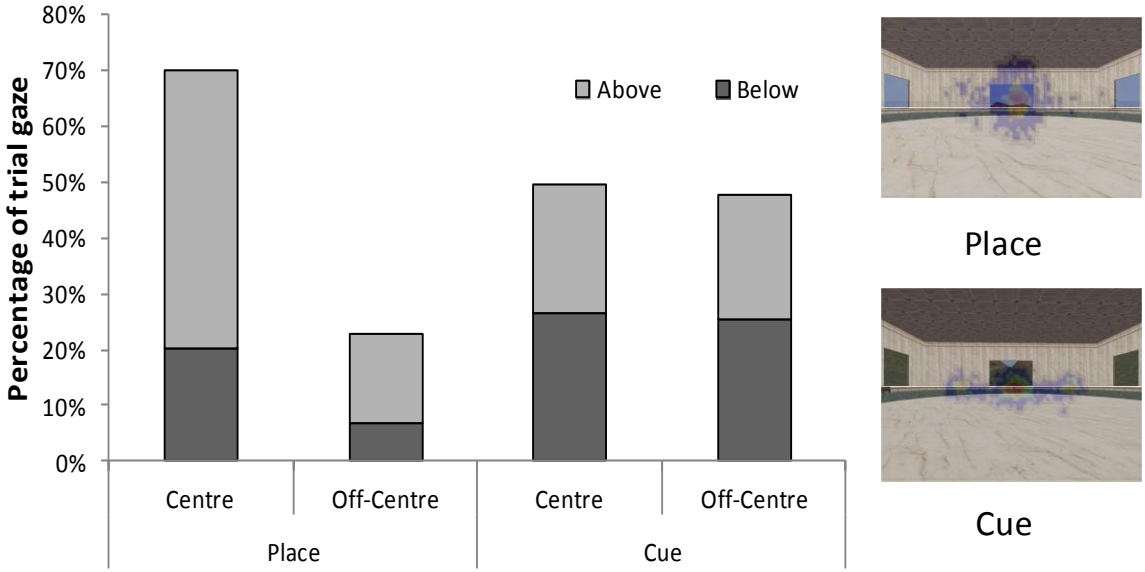


Figure 3.17. Combining vertical and horizontal gaze positions in the Place and Cue mazes. In the Place maze looking was central and above the horizon whereas in the Cue maze looking was distributed more evenly around both the center of the display and the vertical horizon. Inset heat maps illustrate that in each maze participants were looking in regions where useful stimuli were located.

During orientation in the Place maze participants directed most of their gaze (about 70%) in the center of the screen display and further directed 70% of this central gaze above the horizon. During orientation in the Cue maze participants directed only 50% of their gaze toward the center of the screen display with only 40% of this gaze being directed above the horizon. Further, in the Cue maze proportion of gaze in the on-center and off-center regions of the display was roughly equivalent. In the Cue maze, early orientation gaze positions tended to be evenly distributed both around the horizon and across the screen display. These findings suggest that the combination of vertical and horizontal gaze positions best illustrates the differences in looking during early orientation in the Place and Cue mazes (Figure 3.17).

Gaze Position and Navigational Performance

There were no significant correlations between vertical gaze position and the navigation performance variables (distance traveled and probe) in either of the two mazes. In the Place maze there was also no correlation between vertical gaze position (percent trial gaze above the horizon) and latency to the platform. However in the Cue maze there was a significant correlation between vertical gaze position and latency to the platform in the Cue maze, $r = .39$, $p = .02$ indicating that longer latencies to the platform were associated with more upward gaze. In the Cue maze upward gaze would not provide the participant with the cues necessary to solve the task and could explain this correlation. As a caveat it should be noted that a relatively large number of bivariate correlations were conducted for this study and consequently the correlations reported here are tentative due to the possibility of experiment-wise error.

Ancillary Tasks

The majority of participants demonstrated that they understood the three-dimensional nature of the virtual environment and were able to make a cognitive map. Scores on the WTWT were good overall, with 95% of participants indicating that the water was either beside or behind them from their vantage point in the virtual space. Similarly, participants were able to reconstruct the room using pictures. Scores on the RRT were good, with 86% of participants having scores of either 3 or 4, suggesting that they were aware of the spatial layout of the room and the position of the platform. Only three participants were unable to complete this task. There was no effect of maze order on scores in the WTWT or the RRT.

Computer Game Experience

There was no correlation between computer gaming experience and most of the navigation variables (distance travelled, probe trial, DTS trial). However, there were significant correlations of computer gaming experience with latency in the Place and Cue mazes (Place maze, $r = -.43$, $p = .01$; Cue maze, $r = -.39$, $p = .02$). These correlations were negative suggesting that limited gaming experience was related to longer latencies (i.e., a performance deficit) in both mazes. The large number of correlations again makes this finding tentative. There was no correlation between computer gaming experience and vertical or horizontal gaze positions in either the Place maze or the Cue maze.

Discussion

Navigation behaviour was generally good in all maze conditions. When participants had to travel to a visible platform they were able to do so quickly and directly and they also navigated well in both the Place and Cue mazes. Moreover, participants demonstrated good knowledge of the platform location in both mazes, spending a significant proportion of trial time searching for the platform in the correct quadrant of the arena on probe trials. They also demonstrated good knowledge of the platform location on the DTS trial. Participants from both sources (community and student) showed very similar navigation performance.

There were differences in gaze position when participants were orienting in the Place and Cue mazes. When measured during the first second of trials, average gaze position was consistently higher in the Place maze than in the Cue maze. In a trial by trial analysis for Trials 2 to 10, average vertical gaze position was higher in the Place maze than in the Cue maze and the proportion of gaze above the vertical (horizon) and in the

centre of the display were both significantly greater in the Place maze than in the Cue maze. Conversely, gaze position in the Cue maze tended to be just below the horizon and more distributed across the width of the display. A combined analysis of both vertical and horizontal gaze positions revealed that in the Place maze participants tended to look both centrally and above the horizon whereas in the Cue maze they looked across the display and in the areas around or just below the horizon where the objects were located. In all gaze position analyses, participants from both sources (community and student) showed very similar patterns of gaze.

The ability of participants to navigate in the Place and Cue mazes was as expected for a healthy and relatively young sample group. Participants navigated quickly and directly on visible platform trials as well as in both mazes. As expected they were also were slightly faster at finding the platform in the Cue maze than in the Place maze. Presumably this was because in the Cue maze the platform was always marked by the presence of the cue object (the golden urn) whereas in the Place maze this was not the case. Overall, the latencies to find the platform in the Place maze were slightly longer than in previous studies using the current vMWM paradigm (Livingstone-Lee et al., 2011; Mueller et al., 2008). However both the distance travelled to the platform and participant knowledge on probe trials was consistent with past findings. The reasons for the slightly longer latencies are not known but may reflect hesitancy due to the nature of the testing situation. Unlike earlier studies, participants were having their EEG recorded in addition to using a chin rest and a joystick. Wearing an EEG cap requires that participants sit relatively still and this may have caused a slight hesitation in their use of the joystick. But given that most navigation results were consistent with past findings

participants were deemed to have good navigation performance.

Good navigational performance was also indicated by the acquisition curves for the latency and distance variables. For both variables and in both mazes, performance improved across trials and reached asymptote by about the 5th or 6th trial. Participants learned the location of the platform and got better at finding it on successive trials. These results were consistent with those of previous studies using the current vMWM (S. A. Livingstone & Skelton, 2007; Ross, Skelton, & Mueller, 2006), and also with findings from other laboratories using vMWM paradigms (e.g., Astur et al., 2004; Cornwell et al., 2010; Hamilton, Driscoll, & Sutherland, 2002; Hanlon et al., 2006). That is, most participants tended to travel to the maze platform quickly and directly and improved their latency and distance scores across trials.

The current gaze position results confirm those of a recent study examining the utility of the current eye tracking method (Livingstone-Lee et al., 2011). In both studies, horizontal and vertical gaze position during early orientation on trials was a good indicator of allocentric vs. egocentric cognitive strategy. Participants looked in different regions of the virtual environment display depending upon which maze they were navigating. Measures of vertical gaze position showed that overall participants tended to look up more in the region above the horizon in the Place maze whereas in the Cue maze they looked around or just below the horizon. This is important because the stimuli (landscapes) necessary for successful navigation in the Place maze were always located above the horizon whereas the stimuli (objects) necessary for successful navigation in the Cue maze were always located just below the horizon. Similarly, the horizontal gaze position measure indicated the utilization of different strategies in the Place and Cue

mazes. In the Place maze participants tended to look in the centre of the display whereas in the Cue maze participant gaze position was more evenly distributed across the display. But most importantly, in the Cue maze the horizontal gaze position measure showed that participants looked tri-modally in the horizontal vicinity of the three objects that were visible from the start position on every trial. Overall, it was inferred that participant gaze position was an indicator of the strategy being engaged and that participants were utilizing different strategies based on the demands of the navigation tasks. In other words, gaze position indicated whether the participants were using an allocentric or an egocentric cognitive strategy to navigate.

Gaze position was also a good indicator of strategy acquisition in the case where participants were navigating in the first maze (either Place or Cue) presented to them, i.e., without benefit of prior experience in either maze. The change in vertical gaze position from Trial 1 to Trial 3 in both Place and Cue mazes suggests that participants acquired the strategies necessary to solve these tasks early on in behavioural trials. Based on gaze position in the first mazes participants learned, it was clear that in both mazes, participants looked well below the horizon on the first trial, but by the second or third trial they were directing their gaze toward different stimuli depending upon which maze they were navigating. By the third trial in the Place maze participants looked in the upper region of the display which contained the distal room and landscape stimuli and continued to do so for the remainder of the trials. The inference was that by the third Place maze trial most participants acquired an allocentric navigation strategy. A tendency toward the same effect was observed in the Cue maze, but of course, in that maze, the most important environmental stimuli were lower, being situated below the horizon. It

was inferred that when participants were looking in the vicinity of the objects they had acquired an egocentric strategy.

It is important to note that the current experiment was a group study and therefore the effects reported cannot be extended to the measurement of individual performance differences. The gaze position measures were reliable in 75% of individual cases but less consistent for 25% of participants. Thus the effect of the environment on gaze position is significant but not the only factor driving gaze. Further research will be needed to determine the nature of other possible factors but for present the results indicate that the structure and features of the environment are strong determinants of gaze position.

The acquisition data also suggest that, at least in virtual environments, once a strategy is used, it tends to be adhered to until a new navigational task presents itself. Once participants had acquired a strategy (i.e., by Trial 3 in either the Place or Cue maze) they maintained a similar average gaze position on all successive trials. In the Place maze this gaze position was always above the horizon and in the Cue maze it was always below the horizon. This suggests that once participants have decided which stimuli are most useful for navigating in the mazes, they continue to orient toward these stimuli on successive trials. Iaria, Petrides, Dagher, Pike & Bohbot (2003) demonstrated by a combination of behaviour and verbal report that participants spontaneously use one of two strategies (“spatial” or “non-spatial”) in a virtual radial arm maze that could be solved using either strategy. In their experiment, participants sometimes switched from using a spatial strategy to a non-spatial strategy. There was no evidence of trial by trial strategy switching (allocentric to egocentric) in the current study, perhaps because the Place maze was specifically designed to elicit an allocentric strategy.

Present findings indicate that the current combined eye tracking and behavioural methodology is relatively insensitive to the amount of computer gaming experience. The gaming experience score included measures of experience with 2-dimensional and 3-dimensional game environments as well as the game joystick. Although the overall score was negatively correlated with latency it was not correlated with distance travelled or any other navigation measures. Further, gaming was not a factor in gaze position.

The current gaze position results not only replicate previous results (Livingstone-Lee et al., 2011) with a new and larger sample, but also extend them by showing that the method is useful for studying community-based populations as well as young, university students. The current study also confirmed that both vertical and horizontal gaze positions are able to indicate strategy when the navigation environment is designed to elicit either an allocentric or an egocentric strategy. Further the combination of the two gaze types also indicates which strategy participants were using. This combined gaze position analysis that incorporates both vertical and horizontal measures may be better at indicating strategy than either type of gaze on its own. This represents an advance over the previous study because it is now possible to examine regions of interest during orientation in virtual navigation environments.

The present study represents an advance over past work by other authors who have used eye movements to study human spatial navigation. Researchers have previously used gaze position to confirm verbal report after navigation in a virtual environment (Spiers & Maguire, 2006, 2007). This approach required participants to report on which environmental stimuli they were attending to at particular points during a spatial navigation task, in this case while driving a taxi in a virtual city. Interestingly, the eye

movements (saccades toward the relevant stimuli) corroborated verbal report showing that verbal report during navigation converges with where participants look for important environmental information. This result is in agreement with the current finding that important stimuli are looked at more frequently than less important ones. However, there was no analysis of the types of stimuli that were used or any attempt to relate the stimuli to particular navigational strategies.

Jin, Gillner & Mallot (2004) demonstrated that landmarks are learned/acquired, i.e., that the navigator decides which environmental stimuli are important for navigation under the current circumstances. In their study, participants fixated more on stimuli that were relevant for navigating in their virtual environment. This is consistent with the current results showing that participant gaze tends to be allocated in areas of the display that contain the relevant stimuli for solving the current maze tasks. However, Jin, Gillner & Mallot (2004) used a route making task and did not examine the type of strategy participants may have been utilizing. The current study extended this finding to include the analysis of gaze position as an indicator of strategy, either allocentric or egocentric.

In a study of navigational strategy, Gramann, Sharkawy & Deubel (2009) tracked eye movements to differentiate strategies utilized during navigation in a virtual tunnel. Eye movements did not differ depending upon whether participants reported using an egocentric or an allocentric strategy and so could not be used to indicate which strategy was being used at any point in time. However, due to the nature of the question the authors were addressing, their navigation environment was very sparse with the main stimuli being observed changes in the angle of the tunnel corridor as the participant turned corners. Thus eye movements may have been limited by the lack of available

stimuli for navigation. It is also possible that the eye movements indicated a particular egocentric strategy type, i.e., a response strategy that participants used in order to turn corners in the virtual maze while avoiding the tunnel wall. In this case eye movements might not differ depending on the higher order cognitive strategy being employed. The authors concluded that cognitions rather than perceptions dictate navigation strategy. While the current study suggests that eye movements do reflect 'top-down' cognitive processing, present results show that gaze position is also able to indicate the type of cognitive processing (or strategy) that is being utilized based on the type of environment encountered.

The current results are similar to and extend those of two recent studies of gender differences in navigation. A collaboration (Mueller et al., 2008) employing the Place maze and the current eye tracking method, found that participants (male and female university students) looked above the horizon 59% of the time in Place maze trials and had gaze position acquisition curves similar to those found in the current study. Further these participants looked above the horizon only 24% of the time on visible platform trials, suggesting that they adopted differing strategies depending on the presence of differing environmental features. However, the focus of that study was on gender differences in allocentric navigation rather than navigational strategy and accordingly, it did not make extensive efforts to contrast gaze position in different environments. A more recent study of gender differences in navigation (Andersen et al., 2011, in press) employed verbal report to establish that participants spontaneously use either a spatial or a non-spatial strategy to solve a virtual radial arm maze (vRAM) task. Overall, participant gaze was modulated by the number of landmarks present in the environment

such that more time was spent looking at landmarks when more landmarks were made available. However, the virtual environments used in this study were not designed to differentiate egocentric from allocentric strategy use because the focus was on gender differences in related to landmark utilization. The current study extended the findings from these gender studies by directly comparing performance in two mazes biased toward either an egocentric or allocentric strategy and by developing a design where verbal report is not necessary. This latter point is important because some participants are unable to verbalize which features of the virtual environment were utilized (unpublished data), and verbal reports are not always consistent with behaviours observed. Incidentally, the current study screened for gender differences in navigational behaviour and gaze position but these differences did not appear to be sufficiently large or interesting to be worth pursuing.

In a study quite similar to the current investigation, Hamilton, Johnson, Redhead & Verney (2009) measured the eye movements of participants while they navigated in a vMWM. The authors identified two types of navigators, 'direct' navigators who were able to navigate directly to the platform on successive trials and 'indirect' navigators who took longer paths. Direct navigators tended to look at distal navigational key stimuli early in the trial (within the first 3s) whereas indirect navigators tended not to look at distal stimuli until the middle of the trial. The authors reported that in the latter part of trials direct navigators tended to preferentially focus their attention on distal stimuli in the region of the environment where the platform was located more than did indirect navigators. These results validate the methodology of measuring gaze position early in the trial. The current study furthers these results specifically by designing virtual

navigation environments to elicit either allocentric or egocentric strategies and then directly comparing gaze positions in these environments.

There were a number of important technical solutions validated by the current study and a few limitations were noted. The equipment was inexpensive (the eye tracker cost less than $2,000) and analysis was relatively simple (mainly using short MATLAB® scripts, Excel® and SPSS®) once the data were screened and artefacts removed. There are currently two similar studies underway using slightly more sophisticated equipment and the methodology continues to give consistent results. Technical support is available to other labs who may wish to apply this method of gaze position analysis. It should be noted, however, that some problems were encountered. The first was that several participants' eye movements could not be tracked. The reasons for this are varied. First, differences in eye shape, eye musculature and/or low iris to sclera contrast may have contributed to problems with the calibration process. Second, the camera sometimes 'lost' or was unable to follow the eye movements especially if the participant frequently looked away from or near to the edge of the display. However, other studies (e.g., Spiers & Maguire, 2006) also report that a relatively high proportion of participants could not have their eye movements tracked. This proportion may be higher for more complex and dynamic virtual environment tasks and lower for tasks that require participants to make yes/no type responses to static displays (e.g., Butler, Lawrence, Eskes, & Klein, 2009) or that are concerned mainly with optic flow (e.g., Gramann et al., 2005; Gramman et al., 2009).

The current study makes both methodological and theoretical contributions to navigation research. Methodologically, it confirms the effectiveness of combining eye

tracking with a behavioural paradigm that allows navigational strategies (allocentric or egocentric) to be identified without reliance on verbal or self-report. Although verbal report can be a useful correlate to navigation performance or associated brain activity more objective methods are desirable because participants' verbal reports are not always consistent with their navigational movements (unpublished data) and because verbal report does not always accurately reflect cognitive processes (Nisbett & Wilson, 1977).

Gaze position measures of navigation strategy may also contribute to a better understanding of which strategies participants are using independently of the task they are engaged in. This would enable researchers to differentiate navigators who spontaneously select different strategy types to solve the same navigation task. In the current study a visual inspection of individual data revealed that a few participants (n = 5) oriented using an egocentric rather than an allocentric strategy (as expected) in the Place maze. These participants looked below the horizon and at the floor while they were orienting, suggesting that they spontaneously adopted an egocentric frame of reference leading to the utilization of an egocentric strategy (Klatzky, Loomis, Beall, Chance, & Golledge, 1998). Although this is less likely to be a problem in cases where the navigation task is heavily biased toward an allocentric response, some participants may still attempt to utilize "incorrect" or less efficient strategies. In group behavioural studies with large numbers of participants this factor may not weigh very heavily on results. However, the question of strategy selection is methodologically important for navigation studies that employ brain imaging. If humans have different brain networks associated with the utilization of different strategies, then imaging studies could benefit from knowledge of which strategy is being utilized, irrespective of navigation task type.

Typically, imaging studies have fewer participants so there is good reason to identify those who may not be using the anticipated strategy and therefore may not be activating the same brain areas as those who do use the anticipated strategy. Such knowledge would reduce error in imaging results and could also inform task design. For example, eye tracking has been successfully combined with EEG, to mark periods of close attention to virtual environment stimuli that can then be correlated with brain activity (Zeman, P., personal communication, May 2011). This approach allows for the discovery of brain activities associated with the strategies people are using, rather than the task they are engaged in. This becomes particularly important when navigation tasks are more ambiguous, that is when participants are free to use either an egocentric or an allocentric strategy as they would in real world navigation situations. In this case, knowledge of the strategy being utilized is essential for interpreting the associated brain activity.

Another advantage to the described method is that it can be applied to the study of navigation deficits both in and out of the imaging scanner. Such deficits have been noted in a number of psychiatric conditions as well as after acquired or traumatic brain injury (E. D. Bigler, 2001; Grusser & Landis, 1991; Paterson & Zangwill, 1945; Tate & Bigler, 2000). Specifically, research has shown that damage to the brain may result in difficulties with tasks designed to elicit an allocentric strategy (Goodrich-Hunsaker, Livingstone, Skelton, & Hopkins, 2010; Livingstone-Lee et al., 2011). Once navigational deficits can be linked to specific anatomical anomalies, gaze position analysis may provide a useful measure of which strategy patients are using to solve everyday navigation tasks.

The current study provides several contributions to theory, specifically to the understanding of human navigation systems and resulting navigational strategies. It

provides converging evidence for the presence of at least two cognitive navigation systems in the human brain by showing that two types of orientation gaze position can be differentiated at the start of navigation trials. This is consistent with cognitive mapping theory (O'Keefe & Nadel, 1978) which suggests that animals engage in separate locale (mapping) and taxon (guidance) behaviours depending on task requirements. The current findings further converge with those from animal studies suggesting that there are at least two memory systems associated with animal navigation behaviour (Poldrack & Packard, 2003; White & McDonald, 2002) and with those from imaging studies suggesting that the same two systems exist in humans (Doeller, King, & Burgess, 2008; Hartley, Maguire, Spiers, & Burgess, 2003).

The current findings also provide evidence for the theory that cognitive navigational strategies are acquired based on a combination of the navigation environment and individual differences in navigational ability (for review, see Gluck & Fitting, 2003). The gaze position of participants on both allocentric and egocentric tasks changed as more trials were completed, presumably because the majority of participants learned which stimuli were most useful to them. This is important because some studies have suggested that strategy selection is primarily spontaneous especially when the environment is not biased toward one strategy or another. A possible implication of this is that people are innately either allocentric or egocentric navigators. However, another interpretation is that strategies are acquired over time and that the preferred strategy of a navigator depends upon the nature of the environment tasks he/she is most frequently exposed to in combination with the navigational task at hand. The current findings converge with this idea by showing that the strategies people employ may vary from time

to time and depend upon navigational circumstances (for example tasks biased toward the use of either and allocentric or egocentric strategy).As a result, people may prefer one strategy or another, but it is equally likely that the ability of most people to stay oriented to their environment depends upon the ability to flexibly switch strategies with changing navigational circumstances (Etchamendy & Bohbot, 2007; Gluck & Fitting, 2003; Iaria et al., 2003).

The current study also provides evidence for the theory that both bottom-up (sensory/perceptual) and top-down (cognitive) processing contributes to eye movements within the context of a single task. Early work with eye movement tracking was concerned mainly with top-down effects but the bulk of recent work in the field has involved the examination of bottom-up or stimulus driven effects (for review, see Tatler, 2009). More recently researchers have begun to suggest that both types of processing combine to cause the resulting eye movements (DeAngelus & Pelz, 2009). The current study supports this view by showing that both the nature of the environment and the utilization of a strategy are correlated with gaze position. Eye movements appear to result from sensory and perceptual processing of environmental features together with the cognitions related to strategy selection. Some authors (e.g., Angelaki & Hess, 2004) have argued that head movements might be a better or additional measure of spatial orientation, in part because the head is more easily tracked in three dimensions. However, head movement may only be a means of moving the eyes to particular features of the environment thus allowing the appropriate eye movements to occur.

Future applications of the method employed here could include the examination of any time window of interest during a navigation task and therefore could include either

trial-by-trial or within-trial analyses. The method also allows for manipulations of the environmental stimuli for comparison of gaze positions during these different time windows. But one of the most important aspects of this study is that it provides a crucial baseline to study whether experience affects the adoption and use of spatial strategies, including spontaneous selection and switching. Without knowing what people do under conditions where it is clear what strategy is being utilized, it is not possible to interpret gaze behaviour under ambiguous circumstances. This is important because a key goal of navigation research is to ascertain how people utilize environmental information to find their way in real world environments that contain multiple stimuli. Further, this goal must be attained if researchers are to apply eye movement tracking and gaze position analysis to the development of rehabilitation tools. This would allow for the design of purpose built virtual environments for training participants to utilize the stimuli most helpful for navigating in a particular circumstance. Knowledge about where the patient is looking could also be used to provide feedback for this training.

In summary, gaze position analysis is a useful method for distinguishing navigation strategies under different environmental circumstances. Also, its usefulness extends to the community-based population and may therefore be applicable in future studies with brain injury survivors. The construction of the virtual environment is critical to the analysis presented here but more importantly, once the environment is designed the gaze position method allows for analysis in simple or relatively complex environments, as long as appropriate regions of interest can be established. The flexibility of this method thus allows for the analysis of not only strategy use but also the time course of acquisition. Future research using gaze position analysis should be able to identify the

effects of experience on navigational strategy selection. In other words, the method reported here moves researchers closer to answering the question, which strategies do people choose and when do they choose them?

Appendix 3-A
Source Groups

In Experiment 2 the data for two participant source groups was combined in order to increase power to detect the main effect being sought, i.e., effects of experience on navigation performance. The two groups in question were drawn from 1) the Psychology 100 student population at the University of Victoria and, 2) the local community in the city of Victoria, British Columbia. Data from two behavioural conditions (Place maze and Cue maze) were examined for interactions with the origins of the participant samples.

As a reminder, the Place maze task required participants to repeatedly find a hidden platform located in a virtual room with only distal features available for navigation. The location of the platform did not change but participants were required to find it from different starting points in the room. The Cue maze required participants to repeatedly find a hidden platform that was marked by the presence of a local cue/landmark. The location of the platform changed from trial to trial but the platform was always located in front of the same cue/landmark.

Given past research findings (e.g., Livingstone & Skelton, 2007), meaningful differences between the groups would be best indicated by an interaction between group membership and experimental effect. There was some disparity between groups (Table 3-A.1) but the effect sizes were mostly small. The variables tested are listed and described along with their effects in Table 3-A.1. Corresponding figures and statistics are given in the following sections. The variables were selected either because they are conventional measures of navigation performance or because they were found to be key variables in prior eye movement analyses.

Analysis of the data from the two source groups separately showed that the pattern of behaviour and eye movements was similar for student and community participants in both maze conditions (Figures 3-A.1 & 3-A.22; Table 3-A.2). Further, there were no significant interactions of participant origin (student or community) with key navigation and eye movement effects recorded for the Place and Cue mazes. There was some effect of source group on latency in the Cue maze and on vertical gaze position in the Place maze but these effects were small. Community-based participants were significantly slower to find the platform in the Cue maze and had significantly higher gaze position in the Place maze than did students.

Appendix 3-A (continued)
Source Groups

Table 3-A.1.
Summary of variables and their effects for student and community-based group differences.

Variable	Maze x Group interaction? (Table D2)	Group in Maze simple main effect? (Place or Cue)	Student vs. community group difference? (Yes/No)	Large Effect? (Yes/No)
Latency (Fig. D1)	n.s.	Place Cue	No Yes –community slower	No
Distance (Fig. D1)	n.s.	Place Cue	No No	No
Probe (Fig. D1)	n.s.	Place Cue	No No	No
Drop-the-seed (Fig. D1)	n.s.	Place Cue	No No	No
Vertical Gaze Position (Fig. D2)	n.s.	Place Cue	Yes – community higher No	No
Percentage gaze above horizon (Fig. D2)	n.s.	Place Cue	Yes – community higher No	No

n.s. = non-significant

Appendix 3-A (continued)
Source Groups

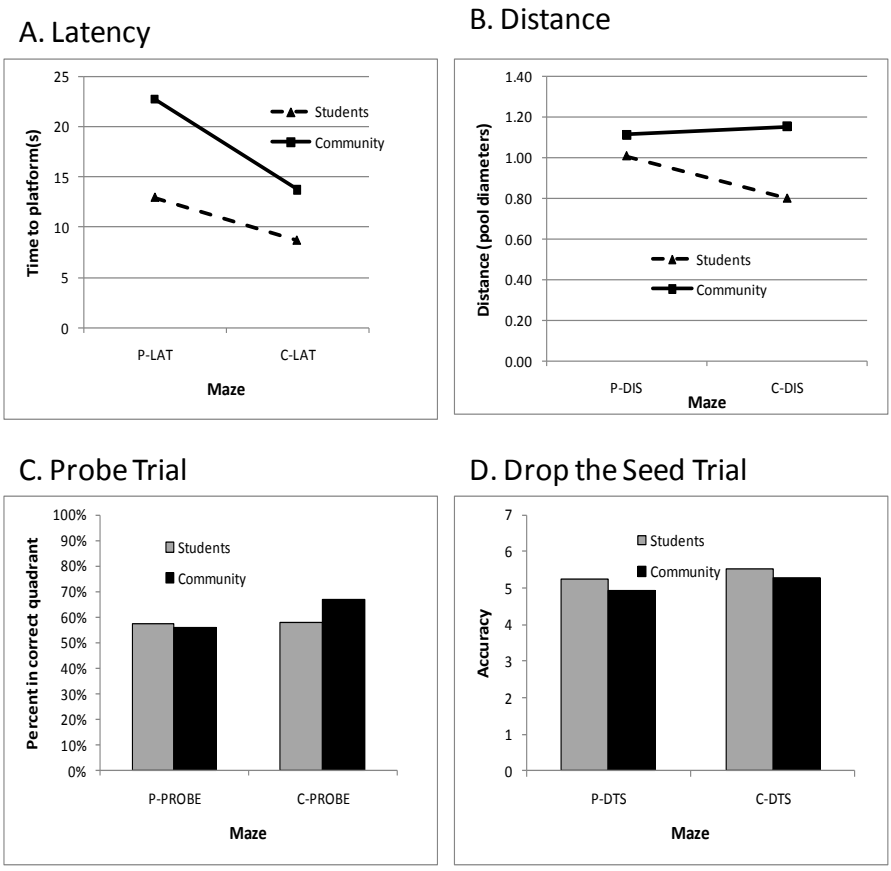


Figure 3-A.1. Comparison of student and community source groups on maze variables. There were no interactions between source group and maze (Place or Cue) for any of the variables. **A**. Students find the platform more quickly than community participants in the Cue Maze. Both student and community participants find the platform more quickly in the Cue Maze than the Place Maze**. B.** There were no differences in distance to the platform in either maze. **C.** Student and community participants were equally knowledgeable about the platform location after completing 10 trials in either maze condition. **D**. Student and community participants were equally accurate in their ability to show (by placing a seed marker) the location of the platform.

Appendix 3-A (continued)
Source Groups

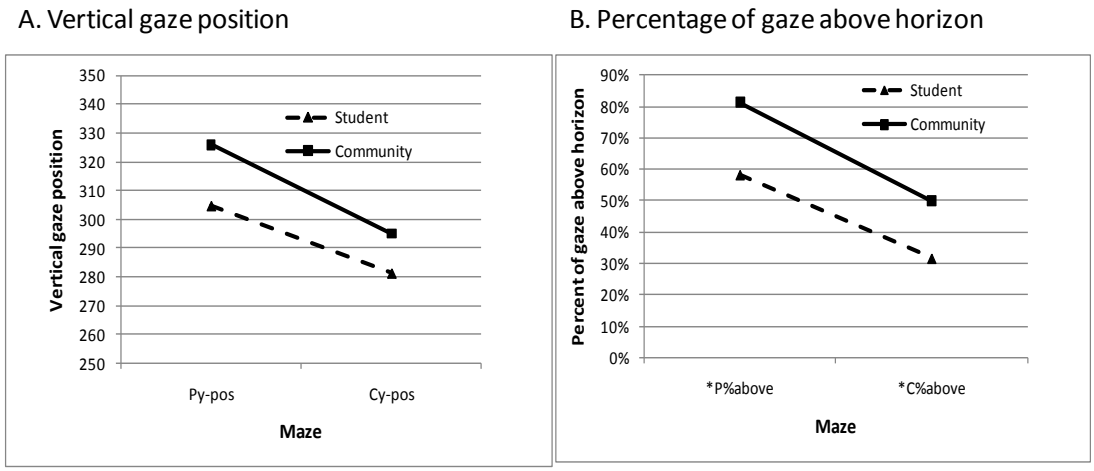


Figure 3-A.2. Comparison of student and community source groups on vertical gaze position variables. There were no interactions between source group and maze (Place or Cue) for the vertical gaze position variables. **A.** Both student and community participants look up more in the Place Maze than in the Cue Maze. Gaze position was slightly higher in the community based group than in the student group. **B.** Both community and student participants had a higher proportion of gaze above the horizon in the Place Maze than in the Cue Maze. The proportion of gaze above the horizon was slightly higher in the community based group than in the student group.

Appendix 3-A (continued)
Source Groups

Table 3-A.2.

Analysis of variance for comparisons of student and community based source groups.

Between subjects				
Effect of Group	F value	Hypothesis df	Error df	P value
Latency	5.74	1	35	.02*
Distance	2.24	1	35	.14
Probe	0.46	1	35	.50
Drop-the-Seed	0.19	1	35	.67
Vertical Gaze position	4.58	1	35	.04
% Gaze Above Horizon	7.39	1	35	.01*
Multivariate statistics				
Effect	F value	Hypothesis df	Error df	P value
Latency: Maze	6.59	1	35	.015*
Latency: Maze x group	0.86	1	35	.36
Distance: Maze	0.34	1	35	.56
Distance: Maze x group	0.74	1	35	.40
Probe: Maze	1.32	1	35	.26
Probe: Maze x group	1.19	1	35	.28
Drop-the-seed: Maze	0.51	1	35	.48
Drop-the-seed: Maze x group	0.01	1	35	.91
Vertical Gaze Position: Maze	39.92	1	35	.00
Vertical Gaze Position: Maze x group	0.78	1	35	.38
% Gaze Above Horizon: Maze	49.67	1	34	.00
% Gaze Above Horizon: Maze x group	0.08	1	34	.78

*significant effect, p<.05

Appendix 3-B
Experiment Protocols

1. <u>Preparation by Experimenters</u>

a. EEG and eye tracking camera setup. Note that technical set-up was provided by Dr. Phil Zeman. EEG results are reported in Dr. Zeman's doctoral dissertation.
b. Preparation of gel syringes, electrode cap, electrodes, surface cleaning (e.g., chin rest).
c. Prepare scripts, run documents, paper tests, clipboard, stopwatch, check mazes, confirm participant number [##,M/F,P/C,X/P/A/C], M=male, F=female, first P=place first, first C=Cue first, X=exploration + visible, P=place, A=dual-strategy (reported in later experiment), C=cue

2. <u>Introduction (in outer lab room)</u>

a. Consent
b. Background information questionnaire
c. Occular dominance test (script below)
   i. *"Extend your arms in front of you with your palms facing away".*
   ii. *"Bring your hands together, forming a small hole by crossing the thumbs and fore-fingers".*
   iii. *" Look at this object (a mechanical object in the laboratory outer room and situated about 15 feet from the participant). With both eyes open, focus on the object as you look through the small hole.*
   iv. *"Close one eye and then the other. When you close one eye, the object will be stationary. When you close the other eye, the object should disappear from the hole or jump to one side".*
   v. *"If the object does not move when you cover one eye, then that eye is dominant. The eye that sees the object and does not move is the dominant eye".*

3. <u>Preparation of Participant</u>

a. Application of electrode cap and electrodes (in outer lab room)
b. Camera calibration (in lab)

4. <u>Eye tracking protocol</u>

(this assumes that game and ET computers have already been turned on)

a. Test for dominant eye (before seating participant in front of camera)
b. Turn on camera [FLYCAP]
c. Seat participant
   i. Adjust chair
   ii. Adjust table/joystick
   iii. Adjust chin rest
d. Participant plays PACMAN game while experimenters set up
e. Start DVD
f. Start eye tracker software [TRACKSTART]
g. Adjust camera
   i. Position tracked (dominant) eye in center of display
   ii. Focus camera
h. Calibrate
   i. Open calibration file
   ii. Participant completes 9 point calibration

   Script: *"You will see a small circle with a letter in it. Please keep your gaze on the circle and repeat the name of the letter out loud. You can mumble the letter so that your jaw doesn't*

Appendix 3-B (continued)
Experiment Protocols

move too much in the chin rest. When the camera is finished calibrating, the circle will move to a new location. This will repeat 9 times at different locations on the screen. Try not to blink when the dot is still. You can blink when the dot is moving."

iii. 'Control L' to start timer
iv. Switch screens to game computer

i. Baseline
  i. Open UnReal map [XX.unr]
  ii. Move tip of pen along horizon (participant tracks this)
  iii. Open baseline file
  iv. Participant tracks ball moving on screen
j. Maze and other tasks (described below)
k. After maze data collected
  i. 'Control T' to stop tracking
  ii. Stop DVD
  iii. Turn off camera
  iv. BACK UP data from ET computer (file types will be provided by Phil)
  v. BACK UP data (dem files) from game computer
  vi. Remove, label and BACK UP (copy) experiment DVD

5. <u>Maze Tasks</u> (X then ABC or CBA, counterbalanced)

X. EXPLORATION + VISIBLE TRIALS UNREAL MAP : X.unr

i) Room Exploration
Exploration of virtual room (practice movement with controller)

ii) Visible Trials
4 Visible Platform Trials

iii) Drop-the-Seed Trial
Single trial with participant explicitly indicating the location of the platform.

A. PLACE TRIALS UNREAL MAP: P.unr

i) Arena Maze Exploration
Exploration of arena without objects.

ii) Invisible Trials
10 invisible platform trials. Platform position stationary.

iii) Probe Trial
Single invisible platform trial with no platform present.

iv) Drop-the-Seed Trial
Single trial with participant explicitly indicating the location of the platform.

B. DUAL-STRATEGY TRIALS **reported in Chapter Four UNREAL MAP: A.unr**

i) Dual-strategy Maze Exploration
Exploration of arena with objects on the wall (steel box is relevant cue).

ii) Invisible Trials, Probe Trial
As for Place Trials.

iii) Differential Drop-the-Seed Trial

Appendix 3-B (continued)
Protocols

Single trial with participant explicitly indicating the location of the platform. Steel box moved to diagonally opposite position on Arena wall. After trial participant is asked if the object moved.

C. CUE TRIALS **UNREAL MAP: Q.unr**

i) Cue Maze Exploration
Exploration of arena with objects on the wall (golden urn is relevant cue).

ii) Invisible Trials, Probe Trial, Drop-the-Seed Trial
As for Place Trials.

6. <u>Other Tasks (in outer lab room)</u>

i) Where's the Water test (in script)
ii) Room Reconstruction Task
iii) Rivermead Test Immediate
iv) Closing questions re: dizziness and fatigue
v) Clock Drawing Task
vi) Bells Test
vii) Rivermead Test Delayed

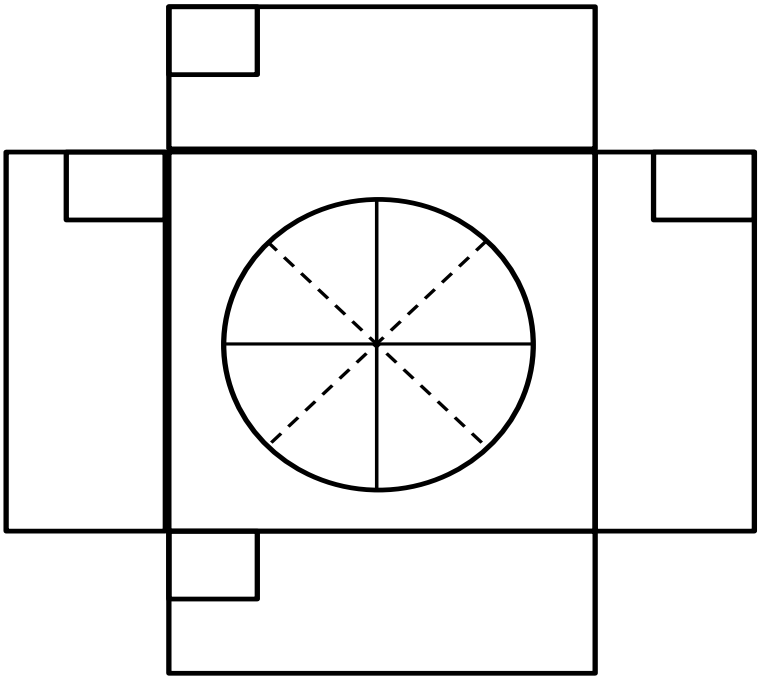
3. Closing

Debriefing and form filling for Psych 100 points **Thank Participant**

Appendix 3-C
Basic Room Reconstruction Task

Room Reconstruction Test Instructions:
Presentation: Lay out the laminated floor of the room and explain that this represents the room and that the circle represents the arena. Give the participant the four laminated walls and then ask, "Based on what you were just doing could you place these walls where you think they were?" Give the participant the laminated green platform and then ask, "Based on the maze with no objects, could you put the green platform where you think it was?"
Recording: On the data sheet record the position of 2 large window and the water. Indicate the placement of the remaining walls, by drawing slopes, the island and the mountains. If you have time, note the order the walls were placed (i.e., which one was placed first) in the little boxes After the participant has placed the platform, place the grid over the arena and use this as a guide to draw the location of the platform on the data sheet.
Scoring:
Walls A: 1 pt if walls adjacent to platform are correct, 1 point for the 2 opposite walls – **A Score: ____**
Walls B: 1 pt if island and mountains are opposite, 1 point if slope walls are correct. **B Score: ____**
Platform: 1 pt if platform in correct hemisphere, 1 pt if in correct quadrant **Score: ____**

A Score + Platform Score = _____ **B Score + Platform Score = _____**



Appendix 3-D
Behavioural Order Effects

Acquisition

Figure 3-D.1 illustrates acquisition curves for the Place and Cue mazes based on order of maze presentation. Visual inspection shows that performance in the visible platform trials was roughly equivalent for both place-first and cue-first conditions.

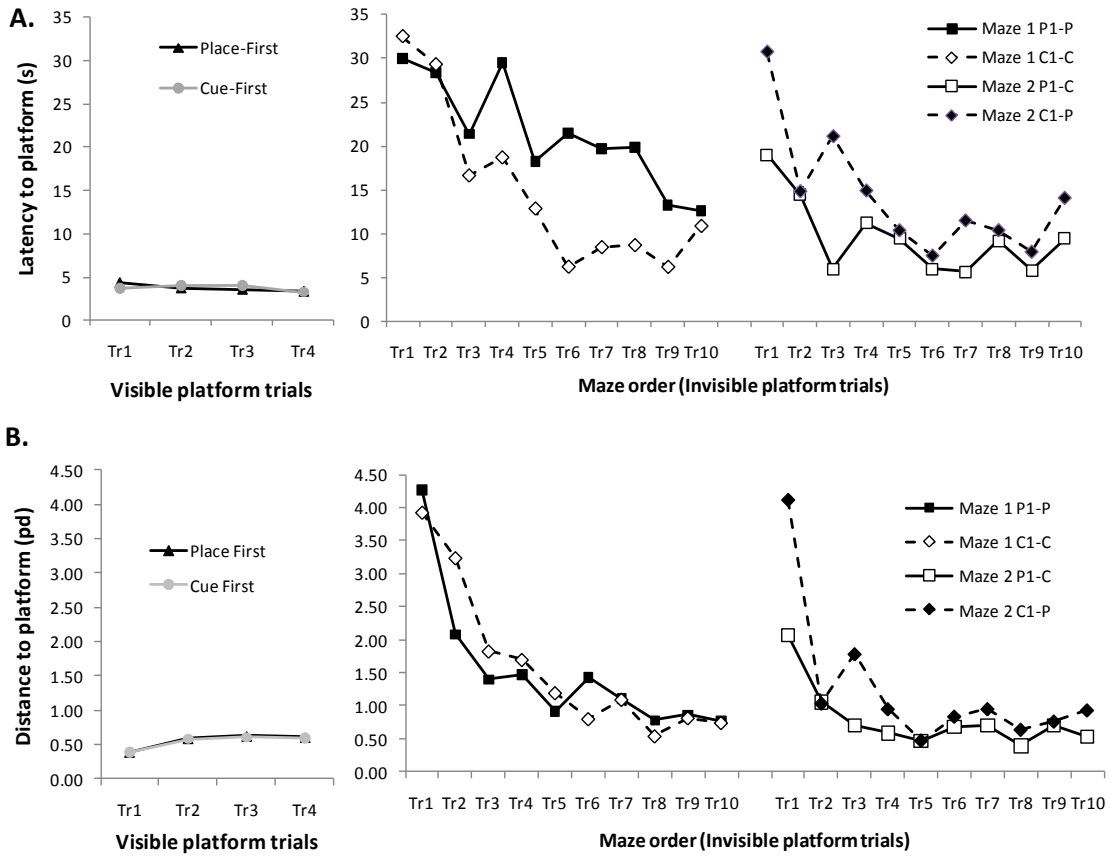


Figure 3-D.1. Trial by trial latency **(A)** and distance **(B)** to the platform in three mazes (Visible platform, Place and Cue) and depending on which maze was completed first(Place or Cue). There were no differences in visible platform trial performance.

Therefore any differences in later navigation performance could not be attributed to differences in the ability to use the game controller or follow task instructions. The acquisition graphs show that when the Cue maze was received second, that is after

Appendix 3-D (continued)
Behavioural Order Effects

participants had first navigated in the Place maze, latencies and distances were initially shorter than when the Cue maze was received first.

Learning was evident on all four sets of invisible platform trials (P1-P = Place maze first, C1-C = Cue maze first, P1-C = Cue maze second, C1-P = Place maze second).

Cue maze Order Effects

To examine order effects we compared performance on four navigation variables (latency, distance, probe and accuracy probe). Order effects were only present for the latency and distance variables in the Cue maze. When performance was compared for Trials 2 to 10 and according to order of presentation, participants who completed the Cue maze first (M = 13.1s , SEM = 1.9) took significantly longer to find the platform than those who completed the Cue maze second (M = 8.6s, SEM = .9), t(23) = 2.07, p = .05, d = .72, equal variance not assumed. To test whether this effect was important to the study we compared performance on both early and late trials (Figure 3-D.1). The noted order effect was only present in early trials (2 to 5) where it was again true that participants who completed the Cue maze first (M = 19.4s, SEM = 3.4) took significantly longer to find the platform than those who completed the Cue maze second (M = 10.3s, SEM = 1.3), t(20) = 2.49, p = .02, d = .87, equal variance not assumed. When performance was compared for Trials 6 to 10 (once it had reached asymptote) no such order effect could be detected.

A similar pattern of order effect was recorded for the distance variable in the Cue maze (Figure 3-D.1). Participants who completed the Cue maze first (M = 1.3pd , SEM = .18) traveled significantly further to find the platform than those who completed the Cue maze second (M = .64pd, SEM = .05), t(19) = 3.69, p = .002, d = 1.3, equal variance not assumed. We again compared performance on both early and late trials (Figure 3-D.2). The noted order effect was only present in early trials (2 to 5) where it was again true that participants who completed the Cue maze first (M = 1.99 pd, SEM = .32) took significantly longer and traveled further to find the platform than those who completed

Appendix 3-D (continued)
Behavioural Order Effects

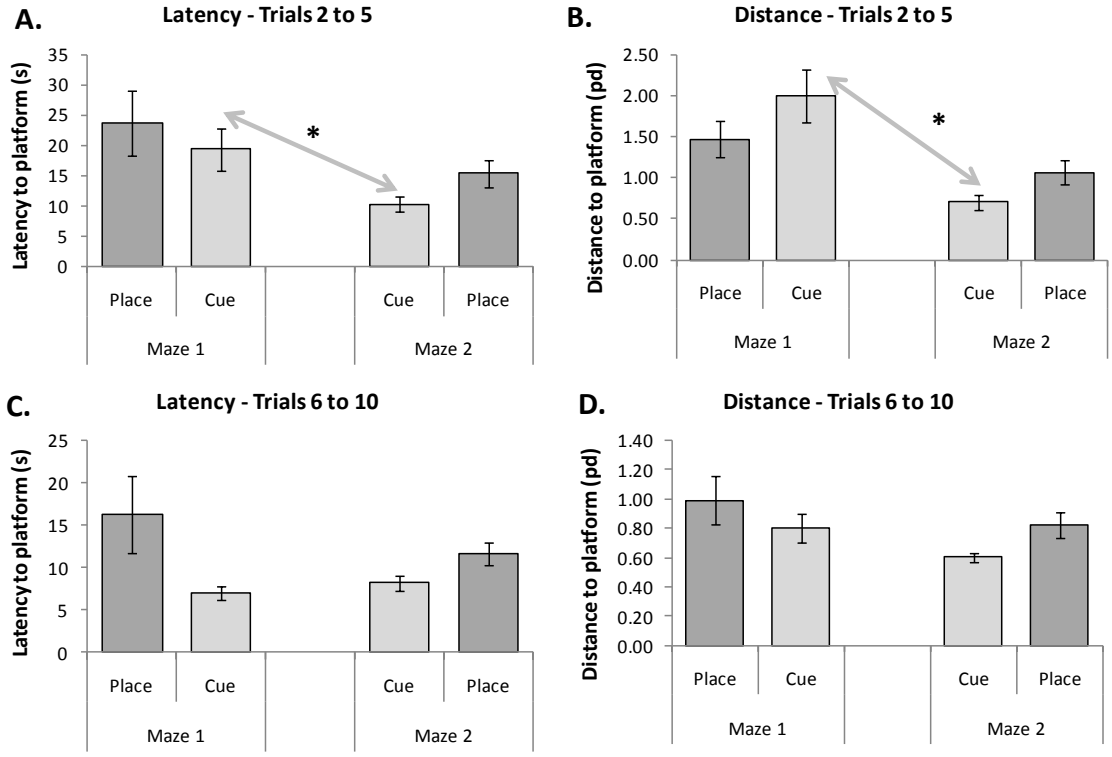


*Figure 3-D.2.*Order effects in latency and distance in the Place and Cue mazes. In early trials (2 to 5) in the Cue maze participants were significantly slower **(A)** and traveled significantly further **(B)** to the platform when they received the Cue maze first. In late trials (6 to 10) there were no differences in latency **(C)** or distance **(D)** to the platform in the Cue maze. There were no order effects in the Place maze. Maze 1 = first maze received (either Place or Cue), Maze 2 = second maze received (either Place or Cue).

the Cue maze second (*M* = .70pd, *SEM* = .09), t(19) = 3.83 , p = .001, d = 1.4, equal variance not assumed. When performance was compared for Trials 6 to 10 (once it had reached asymptote) no such order effect could be detected.

Overall, performance in the Cue maze was considered to be roughly equivalent in the latter half of Cue maze trials regardless of whether participants received the Cue maze first or second. This was taken as an indication that any order effect was resolved by the time participants reached the halfway mark in the Cue maze trials.

Chapter Four

This chapter consists of a manuscript describing a two part study of the relationship of environmental experience to strategy selection in virtual environment navigation tasks. The study reported in this chapter expands on findings from previous work showing that during a virtual environment navigation task people look in different regions of the screen display depending on which strategy type they are using. The present study examines the effects of experience on how these strategies are selected. The main objective was to determine whether antecedent experience influences the strategies people select during later navigation. The second objective was to determine whether eye movements could indicate which strategy was selected in a navigation task where two different strategy types were equally effective for locating the target.

Experience in place-based or cue-based environments determines strategy selection in a virtual Morris water maze: A behavioural and eye-tracking study.

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Abstract

In the study of wayfinding there is considerable controversy over how many strategies people use, and what factors determine when and how strategies are selected. Allocentric strategies rely on the presence of distal, relational stimuli whereas egocentric strategies rely on the presence of proximal or simple guidance stimuli. Strategy use has often been explained by studies of internal factors but little weight has been given to the study of how strategies are selected. The present study examined the effects of recent environmental experience on strategy selection. Methods employed included eye tracking, behavioural strategy probes and verbal report to study the effects of antecedent experience on strategy selection in specially designed virtual environment navigation tasks. Thirty-seven participants were trained either in an allocentrically biased "Place" maze or an egocentrically biased "Cue" maze, versions of a virtual Morris water maze (vMWM). All participants were then tested in the Dual-strategy maze, a version of the vMWM task where both allocentric and egocentric strategies were equally efficient. Strategy selection was measured using a probe trial at the end of testing and was confirmed by subsequent verbal report about the environmental stimuli. Results showed that prior experience in the Place maze was associated with bias towards selection of an allocentric strategy in the Dual-strategy maze at the end of testing whereas experience in the Cue maze was always associated with selection of an egocentric strategy. Verbal report confirmed that allocentric strategists were more aware of features in the virtual environment than were egocentric strategists, suggesting a pathway to strategy selection that is mediated by cognitive mapping. There was no evidence of gender differences in

strategy selection. Eye movements collected during the first, orienting, second of each trial revealed only small differences in the two strategy groups that were limited to the first 250 ms. Together these results suggest that the selection of strategies is strongly related to experience and that experience can be a greater contributor to strategy selection than personal internal factors such as gender. These findings introduce the contribution of cognitive mapping and environmental awareness to strategy selection. The gaze position results do not support the further use of eye-tracking to assess strategy selection in participants with experience in the virtual maze. However, eye-tracking may have utility for the study of spontaneous strategy selection. This research has applications for understanding the cognitive basis of spatial navigation and for the development of brain imaging studies of navigation including studies of navigation deficits.

Navigational Strategy Selection

Wayfinding in the real world is an everyday task for most people, but the means by which people navigate are not completely understood. A number of different categorizations of navigational strategy have been proposed ranging from two components (O'Keefe & Nadel, 1978) to three (Sutherland & Dyck, 1984) or four (Trullier et al., 1997). To date, attention has been paid mostly to strategy identification and use and few have considered the possibility that in a given situation people may be choosing or selecting strategies and that each person may have more than one strategy at their disposal. A key factor in this decision making process, largely overlooked until now, is the effects of experience. A closer examination of the relationship between experience and strategy selection should lead to better understanding of how, when and why people select and use particular navigational strategies. To date, much of the research on strategy use seems to be based on the assumption that strategy use is determined by innate factors such as gender. Understanding the effects of experience on strategy selection should help determine whether the selection or the predilection to select a strategy relies on environmental factors rather than innate abilities.

History of Research on Strategy Use

Prior to the mid-twentieth century, navigation research was focused mainly on stimulus-response behaviours in rats and was strongly influenced by behavioural psychology. According to Tolman (1948) many animal psychologists maintained a firm belief that the behaviour of rats in mazes was driven entirely by stimulus-response mechanisms. In this context, animal learning consisted of strengthening and weakening of connections in a nervous system that was "helplessly responding" (p.189) to the

environment. Thus only one type of strategy was available to the animal. However, Tolman (1948) took issue with this view and proposed instead that animals possess the ability to make a cognitive map (internal representation) that consists of routes, paths and spatial relations between objects and places in the environment. His theory was later expanded by O'Keefe & Nadel (1978) who described the map as a representation of places in space with all the places being systematically related to one another (p.86); they also proposed that the map was independent of the location of the navigator, and that a key brain structure for the map was the hippocampus.

Navigation strategies have been characterized in several different ways. According to the cognitive map theory of O'Keefe & Nadel (1978) navigation can be categorized according to two types of space, labelled "taxon" and "locale". Taxon navigation is accomplished via guidance strategies such at target approach and route making, whereas locale navigation is accomplished via orientation strategies based on cognitive maps. In addition to these categories, Sutherland & Dyck (1984) described a praxis strategy which consists of the recollection of a sequence of body turns. More recently, Trullier et al. (1997) proposed four categories of strategies, target approach, guidance to a target (or series of them), place recognition triggered response, and topological navigation. The first two of Trullier's strategies correspond to the guidance strategies proposed by O'Keefe & Nadel (1978) whereas the topological strategy corresponds to orientation (cognitive map) strategies. The place recognition triggered response strategy may also be a guidance-type strategy (Trullier et al., 1997). In addition to strategies noted here, there are also many task-specific strategies reported in navigation research**.** For example, Kallai, Makany, Karadi, & Jacobs (2005) examined exploration

strategies in humans navigating in a virtual environment and found that participants preferred to use one of two behaviours (circling and criss-crossing). In a real-world building task Hölscher, Büchner, Meilinger, & Strube (2009) compared floor-based and direction (map instruction)-based strategies for wayfinding.

Some researchers have proposed that strategies may be organized hierarchically. That is, strategies could be acquired in a developmental hierarchy (Allen, Kirasic, Siegel, & Herman, 1979) or could be utilized in a hierarchical fashion (Gluck & Fitting, 2003). For example, Siegel & White (1975) described human navigation within a hierarchy of spatial abilities that includes landmark knowledge, route knowledge and survey or map knowledge; they further suggested that landmark knowledge is at the lowest level of this hierarchy and map knowledge at the highest level. Different strategies may be associated with these different types of knowledge and therefore strategies may also be organized hierarchically. Some researchers have proposed hierarchies of strategy that are associated with regions of space, with different strategies selected for nearby and distal regions (Wiener, Buchner, & Holscher, 2009; Wiener, Schnee, & Mallot, 2004). Others have suggested that navigational hierarchies are internal and develop according to the way in which the animal encodes the environment (Jacobs & Schenk, 2003). This encoding may lead to a preference for navigation using a particular strategy. Embedded within this concept of hierarchical strategies is the assumption that every healthy individual should have multiple strategies at their disposal.

Two Navigation Types

Researchers generally agree that there are two different types of navigational strategies, egocentric and allocentric. Egocentric strategies rely on perceptions of the

environment from the perspective of the navigator and may consist of either response-based or cue-based strategies. Response-based egocentric strategies (e.g. a sequence of left and right turns) appear to be used during exploration of an environment (e.g., Kallai et al., 2005) or when a task is well learned and can be accomplished by simple left or right turns (e.g., Heft, 1979; Levy, Astur, & Frick, 2005) . Cue-based egocentric strategies are used to navigate directly to a landmark in the environment (e.g., go to the water) or to construct routes from a series of landmarks each visible from the location of the previous one (e.g., go down the hill, then to the traffic light, then turn to the water) (e.g., Nemmi et al., 2011; O'Keefe & Nadel, 1978). Together these egocentric strategies will allow the person to locate a target in the environment as long as the target is visible or its location can be inferred from the presence of proximal landmarks, or can be found by following a route or a series of body turns.

In some circumstances a target location cannot easily be located utilizing egocentric strategies. For example, navigational targets may not be visible or there may be no proximal stimuli (landmarks) to mark their location. Alternatively, the person might be required to detour from a known route, or might decide to try a shortcut. In this case people may choose to navigate using an allocentric strategy based on the formation of a cognitive map. This type of navigation is often referred to as "allocentric" because it is world-based (Nadel & Hardt, 2004; O'Keefe & Nadel, 1978; Tolman, 1948) that is, based on the ability to imagine the spatial relationships of environmental stimuli independently of one's own perspective. This important aspect of cognitive maps allows people to navigate to unseen target locations in the environment and to make novel routes or detours to these locations, demonstrating the use of allocentric strategies.

Two Cognitive-Neural Systems

The dichotomy of navigational strategies into egocentric and allocentric is confirmed by evidence from laboratory animal and human studies that two strategy types are mediated by neural processing in two different cognitive-neural systems in the brain. These systems have been widely studied in laboratory animals and their functional anatomy is generally agreed upon by researchers (Poldrack & Packard, 2003; White & McDonald, 2002). Each system consists of a set of interconnected neural structures with one structure at the centre of each (White & McDonald, 2002). For example, the hippocampus is at the centre of a system associated with cognitive mapping and the basal ganglia (especially the caudate nuclei) are at the centre of a system associated with stimulus response behaviours. In animals, the hippocampus and caudate systems are thought to act in parallel and they may cooperate or compete with one another to cause the use of a strategy that is best suited to the behavioural task (Poldrack & Packard, 2003; White, 2008; White & McDonald, 2002). White (2008) suggests that this match of strategy to task is a result of coherence so that the system that is best suited to represent incoming information from environment is the system that engages an appropriate navigational strategy. In any case, it seems clear that only one system and one corresponding strategy can be utilized at any given point in time.

Converging evidence from behavioural and brain imaging studies suggests that human strategy use is supported by the same two cognitive-neural systems that are present in animals (for review see, Neil Burgess, 2008). A number of brain imaging studies employing virtual environment navigation tasks have demonstrated that the hippocampus is important for allocentric navigation (e.g., Doeller, King, & Burgess,

2008; Grön, Wunderlich, Spitzer, Tomczak, & Riepe, 2000; Hartley, Maguire, Spiers, & Burgess, 2003). In addition, the presence of two systems is supported by studies demonstrating that hippocampal activity is associated with tasks that require cognitive mapping whereas caudate activity is associated with route following or route recognition tasks (Hartley et al., 2003; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Maguire et al., 1998; Voermans et al., 2004). This anatomical distinction mirrors that found in animal research and suggests that humans also use strategies that are coherent with the task at hand.

Strategies and Experience

Presumably, the strategies animals use to navigate should be determined in part by their experience with the environment. Spatial navigation theories and especially cognitive mapping theory (O'Keefe & Nadel, 1978) suggest that animals (including humans) acquire their ability to navigate by moving through and interacting with the environment during exploration. These interactions when accumulated in the sensory and motor systems of the animal are defined as experiences (O'Keefe & Nadel, 1978). Experience, then, should reflect an accumulation of spatial knowledge that is dependent on the availability of stimuli in the environment (Jacobs & Schenk, 2003; White, 2008). Such knowledge is presumably acquired for the purpose of solving navigational problems (Tolman, 1948).

Experience may be important for the use of both strategy types (egocentric and allocentric). The hallmark of stimulus-response learning was the gradual acquisition of association (or habit) strength (Hull, Felsinger, Gladstone, & Yamaguchi, 1947) through repeated trials (Rescorla & Wagner, 1972), or in other words, through the effects of

experience. Thus, experience is thought to be necessary for the development of egocentric response strategies. Experience may also be necessary for allocentric navigation in at least three ways. Pre-navigation exploration experience may be important for the formation of a cognitive map and for adding information to existing cognitive maps (O'Keefe & Nadel, 1978). Experience could also be an important factor in active navigation by contributing the acquisition of new information based on multiple perspectives of the environment. Further, experience is likely important for the persistence of allocentric navigation behaviour because success in reaching a goal provides experiential knowledge about how to find the goal again using the same strategy. Thus experience may be important for both the development and use of allocentric strategies.

Empirical findings suggest that strategy use is likely affected by both internal and external factors, and that the external factors are environmental and experiential. Considerable research has been devoted to the investigation of internal personal factors such as gender (e.g., Chai & Jacobs, 2010; Saucier et al., 2002) and age (e.g., Moffat & Resnick, 2002). However, far less research has considered that strategy use may also be affected by external factors such as the availability of useful stimuli or the opportunity for experience with these stimuli. This may be due in part to the fact that many navigation tasks are designed in such a way that only one strategy type is likely to be elicited. For example, studies may exclusively investigate either route learning (e.g., Nemmi et al., 2011) or place learning (e.g., Woolley et al., 2010). Indeed, most common type of navigation study appears to employ place-based tasks to study internal factors that might influence the ability to form a cognitive map (and thus use an allocentric strategy) (e.g.,

Kallai et al., 2005; Moffat & Resnick, 2002; Woolley et al., 2009). Thus the study of egocentric and allocentric strategy use and its relationship to environmental experience is relatively new field.

More recently researchers have begun to test strategy use in environments where it is possible to employ either egocentric *or* allocentric strategies to navigate successfully. These ambiguous or "dual-strategy" environments have been used to test the spontaneous use of strategies and to test strategy use across trials. In this context, some researchers have introduced the concept of "preferred strategies" that are used either spontaneously or continuously while navigating. For example, Iaria et al. (2003) noted that in an 8-arm virtual radial arm maze (vRAM) task, participants initially preferred either an egocentric or an allocentric strategy . This preference was indicated by verbal report at the end of testing and showed that each strategy type was used in roughly equal proportions. In another study of preferred strategies, Schmitzer-Torbert (2007) also noted a roughly equivalent preference for either an egocentric or an allocentric strategy early in testing. In this case strategy was measured through random and infrequent probe trials to test whether participants were navigating by a remembered sequence of turns or by a cognitive map of the maze layout. Also, when participants achieved navigational success (found the target in a virtual corridor maze) they tended to continue using the associated, and now preferred strategy on successive trials.

Studies of strategy use in dual-strategy environments have also noted that switching can occur. Iaria et al. (2003) reported that although about half of their participants initially preferred a spatial (allocentric) strategy, only a third used an allocentric strategy by the end of testing. In other words, a substantial proportion of

participants who spontaneously used an allocentric strategy had switched to the use of an egocentric strategy sometime during testing. In a more detailed study of strategy switching Igloi, Zaoui, Berthoz, & Rondi-Reig (2009) tested participants in a 5-arm vRAM that could be solved using either an allocentric or an egocentric strategy. They then used probe trials (every third trial) to measure strategy selection during acquisition. This method resulted in the observation that a third of participants switched strategies very frequently (every few trials). The switches occurred in both directions, from the use of an egocentric to an allocentric strategy and vice versa.

Strategy Selection

Research showing that strategy use changes with time (by preference or by switching) raises the important issue of strategy selection. Theoretically there is a difference between strategy use and strategy selection, the former being concerned with execution or behaviour and the latter with cognitive (not necessarily conscious) choice or decision making. The capacity to switch strategies implies that many (and perhaps most) people have both egocentric and allocentric strategies at their disposal. That is, most people should have intact navigation systems that allow for the selection of an appropriate strategy to meet the requirements of the navigation task at hand. The acknowledgement of flexible switching further implies that people do not navigate solely on the basis of a single innate ability to use one strategy or the other but rather that their navigation systems interact with environmental circumstances in a way that triggers strategy selection and leads to the use of one or the other. However, the precise circumstances of this selection are not understood.

The factor most commonly assumed to control which strategy is engaged at a

given time is familiarity with the environment or route (e.g., Golledge, 1999; Maguire et al., 1998). This familiarity presumably develops via environmental experience. The solutions to navigational problems may depend on familiarity with an environment as well as an ongoing accumulation of new environmental information and thus new experience. Familiarity is crucial to strategy selection because the ability to select a given strategy may depend on both the availability of useful environmental information and the degree of prior exposure to this type information (Burgess, 2006). In other words, for a strategy to be selected relevant stimuli have to be present and the person has to be sufficiently experienced (or familiar) with these stimuli (or similar ones). For example, Jacobs & Schenk (2003) proposed that if the navigating animal has not gained experience with particular types of stimuli then the system that utilizes those stimuli will not be activated (i.e., the corresponding strategy will not be selected). Second, if one system is more dominant, perhaps due to greater experience with a particular stimulus type, that system and its corresponding strategies will be selected more often. Another related point is that if a particular strategy is successful (rewarded) then the animal should be biased toward future selection of the same strategy (and engagement of the same neural system). Thus experience is a key factor in the strategy selection process.

Some researchers have proposed that strategies are selected via activity levels in the egocentric and allocentric navigation systems (Burgess, 2006; Jacobs & Schenk, 2003). The systems are thought to interact either competitively so that ultimately one or the other system engages a strategy and thus controls behaviour (Burgess, 2006). They may also act cooperatively by communicating with one another in situations where one system requires information from the other (Burgess, 2006). However, the mechanisms

behind these interactions are not fully understood (Nadel & Hardt, 2004). One possibility is a "strategy selector" that weighs activity in both systems for the purpose of making a navigational decision. This neural selector could be responsible for determining the selection of a strategy based on levels of activity in either system. There is currently a requirement for research into what factors might affect such a selector (Nadel & Hardt, 2004; Burgess, 2006). Key factors may be the structure of the environment and experience navigating within it (Burgess, 2006).

In order to understand the factors controlling navigation it would appear to be important to investigate the factors controlling strategy selection as well as the factors controlling strategy use. Furthermore, past research seems to have under-recognized experience as a factor in navigation. Accordingly, the objective of the present study was to examine the effects of experience on navigational strategy selection.

Measuring Strategy Selection

In order to study the effects of experience any factor on strategy selection it is necessary to have an environment in which more than one strategy can be used and a way of measuring strategy selection. Virtual environment navigation tasks are ideally suited to this purpose because they provide the opportunity to systematically alter environmental features and bias environments toward the use of different strategies. One task that has been used to study human navigation strategy is a virtual version of the radial arm maze (RAM) task (e.g., Iaria et al., 2003). However, in animals the RAM may not be the best measure of allocentric navigation (Hodges, 1996) and therefore may not be the best choice to elicit allocentric strategies. A more suitable task may be the Morris water maze (MWM) because it is considered to be a good measure of allocentric navigation but can

also be adapted to elicit a cue-based strategy.

The MWM is the gold standard for testing spatial learning and memory in laboratory animals (Brandeis et al., 1989; D'Hooge & De Deyn, 2001). The task (Morris, 1981) requires animals to swim to an invisible Plexiglas™ platform (the target) submerged in a circular pool of milky water and to do this on multiple trials beginning from different positions around the edge of the pool. The wall of the pool is of uniform colour and texture and the only stimuli available for navigating are distal features on the walls of the testing room. After several training trials, rats are able to take relatively direct paths to the platform, regardless of start position, suggesting that they form cognitive maps of the surrounding environment. Morris et al. (1982) demonstrated that damage to the hippocampus disrupted performance on the MWM, indicating that the hippocampus is important for spatial navigation, and especially for cognitive mapping. More recently, the task has been used to differentiate the use of place-based (allocentric) from cue-based (egocentric) strategies in animals (Hamilton, Rosenfelt, & Whishaw, 2004; McGregor, Good, & Pearce, 2004).

Virtual versions of the MWM (vMWM) are also becoming standard in human navigation testing and are beginning to provide converging evidence that there are two navigation systems in the human brain. In healthy participants vMWM tasks have been utilized to test the effects of various environmental factors on human navigation performance (Doeller & Burgess, 2008; Hardt, Hupback, & Nadel, 2009). Virtual MWM tasks also appear to be sensitive to gender differences (e.g., Astur, Ortiz, & Sutherland, 1998; Ross, Skelton, & Mueller, 2006; Woolley et al., 2009), age differences (Moffat & Resnick, 2002), and differences due to brain injury (Goodrich-Hunsaker, Livingstone,

Skelton, & Hopkins, 2010; Livingstone & Skelton, 2007). Recently, the vMWM has been used to differentiate place-based (allocentric) from cue-based (egocentric) strategies in humans (Goodrich-Hunsaker et al., 2010; Livingstone-Lee et al., 2011).

In order to study experience effects on strategy selection it is necessary to differentiate strategy selection from strategy use and to demonstrate the effect of experience on selection. Some researchers have measured strategy via probe trials designed for example to measure strategy acquisition Igloi et al. (2009), strategy use Schmitzer-Torbert et al. (2007) and incidentally, strategy switching. While being good strategy measures, these probe trials by themselves could not examine how participants chose the strategies they used. Other studies have classified strategy use by employing verbal report (e.g., Iaria et al., 2003, Etchamendy et al., 2007; Kato & Takeuchi, 2003; Gunzelmann, 2004) and self report measures (Spiers & Maguire, 2008). This approach may be problematic because people are not aware of the strategies they use. The present study solves the above problems first by providing participants with either allocentric or egocentric training (experience). After testing in a dual-strategy task a specially designed strategy probe trial indicated which strategy type had been selected. This selection was then corroborated (rather than classified) by verbal reporting of environment features used during navigation in the dual-strategy task.

In the present study, strategy selection was measured by probe trials, by verbal report and also by utilizing eye movements to examine strategy selection during orientation in specially designed virtual environments. This relatively new approach applies eye tracking measures to analyze which navigational stimuli (distal or proximal) hold the attention of participants most during tasks that require active navigation (e.g.,

Gramann, Muller, Eick, & Schonebeck, 2005; Hamilton, Johnson, Redhead, & Verney, 2009; Jin, Gillner, & Mallot, 2004; Spiers & Maguire, 2006). The strategies people are using may be revealed by an analysis of which environmental features are attended to most often (Livingstone-Lee et al., 2011). Further, if this analysis is applied to eye movements during orientation in a dual-strategy environment, it may reveal which strategy is being selected. When combined with virtual environment navigation tasks, eye movements have already revealed that gaze position is related to navigational success (Hamilton et al., 2009) and to strategy use (Livingstone-Lee et al., 2011). However this method has not been applied to the study of strategy selection. The present study is a systematic examination of the effect of experience on strategy selection and use that will bring together improved behavioural analysis of navigational strategy with eye-tracking. Eye tracking will permit the analysis of strategy selection on a trial-by-trial basis.

Research Approach

In order to study the effects of experience on strategy selection virtual environment navigation tasks were designed to elicit either an allocentric or an egocentric strategy. The Place maze was a human analogue of the MWM was therefore biased toward the use of allocentric strategies. A second task, the Cue maze, was an adaptation of the Place maze and designed to be biased toward the use of egocentric strategies. This task differed from the Place maze because there were objects (proximal stimuli) situated on the arena wall. One of these objects always marked the location of the platform but its position changed from trial to trial. A third task, the Dual-strategy maze, combined features of both the Place and Cue mazes so that the platform (which always remained in the same location) could be found either by utilizing either the relationships of distal

room features or an object that marked its location. Participants were first trained in either the Place or the Cue maze and were then tested in the Dual-strategy maze; as noted above a probe trial and verbal report assessed strategy selection.

The present study also examined gaze position during navigation in the virtual environments. For this purpose, a crucial design feature of all three virtual environments was that the locations of important proximal and distal stimuli were separated on the screen display. The distal features of the environment (the landscapes) useful for allocentric navigation were always located vertically above a horizon (the vertical midline of the display). The proximal features of the environment (the objects on the arena wall) useful for egocentric navigation were always located below the horizon. Thus it was possible to identify which type of stimuli participants were attending to most while navigating.

Research Questions and Hypotheses

The present study addresses three specific research questions:

1. Will antecedent navigational experience influence strategy selection in the strategy probe trial?
2. Will antecedent navigational experience influence verbal report of strategy selection?
3. Will antecedent navigational experience influence which strategy is selected during orientation in the Dual-strategy task?

It was hypothesized that recent experience navigating by either an allocentric or an egocentric strategy would strongly influence strategy selection in an environment where both strategies are available for navigation. Operationally this would mean that in

the Dual-task maze participants who had been trained in the Place maze would navigate allocentrically using room features and participants trained in the Cue maze would navigate egocentrically using cue objects proximal to the goal. This would manifest in two ways. On the strategy probe trial, training in the Place maze would lead to the selection of an allocentric strategy and training in the Cue maze would lead to the selection of an egocentric strategy. Secondly, the selection of an allocentric strategy would be associated with verbal report of navigation using room features and the selection of an egocentric strategy would be associated with verbal report of navigation using proximal cue objects.

Similarly, eye movements (gaze position) at the start of each trial should indicate which strategy participants selected during orientation the Dual-strategy maze. The hypothesis regarding eye movements was that in the Dual-strategy maze participants who selected an allocentric strategy (at the end of testing) would look upward toward the distal environmental features whereas participants who selected an egocentric strategy would look down toward the cue objects that marked the target location. Operationally, this would mean that the selection of an allocentric strategy would be associated with a higher vertical gaze position (and greater percentage of gaze above the horizon) than would the selection of an egocentric strategy. Also, selection of an allocentric strategy was expected to be associated with more central horizontal gaze position (in the middle portion of the screen display) than was selection of an egocentric strategy.

The methods and results for the present study are reported in two sections, the first (Part A) concerned with navigation behaviour and the second (Part B) concerned with eye movements.

Part A (Navigation Behaviour and Strategy)

Methods

Notes. Methods used in this experiment were largely identical to the methods of the previous experiment (Chapter 3), because the two experiments were embedded within a single study. Some material is replicated here to allow this chapter to stand alone (for manuscript preparation).

Participants. Participants were the same 52 individuals who participated in Experiment 2. They were recruited from two source populations, first year Psychology students at the University of Victoria (n = 33) and volunteers from the local Victoria community (n = 19). The data from these two source groups was combined as described in (Appendix 3-A). This experiment was part of a collaborative study that involved collecting electroencephalography (EEG) data, tracking eye movements and recording navigation behaviour in a virtual maze environment. Participants were excluded from the study if 1) a data set (EEG, eye movement or behaviour) was missing or incomplete due to technical problems, or 2) if participants had experienced a brain injury in the past. Brain injury was defined as having received an injury to the head that required an overnight stay in the hospital. The data from 37 participants (students, n = 23; community volunteers, n = 14) was included in the analysis. Of these 37 participants, 16 were male and 21 female. The mean age of participants in the sample was 25 years (student mean = 22 years; community volunteer mean = 30 years). All participants gave informed consent and the study was approved by the Human Research Ethics Board at the University of Victoria.

Apparatus. Spatial navigation was tested using four versions of a vMWM task; the "Place maze", the "Cue maze", the "Dual-strategy maze", and the "Visible platform maze". These desktop virtual environments were created using the commercially available video game editor, Unreal® (Epic Megagames), and were displayed on a 19 inch LCD monitor at a resolution of 800 x 600. Participants navigated through the trials using a typical gaming joystick that was stable on the desk in front of them. The joystick features were modified so that participants could move forward, left and right, but not in reverse. The Place maze environment was an adaptation of the Arena maze (Skelton et al., 2000, 2006) and consisted of a large circular arena bordered by a low wall and situated in a large square room .The room had large windows in all four walls, providing panoramic views of an outdoor landscape (Figure 4.1). The four walls of the room were arbitrarily assigned cardinal directions of north, south, east and west and the room lacked any distinctive features other than the environment outside the windows. There was a large window on each of the north and south walls and three windows on each of the east and west walls. The views looking out each side of the room were distinct. Mountains were visible through the north window and hills sloped down to a sandy beach outside both the east and west windows. A body of water with a small island could be viewed through the south window. The outdoor landscape provided distal stimuli to aid in navigation to a hidden platform and therefore the Place maze was designed to bias participants toward the use of an allocentric strategy.

The Cue maze (Figure 4.1) was identical to the Place maze except that there were eight objects evenly spaced around the low rising arena wall at cardinal points. These objects served as proximal stimuli (or cues) that the participant could use to navigate to

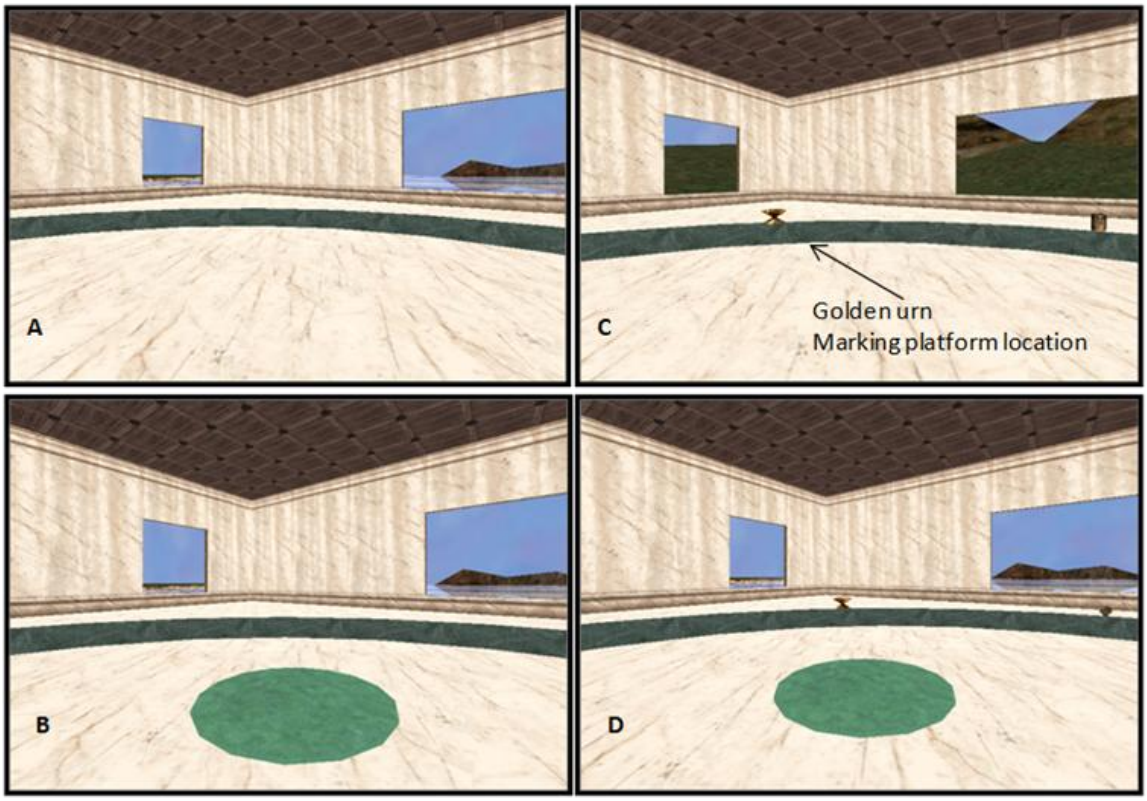

Figure 4.1. The virtual environments used for training. **A**. The Place maze, a vMWM. **B.** The Place maze with the platform visible in its fixed location (i.e., after the participant has stepped on it). Note that during trials, the platform's location could be identified only by a constellation of distal landmarks (windows and landscapes), biasing participants to use an allocentric strategy. **C.** The Cue maze, a virtual landmark maze with the important cue object (the golden urn) shown. **D.** The Cue maze with the platform visible (coincidentally) in the southeast quadrant, marked by the golden urn. Because the platform (and urn) changed quadrants each trial, this proximal object provided the best means of identifying the platform location, biasing participants to use an egocentric strategy.

the hidden platform. Therefore the Cue maze was designed to bias participants toward using an egocentric strategy.

The Dual-strategy maze (Figure 4.2) was identical to the Place maze except that there were eight objects evenly spaced around the low rising arena wall at cardinal points**.** As per the Cue maze, these objects served as proximal cues that the participant could use to navigate to a hidden platform. However, the hidden platform was always in the same location (cf. the Place maze) but was always situated in front of the same cue object (a

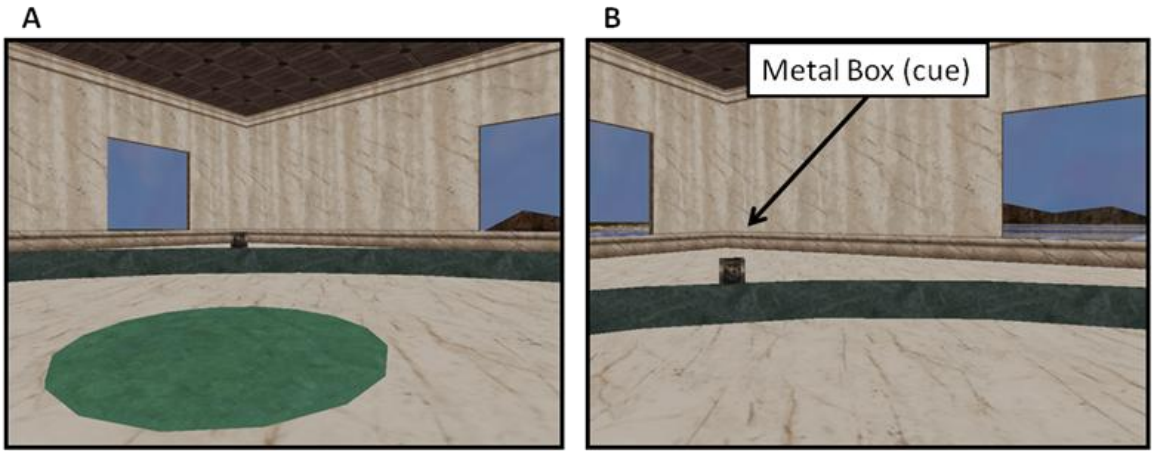

Figure 4.2. Views of the Dual-strategy testing maze from inside the arena. **A.** The green platform was always located in front of the metal box (the important cue object). **B.** The metal box was always located at the southeast cardinal point and the platform (not shown) was always located in front of it. Note that there were 8 objects in total.

metal box) (cf. the Cue Maze). Thus, in this maze, the solution was dual-strategy and participants were free to solve the task by using either room features or proximal cue objects (i.e., by using either an allocentric or an egocentric strategy).

The Visible platform maze (Figure 4.1) utilized the same virtual environment as the Place maze. The platform was always visible on the floor of the arena but its location changed on each trial.

Design. The current experiment was embedded in the design of a previous experiment where the Dual-strategy maze was described as a 'spatial task' (Figure 3.2). Figure 4.3 describes the order of presentation of the mazes and shows the design for the current experiment. All participants first completed the Visible Platform maze. Then half of the participants were presented with the maze sequence Place-Dual strategy -Cue (place-first condition) and the other half the sequence Cue-Dual strategy-Place (cue-first condition). For the purpose of the current experiment the conditions of interest were the

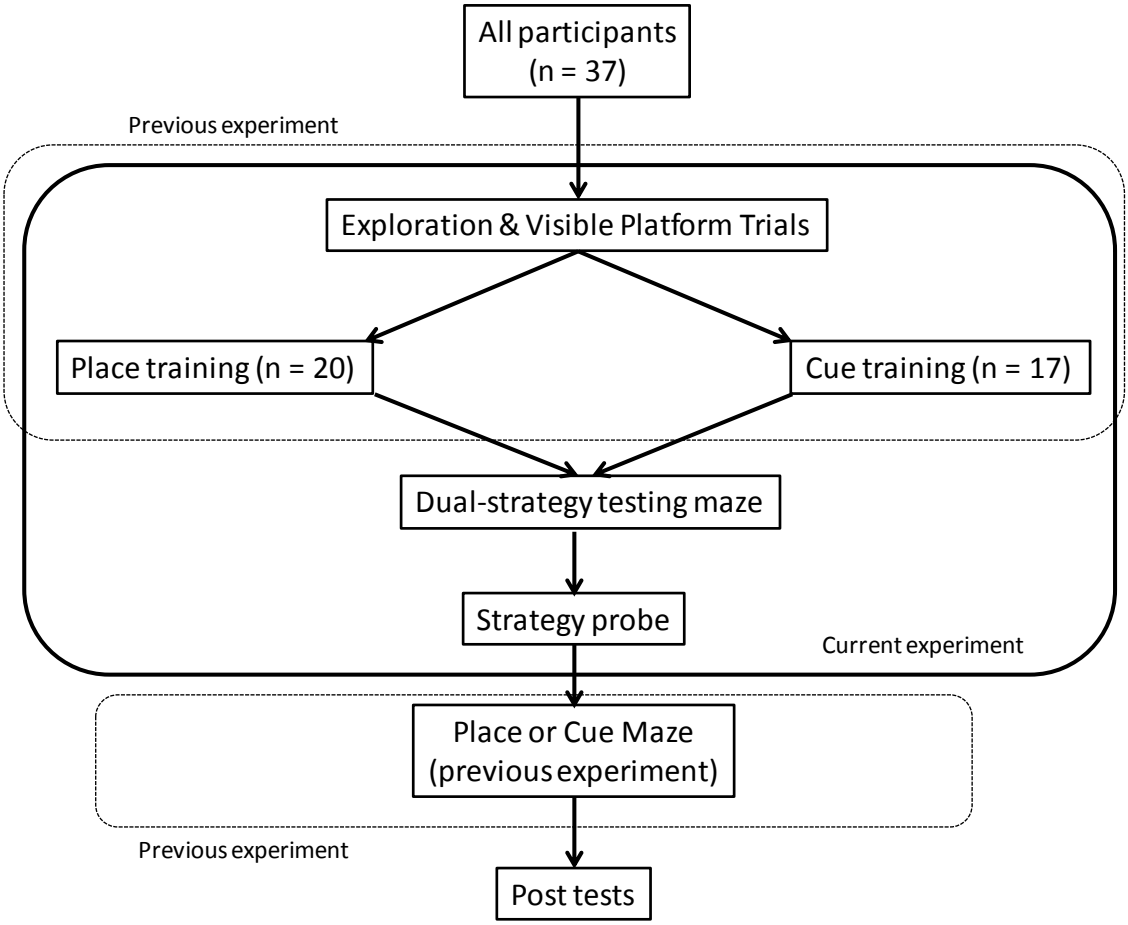

Figure 4.3. Experimental design showing strategy experiment embedded in larger study. Sections relevant to the current experiment are contained within the solid oval box. Dotted lines indicate sections of the previous experiment.

first two mazes in each sequence, that is, "place-trained" (Place then Dual-strategy) and "cue-trained" (Cue then Dual-strategy). The Dual-strategy maze constituted the testing phase of the experiment. Participants were randomly assigned to the two experimental conditions and approximately half (n=20) of the final sample group were place-trained whereas half (n=17) were cue-trained. The results of interest consisted of performance during testing in the Dual-strategy maze and after training in either the Place or Cue maze. All participants completed a strategy probe trial after testing in the Dual-strategy maze.

Procedures. A summary of the experiment protocol is given in Appendix 3-B and Table 4.1 gives a brief summary of maze trials and their purpose. Table 4.2 shows the order of presentation of trials for the two experimental groups (place-trained and cue-trained). Figures 4.4 and 4.5 give schematic aerial views of the training (Place and Cue maze) trials and testing (Dual-strategy maze) trials, respectively. These figures show the number of trials, platform locations and trial start positions. The trial types are described in the following sections.

Room exploration trial. The purpose of this trial was to familiarize the participant with movement using the gamepad/joystick and to provide them with a good view of the outdoor landscape. The trial began with participants situated at the centre of the east wall, outside of the arena and looking toward the middle of the room. Participants were told that they could explore the room for as long as they liked and they were asked to look at the landscape outside each of the windows. The exploration trial ended when the participant indicated comfort with the video game pad and satisfaction with their exploration of the virtual environment.

Visible platform trial. The purpose of these four trials was to confirm that participants were able to navigate to a single visible target in the environment. A large, green, circular platform was visible on the floor of the arena in the centre of a different quadrant for each trial. The start position for each trial was different, with all start positions being just inside the arena wall and at a cardinal point (Figure 4.4). When the participant "stepped" on the platform it made a sound like a bell ringing. Participants were informed that they should stay on the platform until they were ready to proceed to the next trial, the start of which was indicated by a short, high pitched beep.

Table 4.1

Description of maze trials, the number of them presented and their purpose. The order of presentation of the trials depended upon the experimental condition.

Trial type	Purpose	Number of
Room Exploration	To familiarize participants with the environment and using the game joystick	1
Arena Exploration	To familiarize participants with the environment from inside the arena	1
Visible Platform	To familiarize participants with procedural aspects of the task and confirm their ability to navigate to a visible target	4
Invisible Platform	To test participants' ability to navigate to a location in the room	10
Probe	An implicit test of the participants' knowledge of the platform location	1
DTS	An explicit test of the participants' knowledge of the platform location	1
Strategy Probe	A test of the participants' preference for either an egocentric or an allocentric strategy	1

Note. DTS = Drop-the-seed.

Arena exploration trial. The purpose of this trial was to allow participants to become familiar with the environment from the perspective of the arena. The start position was just inside the arena wall at the north cardinal point with the participant facing inward toward the centre of the arena. Participants were informed that they could explore inside the arena for as long as they liked, but that they could not pass beyond the arena wall. The trial ended when the participant indicated satisfaction with their exploration of the arena.

Table 4.2

Experimental design. The order of maze training and testing trials is shown for the two experimental groups (conditions), place-trained and cue-trained.

Test Phase	Experimental Condition	
	Place-first	Cue-first
Explore/Visible	Room explore Visible Platform Maze DTS	Room explore Visible Platform Maze DTS
Training (Place or Cue maze)	Arena explore Place maze Probe DTS	Arena explore Cue maze Maze probe DTS
Testing (Dual-strategy maze)	Arena explore Dual-strategy maze Probe Strategy probe	Arena explore Dual-strategy maze Probe Strategy probe
Cue or Place maze	Reported in previous experiment	Reported in previous experiment
Post-test	Reported in previous experiment	Reported in previous experiment

Note. DTS = Drop-the-seed.

*Place maze invisible platform training trials***.** The purpose of these ten trials was to train participants to navigate to a location in the room when the location was found most easily by using distal room features such as the landscapes outside the windows. The invisible platform was in a fixed location in the centre of the southeast quadrant of the arena. Participants were informed that the platform would always be in the same place and that they should go to the platform as quickly and directly as possible. Start positions were always just inside the arena wall, at one of the four cardinal points and

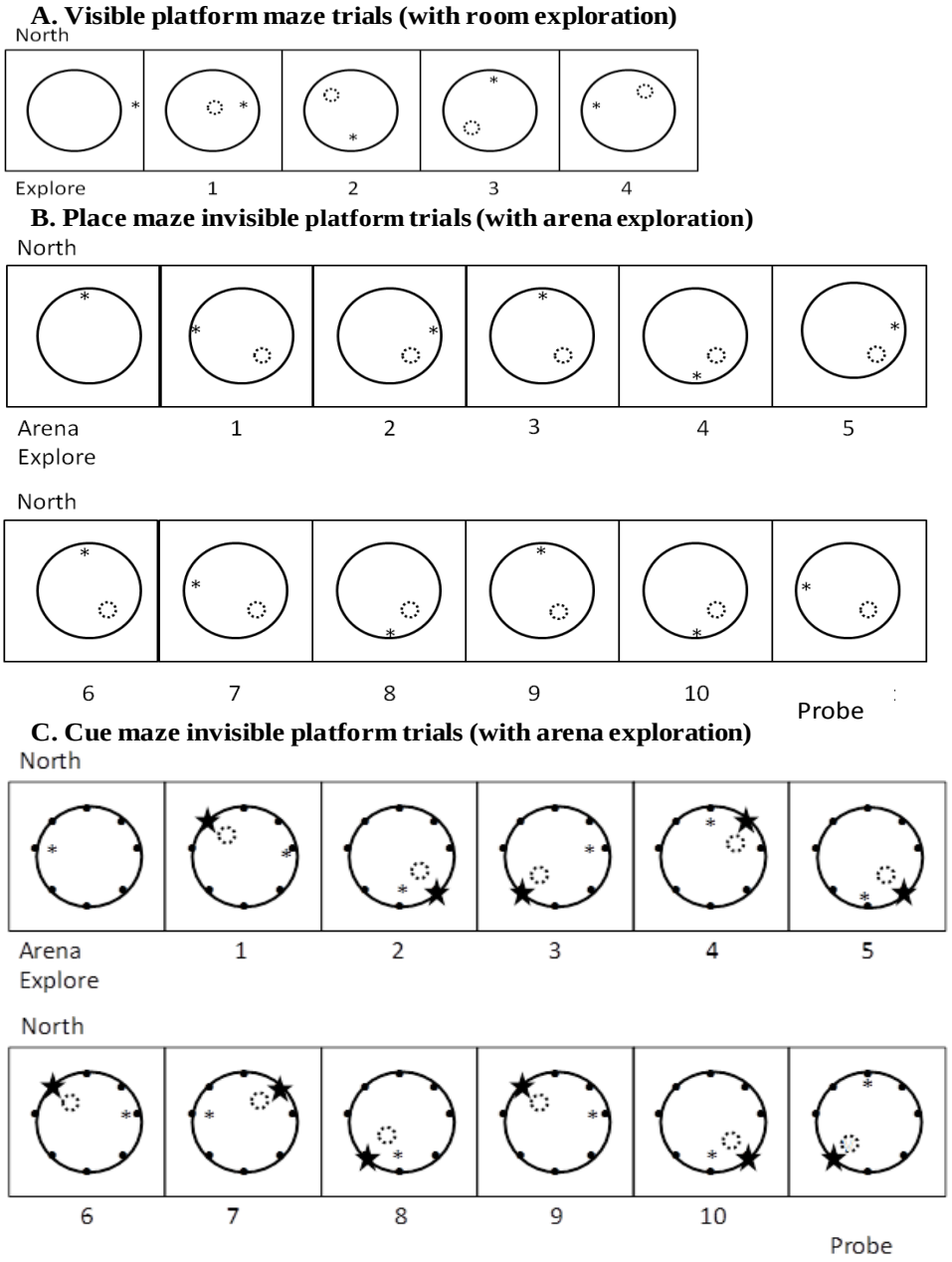

Figure 4.4. Aerial schematic of the Visible Platform maze and the virtual maze training trials (Place and Cue mazes). The arbitrary cardinal 'north' wall of the room is shown. The dotted circle marks the invisible platform location and the asterisk (*) marks the start position of the participant. **A.** Location of visible platform changed on each trial. **B**. In the Place maze, the platform was always in the same location. Note that for the probe trial, the platform was not present but the dotted circle marks its location on previous trials. **C.** In the Cue maze, the platform changed location on each trial but was always located in front of the golden urn cue object (represented by a black star). The other objects perched on the wall are represented by small black dots. On the probe trial the dotted circle marks the location of the platform on previous trials (in front of the cue object).

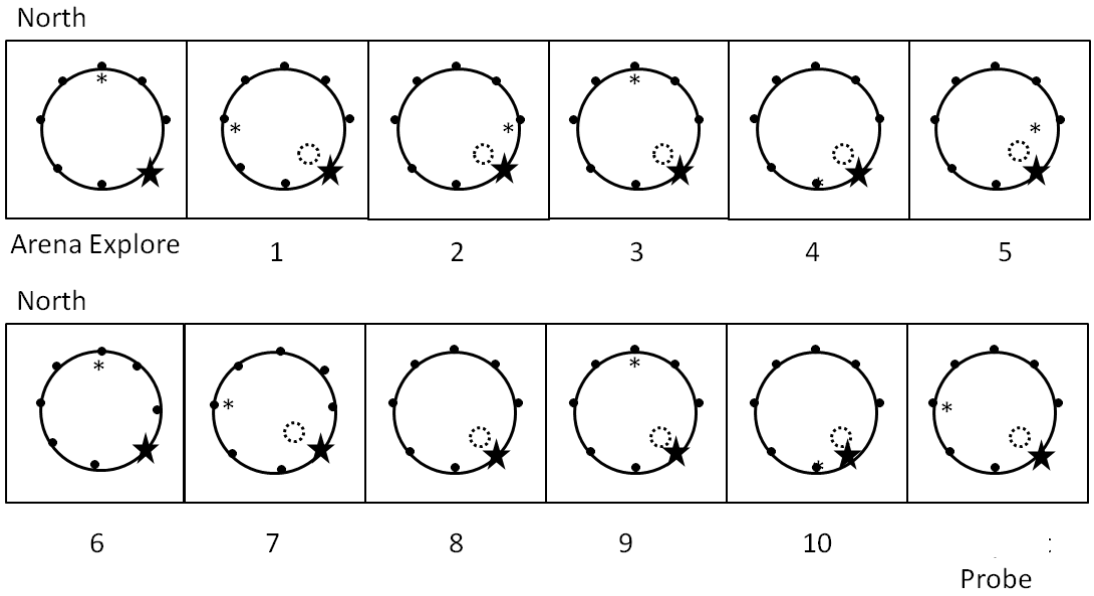

Figure 4.5. Aerial schematic of the virtual maze testing trials (Dual-strategy maze). The dotted circle marks the correct platform location and the asterisk (*) marks the start position of the participant. The platform was always in the same location and was always located in front of the same cue object (a steel box indicated here by a star). The other objects perched on the wall are represented by small black dots. On the probe trial the dotted circle marks the location of the platform on previous trials (in front of the cue object). Note that there is no platform present in the arena exploration trial and that the platform is impossible to find during the probe trial.

varied in a fixed, pseudo-random order. Start positions were also balanced according to whether the participant should make a left or right turn and according to the distance from the start position to the target location (Figure 4.4). The platform remained invisible until the participant stepped on it, at which point it rose up making a sound like a bell ringing. While on the platform, participants were able to look around the room (while remaining on the platform) as much as they liked before proceeding to the next trial, the start of which was indicated by a high pitched beep. After completion of the 10 trials, participants who completed these trials first were referred to as “place-trained”.

*Probe trial***.** The purpose of this trial was to test how well the participants learned the platform location. Prior to testing, participants were informed that on one trial (the probe) the platform would be very difficult to find but that they should continue to search for it anyway. During this probe trial, the platform remained hidden for 50s and the end of the trial was indicated by the usual bell ringing sound.

*Drop-the-seed (DTS) trial***.** The purpose of this trial was to test the explicit knowledge of participants with respect to the platform location. Participants were instructed to go to the spot where they thought the platform should be (based on the trials they were just completing) and once there the experimenter dropped a virtual seed to mark the location. The virtual seed grew into a virtual plant that marked the spot for later scoring on a 0-7 scale. For scoring the DTS trial, a ringed "bull's eye" target was placed over the quadrant where the platform was located during the invisible platform trials, with the centre of the target matched in size to the platform (Figure 4.6). Scores from 0 to7 were assigned based on the location of the participant's marker to the centre of the target (or bull's eye). A score of 0 indicated that the marker was not on the target rings whereas a score of 7 indicated that the marker was placed on the bull's eye (i.e., on the platform location). Participants did not observe the scoring procedure.

*Cue arena exploration trial***.** The purpose of this trial was to allow participants to become familiar with the environment when objects were added to the arena wall. This trial was identical to the Place arena exploration trial except for the addition of an object to each of the 8 cardinal points of the arena wall.

*Cue maze invisible platform training trials***.** The purpose of these ten trials was to train participants to navigate to a location in the room marked by a nearby proximal

Figure 4.6. Scoring for the "Drop-the-Seed" trial. The plant marks the spot where the participant dropped a virtual seed. The task was scored using target rings with the center "bull's eye" matching the size and location of the platform in the maze. Scores ranged from 0 for placement outside the target rings (and outside the correct quadrant) to 7 for placement on the bull's eye. The placement shown would have received a perfect score of 7.

stimulus. Invisible platform testing in the Cue Maze followed the same procedures as for the Place Maze invisible platform trials described above. The platform changed location (from quadrant to quadrant) but was always located in front of the same object, a "golden urn" (Figure 4.1). Participants were told that the platform would not always be in the same location, but that there would always be a clue to its whereabouts. After completion of the 10 trials participants who completed these trials first were described as "cue-trained". The probe trial and DTS trial were as described for the Place maze.

*Dual-strategy arena exploration trial***.** The purpose of this trial was to allow participants to become familiar with the environment when objects were added to the arena wall. This was necessary because the place-trained participants had not yet been

introduced to such an environment. This trial was identical to the Place arena exploration trial except for the addition of an object to each of the 8 cardinal points of the arena wall.

***Dual-strategy maze invisible platform training trials*.** The purpose of these ten trials was to test the ability of participants to navigate to a location in the room when it could be found either by utilizing the distal room features (landscapes) or by utilizing a nearby proximal stimulus. The platform was always in the same location (in the southeast quadrant of the arena) and was also always located in front of the same cue object (a metal box) (Figure 4.2).Invisible platform testing in the Dual-strategy maze followed the same procedures as for the Place maze invisible platform trials described above. Participants were not told anything about the location of the platform so that they were free to use either the landscapes or the metal box in order to find it. The probe trial was as described for the Place maze.

*Strategy probe trial***.** The purpose of this trial was to test which strategy (egocentric or allocentric) participants were utilizing by the end of Dual-strategy testing trials. Instructions for the strategy probe trial were the same as for the DTS trial described above. However, the locations of the cue objects on the arena wall were rotated 180 degrees around the wall so that the object (the metal box) that had been most proximal to the hidden platform during the invisible trials was now in a position diagonally opposite its usual location. Participants were not informed of this change and were simply instructed to "drop the seed" where they thought the platform was, based on the trials they had just completed. They were therefore able to explicitly indicate their knowledge of the platform location by dropping the seed either in front of the important cue object (in its new location) or at the usual location of the hidden platform by using the distal

room cues (windows and landscapes) that remained constant throughout.

The strategy probe was scored according to quadrant placement and accuracy. For this purpose, two bull's eye targets were used to assess accuracy of seed placement both by quadrant and by proximity to the platform location (Figure 4.7). The first target filled

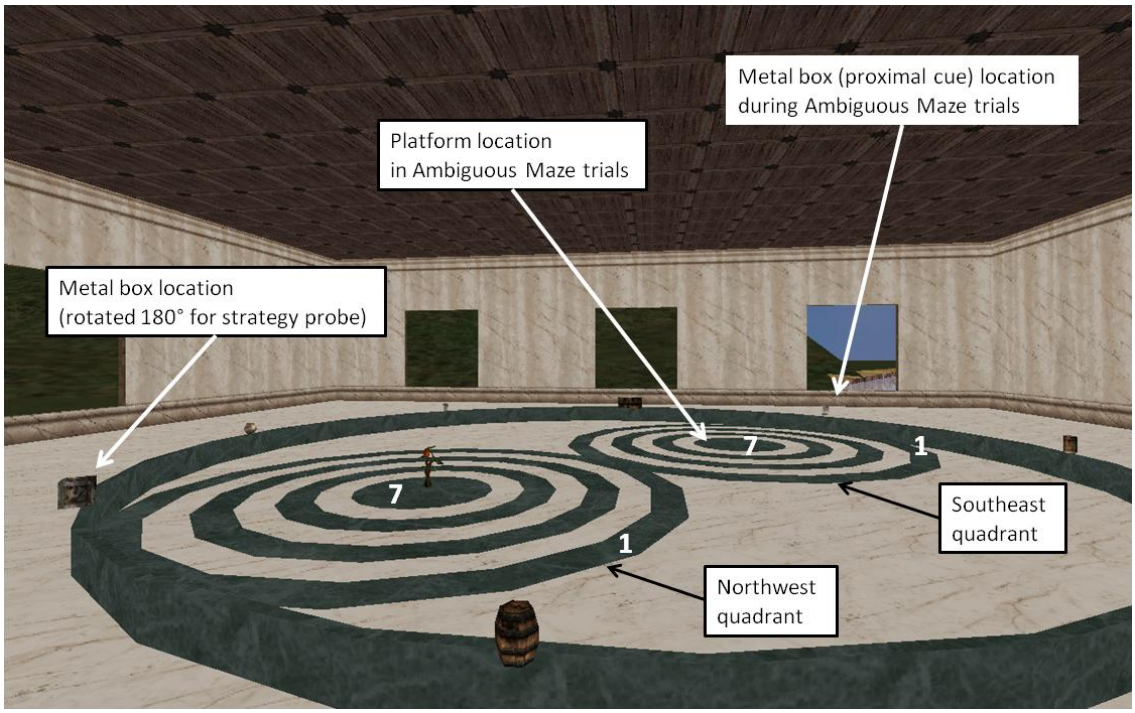

Figure 4.7. Scoring for the strategy probe trial. Two bull's eye targets were placed over the southeast quadrant (where the metal box was located throughout trials) and over the northwest quadrant (because the box was rotated 180° around the arena wall for this trial). A score from 0 to 7 was possible for placing the seed either according to the distal stimuli ('room score' based on windows and landscapes) or the important proximal stimulus ('object score' based on the metal box). In the example shown, the plant represents the spot where the participant dropped the virtual seed and the score is an object score of 7 points indicating the use of an egocentric strategy because the participant used proximal cues to locate the platform. Placement in the southeast quadrant leads to a room score and indicates the use of an allocentric strategy because the participant used distal room features to locate the platform. Placement outside of the target rings indicates no preference (a score of 0).

the quadrant where the platform had been located on the invisible trials and the second target filled the quadrant immediately adjacent to the important cue object that was now

on the opposite side of the arena. Scores ranged from "0" for seed placement outside the target area (and thus not in either 'correct' quadrant) to "7" for seed placement at the platform location. A perfect score of 7 could be achieved by placing the virtual seed either in the centre of the southeast quadrant of the arena (where the platform had been located on previous trials) or in the centre of the northwest quadrant (where the cue object was now located). Thus participants generated one of two scores indicating their accuracy with respect to either the distal landmarks (room and outdoor features) or the proximal cue (the box on the arena wall). These scores were deemed to reflect the use of an allocentric or an egocentric strategy, respectively. Because scores of 0 could not be interpreted, the strategy probe data of participants with a score of 0 was excluded from the analysis. Participants did not observe the scoring procedure.

*Verbal report question***.** The purpose of the verbal report question was to assess participants' environmental awareness. Specifically participants were asked if they noticed that the cue object had changed location for the strategy probe. Participants answered the question, "yes" or "no".

*Ancillary tasks***.** Several ancillary tasks (post-tests) were presented upon completion of the maze tasks. These were described (and the results reported) in a previous experiment but because the results are not relevant to the present experiment, they are not included here.

Computer gaming experience. Because the experiment concerned the effects of training in a virtual environment, participants were asked about their computer gaming experience. The description and reporting of this analysis is given in previous experiments (Experiments 1 & 2, this dissertation).

Demographic variables. Demographic variables were recorded from a background information questionnaire (Appendix 2-A) and included age, gender and education level. These variables were analyzed to assure that there were no confounds of age, sex, education or computer experience with the maze or gaze position variables. The medical variables were recorded for screening purposes. The data of participants who indicated medical problems were generally excluded from analysis if the problem in question was known to affect the ability to navigate.

Analysis. The data were summarized using Excel and inferential statistics were computed using SPSS® (Statistical Package for the Social Sciences). The navigation behavioural analyses were conducted to confirm that performance on maze tasks was similar to performance in prior studies and thus rule out the possibility that there was something unusual about the participant sample. The experimental results of interest were 1) differences in strategy selection based on training in either the Place or Cue maze and 2) differences in environmental awareness as measured by strategy selection and verbal report of whether or not participants noticed the relocation of the cue object in the strategy probe.

Maze variables. The maze data were analyzed using three conventional dependent measures of performance: 1) latency (time in seconds) to reach the platform, 2) distance (in pool diameters) travelled to the platform, and 3) dwell time or percentage of time spent searching in the correct quadrant of the arena on probe trials. Latency and distance variables were analyzed for trials 2 to 10, excluding the first trial because it is considered to be a search trial. The data collected in Unreal® were converted and analyzed using TRAM®, a locally developed software program.

*Statistics***.** Table 4.3 gives a summary of the main statistical tests proposed for this experiment. For the behavioural maze variables (latency, distance, and probe dwell time) a 2 x 2 repeated measures mixed ANOVA was conducted for each to compare performance on invisible platform trials 2 to 10 in the Dual-strategy testing maze to performance on trials 2 to 10 during training in either the Place or Cue maze. The purpose was to show that there was no particular effect of training type on navigation behaviour in the Dual-strategy maze testing trials. Frequency analyses (Chi-square) were conducted for the strategy probe to determine whether prior experience (place or cue training) was associated with which strategy (by room or by object) participants were using by the end of testing. A second frequency analysis was conducted for the verbal report question to show whether the strategy (by room or by object) that participants

Table 4.3.

Table of main statistical analyses for navigation behaviour and strategy selection.

Variable	Groups	Test
Latency	Training (place vs. cue) Testing (Dual-strategy maze)	2 x 2 repeated measures mixed ANOVA
Distance	Training (place vs. cue) Testing (Dual-strategy maze)	2 x 2 repeated measures mixed ANOVA
Probe	Training (place vs. cue) Testing (Dual-strategy maze)	2 x 2 repeated measures mixed ANOVA
Strategy probe	Training (place or cue) Strategy (by room or by object)	Chi-square
Verbal report	Strategy (by room or by object) Environmental awareness (notice or not notice object relocation)	Chi-square

selected was related to their awareness of the environment (noticing or not noticing the relocation of the cue object).

Secondary analyses were conducted to examine potential group differences in mastery of the basic procedural aspects of virtual navigation or in the accuracy of participants' explicit knowledge of the platform location at the end of training. For the Visible platform trials two t-tests were conducted for the variables latency and distance and comparing performance for the two experimental groups, place-trained and cue-trained. A similar test compared accuracy scores on the DTS trial for the two experimental groups.

Results

Visible platform trials. As expected, performance on the visible platform trials showed that all participants were able to follow task instructions and master the use of the joystick and that prior to training there were no detectable differences based on whether participants were assigned to either the place-training ((Latency, M = 3.8s, SEM =.22 ; Distance, M =.6pd, SEM =.004), or cue-training ((Latency, M = 3.7s, SEM =.29 ; Distance, M =.57pd, SEM =.003) condition.

Invisible platform trials. There was no effect of the type of training (place vs. cue) on navigational performance during testing in the Dual-strategy maze (Figure 4.8). A repeated-measures mixed ANOVA with two factors, training type (place or cue) and phase (training or testing) showed no overall effect of training type (place or cue) on latency to the platform and no interaction between training type and phase. However both types of training improved navigational efficiency in the Dual-strategy testing maze, $F(1,35) = 17.44$, $p < .001$, $r = .58$, but this effect was nearly the same, for both place and

cue-trained groups, and there was no significant difference between them. There was also no effect of type of training (place vs. cue) on the distance that participants traveled to the platform during testing in the Dual-strategy maze (Figure 4.8). As per latency, a repeated-measures mixed ANOVA with two factors, training type (place or cue) and phase (training or testing) showed no overall effect of training type (place or cue) on distance to the platform and no interaction between training and phase. Both types of training improved navigational efficiency in the Dual-strategy testing maze, $F(1,35) = 27.48$, $p < .001$, $r = .66$, but this effect was nearly the same, for both place and cue-trained groups, and there was no significant difference between them. Overall, performance during testing in the Dual-strategy maze reflected retention of training, and the effect of experience on navigational performance was that participants in both training groups found the platform more quickly and directly during testing than during training.

Probe trials. Knowledge of the platform location at the end of behavioural trials appeared to be better after testing than after training (Figure 4.8). A repeated-measures mixed ANOVA showed a main effect of training such that overall, participants demonstrated greater knowledge of the platform location on probe trials in the testing phase than in the training phase, $F(1,35) = 4.5$, $p < .05$, $r = .34$. However, this effect was much smaller than the training effects observed for the other navigation variables. Further, given the small variance among scores on the probe trial, it is not clear that the increase in dwell times after testing represents a meaningful improvement in knowledge of the platform's location. Participants demonstrated good knowledge of the platform location on probe trials after both training and testing spending over 55% of trial time

searching in the correct quadrant (Place maze training, *M* = 57%, *SEM* = 5%; Cue maze training, *M* = 58%, *SEM* = 6%; Dual-strategy maze and place-trained, *M* = 64%, *SEM* =5%; Dual-strategy maze and cue-trained, *M* = 61%, *SEM* = 5%). As per distance and latency, probe dwell time scores showed no significant effect of training type (place or cue) and no interaction of training type with phase (training or testing). Thus, the two types of training appeared to result in equivalent knowledge of the platform location and were not associated with differences in knowledge of the platform location at the end of testing.

Training Drop-the-seed (DTS) trial. Prior to testing in the Dual-strategy maze, participants in both training groups (place and cue) demonstrated a good effect of training by showing explicit and accurate knowledge of the platform location (Figure 4.8). Scores on the DTS trial showed that accuracy was slightly greater at the completion of cue training (*M* = 5.3, *SEM* = .6) when compared to place training (*M* = 5.0, *SEM* = .6) but this difference was not significant. On this trial 63% of participants in the cue-trained group and 55% of participants in the place-trained group had high scores of 6 or 7 indicating very good knowledge of the platform location. Most importantly, in both place-trained and cue-trained groups approximately 90% of participants dropped the seed marker in the correct quadrant of the arena indicating good understanding of the requirements of the DTS task, good knowledge of the platform location on invisible trials, and thus, successful training.

Acquisition in the testing phase. Trial by trial acquisition curves showed experience in the training phase (either place or cue) improved but did not eliminate the need for learning in the testing phase. Both latency and distance to the platform were

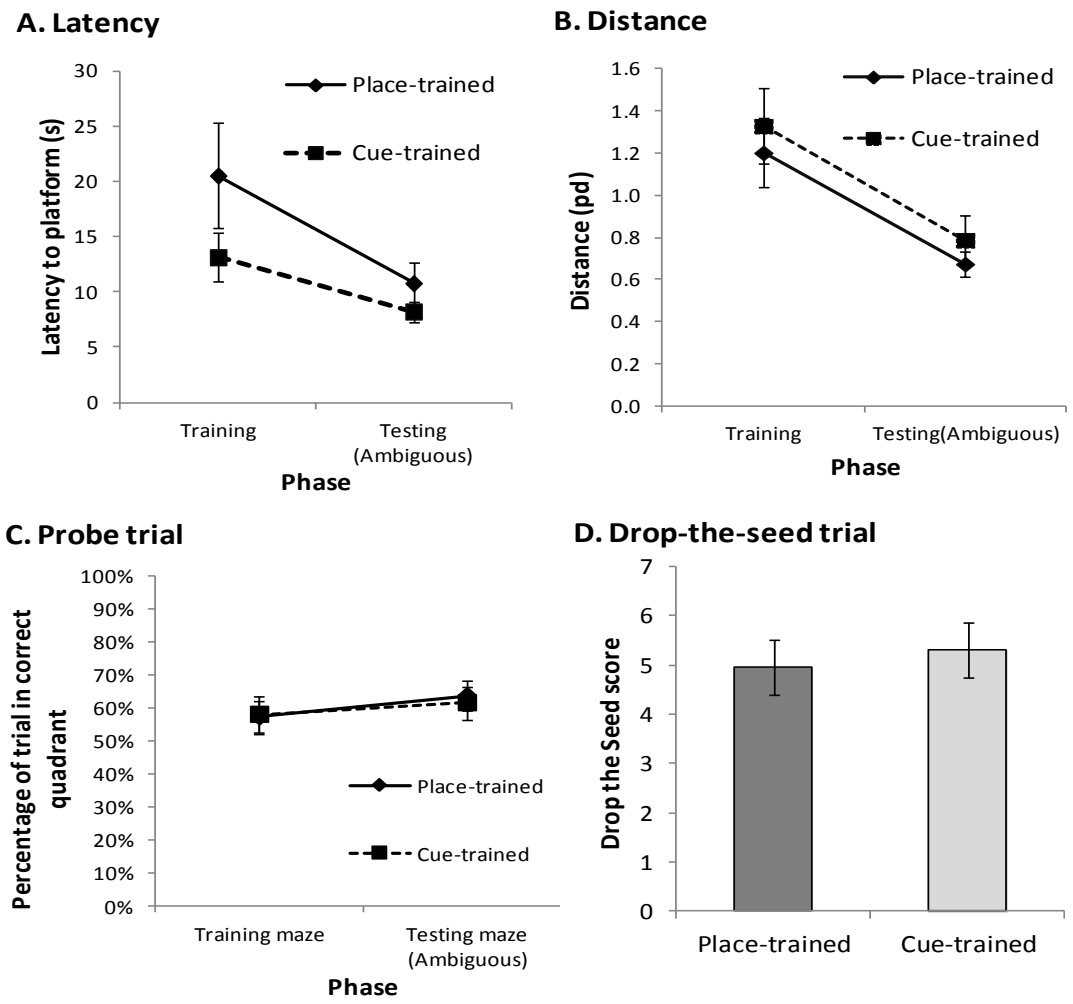

Figure 4.8. Results for navigation variables during training (place or cue) and testing (Dual-strategy maze). In general, performance did not differ for the two training groups. There was a significant difference in probe trial performance after testing. However, this difference was not considered meaningful. Note: pd = pool diameters.

greater on Trial 1 of testing than on the last two trials of training (Figure 4.9) indicating that participants required at least one trial to learn the platform location. The overall pattern of acquisition was similar for the place and cue-trained groups and both latency and distance to the platform improved across trials. By Trial 9 latency to the platform was less than 10s and distance less than .75 pool diameters for both groups indicating that participants were travelling to the platform quickly and directly by the end of testing.

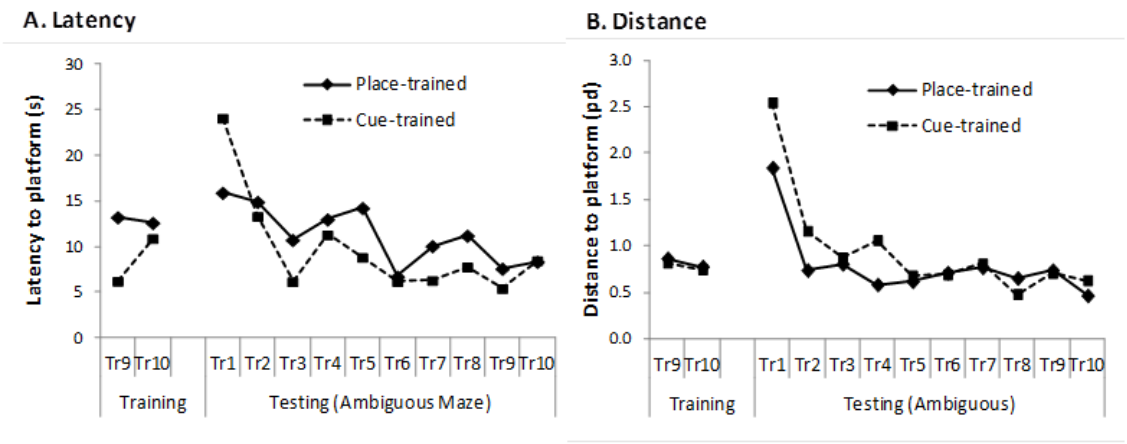

Figure 4.9. Acquisition curves for two navigation variables, latency **(A)** and distance **(B).** Participants took more time and less direct paths to the platform in Trial 1 of testing than in the later training trials. During testing the pattern of acquisition appeared to be similar for the two experimental groups (place-trained and cue-trained).

Identification of strategy groups. At the end of testing in the Dual-strategy maze nearly all participants demonstrated good knowledge of the platform location and a clear choice of strategy on the strategy probe (Figure 4.10). The majority demonstrated a preference to navigate by either the cue object or the room features and landscape. Only two participants scored zero on the strategy probe thus demonstrating incomplete knowledge of the platform location and no clear choice of strategy. Therefore the data from these participants was dropped from further analysis. The resulting sample size for the strategy analyses was 35 (17 cue-trained; 18 place-trained).

The type of training was strongly related to participant's selection of strategies. Cue-training was associated with the selection of an egocentric strategy whereas place-training was associated with the selection of an allocentric strategy. There was a significant association between the type of training (place or cue) and the choice of strategy (by room or by object) in the strategy probe l$\chi^2(1) = 22.09$, $p < .001$, phi = .70 (for this and all other chi-square analyses the likelihood ratio is reported due to the small

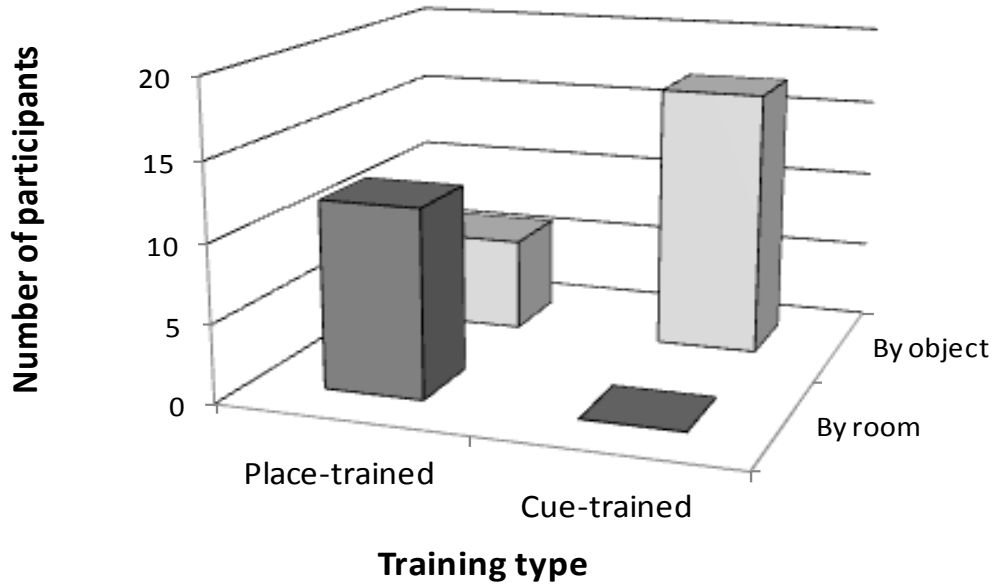

Figure 4.10. Frequency (by training type) of strategy preference at the end of Dual-strategy maze testing. The type of training was significantly associated with preferred strategy (by room or by object). All cue-trained participants indicated a preference for the cue object (cue-trained-egocentric) whereas place-trained participants were divided in their preference for the cue object (place-trained-egocentric) or more distal features of the room (place-trained-allocentric). Overall, two thirds of participants indicated an egocentric strategy whereas one third indicated an allocentric strategy.

sample size). However, the type of training did not perfectly correspond with strategy selection. On the strategy probe, all 17 cue-trained participants (100%) identified the platform location by the (relocated) cue object, indicating they were using an egocentric navigational strategy. Of the 18 place-trained participants, a sub-set of 6 participants (33%) identified the platform by the object whereas the remaining 12 (67%) showed an effect of their place-training by identifying the platform location by room features, indicating that they were continuing to use the allocentric strategy that they had learned in training. For convenience, these three groups of participants will henceforth be referred

to as “cue-trained-egocentric”(n = 17), “place-trained-egocentric”(n = 6), and “place-trained-allocentric”(n = 12).

Strategy selection and environmental awareness. The original intention of asking participants whether they noticed the objects were moved during the strategy probe was to corroborate or validate the strategy probe as a means of categorizing strategies used by individual participants. Indeed, there was a relationship between the strategy participants selected and their awareness of the environment as measured by their awareness of whether or not the cue object was relocated in the strategy probe. There was a significant association between the strategy (by room or by object) participants indicated and awareness (notice or not) of relocation of the cue object, $l\chi^2(1) = 14.29$, $p < .001$ (Figure 4.11). One place-trained participant did not answer the verbal

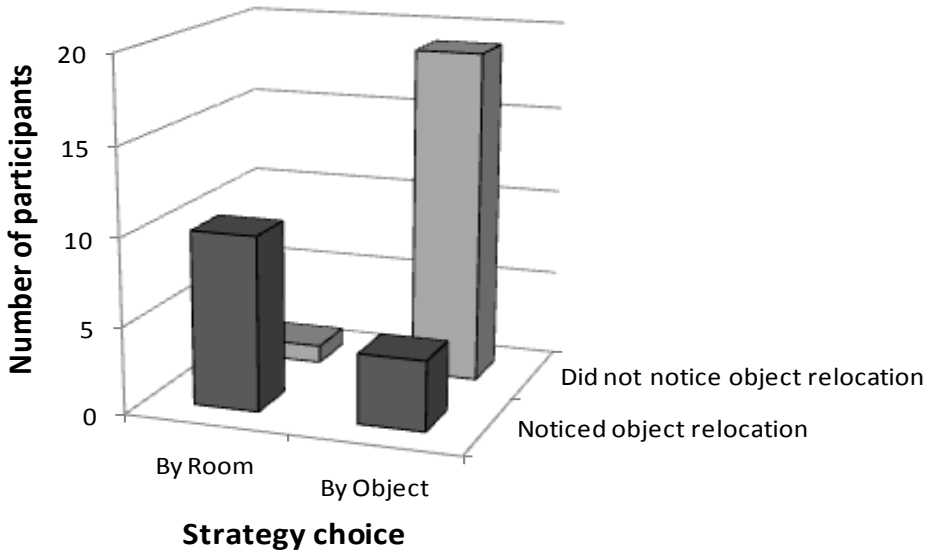

Figure 4.11. Frequency (by strategy) of noticing relocation of the cue object in the strategy probe at the end of Dual-strategy maze testing. Most participants who indicated navigating by the room (an allocentric strategy) noticed that the object had moved. Most participants who indicated navigating by the object (an egocentric strategy) did not notice that the object had moved.

report question and therefore this analysis was conducted for a sample of 34 participants (n = 17 place-trained, n = 17 cue-trained). Based on the odds ratio, participants were 52 times more likely to notice that the object had moved if they indicated navigating by room features than if they indicated navigating by the cue object. The majority (10/11 or 91%) of participants who utilized room features on the strategy probe reported that they had noticed that the object changed location. In contrast, the majority (19/23 or 83%) of participants who utilized the cue object on the strategy probe did not notice that the cue object had been moved. Thus most participants who utilized room features (an allocentric strategy) were aware of the location of the object in relation to these features (i.e., had formed a cognitive map) whereas most participants who utilized the object (an egocentric strategy) during orientation were either not aware of this relationship or chose to ignore it (i.e., had not formed or did not use a cognitive map).

Training and environmental awareness. Further analysis of the verbal reports and their relation to strategy probe results provided some interesting insights as to the processes controlling behaviour. Specifically there seemed to be a relationship between environmental awareness, strategy selection and pre-training. At the end of testing in the Dual-strategy maze, place-trained participants were more likely to indicate that they had noticed the relocation of the cue object than were cue-trained participants. There was a significant association between training type (place or cue) and whether or not participants noticed that the cue object had moved, l$\chi^2(1) = 4.49$, $p < .05$, phi = .36 (Figure 4.12). Based on the odds ratio, participants were 4.73 times more likely to notice that the object had moved if they were place-trained than if they were cue-trained. The majority (10/17 or 59%) of participants who were place-trained reported that they had

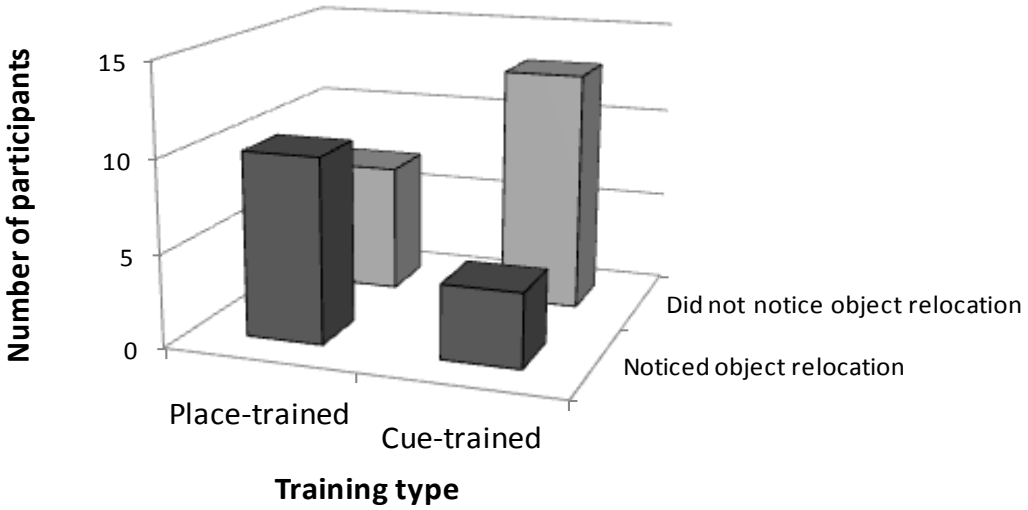

Figure 4.12. Frequency (by training type) of noticing relocation of the cue object in the strategy probe. There was a significant association between type of training (place or cue) and whether or not participants appeared to form a cognitive map by the end of testing in the Dual-strategy maze; i.e., did they notice object relocation during the strategy probe. Place-trained participants were more likely to notice object relocation (form a cognitive map) than were cue-trained participants.

noticed that the object changed location. In contrast, the majority (13/17 or 76%) of participants who were cue trained did not notice that it had been moved.

Proposed path from training to strategy. In order to investigate the apparent relationship of training to awareness of the environment and ultimately to strategy selection, the three variables were examined together. Figure 4.13 illustrates the combination of training (experience), verbal report (environmental awareness of the cue object relocation) and strategy selection (allocentric or egocentric). Participants in the cue-trained-egocentric group were rarely aware of the relocation of the cue object. In contrast almost all participants in the place-trained-allocentric group noticed the relocation of the cue object. Interestingly, all participants in the place-trained-egocentric group reported that they did not notice the relocation of the cue object, thus

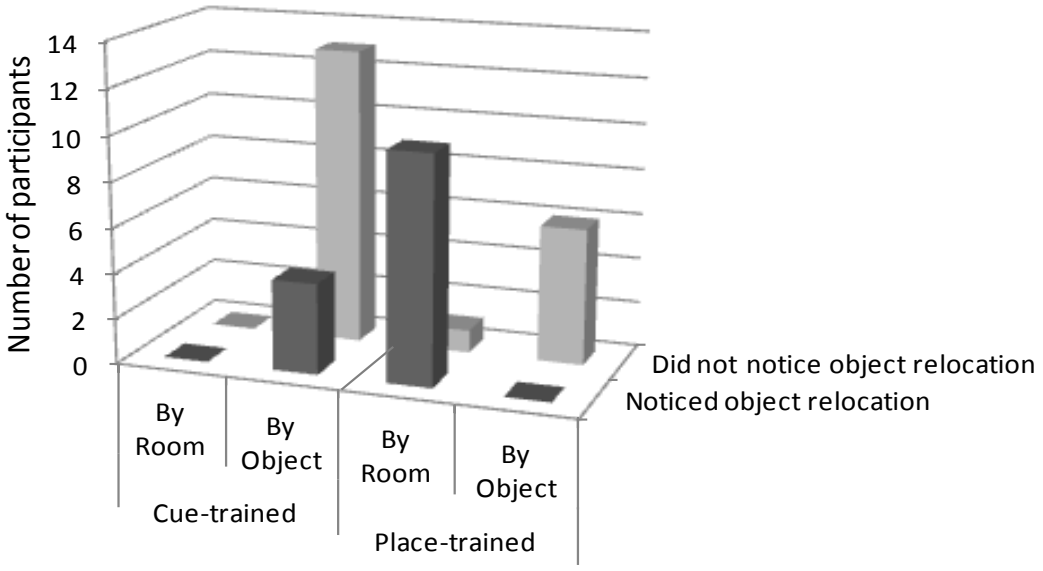

Figure 4.13. The relationship of three variables, training (place or cue), verbal report (notice or not notice object relocation) and strategy selection (by room or by object). All cue-trained participants selected an egocentric, object-based strategy and most reported that the cue object had not been relocated for the strategy probe. Most place-trained participants selected an allocentric strategy and cue object relocation was noticed only by place-trained participants who showed this allocentric strategy.

demonstrating a pattern of data similar to that of the cue-trained-egocentric group. Unfortunately, the sample size required to analyze this data using a loglinear approach is greater (n = 60) than the available sample size in the current experiment (n = 37).

The data reported above suggest a pathway from training (experience) to strategy that is mediated by environmental awareness. This proposed pathway appears to be important for place-trained but not for cue-trained participants (Figure 4.14). Experience in the Cue maze was associated with the selection of an egocentric strategy in all cases, regardless of environmental awareness (of the relocation of the cue object). However, experience in the Place maze, was associated with an allocentric strategy when the

Training	Place			Cue		
# of participants	17			17		
Environmental Awareness (of object move)	**Yes** (M/F)	**No** (M/F)	Sum	**Yes**	**No**	Sum
	10 (6/4)	7 (3/4)		4	13	
Egocentric Strategy (by object)	0	6	6	4	13	17
Allocentric Strategy (by room)	10	1 (0/1)	11	0	0	0

Figure 4.14. The proposed effect of training (experience) and environmental awareness on strategy selection. Environmental awareness appeared to be important for the place-trained but not the cue-trained participants. The black arrows indicate a proposed path from training to strategy via environmental awareness for the place-trained group. The dotted arrow indicates a direct path from training to strategy for the cue-trained group. This table suggests that gender (M = male, F = female) had little or no effect on strategy selection: In essence, place-trained participants who noticed the object move chose an allocentric strategy, and those who did not notice it move did not, regardless of gender.

participant was aware of the environment (i.e., noticed cue object relocation and in 10/11 cases) and with an egocentric strategy only when the participants were not aware of the environmental cues (did not notice cue object relocation). Thus, experience with place-based navigation appeared to be important for the selection of an allocentric strategy during testing, but only in cases where the participant developed an awareness of the environment that included an understanding of local cue objects and their spatial relationship to other more distal features (e.g., landscapes). Without this environmental awareness, place-trained participants responded like cue-trained participants by selecting an egocentric strategy at the end of testing in the Dual-strategy maze (i.e., they formed the place-trained-egocentric group).

Gender effects. Although this study was not directly concerned with gender or sex difference effects, two preliminary observations are reported here. The first is that after place training, gender may have contributed to environmental awareness, although the numbers of participants involved do not allow for any definite conclusion. The ratio of noticing to not noticing (the relocation of the cue object) was approximately 2:1 for males and 1:1 for females (Figure 4.14). That is, two-thirds of place-trained males were aware of the environmental change, whereas only half of place-trained females developed this awareness. However, the second observation is that gender did not contribute to strategy selection. Among the place-trained participants the choice of allocentric or egocentric strategy did not differ by gender. Rather, environmental awareness seemed to be the controlling factor.

Summary. Overall, navigation behaviour was good in all maze conditions and slightly better during testing than during training. The strategies (either allocentric or egocentric) that participants selected at the end of testing were strongly related to the type of training they received and also to their awareness of the spatial relations of stimuli in the environment. Allocentric strategy selection was associated with place training and awareness of the location of the cue object whereas egocentric strategy selection was associated with place training and with limited awareness of the location of the cue object.

Part B (Gaze Position and Strategy)

Methods

In this experiment, eye movements were tracked throughout training and testing. However, for clarity, the results of the behavioural measurements and the gaze position

measurements are being presented separately. Thus the participants, experimental design and behavioural procedures were identical to those reported in Part A. The only exception was that the data from two untrained participants was removed from the analysis because they did not select a strategy and therefore could not be included in the strategy analysis. Thus there were 35 participants in all (cue-trained-egocentric, n = 17; place-trained-egocentric, n = 6; place-trained-allocentric, n = 12). Appendix 3-B gives the experimental protocol, including the protocol for the eye movement tracking. Additional procedures and analyses relevant to the measurement of gaze positions are described below.

Apparatus.

Participant's gaze positions were recorded using a remote eye tracking system consisting of an LED-infrared lighting system (Hamamatsu Corporation) and a Flea Firewire Camera (Point Grey Research). The technology for the tracking device was developed by CanAssist, (Canadian Institute for Accessibility and Inclusion at the University of Victoria). The device recorded monocular positional coordinates at a rate of 60 samples per second. Two computers were set up to simultaneously present the virtual mazes and to log the eye movement data. A television and digital video disk (DVD) player (hidden to the participant) recorded the screen output overlaid with the gaze position. In this manner, the experimenters could directly view the eye movements of participants as they navigated the virtual environment.

Procedures.

Before the experiment began, participants were tested to determine which was their dominate eye so that this eye could be selected for monocular tracking. The test was a variant of the Porta test (reported in Roth, Lora, & Heilman, 2002) (for script see

Appendix 3-B) and based on principles described by Miles (1930). After the dominance test participants were comfortably seated in front of the computer screen with their heads supported in a chin rest for the duration of the maze testing. A 9-point calibration of the eye tracking camera was performed for each participant before testing began (for script see Appendix 3-B). This calibration consisted of participants first fixating on a small circle (containing a letter) in the upper left of the screen display. Participants were asked to verbally repeat the name of the letter (the letter occasionally changed) and to continue staring at the circle. Once calibration of the first location was complete the circle moved to another spot on the display and participants repeated the process for a total of nine locations on the screen. The ability of the participant to name the letters ensured that visual acuity was adequate for completion of the maze tasks and for recording of gaze positions.

Participants also completed a "baseline" task in which they were instructed to follow the movement of the tip of a pen horizontally across the entire width of the display at the vertical midline. The resultant data provided information about individual differences in vertical gaze position. In this way the data for individuals could be adjusted up or down in accordance with their tendency to look either slightly above or slightly below the midline of the screen. This baseline adjustment allowed for the comparison of the gaze positions of different individuals. Once the calibration and baseline tasks were completed, participants began the navigation tasks (Part A) and their gaze positions were recorded for the duration of the experiment.

Analysis. The data were summarized using Excel® and inferential statistics were computed using SPSS®. Heat maps of the eye tracking data were generated using

MATLAB® (Matrix Laboratory). The key variables were vertical and horizontal gaze position. These variables were analyzed with respect to both the type of training (place or cue) participants received and the strategy participants indicated at the end of testing in the Dual-strategy maze.

*Eye tracking variables***.** For this analysis both vertical and horizontal gaze positions were examined. For the purpose of analyzing vertical (or y-axis) gaze position, the size of the objects in the Cue maze and the Dual-strategy testing maze was modified so that they always appeared below a horizon that divided the screen display into upper and lower halves (Figure 4.15). The Place Maze was designed to train participants to utilize the outdoor landscapes (distal stimuli) that always appeared above this horizon. In contrast, the Cue Maze was designed to train participants to utilized objects (proximal stimuli) that always appeared just below the level of the horizon. The Dual-strategy maze was designed to test whether participants utilized the outdoor landscapes or the nearby objects when they were free to choose either strategy. To quantify vertical gaze position, the uppermost point of the screen display was assigned a value of 0 and the lowermost point a value of -600 with the horizon having a value of -300 (Figure 4.15). The variable of interest was vertical gaze position as defined by position on the y-axis. This measures was analyzed for the first second (60 samples) of trial data based on findings from the feasibility work and a recent study (Livingstone-Lee et al., 2011) showing that spatial orientation to the relevant stimuli occurs within this time frame. Horizontal (or x-axis) gaze position was quantified in a similar way to vertical gaze position, by splitting the screen display at the horizontal midline (Figure 4.16). The far left point of the screen display was assigned a value of 0 and the far right a value of 800, with the midpoint of

Figure 4.15. Definition of the vertical horizon on the display. During navigation and from all viewpoints in the arena the objects (proximal stimuli) in the Cue Maze appeared below a horizon (marked here by the black line) that split the screen display in half. All of the outdoor landscapes (distal stimuli) were located above this horizon. The horizon (at a value of -300) was located at the vertical midline of the display.

the display having a value of 400. The display was divided into five equal sections (of 160 units each) with the middle section centred at 400 on the x-axis (Figure 4.16). The sections were labelled far left (0-160), left (160-320), centre (320-480), right (480-640), and far right (640-800). The two variables of interest were horizontal gaze position (defined by position on the x-axis) and the percentage of trial gaze in each of the five sections of the screen. For ease of analysis data from the "off-centre" sections (left, far left, right, far right) were collapsed so that the gaze position variable had two categories, "percentage off-centre" and "percentage on-centre".

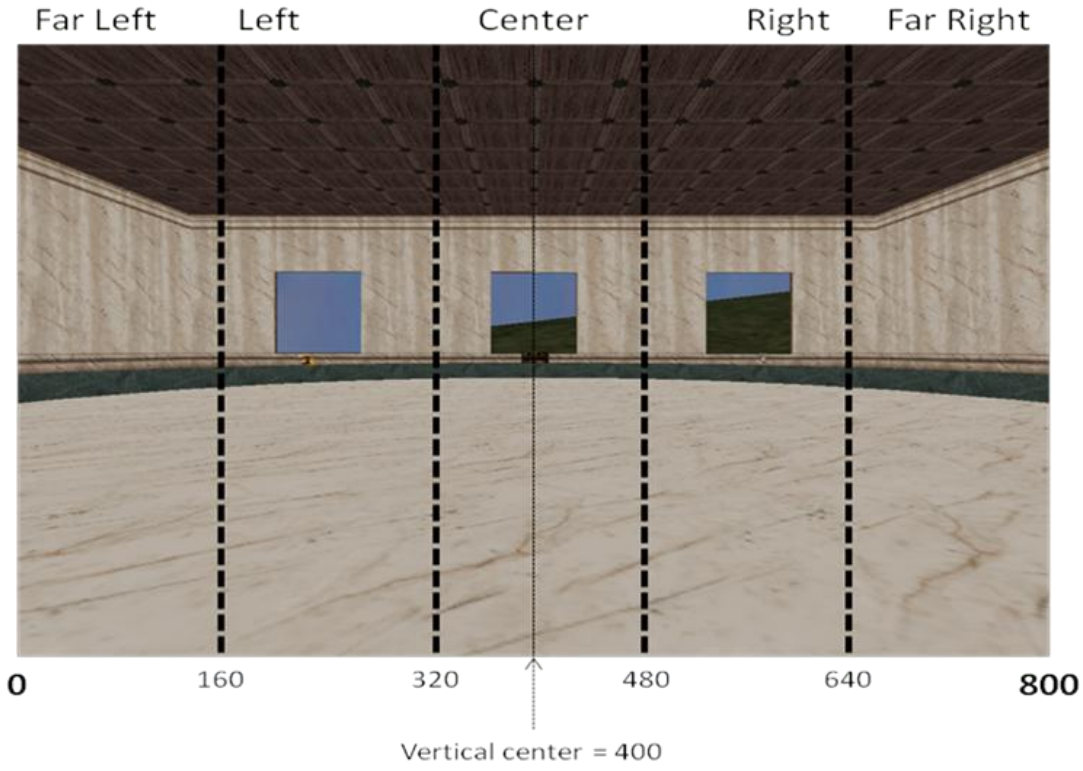

Figure 4.16. Definition of "on-centre" and "off-centre" horizontal gaze position. Screen segments are shown for one Cue maze start position. For analysis the screen display was divided into 5 equal segments with the middle segment defining "on-centre" gaze with a central value of 400. All other segments were defined as "off-centre" gaze. The display was 800 units (pixels) wide and therefore each segment was 160 units wide. Note that the cue objects appeared in the left, center and right segments but not in the far left or far right segments.

*Combining horizontal and vertical gaze positions***.** To analyze horizontal and vertical gaze positions combined, 10 regions of interest were defined (Figure 4.17). These regions were then collapsed into four regions selected to exclude areas of the display where there was little or no participant gaze and to include areas where participants looked most frequently. They captured over 90% of gaze for both the Place and Cue mazes. They four regions were defined as 1) on-centre and above the horizon, 2) on-centre and below the horizon, 3) off-centre and above the horizon, and 4) on-centre and

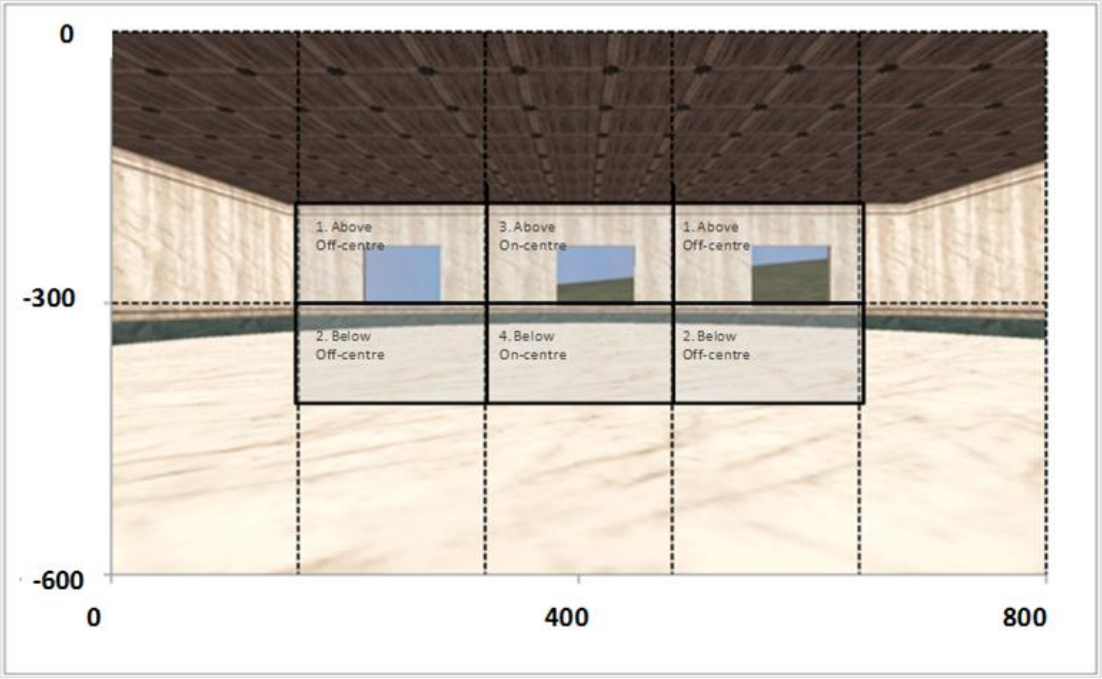

Figure 4.17. Regions of interest combining vertical and horizontal gaze position. View of the Place maze from one of four start positions. The display was divided vertically into two segments (above and below the horizon) and horizontally into five segments. Dotted lines indicate the resulting ten regions of interest. For analysis regions of interest were selected because they incorporated the majority of participant gaze in the mazes. The resulting regions compared were 1) Above and off-centre, 2) Below and off-centre, 3) Above and on-centre, and 4) Below and on-centre.

below the horizon.

*Statistics***.** Table 4.4 gives a summary of the main statistical tests for this experiment. For vertical gaze position in the Dual-strategy maze a one-way ANOVA was conducted for the three strategy groups (cue-trained-egocentric, place-trained-egocentric, place-trained-allocentric) to test the hypothesis that allocentric strategy selection would be associated with higher gaze positions than would egocentric strategy selection. Data from the two egocentric strategy groups were then collapsed so that further contrasts

could be conducted for egocentric and allocentric strategists. The acquisition of vertical gaze was investigated by utilizing t-tests to determine whether gaze in Trial 2 of the Dual-strategy maze was significantly higher than in Trial 1 for both egocentric and allocentric strategists. For horizontal gaze position in the Dual-strategy maze, a t-test compared on-centre gaze for the egocentric and allocentric strategy groups to test the hypothesis that allocentric strategists would have more central gaze than egocentric strategists. An exploratory analysis was conducted for select regions of interest on the display and by combining vertical and horizontal gaze position data. This analysis consisted of a 2 x 2 x 2 mixed repeated-measures ANOVA (vertical gaze x horizontal gaze x strategy) to determine whether egocentric and allocentric strategists differed in their gaze in the regions of interest during orientation in the Dual-strategy maze.

Table 4.4.

Table of main statistical analyses for gaze position and strategy selection.

Variable	Groups	Test
Vertical gaze position	Strategy groups (3) (place-trained-allocentric, place-trained-egocentric, cue-trained-egocentric)	One-way ANOVA
Vertical gaze position (Trial 1 & Trial 2)	Strategy groups (2) (allocentric and egocentric)	t-test (2)
Horizontal gaze position (on-centre)	Strategy groups (2) (allocentric and egocentric)	t-test
Vertical gaze (above/below) Horizontal gaze (on-centre/off-centre)	Strategy groups (2) (allocentric and egocentric)	2 x 2 x 2 mixed repeated- measures ANOVA

A secondary analysis was conducted to determine whether computer gaming experience might have influenced strategy selection. A one-way ANOVA compared experience scores for the three strategy groups (cue-trained-egocentric, place-trained-egocentric, place-trained-allocentric).

Gaze Position Results

Strategy choice and vertical gaze position. The primary objective of the present study was to examine the effect of experience on strategy selection. Two methods were used to assess strategy selection: the strategy probe (described in Part A) and gaze position during orientation on each trial of the Dual-strategy maze. Unexpectedly, training did not appear to affect where participants looked during the first orientation second of trials in the Dual-strategy maze, nor did gaze position in testing predict ultimate strategy choice. The data from one participant in the place-trained-allocentric group was removed at this point because eye movements on some trials during the testing phase were not recorded by the camera. Therefore the sample for the analysis of vertical gaze position consisted of 34 participants (cue-trained-egocentric, n=17; place-trained-egocentric, n = 6; place-trained-allocentric, n = 11). During testing in the Dual-strategy maze, participants looked at or near to the horizon, regardless of which training they received or which strategy they indicated using at the end of trials. Figure 4.18 shows that the differences between the gaze positions of participants in training was no longer present during testing the Dual-strategy maze. A one-way ANOVA comparing average gaze position during testing for the three strategy groups (cue-trained egocentric, place-trained egocentric, place-trained allocentric) was non-significant. Vertical gaze position during the first second of orientation was slightly higher in the place-trained-allocentric

group (*M* = 298, *SEM* = 11) than in the cue-trained-egocentric group (*M* = 291, *SEM* = 5). However, for the place-trained-egocentric group vertical gaze position was highest (*M* = 301, *SEM* = 10).

Because results for vertical gaze position differed from previous findings, the data was examined more closely for outliers. Figure 4.18 shows the group means after the removal of data from one participant (place-trained-egocentric) with a vertical gaze position approximately 1.9 standard deviations beyond the group mean. Although removal of this data did not affect the statistical result, it did show that the trend observed in the feasibility study was similar to that in the current results. Participants indicating an allocentric strategy had slightly higher vertical gaze position than participants indicating an egocentric strategy. Nevertheless, the clear differences in gaze position seen during training were not present during testing in the Dual-strategy maze.

Percentage of gaze above horizon. This measure of gaze position showed the same pattern of results and statistical (non) significance as gaze position.

Average vertical gaze position and the effect of experience. To explore the discrepancy between the current results and those of the preliminary study, the average gaze across the first second of orientation was examined to determine whether the whole time period was equally indicative of attention/strategy selection. As can be seen in Figure 4.19, the overall pattern of orientation gaze was similar for training and testing. Gaze rose gradually to reach a peak at about a third of a second (20 samples) and gradually fell thereafter. Overall, average vertical gaze in the testing maze was lower than gaze during place training and was slightly higher than gaze during cue training. However, while it can be safely assumed that participants in each training condition were

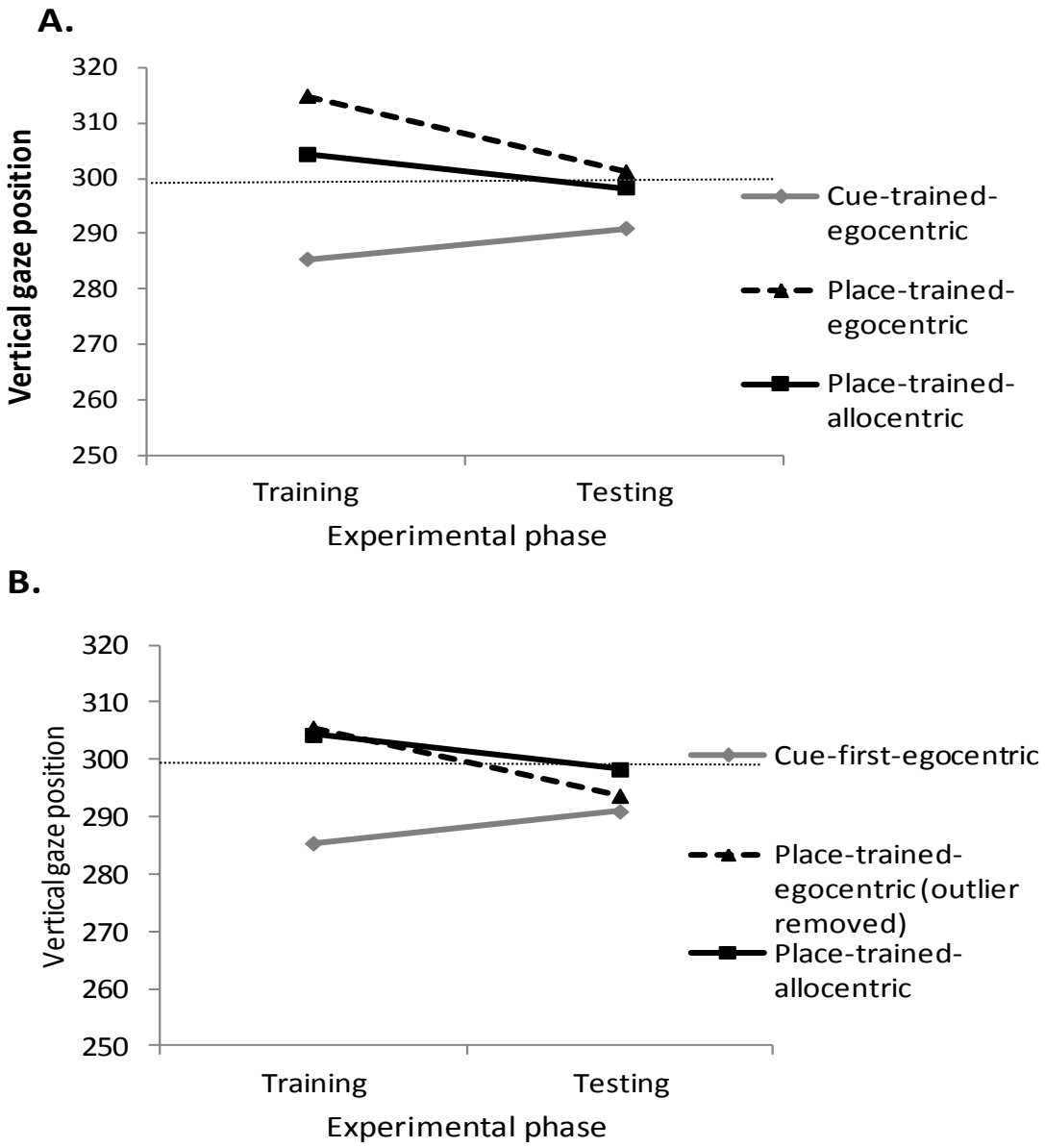

Figure 4.18. Vertical gaze position for the three strategy groups (with and without outlier data). During training vertical gaze positions were higher for place-trained participants than for cue-trained participants. During testing, gaze converged on the horizon, regardless of the strategy (egocentric or allocentric) participants indicated. During testing, the high gaze position of place-trained-egocentric participants **(A)** was unexpected. However removal of data from one outlier **(B)** revealed an expected (but small) trend such that allocentric strategists looked slightly higher than egocentric strategists during testing in the Dual-strategy maze.

following the same navigational strategy, this was not likely to be the case in the Dual-strategy testing maze. Therefore, what is most interesting is the difference in patterns between those navigating using different strategies, that is, the comparison between the three strategy groups.

Although the general pattern of gaze was similar for the three strategy groups (Figure 4.19) gaze position over the first second appeared to have two phases. For all three strategy groups gaze was low in the early part of trials, rising to a peak at about a third of a second and gradually falling thereafter. However, the difference between allocentric and egocentric strategy groups appeared substantial in the first 250 ms (15 samples) of orientation gaze whereas no such difference appeared to be present in the remaining 750ms of orientation gaze. In fact, by about 300ms the gaze appeared to converge on the horizon in all three strategy groups. This pattern of early difference in allocentric and egocentric gaze with later convergence was even clearer when the aforementioned outlier's data was excluded from the average (Figure 4.19). Therefore, in the subsequent investigation of strategy differences only the first 250 ms of gaze were analyzed, the outlier's data were excluded and participants were grouped according to the strategy (either allocentric or egocentric) they selected at the end of Dual-strategy maze testing. Henceforth, these groups will be referred to as allocentric strategists (n = 11) and egocentric strategists (n = 22).

Development of strategy differences. During Dual-strategy maze testing there were fleeting differences in gaze position that corresponded to the utilization of egocentric and allocentric strategies. A trial by trial analysis showed that these strategy differences (as indicated by gaze position) developed early in the testing sequence and

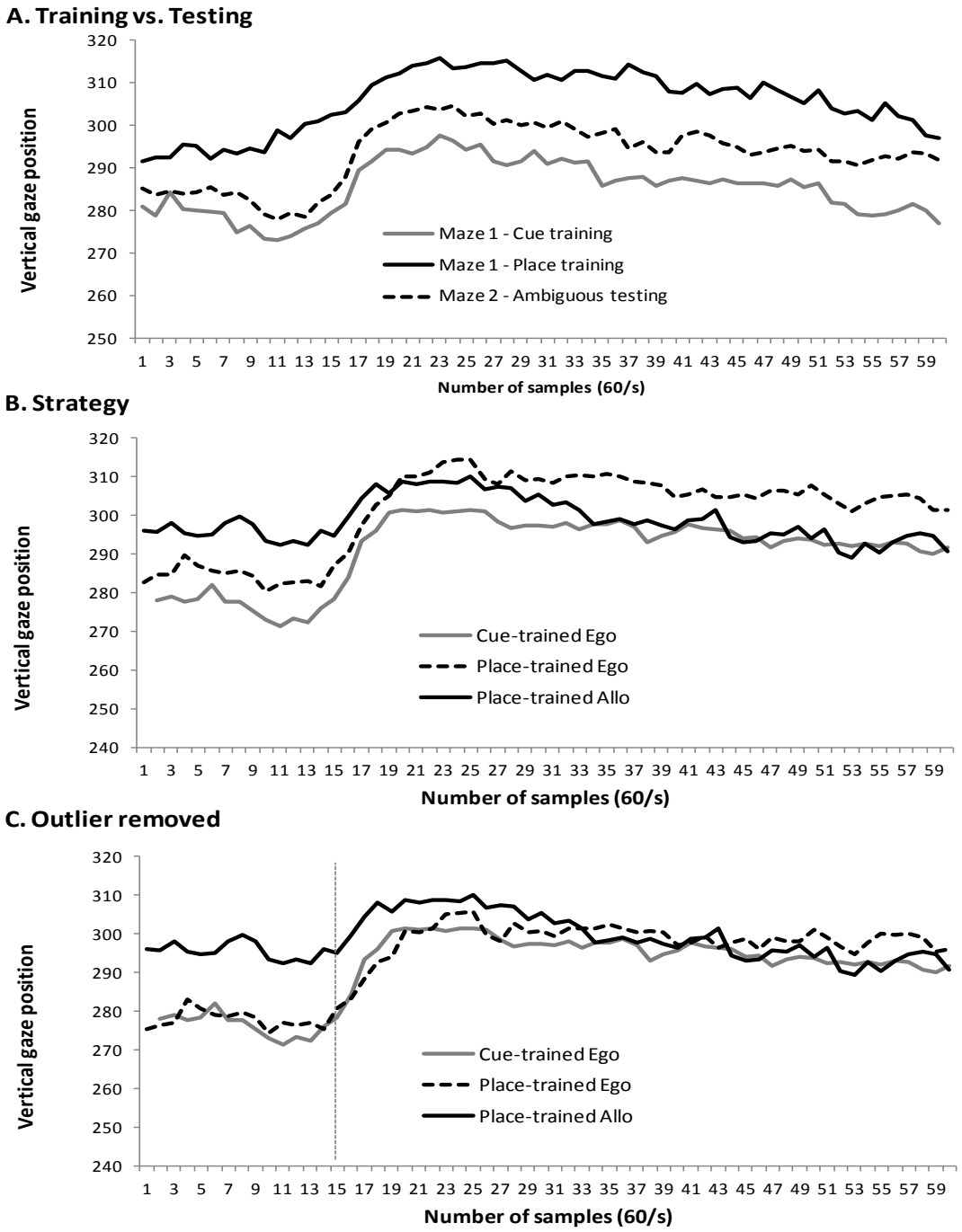

Figure 4.19. Average gaze position during the first second of trials according to maze and strategy. Vertical dotted line represents the 250ms mark of the first second of orientation gaze.

were greatest near the midpoint of the sequence. When vertical gaze position in the first 250 ms was averaged trial by trial and compared for the two strategy types (allocentric

and egocentric) participants in both strategy groups looked well below the horizon on the first 'search' trial but thereafter began to direct their gaze gradually upward (Figure 4.20).

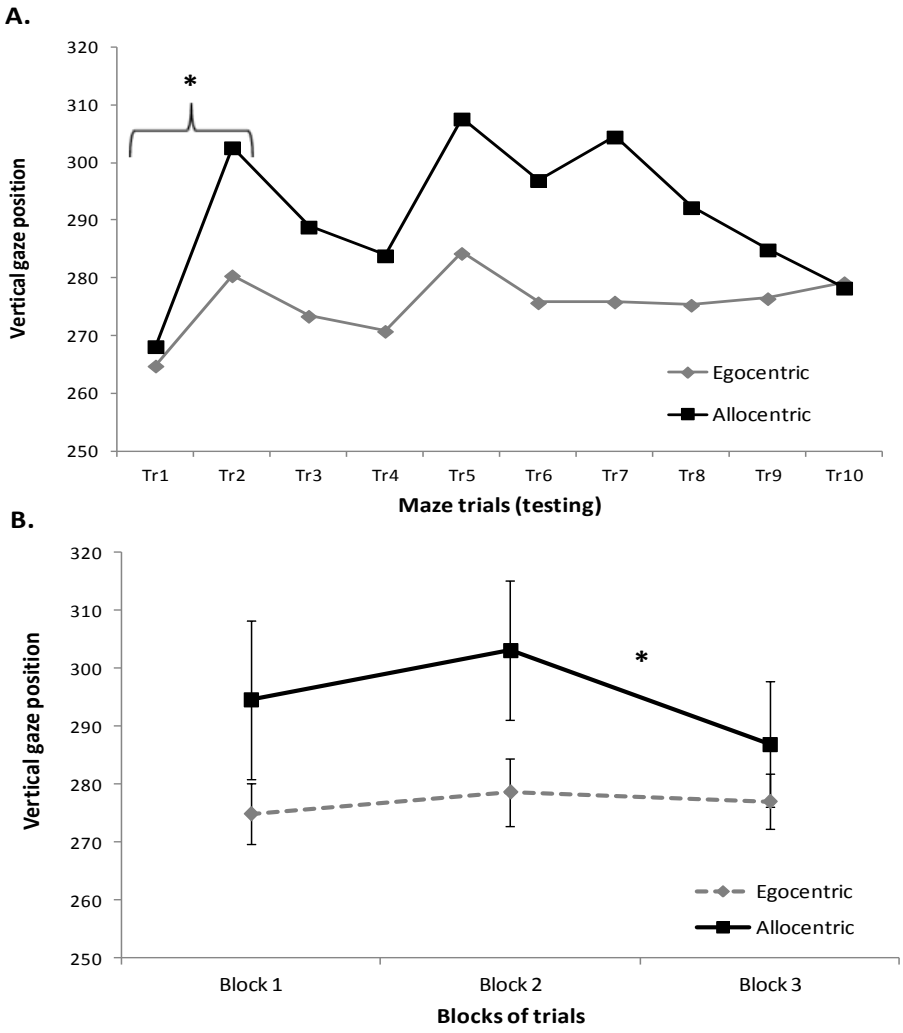

Figure 4.20. Acquisition of vertical gaze position is related to strategy type (allocentric and egocentric) in the first 250 ms of orientation in the Dual-strategy maze. **A.** Participants in both strategy groups had significantly higher gaze (*) in Trial 2 than in Trial 1 (search trial). After trial 1 participants who indicated using an allocentric strategy consistently had higher gaze than those who indicated an egocentric strategy. However, gaze position converged by the 10th trial. **B.** When trials 2-10 were divided into 3 blocks of 3 trials each, gaze position in the middle block (Block 2) of testing trials was significantly higher for the allocentric strategists than for the egocentric strategists and there was a significant interaction (*****) of trial block (2 vs. 3) with strategy type (allocentric vs. egocentric). Note. Trial 1 is not included because it is considered a search trial, i.e., the participant was as yet unaware of the location of the platform and uninformed as to which environmental features would signal its location.

A comparison of change in gaze position from Trial 1 to Trial 2 showed that overall participants looked higher on the screen display in Trial 2 than in Trial 1, $t(32) = 4.08$, $p < .001$, $d = .45$. This effect was also present for both allocentric, $t(33) = 2.14$, $p < .05$, $d = .38$, and egocentric strategists, $t(33) = 3.15$, $p < .01$, $d = .55$, when tested separately. Allocentric strategists looked higher in the first 250ms of testing trials than did egocentric strategists. By the second Dual-strategy maze testing trial a separation of vertical gaze position was observed between the two strategy groups such that allocentric strategists looked higher on the screen display than did egocentric strategists on all but the last trial (Figure 4.20). However, when vertical gaze position in trials 2-10 was compared, the difference between strategy groups was not significant. Therefore a trial block analysis was conducted to identify where in the testing sequence the gaze position of allocentric and egocentric strategists differed. For this analysis three blocks of trials were compared (Block 1 = early trials 2-4, Block 2 = middle trials 5-7, Block 3 =late trials 8-10). In a 2 x 3 mixed repeated measures ANOVA, there was no significant effect of strategy or block. However, simple post hoc contrasts of Block 1 and 3 and blocks 2 and 3 showed that overall vertical gaze position was higher in block 2 (middle trials) than in block 3 (late trials), $F(1,31) = 4.52$, $p < .05$, $r = .36$. An interaction in block 2 and block 3 further indicated that allocentric strategists had significantly higher gaze in Block 2 than did egocentric strategists whereas gaze position for the two strategy groups appeared to converge in Block 3, $F(1,31) = 5.68$, $p < .05$, $r = .39$.

Further analysis of strategy differences. To further investigate the difference between allocentric and egocentric strategies in early orientation, differences in gaze position for the two strategy types were examined utilizing heat maps and measures of

horizontal as well as vertical gaze position. This analysis focused on data from the second trial block (trials 5-7) of testing where vertical gaze position differed for the allocentric and egocentric strategists. However, it should be noted that these strategy differences were ephemeral, occurring only in the first 250 ms of trials and during the middle block of testing trials. Earlier work indicated that differences should have been present in the whole first second of trials and in all testing blocks (Livingstone, 2009). Further, the difference in gaze position for the two strategies was expected to be larger than the effect reported here. Nevertheless, the illustrations below show some separation of gaze position by strategy as well as training, suggesting that orientation for navigation depends on the combination of experience (i.e., training) and preferred strategy.

Heat maps. During early orientation in the middle trials of Dual-strategy maze testing, allocentric and egocentric strategists looked in slightly different places on the screen display. Heat maps of averaged gaze position data were created in order to qualitatively show vertical and horizontal gaze position during early orientation (i.e., the first 250ms) of invisible platform in the middle of testing (i.e.,Trials 5 to 7) (Figure 4.21). Gaze position frequencies were summed by participant and then averaged by group (egocentric and allocentric strategists). Egocentric strategists tended to distribute their gaze widely and primarily below the horizon. Allocentric strategists tended to look more centrally and higher above the horizon.

Horizontal gaze position and strategy. Because the gaze of egocentric strategists appeared to be lower and more distributed, horizontal gaze positions were examined for differences between the strategy groups. Figure 4.22 shows the frequency distributions (in 5-pixel bins) of both vertical and horizontal gaze positions in middle

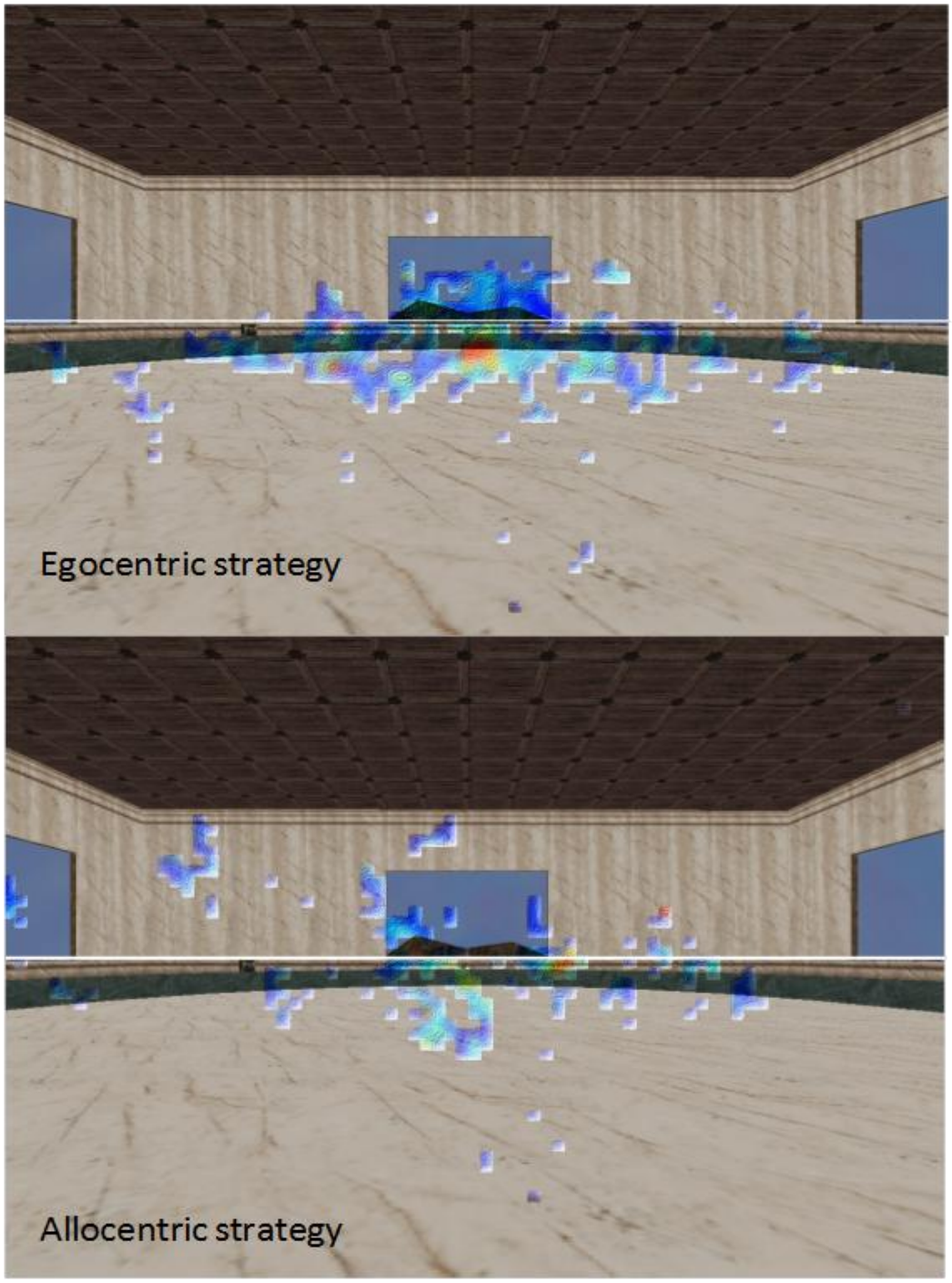

Figure 4.21. Heat maps of gaze positions during the first 250ms of middle testing trials and for two strategy types (allocentric and egocentric). The data contributing to the heat maps was "auto-ranged" so that for each map the colour range of data corresponds to minimum to maximum "heat" for the individual data array. For both images, the horizontal white line indicates the location of the horizon.

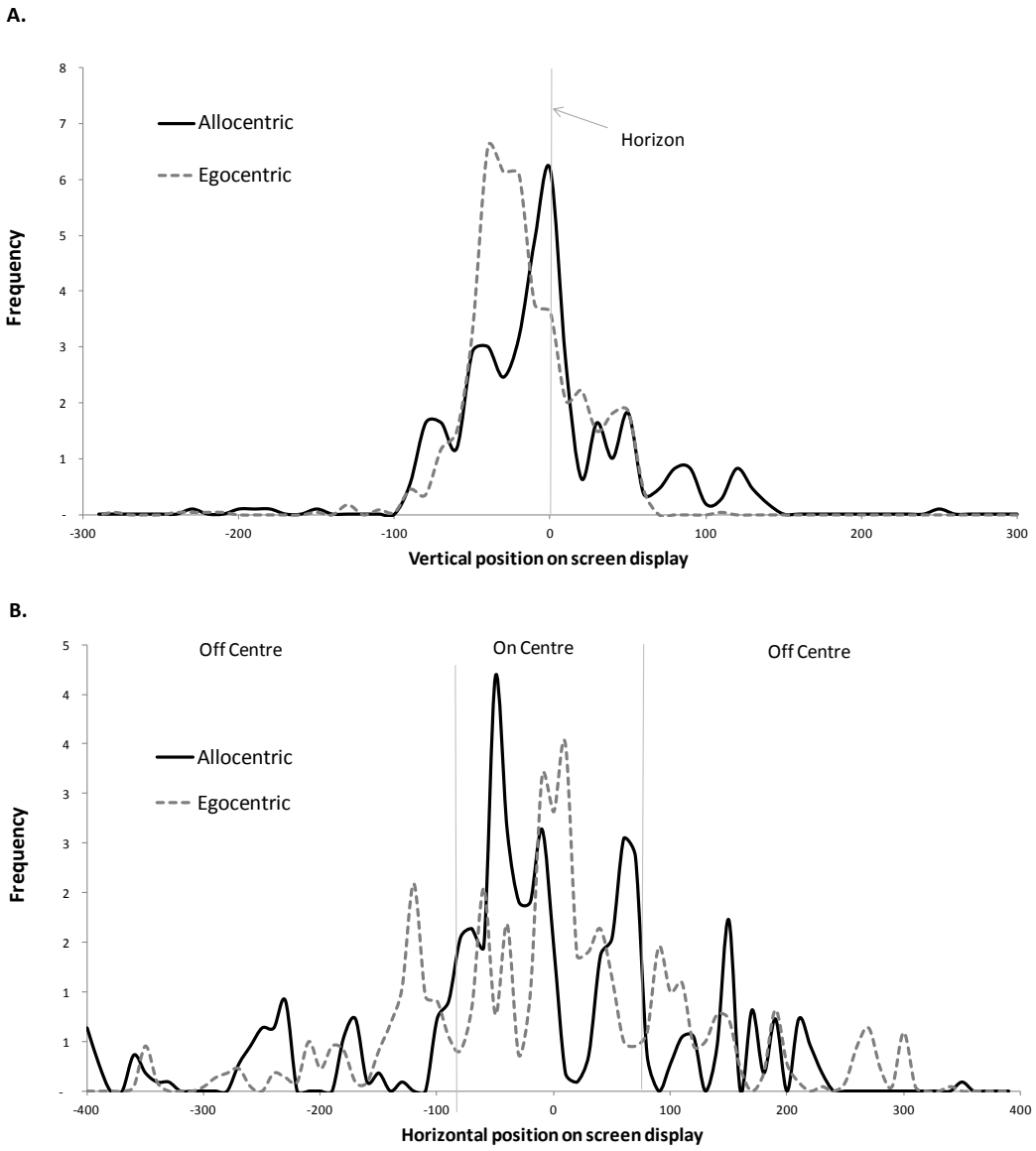

Figure 4.22. Histograms for vertical and horizontal gaze in Trial Block 2 of Dual-strategy maze testing and based on indicated strategy (allocentric or egocentric). **A.** Peak vertical gaze position was higher (further to the right) for allocentric than for egocentric strategists confirming that allocentric strategists looked higher during testing than did egocentric strategists. **B.** Horizontal gaze was distributed across the display for both strategy groups with both groups having more on-centre than off-centre gaze.

trials (5-7) of Dual-strategy maze testing and for the first 250ms of orientation. The vertical distributions confirm that allocentric strategists looked higher on the display than did egocentric strategists. The peak of vertical gaze was near the horizon for the

allocentric strategists and below the horizon for the egocentric strategists. The horizontal distributions also illustrated some differences between the two strategy groups (Figure 4.23) but these differences appeared to be small. Gaze was distributed across the display

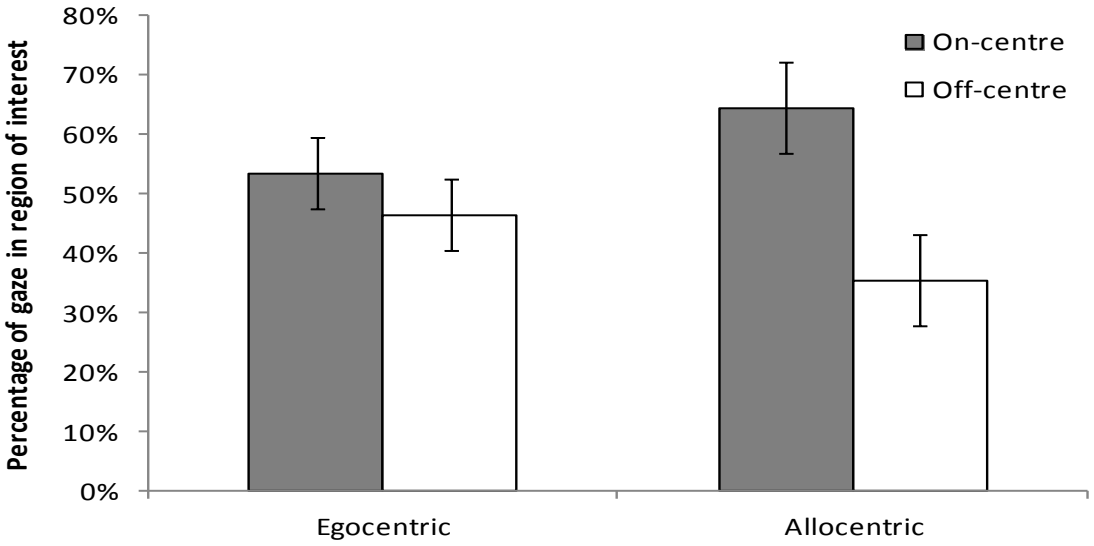

Figure 4.23. Comparison of horizontal gaze in on and off-centre regions of the display for allocentric and egocentric strategists. The gaze positions of egocentric strategists were slightly more distributed than those of allocentric strategists. However, for off-centre gaze the difference between the strategy groups was not significant.

for both strategy groups (allocentric and egocentric strategists) with both groups appearing to have more on-centre than off-centre gaze. However, allocentric strategists had a slightly greater proportion of central gaze (M = 65%, SEM = 8%) than did egocentric strategists (M = 54%, SEM = 6%). In contrast, egocentric strategists had a slightly higher proportion of off-centre gaze (M = 46%, SEM = 6%) than did allocentric strategists (M = 35%, SEM = 8%). However, a t-test comparing off-centre gaze for allocentric and egocentric strategists was non-significant.

Analysis of regions of interest. To investigate whether gaze position in different strategy usages was a matter of a combination of horizontal and vertical gaze positions a 'region of interest' analysis was conducted for the first 250 ms of orientation and for middle trials (5-7). Gaze position in the training maze appeared to be somewhat related to the combination of training and strategy. Gaze in the two regions below the horizon was similar for egocentric and allocentric strategists, both on centre and off centre, except that the allocentric strategists did not look much below the horizon during off-centre gaze (Figure 4.24). Gaze in the two regions above the horizon was quite similar for egocentric

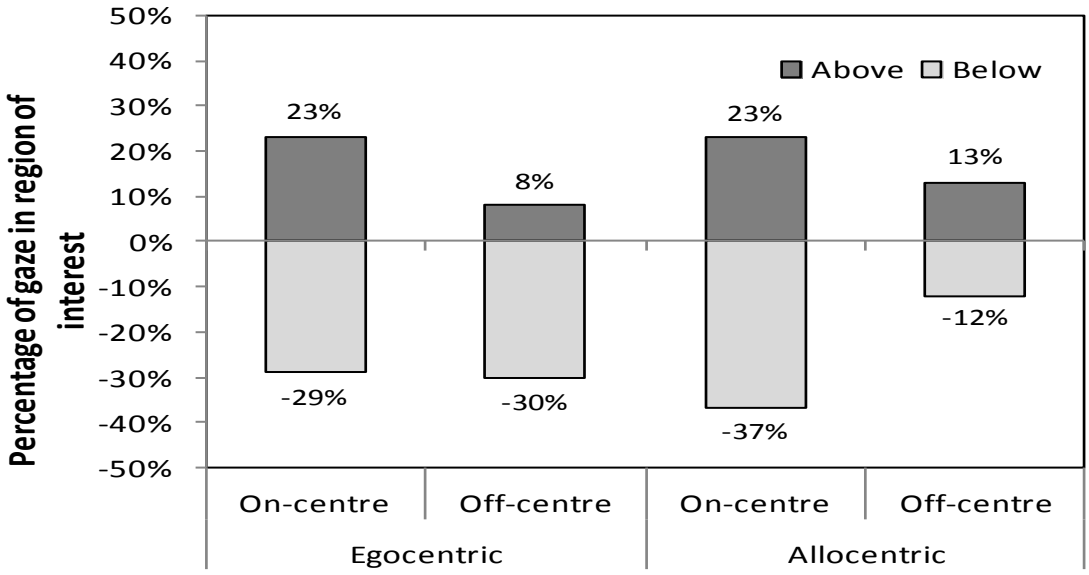

Figure 4.24. Percentage of trial gaze in regions of interest and according to strategy. Percentage of trial gaze is shown for four regions of interest (above & on-centre, above & off-centre, below & on-centre, below & off-centre) and the two strategy groups (egocentric and allocentric) as indicated by the strategy probe trial. Gaze was similar for allocentric and egocentric strategists except that allocentric strategists had slightly more central gaze and did not look much below the horizon in the off-centre region of the display.

and allocentric strategists, with both groups looking more on-centre than off-center. Percentage of gaze data from four regions of interest (Figure 4.17) was entered into a

2 x 2 x 2 repeated measures ANOVA with three factors: 1) strategy (allocentric or egocentric) and 2) on-centre gaze (above and below the horizon), and 3) off-centre gaze (above and below the horizon). The four regions of interest were: 1) on-centre and above the horizon, 2) on-centre and below the horizon, 3) off-centre and above the horizon and, 4) off-centre and below the horizon. The percentage of gaze in each of the four regions was compared according to whether participants indicated an egocentric or an allocentric strategy at the end of testing in the Dual-strategy maze. There was no overall interaction of strategy with on-centre and off-centre gaze. There was a significant main effect of on-centre gaze such that more on-centre gaze was concentrated below than above the horizon, $F(1, 31) = 6.67$, $p < .05$, $r = .42$. There was no significant main effect of strategy although it appeared that those in the place-trained-allocentric group tended to look on-centre. That is, gaze position by strategy was mostly a relation with horizontal position, and not a combination of horizontal and vertical gaze positions, i.e., looking into particular regions of interest. However, as noted above (Figure 4.23) the interaction of strategy and horizontal gaze position was not significant.

Other Explanations

Because the pattern of gaze positions during Dual-strategy maze testing was unexpected, other explanations were sought for the experimental outcome. Specifically, gaze positions during training and computer gaming experience were further studied for their potential effects on gaze position during testing.

Performance in training. The data were examined for the possibility that differences in gaze in the training maze (as measured by gaze position) may have carried through to the Dual-strategy maze and so unduly influenced gaze positions during Dual-

strategy maze testing. Correlations of gaze position during training with gaze position during testing were similar for the two training types (place and cue) (Figure 4.25). Gaze during cue-training was significantly correlated with gaze during testing, $r = .70$, $p < .001$ and gaze during place-training was similarly correlated with gaze during testing, $r = .89$, $p < .001$. These correlations could be explained in one of two ways. One possibility is that participants could have come to the experiment with a bias as to where to look in the maze, and this bias manifested in both training and testing. Alternatively, it could mean that the participants learned where to look during training, and continued to look in the same region during testing. Given that participants were assigned randomly to groups, it seems more likely that the high correlation between the two mazes was due to the effect of experience.

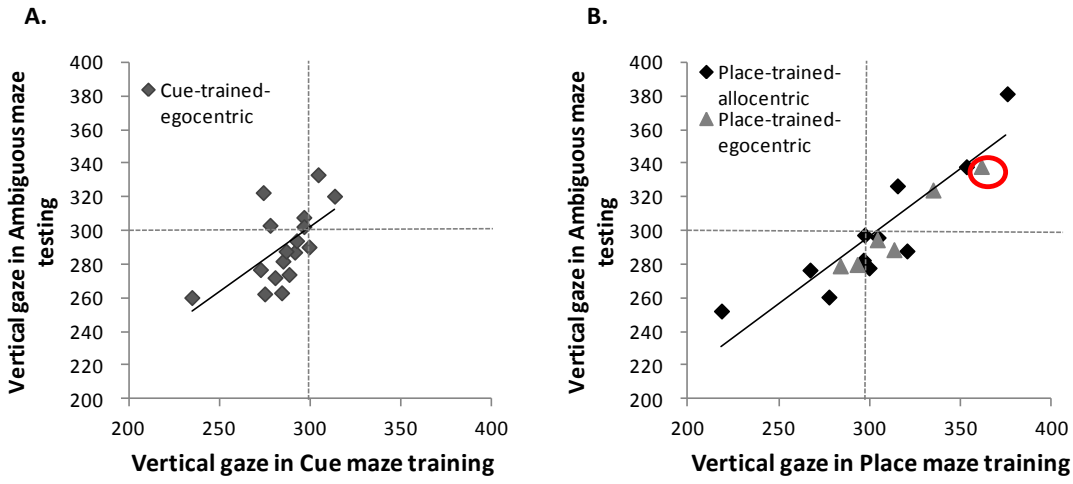

Figure 4.25. Correlations of vertical gaze position in training versus testing phases. Correlations were similar (and significant) for cue-trained **(A)** and place-trained **(B)** participants. The linear trend is indicated by the solid line and the dotted grey lines show the location of the horizon. The red circle indicates the outlier identified in the place-trained-egocentric group.

Computer experience. Computer gaming experience did not appear to contribute to the unexpected pattern of gaze positions observed during testing in the Dual-strategy

maze. To rule out computer gaming experience as a factor influencing gaze position, the strategy groups were compared according the gaming experience they had reported on their background information questionnaires. A one-way ANOVA comparing overall gaming experience for the three strategy groups (cue-egocentric, place-egocentric, place-allocentric) identified by the strategy probe was non-significant. Moreover, a second ANOVA comparing experience with three-dimensional (first-person shooter type) games was also non-significant.

Gender. The gender of participants did not appear to contribute to the pattern of results. Overall, vertical gaze positions of males and females during the testing phase (trials 2-10) were very similar (Males, M = 284, SEM = 6.52; Females, M = 285, SEM = 8.00). When the data were examined according to strategy selected (egocentric or allocentric) and for the middle testing trials gaze positions of males and females still appeared very similar (Figure 4.26).

Effect of Strategy on Navigation Performance

There were very few correlations between measures of gaze position and navigation performance. Neither distance to the platform nor probe trial measures were correlated with vertical gaze position or percentage of gaze above the horizon (for trials 2 to 10). However, during testing, latency to the platform was correlated with both vertical gaze position, $r = .50$, $p < .01$, and percentage of gaze above the horizon, $r = .30$, $p < .05$. The direction of this relationship was unexpected, since it showed that higher gaze position was correlated with longer latencies to the platform during testing. There was only one significant correlation of training (place or cue) or strategy (egocentric or allocentric) with measures of gaze position. Vertical gaze position was correlated with strategy

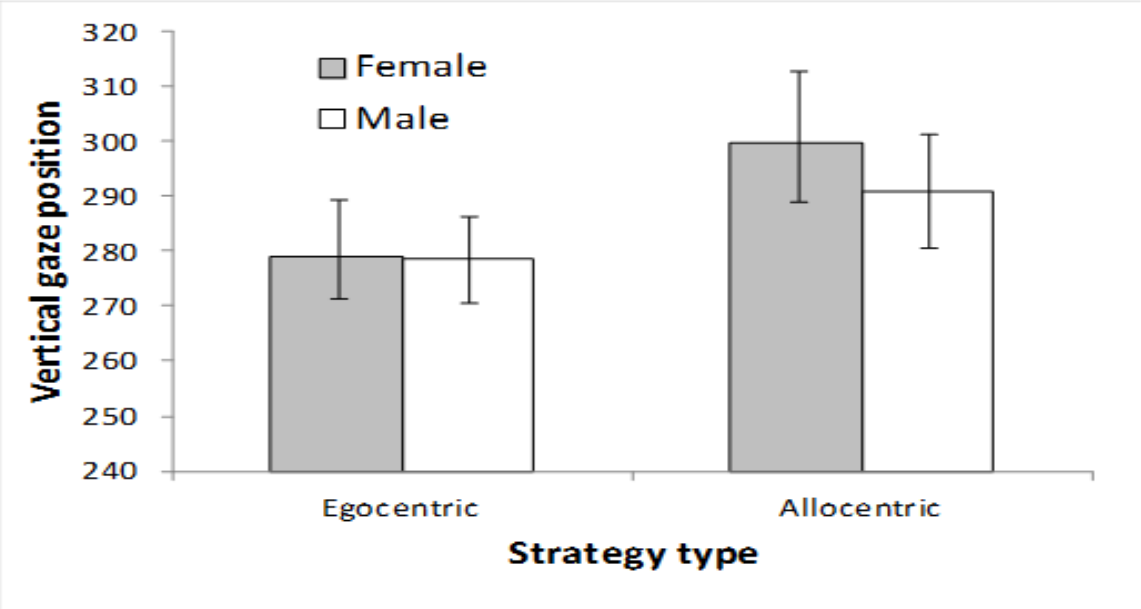

Figure 4.26. Similarity of gaze position for the two genders (male and female) during testing in the Dual-strategy maze. Vertical gaze position in the first 250 ms of middle testing trials is similar for the two genders in both the egocentric and allocentric strategy selection groups.

selected ($r = .38$, $p < .05$) in the first 250ms of middle testing trials as was expected based on the previous analysis. It is important to note that a large number of correlations were performed during data screening and may have led to Type 1 error. Nevertheless, performance in the Dual-strategy testing maze did not appear to be related to which cues participants were looking at in the maze, at least not during the initial orientation period of each trial.

Summary

The results for gaze position were unexpected and there was little relationship of gaze position (either vertical or horizontal) to the strategy participants chose in the strategy probe. There was a small effect in the expected direction during middle trials of the Dual-strategy maze but only briefly in the first 250 ms of orientation. During this time

window, participants who chose an allocentric strategy had higher vertical gaze positions than did participants who chose an egocentric strategy. Allocentric and egocentric strategists did not differ in terms of horizontal gaze position or gaze in the important regions of interest.

Discussion

Summary of Navigation Results

Navigation behaviour was good in all maze conditions. Participants were able to travel to the visible platform quickly and directly and they navigated well during training in both Place and Cue mazes. Navigation performance was also similar in the two training mazes although participants found the platform more quickly during cue training than during place training. Further, participants demonstrated good knowledge of the platform location at the end of training in both the Place and Cue mazes by spending a significant proportion of trial time searching for the platform in the correct quadrant of the arena on the probe trial. Participants also explicitly demonstrated good knowledge of the platform location on the DTS trial at the end of training.

Overall, navigation performance was better during testing than during training. Participants traveled to the platform more quickly and directly in the Dual-strategy maze than in either the Place or Cue mazes. However, performance during testing was similar, regardless of which training maze (Place or Cue) participants completed. All participants demonstrated good knowledge of the platform location on the probe trial at the end of testing.

Training did not prevent learning during the testing phase. Latencies and distances were longer during the first trial of testing than during the latter training trials. Further,

the shape of acquisition curves for the navigation variables latency and distance were similar in training and testing phases.

Strategy choice was related to experience, that is to which training maze participants had completed. At the end of testing, all cue-trained participants utilized an egocentric strategy whereas place-trained participants were divided in their choice of strategy. One third of place-trained participants utilized an allocentric strategy and two thirds utilized an egocentric strategy. Participants' awareness of the environment corroborated their choice of strategy at the end of testing. Participants tended to choose an allocentric strategy if they had noticed that the cue object was relocated in the strategy probe. In contrast, participants tended to choose an egocentric strategy if they had not noticed that the cue object was relocated.

Summary of Gaze Position Results

The results for gaze position were unexpected. There was little relationship of gaze position (either vertical or horizontal) to the strategy participants chose at the end of testing, at least during orientation in the first second. There was a small effect in the expected direction during middle trials in the testing phase but only briefly in the first 250 ms of orientation. During this time window, participants who chose an allocentric strategy had higher vertical gaze positions than did participants who chose an egocentric strategy. However, the overall effect during testing was for vertical gaze to converge on the horizon, regardless of which strategy (allocentric or egocentric) participants chose. That is, during orientation in the first second of Dual-strategy maze testing all participants tended to look at or near to the horizon (in the vicinity of the objects on the arena wall).

There was no notable relationship of horizontal gaze position to strategy choice. However, there was a slight tendency for participants who chose an allocentric strategy to look centrally during testing. Participants who chose an egocentric strategy had slightly more distributed gaze. The analysis of the combination of vertical and horizontal gaze positions confirmed that there were no differences between strategy groups according to gaze in important regions of the screen display, i.e., the area surrounding the horizon. Ultimately, patterns of gaze during testing in the Dual-strategy maze were similar for allocentric and egocentric strategists.

Discussion of Navigation and Gaze Position Results

Performance during training in the Place and Cue mazes was as expected for a healthy and relatively young sample group. Participants found the platform quickly and directly on visible platform trials, regardless of the type of training (place or cue) they later received. This was important because differences in the ability to understand procedures or master the use of the joystick could have influenced later performance.

Participants were slightly faster at finding the platform during cue training than during place training. Presumably this was because during cue training the important cue object (the golden urn) always closely marked the platform location. No such proximal cue was available during place training. However, the distance travelled to the platform was similar for the two training groups. The reasons for the slightly longer latencies are not known but may reflect hesitancy due to the nature of the testing situation. Unlike earlier studies, participants were having their EEG recorded in addition to using a chin rest and a joystick. Wearing an EEG cap requires that participants sit relatively still and this may have caused a slight hesitation in their use of the joystick. But given that most

navigation results were consistent with past findings participants were deemed to have good navigation performance during training.

Performance on probe trials was better after testing than at the end of training. As noted in the results, there was very small variability in probe trial scores and this might have contributed to the observed significant difference. However, the percentage of trial time spent searching in the correct quadrant was relatively high for both training groups and consistent with past findings using the Place maze (Goodrich-Hunsaker et al., 2010; Livingstone & Skelton, 2007; Mueller, Jackson, & Skelton, 2008). Further the percentage of time spent in the correct quadrant at the end of testing in the Dual-strategy maze was consistent with the score recorded after testing in one other study employing this maze paradigm (Livingstone & Skelton, 2007). In short, the difference in probe trial scores is not considered meaningful and the more important observation is that after either place or cue training participants showed good knowledge of the platform location.

Performance was as expected during testing in the Dual-strategy maze. Latency and distance to the platform were good and better (shorter) during testing than during training. This result indicates an effect of experience (or "practice effect") on navigating in this environment. However, learning was still evident during testing in the Dual-strategy maze. When acquisition curves were examined it was clear that participants took longer to navigate in the first search trial than on later training trials. Furthermore, asymptotes for latency and distance were not reached until about the half way through testing. This result was expected because although the virtual environments were very similar (same virtual room, same arena) the features and requirements of the Dual-strategy maze differed somewhat from those of either the Place or Cue mazes.

Specifically, place-trained participants were presented with objects (perched on the arena wall) that were not present during training and also had to learn a new platform location. Conversely, cue-trained participants were presented with a different important cue object (the steel box rather than the golden urn). Regardless of these changes, navigational performance during testing was generally good and for both training types (place and cue) and performance improved across trials.

The current navigation results were consistent with those of previous studies using the Place maze or Arena maze (Livingstone & Skelton, 2007; Mueller et al., 2008; Ross et al., 2006) and also with findings from other laboratories using vMWM paradigms (e.g., Astur, Tropp, Sava, Constable, & Markus, 2004; Cornwell et al., 2010; Hamilton, Driscoll, & Sutherland, 2002; Hanlon et al., 2006). That is, most participants tended to travel to the maze platform quickly and directly and improved their latency and distance scores across trials. Overall, participants understood task requirements, were able to navigate to a visible target in the virtual environment and were able to successfully navigate to the platform in both training and testing phases. Participants showed better performance during testing than during training but nevertheless demonstrated a pattern of learning similar to that observed for the training mazes.

As hypothesized, prior navigational experience was strongly related to the strategy selected by participants at the end of testing. The original hypothesis was that place-trained participants would be more likely to select an allocentric strategy whereas cue-trained participants would be more likely to select an egocentric strategy. Results were primarily as expected, however the place-trained participants were divided in their selection of the two strategies at the end of testing. Surprisingly, experience in the Cue

maze was perfectly related to strategy selection so that all cue-trained participants selected an egocentric strategy at the end of testing.

As expected, the type of strategy (egocentric or allocentric) participants selected was corroborated by their verbal report. When asked whether the cue object had been relocated for the strategy probe trial, participants were much more likely to report noticing the change in object location if they had selected an allocentric strategy than if they selected an egocentric strategy. Participants who selected an allocentric strategy tended to know that the cue object had been relocated but ignored this knowledge in favour of navigating by distal room features. Thus they were aware of the relationship of the object's location to distal room features. This awareness of the environment is interpreted as an indicator that those who selected an allocentric strategy had formed and were using a cognitive map. In contrast, participants who selected an egocentric strategy (regardless of their training) tended not to notice that the cue object had been relocated and therefore used the cue object to navigate in the strategy probe. These participants appeared to have little awareness of the relationship of the object's location to the distal room features. This is taken as an indication that participants who selected an egocentric strategy either had not formed or did not utilize a cognitive map.

There are several alternate explanations for the findings regarding strategy selection. The first of these is that egocentric navigation behaviour is dominant even in situations where both strategies are equally useful for locating the target. In the current experiment all participants who were cue-trained appeared to prefer the egocentric strategy that they had learned in the Cue maze. This perfect relationship between training and strategy selection suggests that cue-trained participants were biased toward the use of

the proximal objects when navigating in the Dual-strategy maze and therefore that egocentric strategies dominate in these circumstances. Furthermore, one third of place-trained participants also selected an egocentric strategy at the end of testing. This group of participants appeared either to have ignored the room features during testing or to have made no link between the locations of these features and the location of the cue object which was always located close to the target platform. For these participants, the objects on the arena wall may have dominated over the information available from room features such as the landscapes outside of the windows. However, egocentric navigation was not completely dominant since two thirds of place-trained participants still selected an allocentric strategy at the end of testing. Thus for most place-trained participants the preferable stimuli appeared to be the distal room features. These findings are consistent with the view that task demand and available environmental stimuli determine the reference frame (egocentric or allocentric) adopted by the navigator (Doeller, King, & Burgess, 2008; Etchamendy & Bohbot, 2007) in combination with individual differences (Wolbers & Hegarty, 2010). However it is clear from the current results that experience was a key factor.

An explanation related to the above is that egocentric navigation is simply easier than allocentric navigation. Although this may seem intuitive, it is unlikely to be the case. In the current experiment, although there was a difference in latency to the platform in the Place and Cue mazes, the distance that participants traveled to reach the platform was very similar when compared for the two mazes. These findings coincide with others suggesting that navigation in a vMWM does not differ in difficulty depending on whether stimuli are within the arena or are linked to either the arena wall or the distal landscape

(e.g., Chamizo, Aznar-Casanova, & Artigas, 2003; Doeller et al., 2008). Further, if an egocentric strategy were easier the expectation would be that all participants would select an egocentric strategy after testing in the Dual-strategy maze. This was clearly not the case since two-thirds of place-trained participants still chose an allocentric strategy in the strategy probe even when presented with the useful cue object in the Dual-strategy maze.

It could also be speculated that differences in strategy choice were related to differences in previous computer game experience. It has been shown that limited experience with computer interfaces may contribute to an inability to point accurately (a measure of cognitive mapping) in virtual space (Richardson, Powers, & Bousquet, 2011; D. Waller et al., 1998). Since game experience could be correlated with cognitive mapping ability it is possible that participants with less computer gaming experience might have been impaired in their ability to form a cognitive map and thus use an allocentric strategy. However, this did not seem to be the case. There were no differences in computer gaming experience (including joystick use and experience with three-dimensional games) for the three strategy groups that emerged at the end of testing. Thus it appears that the strategies selected by participants were related to their recent experience during training rather than to the utility of proximal cues or to previous computer gaming experience.

The finding that environmental awareness was related to both strategy selection and experience led to the tentative proposal of a pathway from experience to strategy selection that for allocentric strategists is mediated by cognitive mapping. In the present study awareness of the environment meant that participants had encoded the relationship of the platform location to both room features and the proximal cue object. This was

interpreted as evidence for the formation of a cognitive map. In environments like the Cue maze where goal locations are marked by proximal cues, participants simply follow these cues, appear to ignore the environment and thus may not form useful cognitive maps. In the present study, this experience led to later selection of an egocentric strategy. However for environments like the Place maze where goal locations are marked by the relationships of more distal cues (like the outdoor landscapes) the pathway to later strategy selection may be mediated by cognitive mapping. Experience with relational stimuli appeared to promote environmental awareness and thus the formation of a cognitive map. This experience may have led to later selection of an allocentric strategy. But most importantly, an allocentric strategy was only selected when participants were both place-trained *and* aware of the relationships of environmental features. This suggests that in order for people to select an allocentric strategy they must first have formed a cognitive map. Thus there may be a pathway from experience to allocentric strategy choice that is mediated by attention to the environment and cognitive map formation. One caveat to this discussion is that the sample size reported here is relatively small (n = 11 allocentric strategists) preventing a complete analysis of the interaction between experience, strategy and environmental awareness.

In the present study, the relationship between cognitive map formation and navigational strategy use was not one-to-one. It is important to note that the selection of an egocentric strategy by itself does not preclude the possibility that participants had formed a cognitive map. Such maps may be formed automatically (O'Keefe & Nadel, 1978) but later may be ignored. For example, in the current study a few cue-trained participants were aware that the cue object had been relocated (had formed a cognitive

map) but nevertheless selected an egocentric strategy. Further, it is possible that cognitive maps may be impoverished, that is not sufficiently formed to be useful in later situations (Iaria, Palermo, et al., 2009). Interestingly, the place-trained participants who selected an egocentric strategy in the strategy probe were all unaware that the cue object had been relocated. Presumably these participants either had not formed a sufficient cognitive map or had not integrated the object's location into an existing map.

In summary, cognitive mapping (via environmental awareness) was related to strategy selection but only when participants had experience navigating in an environment that promoted the utilization of distal, relational features. Presumably this direct navigational experience contributed to the formation of a cognitive map and the later selection of an allocentric strategy.

One interesting and unexpected finding of the present study was that strategy choice did not appear to be related to the gender of participants. The experiment was not designed to study gender or sex differences in strategy selection but these were briefly examined because of their importance in the literature concerning spatial navigation and spatial cognition. Males and females who were place-trained chose allocentric or egocentric strategies in equivalent numbers at the end of testing in the Dual-strategy maze. When data from the place-trained group (which contained an equivalent number of males and females) was examined for strategy choice, there were no gender differences in the number of egocentric and allocentric strategists and both strategies were selected at an equivalent rate. However, the data did suggest that there may be gender differences in cognitive map formation. More males than females were aware that the cue object was moved and therefore may have been more aware of the distal room features than were

females. This is consistent with research showing that males tend to orient to distal cues more accurately than do females (Woolley et al., 2010). However, it should be noted that the sample size in the current study was too small for any definitive result to be reported.

Unexpectedly, eye movements were not good indicators of the strategy that participants selected at the end of training. Preliminary work had led to the hypothesis that during testing egocentric strategists (regardless of training) should have lower gaze positions than allocentric strategists. Instead it was found that vertical gaze positions did not differ for the strategy types and further that gaze tended to converge on the horizon, regardless of which strategy participants selected at the end of testing. Some very ephemeral effects were discovered very early in trials (during the first 250 ms) but these were present only in the three middle trials of testing in the Dual-strategy maze. Thus the conclusion was that eye movements are not useful indicators of strategy selection, at least in the one second time window selected for analysis.

There are several possible explanations the failure of eye movements to indicate strategy selection in this experiment. These include selection of the time window of interest, design of the virtual environment and the effects of experience on gaze position. The initial second time window was chosen based on previous work showing successful differentiation of gaze position in the Place and Cue mazes (Livingstone-Lee et al., 2011; Chapter Two, this dissertation). Further, other researchers have used information from the first second of trials to capture differences in gaze for participants who navigate directly or indirectly to the platform in a vMWM (Hamilton et al., 2009). An early time window was also employed by Cazzato, Basso, Cutini, & Bisiacchi (2010) to show differences in strategy on a mapping task. These previous results suggest that the one-second time

window should contain information that correlates with strategy selection. It is possible, however, that the one-second time window does not capture experiential differences in gaze position. Attempts to identify a more useful window within the one-second interval were only partially successful and experience effects were small. Further research may be necessary to identify other time windows of interest. One possibility is the inter-trial interval when participants are looking around the virtual room from the perspective of the platform.

Another explanation for the failure of eye movements to indicate strategy selection may be the design of the Dual-strategy maze environment. Specifically, the cue objects were located just below the horizon and not far (vertically) from the lower portion of the windows that contained the distal landscape features. This small separation of stimulus types may have contributed to the convergent gaze because gaze positions of the allocentric and egocentric strategists might have overlapped one another.

The final and most compelling reason for the convergence of gaze in the Dual-strategy maze is the effect of experience. The current study differed from previous work in that participants were trained and were therefore not naive to the virtual environment at the start of testing. The prior experience of participants in either the Place or Cue maze may have caused less pronounced differences in gaze position in testing due to the fact that some aspects of the environment had already been encoded and therefore were no longer the focus of visual attention. It is also possible that with experience participants required less gaze time to formulate and utilize a strategy, especially if that strategy was employed consistently across trials. Cazzato et al. (2010) reported that on the Maps Test (a two dimensional task) the number of fixations was reduced with constant strategy (i.e.,

with experience using the same strategy) but was high when participants were changing strategies. This finding suggests that the number of fixations may have been high during training when a new strategy was being acquired and low during testing when the strategy had been utilized repeatedly. Another study (Becic, Boot, & Kramer, 2008) using a mapping task found that covert looking (i.e., fewer fixations) was associated with better performance than was overt looking (i.e., more fixations) but this finding has not been tested in three-dimensional virtual environments. Ultimately, the failure to find a strong association between strategy choice and eye movements in the Dual-strategy maze was likely the result of a combination of factors including virtual environment design and the changing nature of gaze fixations with experience.

The present study represents an advance over past work concerning navigation strategies in humans by demonstrating that experience strongly influences the selection, development and utilization of allocentric or egocentric strategies. This study is one of only a few designed to study strategy utilization by manipulating navigation experience and is the first to compare an allocentric strategy to an egocentric cue-based strategy as opposed to an egocentric response-based strategy. The current experimental approach is an important extension of previous work because it allows for the study of how particular experiences with an environment influence the ability to navigate, perhaps to an even greater degree than do innate abilities or other individual differences so commonly studied in the field of navigation research (for review see Wolbers & Hegarty, 2010). Furthermore, testing an egocentric cue-based strategy is important because the ability to associate a cue with a location is necessary for route learning and route navigation (Maguire, Burgess, & O'Keefe, 1999; Moffat, 2009; O'Keefe & Nadel, 1978) and

probably differs from more automated response-based strategies which consist of body turns (left or right).

The current findings suggest that experience has a direct and relatively large effect on strategy choice. Place training and cue training were strongly related to the later choice of an allocentric and an egocentric strategy, respectively. This experience effect was previously hinted at in findings from two studies (Etchamendy & Bohbot, 2007; Iaria et al., 2003) showing by verbal report that some participants change strategies (from allocentric to egocentric) with experience across trials as they navigate in an dual-strategy vRAM environment. The current study expanded on this work by directly manipulating environmental experience and by testing strategy selection using a probe trial rather than verbal report. Findings indicated that strategies can indeed be trained and that the type of strategy selected later is frequently related to that training. A similar result was demonstrated by Schmitzer-Torbert (2007) who showed transfer of strategy (allocentric place-based and egocentric response-based) from training to performance in a dual-strategy virtual environment. The current study extends this work by showing the continuity of strategy in a vMWM rather than a virtual corridor maze and by comparing allocentric strategies to egocentric cue-based strategies rather than response-based strategies like left and right turns.

The finding that strategy selection is strongly affected by experience implies that strategy switching may occur in response to changes in the environment. For example, in the current experiment, some place-trained participants (approximately 33%) indicated utilizing an egocentric strategy on the strategy probe. Although strategy switching was not tested it is possible that these participants had been utilizing an allocentric strategy in

training but switched to an egocentric strategy in the Dual-strategy maze. Interestingly, Igloi et al. (2009) reported a similar effect in their study employing a virtual star maze to study strategy selection. A proportion (30%) of their participants switched strategies as they gained experience in a dual-strategy maze environment.

The experience effect reported here was striking first because all participants who were trained in the Cue maze appeared to continue utilizing an egocentric strategy throughout Dual-strategy maze testing trials. This finding has important implications for the interpretation of studies utilizing more than one virtual environment navigation task. For example, Levy, Astur & Frick (2005) studied gender differences in navigation by presenting three virtual environment navigation tasks (vRAM, virtual T-maze, vMWM) in sequence. Each task was designed to be dual-strategy in nature, i.e., could be solved using either an egocentric or an allocentric strategy, however by the end of testing in the vMWM, all participants selected an egocentric strategy on the strategy probe. The authors were surprised by this outcome, having expected some participants to utilize an allocentric strategy in the dual-strategy vMWM. However, the authors themselves note that the environmental stimuli in the vRAM may have promoted the utilization of egocentric strategies (at least in female participants). Given the large experience effects found in the current study, it could be speculated that experience in the (cue-based) vRAM influenced strategy selection on succeeding maze tasks. In any case, the possibility of experience effects should probably be considered in all navigation studies utilizing virtual environments.

In the current study, preliminary findings suggest that gender does not contribute to strategy selection in navigation tasks. Although the groups sizes were quite small when

divided by gender, a few interesting relations are worth noting. When females were trained in the Place maze (with a bias toward the use of distal room features) they later chose an allocentric strategy at the same rate as did males. In a parallel fashion when males were trained in the Cue maze (with a bias toward the use of proximal stimuli) they later chose an egocentric strategy at the same rate as did females, that is, all of the time. It is important to note that strategy selection took place at the end of the testing in the Dual-strategy maze thus revealing a persistent effect of training. Two previous studies utilizing a vRAM (Andersen et al., 2012; Iaria et al., 2003) found no gender differences in spontaneous strategy selection when allocentric strategies are compared to egocentric response-based strategies. Similarly van Gerven, Schneider, Wuitchik, & Skelton (in press) utilized the Dual-strategy maze and found no gender differences in spontaneous strategy selection when comparing allocentric strategies to egocentric cue-based strategies. The current study expands on these findings by showing that experience outweighs the effect of gender in the selection of either an allocentric or an egocentric cue-based strategy.

The current study also identified a possible gender difference related to awareness of the environment during orientation. In the Dual-strategy maze the place-trained males did appear to have slightly greater awareness of the room features and their relationship to the location of the cue object than did place-trained females. However, this advantage was not associated with better performance (i.e., improved latency and distance scores). Further, the place-trained females did not necessarily switch to the use of an egocentric strategy even when useful positional cues were presented to them in the Dual-strategy maze. This contradicts findings from studies suggesting that males and females differ in

their preference for proximal and distal environmental stimuli and that this difference is reflected in navigation performance. For example, Chai & Jacobs (2010) found that in an open air vMWM males had difficulty navigating in the absence of directional cues (for example directional landmarks or the slope of the ground) whereas females had difficulty navigating in the absence of positional cues, i.e., landmarks. Further, by utilizing a vMWM task, Wolley et al. (2010) found that males demonstrated better heading direction than females early in trials, suggesting that males were better at processing information from the distal environment. Although the present study found a potential advantage for males in environmental awareness, there was no evidence that this influenced either strategy selection or performance in the maze tasks. Rather, navigational experience seemed to influence the choice of strategy to a greater degree than gender. This is consistent with the observation that although gender differences appear to be consistent for some spatial tasks, these differences are small (Gluck & Fitting, 2003) and like other gender differences in spatial ability may be influenced by cognitive styles that could be changed or eliminated with training (Bosco, Longoni, & Vecchi, 2004).

With respect to eye movements, the results of the present study suggested that in the current context eye movements are not a good measure of strategy selection. The findings differed from those of feasibility work suggesting that higher vertical gaze positions would be associated with selection of an allocentric strategy and lower gaze positions with the selection of an egoocentric strategy. Instead, no differences in gaze were found according to strategy and in the testing phase gaze tended to converge on the horizon regardless of which strategy participants indicated using. This was surprising given the work of Hamilton et al. (2009) showing that during orientation in a vMWM

participants who navigated directly to the platform were more likely to concentrate their gaze on distal features of the environment whereas participants who navigated indirectly concentrated their gaze within the arena space. This finding would suggest that direct navigators may have been forming an allocentric strategy (at least during orientation) and indirect navigators an egocentric strategy. However Hamilton et al. (2009) studied spontaneous development of strategies within trials rather than the effects of experience. In the current study, effect of strategy (as measured by eye movements) may have been overwhelmed by the combined effect of experience and available environmental stimuli in the Dual-strategy maze.

Research Applications

There were some technical solutions and limitations noted during the current study. Most importantly the method employed is effective in identifying gaze positions associated with environmental stimuli designed to elicit either allocentric or egocentric strategies. The equipment was inexpensive and the data analysis was relatively simple once the data were screened and artefacts removed. It should be noted, however, that some problems were encountered. The first was that several participants' eye movements could not be tracked. The reasons for this are varied. First, differences in eye shape, eye musculature and/or low iris to sclera contrast may have contributed to problems with the calibration process. Second, the camera sometimes 'lost' or was unable to follow the eye movements especially if the participant frequently looked away from or near to the edge of the display. However, other studies (e.g., Spiers & Maguire, 2006) also report that a relatively high proportion of participants could not have their eye movements tracked. This proportion may be higher for more complex and dynamic virtual environment tasks

and lower for tasks that require participants to make yes/no type responses to static displays (e.g., Butler et al., 2009) or that are concerned mainly with optic flow (e.g., Gramann, Muller, Eick, & Schonebeck, 2005; Gramman, Sharkawy, & Deubel, 2009). As noted previously, another issue is that the design of the virtual environment may have prevented the recording of eye movements associated with strategy selection in the Dual-strategy maze. Future studies in the laboratory will assess this possibility.

The current study makes several contributions to navigation research. It confirms the effectiveness of the vMWM as a method for studying human navigational strategies. Further, the behavioural design in combination with the strategy probe and verbal report allows for both training and testing of navigational strategy selection. This represents a new methodological direction because it acknowledges the importance of antecedent experience for strategy selection and thus refines the study of navigation behaviour. The introduction of a direct test of experience on strategy selection allows for improvements in studies of gender differences, aging and brain injury. For example, such studies would benefit from knowledge concerning the effects of training and whether they improve navigational efficiency or promote the utilization of new and more effective strategies.

The current study also confirms the effectiveness of combining eye tracking with a navigational paradigm for the identification of strategies in environments that are biased toward the utilization of either allocentric or egocentric strategies. Unfortunately the method described was unsuitable for detecting strategy selection in the Dual-strategy maze. However, as a first study it was effective in showing a small difference in early gaze orientation. Further, eye movements may still be useful measures of strategy selection in dual-strategy environments as long as the effects of experience on

gaze can be identified.

The current behavioural paradigm may also be useful when combined with functional brain imaging. The ability to identify and predict strategy selection is very important for navigation studies that utilize brain imaging to determine what brain activity corresponds to a particular cognitive or behavioural measure. Although tasks can be designed to reasonably elicit a strategy it is important to discover participants who do not used the anticipated strategy, especially in studies with small numbers of participants. For example the current behavioural and eye tracking paradigm is presently being combined with EEG to identify connectivity between brain regions that corresponds to gaze in particular regions of the virtual environment (P. Zeman, personal communication, May, 2012) and to the selected strategy. This approach may be useful for identifying individuals who utilize alternate strategies or switch strategies as they navigate in either a place-based or cue-based task environment. Further adaptations will be necessary to study brain activity in dual-strategy environments.

Another advantage to the described method is that it can be applied to the study of navigation deficits both in and out of the imaging scanner. Such deficits have been noted in a number of psychiatric conditions as well as after acquired or traumatic brain injury (e.g., Grusser & Landis, 1991). Specifically, research has shown that damage to the brain (and especially the hippocampus) may result in difficulties with tasks designed to elicit an allocentric strategy (Goodrich-Hunsaker et al., 2010; Maguire, Nannery, & Spiers, 2006). The method described here could provide a useful measure of which strategies brain injury survivors utilize on place-based tasks and identify corresponding brain activities.

Contributions to Theory

The current experiment provides converging evidence for the theory that there are two navigation systems in the human brain by showing that two types of orientation gaze position can be discriminated during training in virtual environment navigation tasks. These two types of gaze orientation were generated by creating a bias in the virtual environment toward the utilization of either distal or proximal stimuli and are there thought to have reflected activity in the allocentric and egocentric systems, respectively. This is consistent with O'Keefe & Nadel's (1978) cognitive mapping theory which proposes that animals perform either locale (mapping) or taxon (guidance) behaviours in response to the requirements of the navigation task and available environmental stimuli. The current findings also converge with accumulating evidence suggesting that there are two memory systems associated with animal navigation behaviour (Poldrack & Packard, 2003; White & McDonald, 2002; White, 2008) and that there are two corresponding cognitive/memory systems in humans (e.g., Doeller, King, & Burgess, 2008; Hartley et al., 2003).

The present study also supports cognitive map theory by demonstrating the significance of environmental experience for map formation and by showing that environmental awareness is more important for allocentric than for egocentric navigation. Overall, it confirms the view that experience with locale space supports navigation using places or configurations of more distal cues (allocentric navigation) whereas experience with taxon space supports navigation using local, proximal cues (egocentric navigation) (O'Keefe & Nadel, 1978). The enhanced environmental awareness of allocentric strategists coincides with the proposition that in order to update a cognitive map the

navigator must first be able to notice new features in the environment and then to locate them in the current map (O'Keefe & Nadel, 1978). In the present study this ability was demonstrated only by the allocentric strategists supporting the view that awareness of the environment is necessary for cognitive mapping but not for stimulus-response type behaviours.

The current behavioural findings support the proposition that navigational strategies are not innate but rather can be selected through a combination of experience and environmental awareness. Researchers in the field of spatial navigation generally agree that strategies are selected based on a combination of environmental stimuli, task requirements and individual differences in the navigating person (e.g., Gluck & Fitting, 2003; Kallai et al., 2005) with each of these factors making roughly equivalent contributions to the cognitive map. However, studies of individual differences have sometimes concluded that spatial ability, including the ability to form a cognitive map, is an innate (i.e., biologically determined) factor. Due to this assumption, gender differences in navigation studies have been attributed to evolution (Silverman et al., 2000), latent hormonal factors (Burkitt et al., 2007; Choi & Silverman, 2002; Sandstrom et al., 1998) and differences in brain function (Grön et al., 2000; Sandstrom et al., 1998) without considering strategy use or the effects of experience on the strategies people select. Similarly, some researchers have suggested that apparent deficits in navigation performance due to aging are entirely attributable to internal factors such as brain atrophy (e.g., Moffat, Zonderman, & Resnick, 2001) without considering the influence of experience or strategy use.

Recently some researchers have begun to question the assumption of innate

differences, by demonstrating for example that males and females employ the same brain structures when navigating (Blanch et al., 2004) and that older individuals can improve navigational performance with training (Becic et al., 2008). Some studies have even concluded that strategy use and experience are factors that should always be considered in spatial cognition research (e.g., Gluck & Fitting, 2003).

Given the current state of the literature concerning individual differences, it is important to consider the effects of environment and experience on strategy selection. As O'Keefe & Nadel pointed out in their seminal work on the cognitive map theory, individual differences in spatial ability do not necessarily imply that such abilities are innate. Logically this suggests that the ability to select a strategy is not fixed but rather is flexible and amenable to change based on external factors. In other words, people are not inherently egocentric or allocentric navigators. Instead, each person likely has two navigation systems and two available strategy types from which they can select based on a combination of immediate environmental features, past experience and possibly fluency or competency with that strategy. The present study supports this view by showing that strategy selection is strongly associated with antecedent experience and with the type of stimuli available for navigating. Given that people were randomly assigned to the two different training mazes (place or cue) and selected strategies mainly according to this training, it seems likely that experience effects outweighed any individual differences.

Similarly, the effect of experience appeared to outweigh gender differences in contributing to the strategies people selected for navigation. Preliminary findings add to a growing body of work showing that commonly accepted gender differences in spatial ability are frequently small and may be outweighed by other effects (Gluck & Fitting,

2003). A tentative male advantage was found for environmental awareness (and possibly cognitive mapping) suggesting convergence with the assertion that males consistently outperform females on place-based navigation tasks. However the current preliminary results concerning the effect of experience are quite consistent with the view that gender differences in spatial ability are small and may even disappear given the correct circumstances. In the present study males and females performed equally well on all navigation tasks. They also selected allocentric and egocentric strategies with equal frequency and apparently based on antecedent experience rather than other factors.

The present study contributed to eye movement theory by suggesting that eye movements can be adapted for efficiency based on top-down effects. Eye movements in the Dual-strategy maze did not correspond to the strategies people selected however the convergence of gaze toward the horizon suggested that participants had learned to be more efficient with their gaze once a strategy was selected. This top-down effect was present only during testing. During the training phase of the experiment eye movements were directed toward the most useful stimuli in the environment, suggesting a bottom-up effect during the acquisition of strategy. These findings are consistent with the theory that eye movements are the result of both bottom-up (sensory/perceptual) and top-down (cognitive) processing (DeAngelus & Pelz, 2009; Tatler, 2009).

Future Applications and Proposed Research

Future applications suggested by the current experiment include eye tracking studies and behavioural investigations. The eye tracking method described here continues to have utility for discriminating gaze associated with biased (place or cue-based) navigation tasks and may be useful in situations where the acquisition of behavioural

strategies is the focus of study. For example, the method could be applied to investigation of spontaneous strategy acquisition in the Dual-strategy maze to study how strategies are utilized in everyday environments where multiple cues and stimulus types are present. Furthermore, the method has yet to be applied to detailed trial-by-trial analysis or comparative analysis of differing time windows. Eye tracking studies could also test the effects of experience on gaze efficiency in navigation tasks. Together, such studies may further clarify the nature of strategy acquisition and the timing of strategy selection.

The behavioural paradigm described here also provides a baseline for the further study of the effects of experience on strategy selection. One desirable outcome of such research is the ability to predict how interaction with the environment may determine which strategies people use. Such work has applications in community design, especially of buildings and road systems.

Studies analyzing changes in strategy selection with experience also have implications for research into sex and gender differences. The finding that strategy selection can be trained through environmental experience suggests that spatial ability is not a fixed trait and therefore that gender differences in spatial navigation performance may be malleable. Future studies could systematically test this assertion by comparing training outcomes for the two genders.

The current work also provides a foundation for basic research into navigation deficits as well as more advanced research into the effect of environmental experience on strategy selection after brain injury. An early part of this process is described in the following feasibility chapter and includes establishing the patterns of eye movements shown by brain injury survivors on place-based and cue-based navigation tasks. This step

is important because individuals with brain injury may simply not visually attend to all of the available cues in an environment. In other words, their navigation deficits may result partly from an inability to notice or encode environmental stimuli. If eye movements show that brain injury survivors have navigation deficits exclusively in the place-based domain (as suggested by, Livingstone & Skelton, 2007; Goodrich-Hunsaker et al., 2010), then this would indicate that deficits are linked to a failure either to notice the distal environment or to incorporate distal features into a cognitive map. It is also important to establish whether the selection of a navigation strategy is linked to experience and environmental awareness as it is in the healthy population. Such knowledge would contribute to a better understanding of human brain function and to interventions for improving navigational performance.

Conclusion

In conclusion, the behavioural analysis described here was able to identify important effects of experience on the selection of a navigation strategy and argues against the idea that strategy use is innately determined. The present results indicate that strategies people select for navigating are associated with the nature of antecedent experience with environments containing different types and combinations of environment stimuli. Furthermore, cognitive mapping may mediate the pathway from experience to strategy selection. This is especially important for the selection of an allocentric strategy which seems to depend on experience navigating in environments containing useful distal features and on awareness of the spatial relationships of environmental stimuli. Eye tracking was able to capture only a brief effect of strategy (allocentric or egocentric) very early during orientation to the environment. Other

measures of gaze may be required to corroborate strategy selection. Continued improvements in measures of strategy selection will contribute technically to improvements in vMWM task design and to development of tasks for brain imaging studies of navigation. Such improvements could play a part in the study of navigation differences especially as they relate to gender and aging. Understanding the factors contributing to strategy selection may also improve understanding of navigation deficits and the development of better rehabilitation tools to address these deficits.

Chapter Five

The following is a feasibility study and will not be published on its own. Accordingly, it is written as a part of the dissertation, and as a preliminary report rather than a stand-alone manuscript. The study investigates the feasibility of applying eye tracking measures to assess navigation deficits and spared navigational function in survivors of traumatic brain injury.

A preliminary study of the utility of eye-tracking measures for assessment of navigation deficits in survivors of traumatic brain injury.

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Abstract

Wayfinding in the real world is an everyday task for most people, but survivors of traumatic brain injury often have problems with wayfinding and navigating. The deficit in navigational ability may be related to the inability to form or use a cognitive map and therefore to select or use allocentric strategies. Allocentric strategies rely on the presence of distal, relational stimuli whereas egocentric strategies rely on the presence of proximal or simple guidance stimuli. The current study investigated the feasibility of combining a new method of eye tracking with specially designed virtual environments (based on the Morris water maze task) to study navigational strategy use in three TBI survivors. Eye tracking results showed that the TBI survivors had much lower gaze than did comparison participants in an environment where only distal room features were provided whereas their gaze positions were similar to those of comparison participants when useful proximal stimuli were present in the environment. The combination of eye tracking and virtual environment navigation tasks appears to be feasibility and may be useful for the assessment of navigation deficits after brain injury and for the development of rehabilitation tools.

Feasibility Study of Strategy Use after Traumatic Brain Injury

Traumatic brain injury (TBI) is a common cause of injury in the human population (Phillips, Voaklander, Drul, & Kelly, 2009; Thornhill et al., 2000) and problems with wayfinding appear to be quite common after damage to the brain. Wayfinding deficits have been shown to occur after acquired brain injury such as stroke (Barrash et al., 2000) as well as TBI (Skelton et al., 2000, 2006). However the reasons for deficits in spatial navigation after a traumatic injury are not well understood. Indeed, little attention has been paid to assessing the nature of these deficits or to their time course.

A possible explanation for the existence of wayfinding deficits after TBI concerns the nature of the brain's navigation systems and their anatomical substrates. Research with both animals and humans suggests that there are two types of navigation associated with two cognitive navigational systems in the brain (Burgess, 2008; White & McDonald, 2002). Each system consists of a number of structures and connections and each has one important central structure (Anderson & Bigler, 1994; Goodrich-Hunsaker, Livingstone, Skelton, & Hopkins, 2010; Livingstone & Skelton, 2007). The allocentric system supports navigation using cognitive maps and the spatial relations of features in the environment and its central structure is the hippocampus. The egocentric system supports navigation using responses to simple environmental cues (or sequences of them) and its central structure is the caudate. There are few studies of human navigation performance and it neural correlates in TBI. However, existing research suggests the possibility that TBI can damage the allocentric system while leaving the egocentric system mostly intact (Anderson & Bigler, 1994; Goodrich-Hunsaker et al., 2010; Skelton et al., 2006).

The key problem in assessing the effects of TBI on navigational cognition is that the pattern of deficits and spared abilities has not been fully described. Linked to this problem is the absence of good tests of navigational ability appropriate for use in the TBI population. Currently most testing is either of the table top or pencil and paper variety , for example the stylus maze task (Milner, 1965), the mental rotation task (Levin, Mohamed, & Platek, 2005) or map reading (Dabbs, Chang, Strong, & Milun, 1998). Because these tests are presented in tow dimensional format and in the near space of the participant they do not address problems spatial navigation in a three dimensional environment utilizing stimuli in both near and far space. A preferable method would be to assess spatial navigation in real world settings. However, there are few such tests available and they have several problems including that they are labour intensive and difficult to administer. These types of tests often involve assessing (or training) the ability of hospital patients to follow routes in building corridors (e.g., Barrash, 1994) although at least one research group have undertaken an outdoor assessment (Iaria, Bogod, et al., 2009). More recently, researchers have devised experimental virtual environments for assessing cognitive map function while participants navigate in virtual rooms, towns or cities (Hamilton et al., 2002; Maguire et al., 1998; Nadel et al., 1998; Spiers & Maguire, 2006) but the focus of these studies has mainly been on the understanding of place learning rather than the relative contributions of the two systems of navigation.

Clearly there is a need for new methods of assessing navigational function in individuals who have sustained brain injuries, including but not limited to TBI. Such tests should be able to be standardized, that is, systematic and applicable across different laboratory and diagnostic settings. They should also be ecologically valid (Rizzo et al.,

2004) and should therefore test navigation in large scale space in a manner that demonstrates effects on navigation in everyday situations. Tests of navigational function should also be able to differentiate which system (allocentric or egocentric) is being used or has been selected. This is important because residual function needs to be assessed before rehabilitation methods can be devised (Wilson, 2002).

The present study is designed to test the feasibility of a new method of navigation assessment that combines virtual environment navigation tasks with eye tracking to assess the pattern of navigational deficits and abilities after TBI. The use of virtual environment navigation tasks is proposed because virtual environments are considered ecologically valid (e.g., Rizzo, Buckwalter, & Neumann, 1997; Ross, Skelton, & Mueller, 2006) and because they have already shown promise in testing, assessment and rehabilitation of cognition and memory after damage to the brain (Rose, Brooks, & Rizzo, 2005). The tasks employed in the current study are virtual versions of the Morris water maze (MWM) (Morris, 1981), a consistently reliable measure of deficits in spatial navigation and memory in laboratory animals (D'Hooge & De Deyn, 2001). In animals the MWM has been used to identify deficits in cognitive mapping associated with damage to the hippocampus (Morris et al., 1982) and to differentiate the two cognitive navigation systems (allocentric and egocentric) (McDonald & White, 1994). In human studies, virtual versions of the task have been used to show corresponding navigation deficits associated with damage to the hippocampus (Astur et al., 2002; Goodrich-Hunsaker et al., 2010) and also to show cognitive navigational deficits in survivors of TBI (Skelton et al., 2006).

The present study also proposes tracking the eye movements of TBI survivors

because gaze position is an objective and implicit measure of which regions of virtual space are being attended to for orientation during virtual navigation tasks (Hamilton et al., 2009; Livingstone-Lee et al., 2011). When healthy participants orient at the beginning of navigation trials they look in different regions of the virtual environment display depending upon which stimuli are most relevant to solving the task. In place-based tasks these stimuli tend to be configurations of distal features whereas in cue-based tasks participants tend to look in regions of the display containing the important cue. However, there is a need to confirm that tracking eye movements during navigation is feasible with the TBI population.

Research Approach, Objectives and Rationale

The present feasibility study combines eye tracking with three virtual water maze tasks to test where TBI survivors look when they are orienting for navigation. The maze tasks are described in the previous chapters but as a reminder they consist of the Place maze, the Cue maze and the Dual Strategy maze. The Place maze was designed to elicit allocentric strategies whereas the Cue maze was designed to elicit egocentric strategies. The Dual Strategy maze could be easily solved using either strategy type. The stimuli most useful for solving the tasks were located in specified regions of the screen display and the frequency of gaze in these regions was recorded using an eye tracking camera. A probe trial was employed to test whether participants selected an egocentric or an allocentric strategy at the end of testing in the Dual Strategy maze.

The main objective of the current experiment was to examine the feasibility of using eye movement tracking to assess navigation deficits in TBI survivors. Another primary objective was to explore the possibility that method described below could

provide the foundation for future studies to better delineate patterns of deficits and preserved navigational function after TBI. No specific hypotheses were tested however, it was anticipated that the TBI survivors would exhibit some behavioural deficits on the Place maze task.

The decision to conduct a feasibility study was made for several reasons. The first was that a full scale study of the effects of experience on strategy selection was beyond the scope of this dissertation. Furthermore, prior experience in developing experiments with the TBI population (Livingstone & Skelton, 2007) has shown that in order to conduct a full study at least a year is required to recruit and test a relatively small sample (~12) of TBI participants and matched comparison participants. However, given the direction of the present research program, there appeared to be value in investigating the feasibility of using eye movements in this population before embarking on a full scale study.

Methods

The methods for this experiment (general procedures, virtual environment navigation tasks and eye tracking) were as described in Chapters 3 and 4. However, some minor changes (described below) were made to accommodate the brain injury survivors. Electroencephalography (EEG) data was recorded from the TBI participants as part of a collaborative study and as described in Chapters 3 and 4. The EEG results are to be reported elsewhere.

Participants

The participants were three male traumatic brain injury survivors recruited from the Brain Injury Society in Victoria, British Columbia (via a poster displayed at the

society office) and 15 male comparison participants (community based and student) matched only for gender. The comparison participants formed part of the sample studied in a previous experiment (see Chapter Four) and all agreed to have their data used in this second analysis. The average age of the comparison group was 25 years with a range of 19 to 46 years. Participants in the comparison group had no documented history of neurological or psychiatric disorders and only one individual was taking a medication (AndroGel® testosterone replacement) which was not deemed to influence navigation performance. The majority (13/15) of comparison participants had either a partial university education or an undergraduate degree. One comparison participant had a partial high school education and one had a graduate degree.

The TBI survivors were Participant 1 (P1, aged 42 years), Participant 2 (P2, aged 35 years) and Participants 3 (P3, aged 30 years). These participants answered questions about their injury (Appendix 5-A) and Table 5.1 gives a summary of their demographics. All were classified as brain injured after reporting that they had been hospitalized for loss of consciousness. One participant (P3) reported being in a coma for three weeks. By self-

Table 5.1

Background demographics of TBI survivors.

Participant	Age (years)	Education	Time since injury	Cause of injury	Injury type (self report)
P1	42	Graduate degree	>1 year	Motor cycle accident	Concussion (area not known)
P2	35	Some university	9 years	Car accident	Mild frontal
P3	30	University degree	8 years	Sports injury	Severe temporal (coma)

report P2 received a mild frontal lobe injury and P3 received a right temporal lobe injury. P1 reported a concussion but could not provide details of the area of damage. The TBI survivors had no documented history of neurological disorder or psychiatric condition before their injury. One participant (P3) reported having depression which was well controlled by medication and occasionally he took muscle relaxants to combat muscular pain. The time since injury ranged from just over a year to 9 years (P1 = over a year, P2 = 9 years, P3 = 8 years). The injuries were caused by motor vehicle accidents (P1 and P2) and sports injury (P3). Education levels were some university (P2), a completed university degree (P3) and a graduate degree (P1). Extra care was taken to make sure that the TBI survivors understood the informed consent and participant debriefing. All TBI and community based participants were paid an honorarium of $30 for their time and for travelling to the university. The University of Victoria Human Research Ethics Committee approved the research.

Apparatus and Procedures

The apparatus and procedures were as described in Chapters 3 and 4. Briefly, participants completed four virtual environment navigation tasks based on a human analogue of the MWM. The Visible Platform maze required participants to repeatedly travel to a platform visible in the environment. The Place maze biased participants toward using distal room features (an allocentric strategy) whereas the Cue maze biased participants toward using a cue object located on the arena wall (an egocentric strategy). In the Dual Strategy maze the environment did not contain any allocentric or egocentric bias and therefore participants were free to select either strategy type to find the platform. After completion of the Dual strategy maze participants completed a strategy probe trial

to test whether they selected an allocentric or an egocentric strategy. Eye movements (gaze positions) were recorded during the first orientation second at the start of trials.

In addition to the above procedures, care was taken to monitor the fatigue level of the TBI survivors, since fatigue is one of the most common after effects of brain injury (Belmont, Agar, Hugeron, Gallais, & Azouvi, 2006). When TBI participants were recruited they were asked when during the day they feel most alert and an effort was made to schedule appointments at these times. Further, TBI participants were questioned about their level of fatigue at the end of each set of maze trials and given the opportunity to rest if necessary.

Design Note

The participants received the mazes in differing orders as follows: P1 (Place then Dual Strategy then Cue), P2 (Cue then Dual Strategy then Place), P3 (Dual Strategy then Place then Cue). Experience effects were not studied although their presence is likely based on findings reported in Chapter 4. The possible influence of these effects is considered in the discussion section below.

Ancillary Tasks

Cognitive mapping tasks. Participants completed the Where's the Water Task (WTWT) task to ascertain whether they felt a sense of "presence" in the virtual environment (see Appendix 2-B). Participants indicated by pointing where they thought the water was located in the environment. The task was scored on a 3-point scale. Participants also completed the Room Reconstruction Task (RRT) to assess the degree to which they had formed a cognitive map (see Appendix 3-C). As a reminder participants reconstructed the main features of the room (including the platform location) using two

dimensional pictures. The task was scored on a 4-point scale.

Neglect tests. Two tests, the Clock Drawing Task and the Bells Test were used to establish whether or not the TBI survivors exhibited signs of visual neglect. Such neglect can impair navigational performance (Nico et al., 2008; Piccardi, 2009). The clock drawing task required participants to draw a circle (representing a clock face) on a blank sheet of paper and then to draw the numbers 1 to 12 in the correct positions. Participants were then asked to draw hands in the twenty-to-four position on the clock face. The task was scored on a scale of 1 to 10 as described in Spreen & Strauss (1998) with scores greater than 7 being considered in the normal range. A second task, the Bell's Test, was employed because it may be more sensitive than the clock drawing task and more useful for evaluating mild cases of visual neglect (Gauthier, Dehaut, & Joanette, 1989). Participants were required to circle pictures of bells on a sheet that also contained multiple distracter pictures. For scoring purposes a global score was calculated (from a possible total of 35) along with scores for the left and right side of the sheet.

One test item labelled "immediate and delayed recall" from the Rivermead Behavioural Memory Test (RBMT) (Wilson, Cockburn, Baddeley, & Hiorns, 1991) was used to indicate the severity of verbal memory problems in the TBI survivors. This test item was selected because it requires participants to listen to and remember the contents of a short verbal passage both immediately and at a later time. The ability to do this is important for listening to and remembering instructions during testing. Consequently, a deficit on the RBMT test item could indicate that participants had difficulty following task instructions. The item was scored according to instructions given with the RBMT, with one point given for each important word/phrase recalled, to a total of 21 possible

points.

Computer Game Experience

Because the experiment concerned the effects of training in a virtual environment, participants were asked about their computer gaming experience. They were asked whether they play two and/or three dimensional games, how often they play (now and as children) and about their experience with game controllers/joysticks. Participants responded on a 6-point Likert-type scale (Appendix 2-A) by circling one of the following responses: “never”, “occasionally”, “monthly”, “weekly”, “every few days”, or “daily”. Results were tabulated by examining each question separately for TBI and comparison participants.

Analysis

The derivation of the behavioural and eye movement variables was as reported in Chapters 3 and 4. Briefly, for navigation behaviour the key variables were latency to the platform, distance traveled to the platform, maze probe, DTS score and strategy probe. The eye movement analysis was limited to vertical gaze for simplicity and the important variable was vertical gaze position (above or below the horizon). As a reminder the horizon divided the screen display into equal sized upper and lower halves. The objects useful for navigation in the Cue and Dual Strategy mazes always appeared below the horizon whereas the distal room features useful in the Place and Dual Strategy mazes were always above the horizon.

Statistics. The analysis was descriptive in nature due to the small number of TBI participants. Means and standard deviations were reported where appropriate, for example, for the behavioural measures (latency, distance and maze probe) and for the

variable vertical gaze position above the horizon. Individual scores were reported for the DTS trials and frequency of selection was reported for the strategy probe trial. To assess whether individual TBI survivors performed differently or had different patterns of looking than the comparison group, confidence intervals were calculated for the comparison mean scores. In this way, "norms" were established for latency, distance, probe trial scores and the vertical gaze position variable. Scores of TBI survivors were assessed according to whether they fell inside or outside the limit identified by the confidence intervals of the comparison group mean. Scores outside these intervals were taken to indicate that the individual's performance differed from that of the comparison group.

Results

Note: The following results are preliminary and descriptive. Therefore terms such as "greater than" or "similar to" do not refer to statistically significant differences. Rather, these expressions refer to descriptive statistics or observations made by visual inspection of the data.

Navigation Results

TBI participants were able to master use of the joystick and were able to follow instructions well enough to complete the maze tasks. TBI participants performed nearly as well on the visible platform trials (Latency, M = 4.2 s, SD = 2.0; Distance, M = .70 pd, SD = .28) as did the male comparison group (Latency, M = 3.5s, SD = 1.0; Distance, M = .6, SD = .01). However, latency and distance scores on the second visible platform trial were greater than expected for the TBI group. This was the result of one trial for one participant (P3) who initially misunderstood task directions. Upon clarification,

this participant was then able to navigate to the visible platform with ease.

The TBI survivors did not perform as well in the Place maze as did the comparison participants (Figure 5.1). Visual inspection of the data shows that both latency and distance scores of the TBI survivors tended to be highly variable. All three participants took longer to find the platform (P1, *M* = 27 s; P2, *M* = 14 s; P3, *M* = 15 s) than did comparison participants *(M* = 12.4 s, *SD* = 7.1). Two TBI survivors also took longer routes (P1, *M* =4.3 pd; P2, *M* = 2.1 pd) to the platform than did the comparison participants. Differences in latency and distance scores were especially noticeable during the later trials (6 – 10).

The observed differences in Place maze performance were confirmed by comparing the individual scores of TBI participants to the 95% confidence intervals calculated for the comparison group means (Figure 5.2). Table 5.2 gives the navigation behavioural scores (latency, distance and probe trial) for the three TBI participants and confidence intervals for the comparison group. For latency on trials 2 – 10 in the Place maze, only one participant (P1) had scores falling outside the range of the comparison confidence intervals, suggesting that the time taken to find the platform was within the normal range for the other two participants (P2 and P3). However, when latencies in the Place maze were examined for later trials (6 – 10), all three TBI participants had scores that exceeded the normal range, indicating that they took longer to find the platform than did the comparison participants (Figure 5.2).

For the distance travelled to the platform on trials 2 – 10 in the Place maze, two TBI participants (P1 and P2) had scores exceeding the normal range and thus took longer paths to the platform than did the comparison participants (Figure 5.2). The

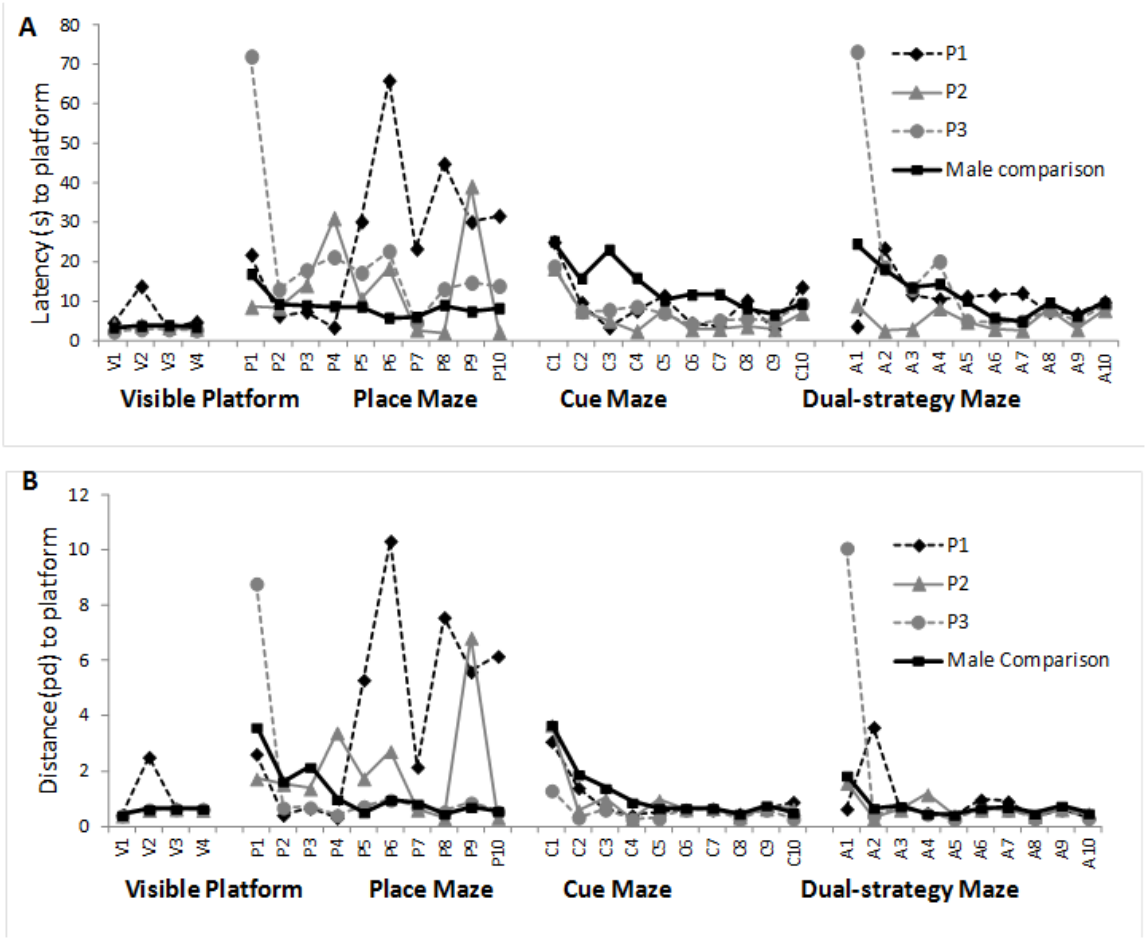

Figure 5.1.Acquisition curves comparing performance of TBI survivors and male comparison participants in three mazes (Place, Cue and Dual Strategy). Relative to comparison participants, TBI survivors had similar latencies **(A)** and distance traveled **(B)** to the platform in the Cue and Dual Strategy mazes. Relative to comparison participants, TBI survivors had impaired performance (longer latencies and distances to the platform) in the Place maze.

exception to this was P3 whose paths to the platform were the same length as those of the comparison participants.

TBI participants had latency and distance scores that were mostly within normal

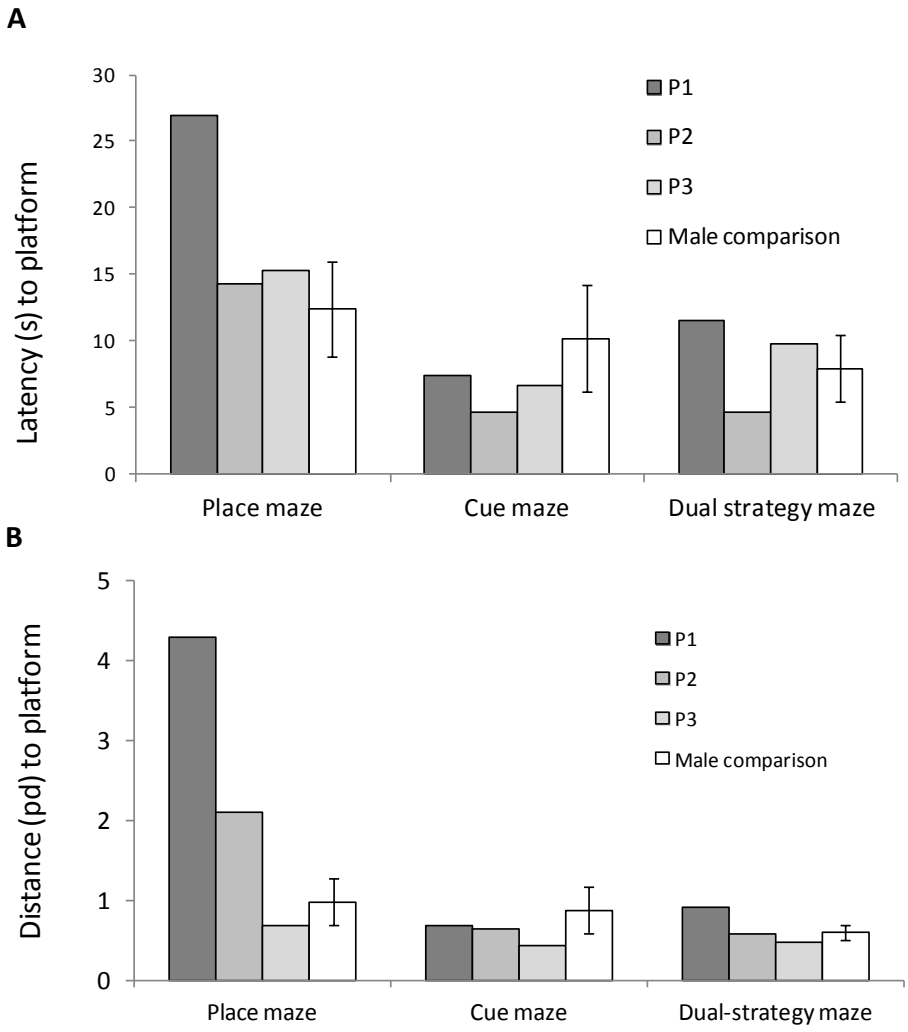

Figure 5.2. Mean latency and distance scores for TBI participants compared to confidence intervals for the comparison group in all three navigation tasks, Place maze, Cue maze and Dual Strategy maze (Trials 2 – 10). **A.** Participant 1 had high latencies in both the Place maze and the Dual Strategy maze. **B.** Participants 1 & 2 had high distance scores in the Place maze and Participant 1 also had high distance scores in the Dual Strategy maze. All TBI participants performed well in the Cue maze. Bars indicate the 95% confidence interval around the mean for the comparison group.

limits in both the Cue maze and the Dual Strategy maze (Figure 5.1 and Table 5.2). The single exception was P1, who had latency and distance scores that both exceeded (were worse than) the comparison group limits in the Dual Strategy maze. However, this participant had latency and distance scores within the confidence intervals for the

Table 5.2.

Navigation behavioural scores for TBI participants compared to confidence intervals for male comparison group. Variables of interest are latency to the platform, distance to the platform and percentage of trial in correct quadrant on the probe.

Participants & confidence interval	Latency (s) (trials 2-10)	Latency (s) (later trials 6-10)	Distance (pd) (trials 2-10)	Probe %
		Place Maze		
P1	27*	39*	4.3*	28*
P2	14	13*	2.1*	37*
P3	15	14*	0.7	63
Comparison group mean	12	10	1.0	62
95% confidence interval	8.9 to 16.0	6.3 to 12.9	0.7 to 1.3	54 to 71
		Cue Maze		
P1	7	7	0.7	78
P2	5	4	0.6	44
P3	7	6	0.4	89
Comparison group mean	10	7	0.9	63
95% confidence interval	6.3 to 14.3	5.2 to 9.0	0.6 to 1.2	53 to 72
		Dual Strategy Maze		
P1	12*	9	0.9*	58
P2	5	5	0.6	53
P3	10	6	0.5	94
Comparison group mean	8	7	0.6	63
95% confidence interval	5.4 to 10.4	4.3 to 9.8	0.5 to 0.7	53 to 74

Note. P1 = Participant 1; P2 = Participant 2; P3 = Participant 3; pd = pool diameters.
* = outside of confidence interval and performance worse than that of comparison group.

comparison group on later trials 6 - 10 (data not shown). The differences in performance in the three maze conditions did not appear to be a result of an experience effect. That is, there appeared to be no order effect that could explain the difference between

performance in the Place maze and the other two mazes (Appendix 5-B).

Overall, TBI participants did not perform as well on the Place maze probe trial as did the comparison participants. In contrast, TBI participants had good scores on probe trials in the Cue maze and Dual Strategy maze, tending to perform as well as comparison participants on these trials. However, some individual differences were observed in the TBI group.

On the Place maze probe trial, two TBI survivors (P1 and P2) were less able to focus their search for the platform than were comparison participants. These two participants spent less time searching the correct quadrant of the arena than did the comparison participants and their scores fell below the range of confidence intervals calculated for the comparison group (Figure 5.3). In fact, the proportion of the probe trial that Participant 1 spent in the correct quadrant was barely above chance. However, Participant 3 performed well on the probe trial, focusing his search in the correct quadrant for about 60% of the trial and at the same rate as the mean for the comparison group.

On the Cue maze probe trial, two TBI survivors (P1 and P3) focused their platform search as well as did comparison participants and their scores were within or exceeded (were better than) the confidence intervals calculated for the comparison group (Figure 5.3). Participant 2 did not focus his search as well as the comparison participants and his scores were below the comparison group limits. Interestingly, this participant had good latency and distance scores in both the Cue maze and the Dual strategy maze.

On the Dual Stratgey maze probe trial all three TBI survivors performed within or exceeded normal limits (Figure 5.3).

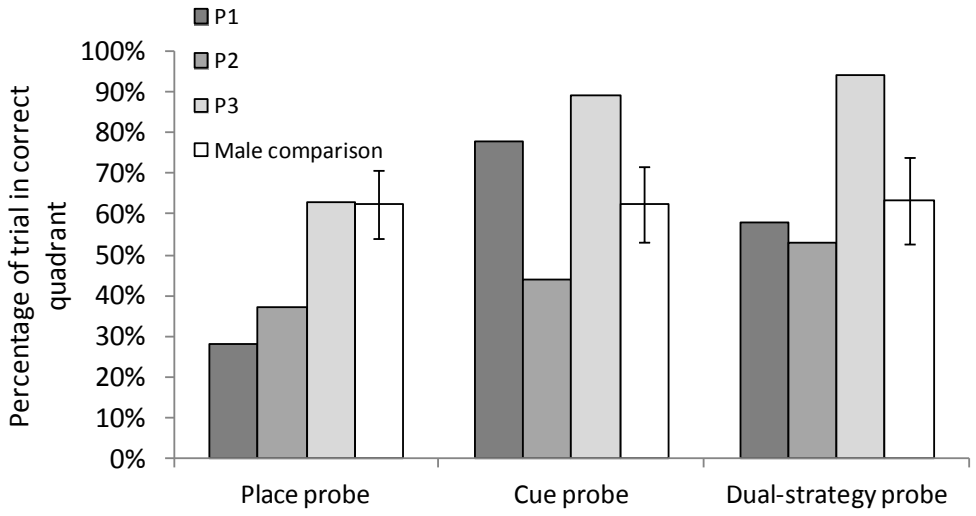

Figure 5.3. Probe trial scores comparing performance of TBI participants to confidence interval of comparison group for three tasks, Place maze, Cue maze and Dual Strategy maze. Two TBI participants had low scores on the Place maze probe and one had a low score on the Cue maze probe. All three TBI participants performed well in the Dual Strategy maze probe.

Drop-the-seed Trials

The TBI survivors were able to explicitly indicate the location of the visible platform by dropping a virtual seed at its centre. Thus they were able to understand and execute the task requirements for DTS trials. On the Place maze DTS trial two TBI survivors (P2 and P3) had perfect scores of 7, indicating that they were able to explicitly identify the location of the platform (now hidden) in the virtual environment. However, Participant 1 had a score of 0, and indicated that the platform location was outside of the correct quadrant of the arena. In the comparison group about 60% of participants had scores of 6 or 7 on the DTS trial and no participant received a score of 0. On the Cue Maze DTS trial all three TBI participants had perfect scores of 7, indicating that they were able to accurately locate the platform in the virtual room. About 75% of comparison participants had very good scores of 6 or 7 on this trial.

Strategy Probe Trial

On the strategy probe trial after the Dual Strategy maze, all three TBI survivors selected an egocentric strategy. They dropped their virtual seed markers in front of the cue object (the steel box). Furthermore, by verbal report all three participants were unaware that the cue object had been relocated for this trial. In the comparison group, six participants selected an allocentric strategy and dropped their virtual seed markers according to the spatial relations of the room features; nine participants selected an egocentric strategy and dropped their seed markers in front of the cue object. All comparison participants who navigated by the room features on this trial noticed that the object had been moved. Furthermore, the majority (8/9) of comparison participants who navigated by the object did not notice that it had been moved.

The TBI survivors were slightly less accurate than comparison participants in their placement of the seed marker. However, their performance was still good, i.e., in the correct quadrant of the arena and close to the platform location. Two TBI survivors (P1 and P3) had very good accuracy scores of 6 and the third TBI survivor (P2) had a good accuracy score of 5. The overall accuracy of comparison participants on this trial was a very good score of 6.3 (placement by steel box = 7.0; placement by room features = 5.3).

Gaze Position Results

Average gaze during orientation. Overall, the shape of average orientation gaze (for the first second) was similar for TBI and comparison participants (Figure 5.4). Gaze rose gradually to reach a peak at about a third of a second (20 samples) and levelled off thereafter. In the Place maze the average orientation gaze of the TBI survivors was substantially lower that of comparison participants (Figure 5.4). Further, the average

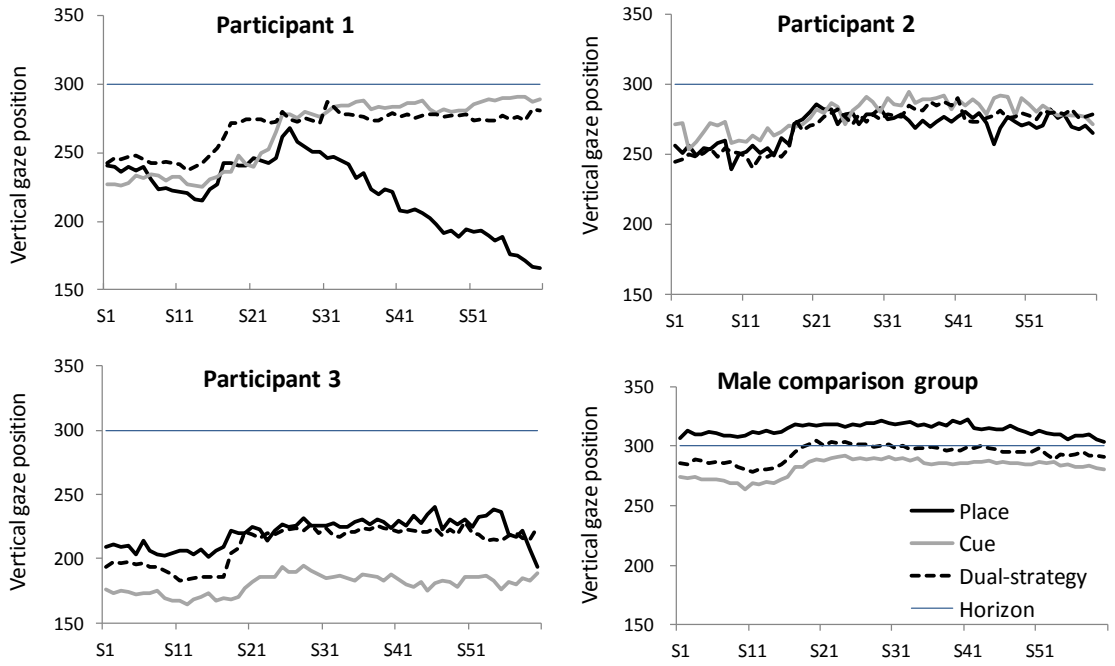

Figure 5.4. Average vertical gaze position for TBI survivors and comparison participants in Place, Cue, and Dual Strategy mazes in the first orientation second of trials. Sampling rate was 60 samples per second and appears on the horizontal axis. The blue line indicates the horizon defined at the vertical midline on the screen display.

orientation gaze of TBI participants never rose above the horizon, whereas average gaze for the comparison group was always above the horizon. This indicates that TBI participants were likely not utilizing the distal room features during orientation in the Place maze. One TBI survivor (P1) had an unusual pattern of gaze that consistently dropped off at the midway point of the first orientation second. This participant may have been looking mainly at the floor although the useful stimuli (outdoor landscapes) were located above the horizon.

In the Cue maze the average gaze of two TBI survivors (P1 and P2) was similar to the gaze of comparison participants. These two participants looked in the vicinity of the

horizon during the first orientation second suggesting that they were orienting toward the objects on the arena wall (by looking at or just below the horizon). The exception to this was Participant 3 whose average gaze was very low suggesting that this participant looked mainly at the floor during orientation in the Cue maze.

In the Dual Strategy maze, the average gaze of two TBI survivors (P1 and P2) was very similar to their gaze patterns in the Cue maze. However, Participant 3 (whose gaze was always low) appeared to have a gaze pattern similar to his average gaze in the Place maze.

Trial by trial vertical gaze position. Visual inspection of trial by trial data showed that in the Place maze TBI survivors consistently looked lower on the screen display than did comparison participants (Figure 5.5). During orientation in this task the vertical gaze positions of the TBI survivors were lower and more variable than were the gaze positions of the comparison group. Further, on the majority of trials the vertical gaze of each TBI survivor was below the horizon whereas the mean vertical gaze position for comparison participants was above the horizon on all but the first trial. Interestingly, Participants 1 and 2 had vertical gaze positions similar to those of comparison participants in the first few trials, but their gaze tended to drop thereafter. Participant 3 had low gaze throughout the Place maze trials although he exhibited a slight rise in gaze during early trials. When the trial by trial gaze positions of the TBI survivors were compared to those of the comparison group, all three participants had gaze positions that fell outside of the 95% confidence interval calculated for the comparison participants (Figure 5.6). These results indicate that across Place maze trials TBI survivors oriented by looked mainly below the horizon either at the arena wall or at the floor. Thus they did

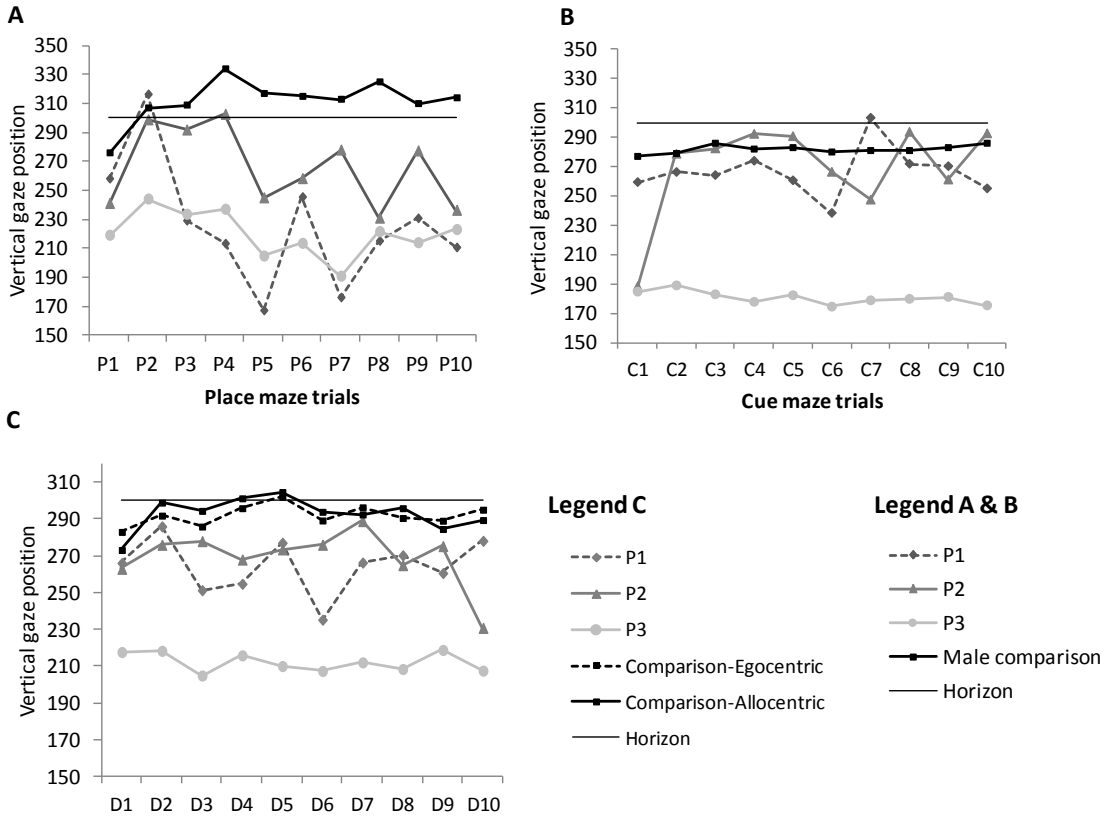

Figure 5.5. Vertical gaze position across trials for TBI and comparison participants. In the Place maze **(A)** all three TBI participants had lower gaze positions than did the comparison participants. In the Cue maze **(B)** two participants had gaze positions similar to the comparison participants. In the Dual Strategy maze **(C)** TBI participants looked lower than did comparison participants. Participant 3 had very low gaze positions in both the Cue and Dual Strategy mazes. The horizontal line represents the horizon on the screen display.

not appear to orient toward the distal room features that were the stimuli most useful for navigating.

In the Cue maze TBI survivors tended to orient in a manner similar to the comparison participants. Participants 1 and 2 had vertical gaze positions very similar to

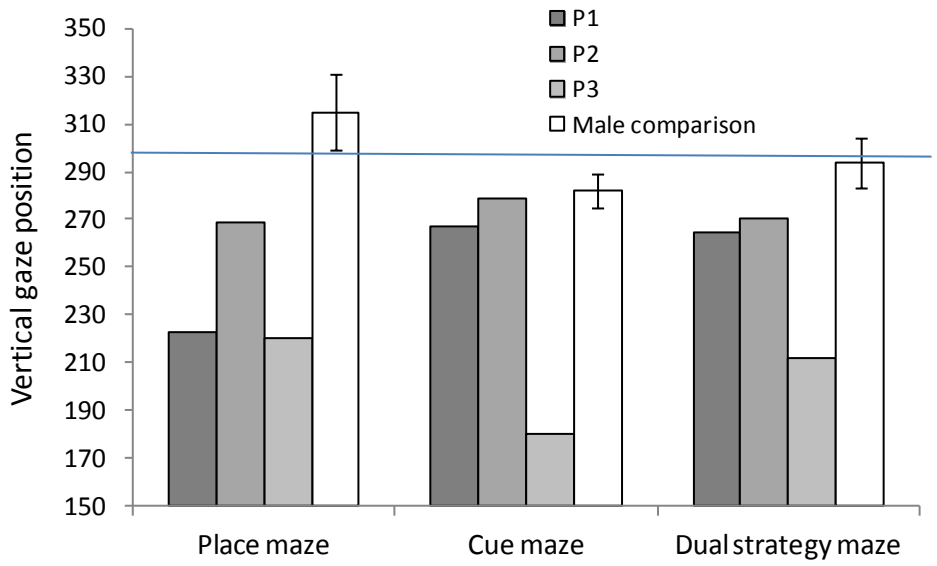

Figure 5.6. Mean vertical gaze positions for TBI participants compared to confidence intervals of comparison group for three tasks, Place maze, Cue maze and Dual Strategy maze. In the Place maze, all TBI participants had lower gaze position than did comparison participants. In the Cue maze two TBI participants (P1 and P2) had gaze positions similar to the comparison group. In the Dual Strategy maze all participants had lower gaze positions than did comparison participants. The horizontal line represents the horizon at the vertical midline of the screen display.

those of the comparison participants (Figure 5.5). Gaze was low on the first trial but rose to a region just below the horizon, where it remained for the rest of the trials. Also, trial by trial gaze positions of Participant 1 fell within the confidence interval limits for the comparison group (Figure 5.6) and those of Participant 2 closely approached these limits. The results indicate that these participants were probably orienting toward the useful cue objects located on the arena wall. The exception to this was Participant 3 whose gaze was consistently low with an average in the bottom third of the screen display. He appeared to be looking mostly at the floor.

In the Dual Strategy maze the TBI survivors tended to orient in the same way that they had in the Cue maze, however their gaze remained lower than that of comparison participants (Figure 5.5). When comparison participant gaze positions were grouped

according to whether they had selected an allocentric or egocentric strategy on the strategy probe, there were small differences in vertical gaze such that allocentric strategists had higher gaze in early to middle trials. The trial by trial gaze positions of all three TBI survivors fell outside the confidence interval limits of the whole comparison group (Figure 5.6) and also those for the comparison participants when they were grouped as either egocentric or allocentric strategists (data not shown). However, it should be noted that the comparison participants had slightly higher gaze positions in the Dual strategy maze than in the Cue maze. As per the Cue maze, Participant 3 had consistently low gaze and appeared to be looking mainly at the floor during the orientation phase of trials.

Ancillary Tasks

Where's the Water Task. On the WTWT, two of the TBI survivors (P1 and P3) indicated by pointing that the water was located behind them. These participants had perfect scores of 2 on this task indicating that they felt immersed in the virtual environment and understood its basic layout. Participant 2 had a score of 0 and pointed at the screen to indicate the location of the water. He may have had difficulty perceiving the environment in three dimensions or he may simply have been unaware of the existence of the water outside one of the windows. The majority of comparison participants had a score of 2 on this task.

Room Reconstruction Task (RRT). TBI survivors were relatively successful at reconstructing the features of the virtual room and performed as well as comparison participants on the RRT. Their scores were as follows: P1 = 3, P2 = 3, P3 = 4. The majority (12/15) of comparison participants had scores of 4 and only 2 comparison

participants performed poorly (scores of 0 or 1) on the task. However, it should be noted that Participants 1 and 2 were able to reconstruct the layout of the room but were unable to place the platform in the correct quadrant of the arena.

Clock Drawing Task. TBI survivors did not show visual hemi-neglect according to the Clock Drawing Task. Participants 1 and 2 had scores of 9/10 and Participant 3 had a perfect score of 10/10. Scores of 7 and above are considered within normal limits.

Bells Test. The results of the Bells Test indicated that none of the TBI survivors had residual visual neglect. Global scores on this task were similar for the TBI participants (P1 = 35, P2 = 33, P2 = 33, P3 = 35) and comparison participants (=34). The criterion for attentional problems is a score of less than 32, that is, the omission of more than three bells (Gauthier et al., 1989). Participants 2 and 3 circled fewer bells on the left side (P2 = 13, P2 =14) than they did on the right side (P1 = 15, P2 = 15) of the sheet whereas the average left vs. right scores for the comparison group were 14.5 and 14.5 respectively. However, visual neglect is only suspected if a participant omits 6 or more bells on either side. Thus by the test criteria none of the three TBI survivors exhibited neglect.

RBMT test item. The TBI survivors demonstrated good verbal memory both immediately and after a short delay. Their scores on the RBMT immediate (P1 = 8.5, P2 = 8.0, P3 = 7.5) and delayed (P1 = 6.0, P2 = 8.0, P3 = 7.0) recall test item were as good as those of comparison participants (Immediate = 7.3, 95% CI = 1.3; Delayed = 6.8, 95% CI = 1.5).

Comparison of Measures

When performances of the three TBI survivors were compared on the key

navigational measures (latency, distance, probes and ancillary tasks), deficits appeared on tasks that were designed to test cognitive mapping, i.e., in the Place maze, RRT and WTWT. Table 5.3 gives a comparison of the navigation performance in the Place and

Table 5.3

Summary of navigation behavior, gaze position and ancillary task scores for the TBI survivors. Note that there were deficits in behavior and apparent deficits in gaze position in the Place maze but not in the Cue maze. TBI survivors selected egocentric strategies. P3 had better behavioural performance than the other two TBI survivors.

	Place maze			Cue maze			Dual Strategy		Ancillary tasks	
Participant	SS	DTS	Vertical gaze	SS	DTS	Vertical gaze	DTS	Vertical gaze	WTWT	RRT
P1	*	*	*	-	-	-	Ego	Ego	-	*
P2	*	-	*	-	-	-	Ego	Ego	*	*
P3	-	-	*	-	-	*	Ego	Ego	-	-
Comp							Ego/Allo	Ego/Allo		

Note1. SS = Spatial score; DTS = Drop-the-seed; WTWT = Where's the Water Task; RRT = Room Reconstruction Task; P1 = Participant 1; P2 = Participant 2; P3 = Participant 3; Allo = Allocentric strategy or gaze, Ego = Egocentric strategy or gaze; Ego/Allo = Majority (9 of 15) of comparison participants chose egocentric strategy.
*= apparent deficit, - = no deficit.

Cue mazes and the gaze positions of the three TBI survivors. Navigation performance was quantified using the spatial score measure (Skelton et al., 2006) to combine latency, distance and probe dwell time measures:

Spatial Score= (0.5 x probe z-score) – ((0.25 x latency z-score) + (0.25 x distance z-score))

When summarized in this way it became apparent that Participants 2 and 3 had problems in the Place maze and also on the RRT. These same two participants looked mainly below the horizon in the Place maze and one of these participants (P2)

also had difficulty pointing out the location of the water, a key outdoor feature of the virtual environment. However, Participant 3 had fewer navigation problems although he did have very low orientation gaze in all maze conditions. According to two previous studies (Livingstone & Skelton, 2007; Skelton et al., 2006), most but not all TBI survivors exhibit spatial navigation deficits. It is therefore not surprising that in the present study one TBI survivor demonstrated reasonably good navigational ability.

Computer Game Experience

The computer game experience of TBI survivors differed only slightly from that of the comparison participants and reported joystick/gamepad experience was similar for the two groups of participants. Participants 1 and 2 currently indicated playing computer games less frequently (only occasionally) than the average of the comparison group which was monthly computer game play. Participant 3 indicated playing computer games on a weekly basis. The nature of computer game play was also somewhat different for TBI survivors who indicated playing three dimensional computer games occasionally whereas the average for the comparison group was monthly three dimensional game play. However, about a third of the comparison group also indicated playing three dimensional games only occasionally. All three TBI survivors had average or greater than average experience with computer joysticks and/or gamepads.

Discussion

Summary of Navigation Results

In the present feasibility study, TBI survivors and comparison participants were equally capable of understanding task instructions and mastering the use of the joystick. TBI survivors had good latency and distance scores on the Visible Platform trials and

their scores were similar to those of the comparison participants. Furthermore, the TBI survivors were as capable as comparison participants at navigating in the Cue maze environment where clear proximal cues were provided for orientation. All three TBI survivors had latency, distance scores that were similar to those of the comparison participants. Two of the three TBI survivors also had probe trial scores similar to those of the comparison participants and all three TBI survivors placed the marker accurately on the Cue maze DTS trial.

The TBI survivors tended to be impaired in their performance in the Place maze where they were required to navigate without the presence of clear proximal cues. Two of the TBI survivors had latency and distance scores that were higher (worse) than those of the comparison participants. These same two participants were also unable to focus their search for the platform on the probe trial. A third TBI survivor had higher latency scores but had distance probe trial scores that were similar to those of the comparison participants. On the DTS trial one TBI survivor had difficulty and placed the seed marker outside the correct quadrant of the arena. Surprisingly, the other two TBI survivors had good scores on this trial.

As expected, TBI survivors performed nearly as well as comparison participants in the Dual Strategy maze where the survivors could use either distal or proximal cues to find the platform. Only one TBI survivor had some initial difficulty with the task, but on later trials had latency and distance scores similar to those of the comparison participants. On the probe trial all three TBI survivors were able to focus their search as well as the comparison participants. On the DTS trial, the TBI survivors were as accurate as were the comparison participants. It is worth noting that all three dropped their seed markers in

front of the cue object, indicating that they were navigating using an egocentric strategy. This strategy is similar to the strategy elicited by the Cue maze.

Summary of Eye Tracking Results

In the Cue maze the comparison participants and TBI survivors appeared to orient in a similar fashion. Like the comparison participants, two TBI survivors focused their gaze near the region of the display that contained the cue objects. One TBI survivor did have much lower gaze and appeared to look mainly at the floor while orienting. In contrast, in the Place maze TBI survivors appeared to orient differently than did comparison participants. The gaze positions of comparison participants were consistently high and directed toward the area of the display containing the distal room features (outdoor landscapes) whereas the gaze positions of TBI survivors were consistently low and directed toward the region just below the arena maze wall or toward the arena floor.

In the Dual Strategy maze the TBI survivors appeared to orient in the same way that they had in the Cue maze. However their gaze was lower than that of the comparison participants who had slightly higher average gaze in the Dual Strategy maze than in the Cue maze.

Discussion of Navigation Results

The navigational deficits seen here in the Place maze but not the Cue or Dual Strategy mazes, and the choice of an egocentric strategy in the Dual Strategy maze were as expected based on previous work showing that TBI survivors have deficits on place-based but not cue-based navigation tasks (Livingstone & Skelton, 2007). These deficits may occur because TBI survivors have difficulty either forming or using cognitive maps and is consistent with the finding that TBI frequently results in damage to the

hippocampus (Bigler, 2001; Bigler et al., 1997) a structure known to be important for spatial navigation in both animals (Morris et al., 1982) and humans (C. F. Doeller et al., 2008). Damage to the hippocampus or its connections has been associated with a cognitive mapping deficit (Barrash et al., 2000; Feigenbaum, Polkey, & Morris, 1996; Goodrich-Hunsaker et al., 2010) as shown by difficulty navigating in situations where there are no proximal cues to mark the location of a target or where the target location cannot be seen from the start position. This may occur because of an inability to utilize allocentric strategies.TBI survivors appear to have no difficult when navigating using clear, proximal cues. Interestingly, research has shown that TBI does not result in noticeable damage to the striatum or caudate (Anderson & Bigler, 1994; Primus et al., 1997). This may explain in part why egocentric strategies such as navigating to a single guidance cue may be spared after TBI. At least one study has shown a double dissociation such that in humans the hippocampus and caudate systems appear to function separately from one another (Voermans et al., 2004). The pattern of impaired and spared ability observed in the TBI survivors supports this proposition as does the finding that TBI survivors selected an egocentric strategy in the strategy probe trial. The capacity of the current behavioural paradigm to elicit both impaired and spared behaviours contributes to the feasibility of the methods described here.

Although the sample size here is very small, it is worth noting that this is the first time that brain injury has been shown to affect strategy selection, and indicates that deficits in navigation may result from the inability to use an allocentric strategy, not from the inability to select a strategy appropriate to the circumstances.

Discussion of Eye Tracking Results

The present findings demonstrate the feasibility of applying eye tracking methods to the study of spatial navigation in survivors of TBI. The eye tracking results demonstrated that the gaze of TBI survivors and comparison participants differed in the Place maze and not in the Cue maze. This suggests that the current paradigm is useful for assessing orientation strategies in the TBI population.

The low gaze of TBI survivors in the Place maze indicates that these individuals were not looking in the regions of the screen display containing the distal room features and thus were probably not using allocentric strategies. The Place maze is an analogue of the MWM and is therefore designed specifically to provide only distal, extra-maze stimuli for navigation. Comparison participants tended to look in the regions containing these stimuli about two-thirds of the time during orientation (data not shown) and had an average vertical gaze position that was located within this region. This was taken to mean that the comparison participants formed cognitive maps and navigated by using allocentric strategies that were based on the spatial relationships of the available room features. However, during orientation the TBI survivors had average vertical gaze positions that were located in the bottom half of the display, sometimes in the region just below the arena wall and sometimes on the floor of the arena suggesting that they were not utilizing the room features. In other words, the TBI survivors were either not forming or not using cognitive maps (and corresponding allocentric strategies) while navigating in the Place maze.

The trial by trial orientation gaze of two TBI survivors (P1 and P2) in the Place maze surprisingly showed a pattern that appeared to correspond to their navigation

behavioural scores for latency and distance. On early trials the TBI survivors had high average gaze and low (good) latency and distance scores (much like the comparison participants). However as trials progressed, the TBI survivors demonstrated progressively lower gaze accompanied by higher (worse) latency and distance scores. This is an interesting finding because previous work with healthy participants has been unable to identify correlations of behaviour with gaze positions.

The eye tracking results from the Cue and Dual Strategy mazes indicate that TBI survivors can identify, and focus their attention on, navigationally relevant stimuli. Two of the TBI survivors looked close to the horizon and in the vicinity of the objects while orienting in these mazes. Therefore, the deficits observed in the Place maze were not due to deficits in the ability to drive gaze. This suggests that the gaze position variable is meaningful for discriminating strategy use in the TBI population.

In the Cue maze, the vertical gaze positions of the TBI survivors support the proposition that egocentric strategies (and thus the egocentric system) are spared after TBI. Two participants had trial by trial gaze positions remarkably like those of the average for the comparison participants, with gaze focused mainly in the area just below the horizon and where the useful objects were located. It has been shown that TBI survivors who have topographic disorientation rely on landmarks and body positions for guidance and wayfinding in outdoor environments (Antonakos, 2004). In the current study the Cue maze task was constructed so that one cue object (the golden urn) always predicted the location of the platform and likely acted as a single guidance cue that the TBI survivors were able to utilize for navigation. One participant (P3) looked mainly at the floor during orientation (as he also did in the Place maze) and therefore may have

been adopting an egocentric response-based strategy based on body positions. The ability of the TBI survivors to use egocentric strategies is also supported by their ability to explicitly indicate the locations of the platform on the DTS trial.

The trial by trial orientation gaze of TBI survivors in the Dual Strategy maze was remarkably similar to their orientation gaze in the Cue maze, suggesting that in the Dual Strategy maze the TBI survivors were also using egocentric strategies. Unexpectedly, the TBI survivors looked down more than did the comparison participants in the Dual Strategy maze. A partial explanation for this is that some of the comparison participants used an allocentric strategy to solve the task and therefore had higher gaze positions. Indeed the comparison participants who selected an allocentric strategy did have slightly higher gaze positions in early trials than did those who selected an egocentric strategy.

Discussion of Feasibility

The present findings are among the first to suggest that it is not only feasible to collect eye movements, but that such data may have utility for indicating cognitive navigational deficits in survivors of TBI. Previously, eye tracking has been used to measure oculomotor deficits after brain injury (Ciuffreda et al., 2007; Heitger, 2003) and to study the well-known phenomenon of visual neglect (Làdavas, Zeloni, Zaccara, & Gangemi, 1997). However the present study is one of only a handful of studies applying eye tracking to the problems TBI survivors face in everyday life and is the first to examine gaze position during wayfinding. Linden Crothers & Rauch (2006) successfully measured eye movements (saccades and fixations) in TBI survivors and showed that individuals with attentional deficits had different patterns of eye movements than did healthy comparison participants. These researchers employed everyday tasks such as

finding a product on a supermarket shelf and finding a landmark on a map. However, these tasks were presented in a two-dimensional format so that they resembled paper and pencil type tasks. The current findings improve on this by employing a three-dimensional virtual environment and eye movements to successfully identify differences in where TBI survivors and comparison orient while navigating.

There were several challenges to feasibility noted during this study. These could confound results but mainly they suggest limitations to the population from which participants can be recruited. The most important challenges may be due to personal history of the TBI survivors, physical limitations, cognitive limitations and status of the visual system.

In the present study, the pre-injury state and experiences of the TBI survivors was unknown and thus could have contributed to performance in the mazes or to the eye tracking results. The paradigm described here cannot take into account the prior navigational ability of TBI survivors and so it may be difficult to assess deficits on an individual basis. This is a common problem in the field of neuropsychological assessment (Banich, 1997, p. 87) and appears to have few reliable or valid solutions. However, the problem could be partially addressed by asking TBI survivors (and significant others) about their wayfinding experiences prior to injury.

Another prior experience that could affect behavioural performance (and perhaps eye movements) in virtual navigation tasks is computer game play. In the present study, the TBI survivors had slightly less computer game experience and tended to play games occasionally rather than on a monthly basis as reported by the comparison participants. However, a third of the comparison participants had similar levels of computer game

experience to the TBI survivors and all three TBI survivors had average or better than average experience using joysticks and gamepads. Although game experience did not appear to be a factor in the current study it should be considered in future developments of this paradigm.

Physical problems after TBI could also be a challenge to feasibility and may include motor deficits, reaction time problems or fatigue. There are limits to participation in the study because TBI survivors must be able to sit for some time in front of a computer monitor, adapt to a chin rest and operate a joystick. Given that TBI survivors may also have sustained other physical injuries, some of them would not be able to cope with the motor demands of the current paradigm. Some TBI survivors may also have reaction time deficits that could confound navigation results (Stuss, Pogue, Buckle, & Bondar, 1994). This did not appear to be the case in the current study because TBI survivors found the platform quickly on the visible platform trials and in the Cue and Dual Strategy mazes where their performance was similar to that of comparison participants. However, it would be advisable to test reaction times if this paradigm were going to be applied to study of acutely injured or older TBI survivors. A third potential physical limitation is the presence of fatigue which is a very common problem after TBI (Belmont et al., 2006). The present experimental paradigm required that participants be able to remain alert for about an hour. While the TBI survivors tested here reported no fatigue, its presence should always be suspected when designing studies with this population. Solutions involve scheduling at suitable times of the day, rest periods between blocks of maze trials and completion of some ancillary tasks during a second session.

Cognitive problems may also present a challenge to feasibility. In the type of study presented here, the main concern is whether or not TBI survivors can understand, remember and follow task instructions.In the current study these problems were largely ruled out because of the very good performance of TBI survivors on all but the Place maze and associated mapping tasks. Furthermore, all three TBI survivors did as well as comparison participants on the RBMT verbal memory test item thus demonstrating that they could remember important parts of a verbal passage immediately after it presentation and also sometime later. However, the TBI survivors in the current study were all more than one year beyond the date of injury and therefore may have experienced some recovery of language or memory function (Wilson, 2002). Because of the small sample size studied here and because memory problems are strongly associated with TBI, care should be taken to assess memory function in future studies.

Disturbances in visual function may also present challenges to feasibility. Subtle oculomotor and vision problems can be a consequence of traumatic brain injury (Ciuffreda et al., 2007). These were not likely a problem in the present study in part because the TBI survivors were able to complete the calibration task which required them to fixate on relatively small targets located in all regions of the screen display. They also completed the baseline task and so were able to follow the movement of an object across the screen at the level of the horizon. However, subtle differences in saccades and fixation duration were not tested for.

Another challenge to feasibility, especially in participants with right hemisphere damage, is the possible presence of contralateral visual neglect. Although this condition can be very striking in the acute phase after injury or stroke (Bisiach & Luzzatti, 1978) it

may also be associated with ongoing and more subtle deficits (Gauthier et al., 1989). The TBI survivors in the present study did not show residual signs of neglect (left or right) on either the Clock Drawing Task or a more sensitive cancellation task (Bells Test). The participants were not tested for selective neglect of either near or far space although the Bells Test has recently been adapted for this purpose (Aimola, Schindler, Simone, & Venneri, 2012). The results of this adaptation showed that participants with right hemisphere damage (due to stroke or tumour) were more likely to demonstrate residual deficits in near rather than far space. These findings should be taken into account in future studies and may limit participation in the acute phase after injury.

Although there were some limitations, there were also several findings suggesting that the present feasibility study was a success. The first was that tracking eye movements during virtual navigation tasks was a useful method for discriminating strategy use in TBI survivors. Gaze positions in the Place and Cue mazes suggest that TBI survivors look for proximal cues when orienting for navigation and do not orient toward distal configurations of stimuli. Thus TBI survivors did not appear to use cognitive maps or allocentric strategies, even when navigating in the Place maze. The discrimination of strategies used by TBI survivors is important both for assessment and for the development of rehabilitation tasks to improve wayfinding function. For example, if a larger scale study shows that the present findings are consistent then training paradigms could be designed to improve cognitive mapping function or to compensate for lost mapping ability. A secondary but important contribution of the present study was to show that survivors of TBI are capable of having their eye movements successfully tracked, i.e., could complete calibration tasks and could stay focused on the screen

display throughout testing. Further the presence of a chin rest did not appear to interfere with performance on the maze tasks. This is important because without restraints TBI survivors can have a tendency to make sudden head movements (Linden et al., 2006) and therefore require constant re-calibration of the camera.

With further development the current paradigm has potential applications in diagnosis and rehabilitation of wayfinding deficits. The present study demonstrates the feasibility of combining eye tracking with an errorless learning approach so that navigational ability can be measured objectively and within the context of a task that patients find enjoyable and interesting. This is important because the ability to combine objective measures such as eye tracking with errorless learning tasks in a practical context could greatly benefit cognitive rehabilitation practice (Lloyd, Riley, & Powell, 2009; Wilson, 2002). Many existing tests of cognitive function after brain injury involve verbal or memory tests that assess deficits by the number of errors participants make. This approach often leaves the TBI survivor aware of his/her deficits and can lead to non-optimal performance on memory tasks (for short review see Wilson, 2002). In contrast, the virtual environment tasks employed here provide the opportunity for errorless learning because the participants are generally unaware of what constitutes good performance, i.e., whether they have been searching for too long or have travelled too far. Furthermore participants almost always attain the goal by finding the target platform and so receive positive feedback about their learning. The general comment of TBI survivors (and indeed the comparison participants) was that the environments were interesting and enjoyable and that the tasks were not stressful.

The present findings also point to the feasibility of providing a method to

distinguish behavioural compensation from recovery of function after TBI. Distinguishing compensation from recovery has been a problem in assessment and rehabilitation of cognitive function (Wilson, 2002). For example, it can be difficult to know whether a treatment is having an effect on recovery or whether the recovery has happened spontaneously. It is also not known what factors make particular TBI survivors more or less able to compensate for their cognitive losses (Wilson, 2002).

One possible path to behavioural compensation is through learned irrelevance i.e., through learning that some environmental information is no longer useful. An example from the current study is that TBI survivors may already have learned that some types of stimuli are simply not useful for navigating. Problems navigating using the spatial relationships of features in the environment may cause TBI survivors to ignore these spatial relationships. This may explain why, in the Place maze, TBI survivors ignored the stimuli above the horizon and looked mainly below the horizon and in near space. The reasons for this may be twofold and related to the availability of strategies. First, in the absence of useful allocentric strategies TBI survivors may attempt to use egocentric strategies to solve all navigation tasks. Second, the continued use of the egocentric system may strengthen this system leading to very good performance in some situations (as observed, for example, in the Cue maze). With time, these egocentric strategies may even become practiced enough that the resulting behaviour can look like recovery of function. For example, Participant 3 performed reasonably well in the Place maze (at least on the distance) measure but he appeared to be using an egocentric strategy and looked mostly at the floor. An important strength of the current paradigm is that it could be applied to assess such strategy use independently of the behavioural result. In other

words it can assess whether the TBI survivor is recovered, i.e., is looking in the same regions of the display as the comparison participants or is compensating (and therefore looking elsewhere).

The present findings suggest that there would be value in continuing to utilize eye tracking to measure navigation performance in the TBI population. The experimental paradigm described here would be of benefit for testing the degree of deficit, for example in relation to time since injury or injury severity. In combination with brain imaging, it might also reveal which networks of brain structures are activated during navigation on place-based tasks. An exploratory study of this kind is underway using the EEG data collected from the TBI survivors in the present experiment.

The paradigm described here might also be applied to the assessment of other types of brain injury for example concussion or mild TBI that do not necessarily require hospitalization. It could also have applications in the study of psychiatric conditions such as Post Traumatic Stress Disorder and Alzheimer's Disease, that are known to damage the hippocampus system (Reisberg et al., 2008; Smith, 2005, respectively) and may therefore cause cognitive mapping deficits (Astur et al., 2006).

Conclusions

In summary the results reported here show the feasibility of combining eye tracking with virtual environment tasks for testing navigational ability after TBI. There are some challenges to implementation of the method but these can mainly be overcome by screening measures applied when recruiting TBI survivors for future studies. The success of the current study suggests that further larger scale studies could be conducted to better explain the nature of cognitive navigational deficits after TBI. These methods

also provide the foundation for developing an assessment tool that could ultimately be used in a rehabilitation setting.

Appendix 5-A
TBI Background

Questions for participants with brain injury:
It is not uncommon for people who have had a brain injury to have trouble remembering what happened. I'm going to ask you a few questions about what you remember around the time of the injury and your hospital stay. Please answer them as best you can. For some people, discussing these topics may be difficult or upsetting for them. If you find our discussion upsetting, please let me know and we can move on.

12. When were you injured? (month, year) _____

13. Could you go over **how you got your brain injury**? *{Record MVA, fall, stroke etc, and a few details}*

_____

_____

_____

14. Were you hospitalized after your brain injury? Y / N

{If yes} For how long? _____

{If injury is within the past year, ask} How long have you been out of the hospital?

_____

15. Did you lose consciousness or were you in a coma after you brain injury? Y / N

16. What is the last thing that you remember before losing consciousness?

_____

17. What is the first event you can remember after regaining consciousness?

_____

18. After brain injuries, many people have large gaps in their memory. For example, they may have a period of a day, a week, or a month where they don't remember things that happen, things they've done or visitors they've had. This is called "Post-Traumatic

Appendix 5-A (continued)
TBI Background

Amnesia". Did you have any gaps like that? Y / N *{If yes}* When did you stop having these gaps? (How long after your injury?) ____

*NOTE: try to get an **estimate of Post Traumatic Amnesia** duration and circle one of the following:*

10 minutes or less	*An hour or less*	*A day or less*	*A week or less*	*1-2 weeks*	*A month or more*

Appendix 5-B
Order effects on maze tasks for TBI survivors

One explanation for the good performance of TBI survivors in the Cue and Ambiguous mazes is that the order of presentation may have provided experience with the environment and the opportunity for participants to solidify their use of a strategy. The inspection of trial by trial acquisition curves showed that this did not seem to be the case; good performance on later trials in one maze did not usually lead to good performance in the first trial of the next maze. Also, performance appeared to be similar in the Cue maze regardless of presentation order. A further examination of the latency and distance data (Figure 5-B.1) revealed that experience in the maze environments could not completely account for the differences observed in performance in the Place maze when compared to the other two mazes. A strong order effect would have been indicated if latencies and distances became shorter with each progressive maze task. However, only the data from Participant 1 could be interpreted in this way. This participant completed the mazes in the order Place then Dual Strategy then Cue. When the data were organized by maze type it was clear that this factor was more important the order in which the mazes were presented. Subtle effects of experience may be present in the Dual Strategy maze but overall the effect of the mazes was consistent.

Appendix 5-B (Continued)
Order effects on maze tasks for TBI survivors

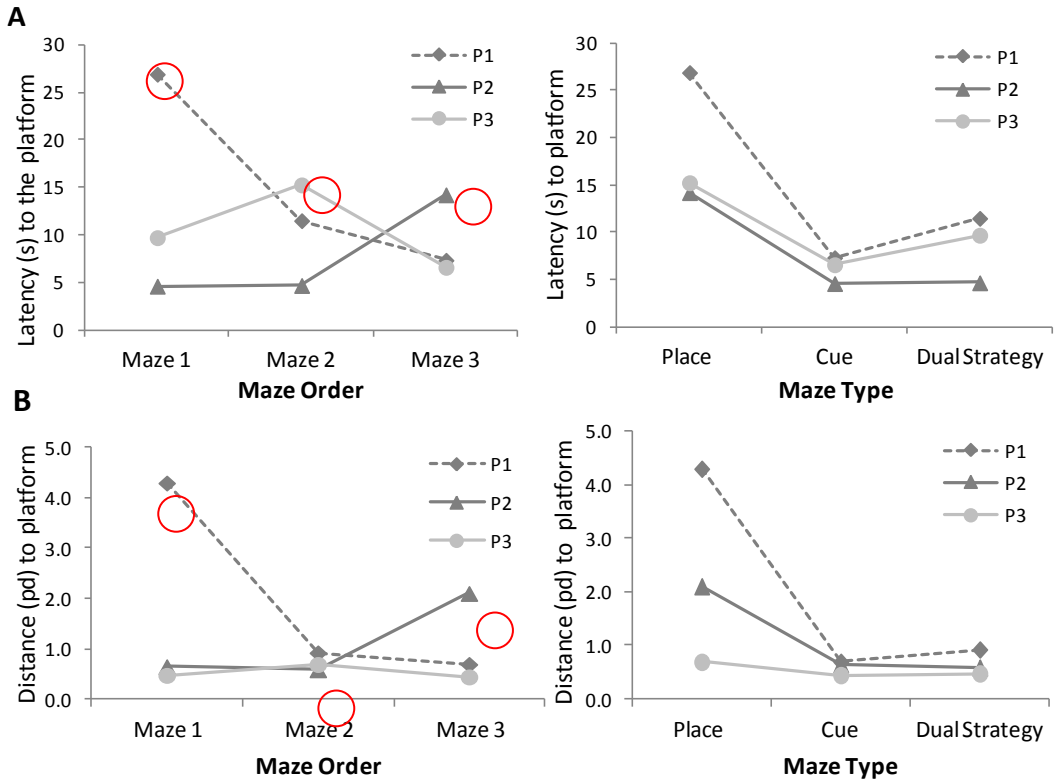

Figure 5-B.1. Comparison of the influence of maze type and maze order on navigation behaviour in TBI survivors. The patterns of data show that the type of maze was more important than order effects. Red circles indicate Place maze performance.

Chapter Six

This chapter consists of a general discussion and integration of findings from the four experiments described in this dissertation. It therefore is not a manuscript and its contents are formatted according to APA style guidelines. The only exception is the page numbering system which follows the same pattern as previous chapters.

Summary of Experiments

The research reported in this dissertation examined the effects of environment and experience on human spatial navigation, specifically with respect to human egocentric and allocentric navigation. Chapter 1 described the state of the literature regarding spatial navigation in humans and non-human animals and provided rationale for the research program. Chapters 2 to 4 described three human navigation experiments employing virtual Morris water maze (vMWM) tasks, with the latter two experiments employing eye tracking to study strategies during orientation. In Chapter 5 a fourth experiment reported on the feasibility of using the methods developed in Chapters 3 and 4 to test survivors of traumatic brain injury (TBI).

The first (exploration) experiment was conceived because there is a lack of research into exactly when and how people form cognitive maps. Although laboratory animals appear to form maps via exploration of the environment, this assumption had not previously been tested in humans. Furthermore an informal review showed that for vMWM tasks participants seemed to do better when they were given the opportunity to explore before testing. However this proposition had not been tested. Therefore, participants ($n \approx 100$) were tested in either a place-based or a cue-based vMWM task and were either given the opportunity to explore or were not. Participants who had the opportunity to explore the environment before the place-based task did much better on the task than did participants who were not permitted to explore beforehand. No such difference was observed for the cue-based task. Thus this experiment was the first to show that exploration is critical to the formation of cognitive maps in humans and most importantly, that pre-task exploration improves performance on place-based tasks. The

importance of exploration to place navigation has implications for cognitive map theory that will be discussed below.

The second (strategy) experiment was designed as a replication and extension of previous research showing that eye movements indicate the strategies people use to orient for navigation. Important extensions included the testing of community-based participants and the addition of new analyses of eye movements. The purpose was to establish a valid and reliable method for testing strategy use and selection in different populations and to investigate new eye tracking measures of strategy use. Participants (n = 37) were tested in both a place-based and cue-based vMWM task and their eye movements were measured according to whether they looked above or below a horizon at the vertical midline of the screen display. Eye movements were recorded during the first second of behavioural trials when they were orienting themselves (i.e., discerning their own position) within the virtual environment. In the place-based task participants looked above the horizon at the room features most useful for navigation. In contrast, in the cue-based task participants looked near or below the horizon where the useful cue objects were located. These patterns of gaze were established within the first few trials and maintained for the duration of testing. Further, in the place-based task participants looked more at the centre of the display whereas in the cue-based task their gaze was more evenly distributed across the display. These results were taken to mean that gaze position accurately indicated and differentiated when participants were using allocentric strategies and when they were using egocentric strategies, i.e., in the place and cue-based tasks respectively. Gaze positions and strategies during orientation were similar for university students and community-based participants suggesting that the method can be applied to

study both populations. The success in identifying strategies during orientation further suggested that the method could be applied to study the effects of experience on strategy selection. The importance of environmental features to strategy use has implications for cognitive map theory that will be discussed below.

The third (experience) experiment was based on two premises: 1) the observation that behavioural studies of navigation frequently do not discern what strategies people are using when they navigate and 2) that experience with an environment and associated strategies should affect later strategy selection and possibly navigational performance. A common methodological approach is to force the use of a strategy (often without training) and then to measure behavioural differences according to subject variables such as gender or age. Thus the influence of experience with different types of environments and stimuli is ignored. Other study types confound the strategies used because the environments employed allow for the selection of more than one strategy type. That is, because of the arrangement of environmental features different strategies may lead to the same behavioural outcome. A more desirable approach is to identify what strategies people are using and then to study the way in which their experiences influence the selection of these strategies.

The experience experiment was the first attempt at discerning the effects of prior experience on the strategies people select when more than one strategy type will suffice to find the target. Participants (the same sample tested in the strategy experiment) were trained to use either an allocentric or an egocentric strategy and were later tested in a Dual-strategy vMWM. Eye tracking measures were used to indicate strategies used during orientation in the Dual-strategy environment and a behavioural probe trial

measured strategy selection at the end of testing. Training (experience) in the place-based and cue-based tasks was strongly correlated with strategy selection but eye movement analysis failed to show a strong effect of experience on the strategies participants used during orientation. Because of the strong effect of experience on strategy selection further behavioural analyses were undertaken. The combination of probe trials and verbal report showed that selection of an allocentric strategy was related to participants' awareness of the environment, i.e., to whether or not they had formed a cognitive map. Furthermore this effect outweighed the effect of gender. Recent emphasis on individual differences such as gender or age has obscured the importance of experience for strategy selection and efficient navigation. However, the findings reported here suggest that researchers should revisit the concept of experience as a very strong factor in determining how people navigate. The importance of experience for later navigation performance has implications for cognitive map theory will be discussed below.

The fourth (brain injury) experiment was based on prior research with survivors of TBI showing that they had difficulty navigating in a place-based vMWM but could navigate well in vMWM tasks where a nearby cue marked the location of the platform (Livingstone & Skelton, 2007). The experiment tested the feasibility of using eye movements to study navigation deficits in survivors of TBI. In the place-based task TBI survivors tended to have lower gaze and worse behavioural outcomes than did the comparison participants. However, in the cue-based task TBI survivors performed as well as comparison participants and had similar gaze (directed toward the cue objects). In the Dual-strategy maze all three TBI survivors appeared to use egocentric strategies and all

three selected an egocentric strategy at the end of testing. The experimental method was judged to be feasible and although there were only three participants, this is the first study to show that strategy selection may be affected by brain injury. Specifically, deficits in navigation may be the result of an inability to use allocentric strategies rather than an inability to select the appropriate strategy for the task.

Limitations of Experiments

There were a number of limitations noted during the course of the experiments reported in this dissertation. Detailed descriptions of these have already been provided but the most critical limitations are summarized below.

A potential (and general) limitation of the current findings is that the experimental paradigm does not allow for the measurement of sensory-motor integration during navigation. This path integration (or dead reckoning) is hypothesized to support the development and updating of the cognitive map (Gallistel & Cramer, 1996) by allowing the animal to continually update its position according to its movements. Path integration is thought to be the means by which animals are able to return to a start position based only on metering of their body movements. For example, animals may know their position in the environment based simply on integrating the movements they have made with their existing cognitive map (Gallistel & Cramer, 1996). However, in the context of the experiments reported in this dissertation it is important to note that the participants' movement through the environment in combination with the available visual stimuli appeared to provide enough information for the formation of cognitive maps. Indeed, movement through space is a fundamental aspect of navigation considered in the current experiments (Chapter One, p. 8-9). However, it is possible that better quality maps could

be achieved in real-world navigation tasks since participants would receive additional information from their own body movements. The question of ecological validity of virtual environment navigation tasks centers mainly on this issue but thus far it seems to be true that cognitive maps can be formed in the absence of proprioceptive and vestibular input (e.g., Jacobs et al., 1998). In short, human path integration may be possible based mainly on visual input. The question of whether this is the case was beyond the scope of the current research.

In the exploration experiment, findings were restricted to the effects of exploration before testing and from the goal location. Although the importance of this exploration for later performance was clearly established, other forms of exploration were not taken into account. For example, participants may have explored by visual scan at the end of trials (from the perspective of the platform) or while navigating, especially in early trials. Also, participants in the cue condition may have explored during the later portion of the probe trial, though this would have affected Room Reconstruction but not performance on the test trials. Future experiments should be designed to dissociate these other forms or exploration and their relative effects on navigation performance.

Limitations to the experiments on strategy and experience were mainly the result of constraints in either the apparatus or select analyses. The eye tracking camera sometimes failed to record eye movements adequately either as a result of failure of the calibration task or loss of tracking when participants looked away from the display. Although every effort was made to prevent these problems, it must be acknowledged that they did occur. This had the effect of reducing the sample size because no eye movement data could be collected for some participants. There may also have been a deficiency in

the design of the Dual-strategy water maze task. In the experience experiment eye movements differentiated the strategy used during training but during testing eye movements were not good indicators of strategy selection. Clear separation of gaze positions according to strategy may not have been observed because the environmental stimuli important for navigation were located quite close to one another. The objects useful for egocentric navigation were just below the horizon whereas the features (landscapes) most useful for allocentric navigation were located just above the horizon. This relatively small separation of the stimuli may have contributed to the finding that regardless of prior experience, participants appeared to focus their gaze near to the horizon. Future adaptations of the Dual-strategy maze should ensure that egocentric and allocentric stimuli are located in more distinctly different regions of the display.

The analyses employed in the strategy and experience experiments were somewhat limited by the analysis time window selected for eye tracking and also by the sample size. The window selected for the eye movement analysis was the first orientation second at the start of each trial. Previous research had indicated that important information about strategy was contained within this window. However, for the Dual-strategy maze the effects observed in the first orientation second were very brief and relatively small. A possible solution is to examine other time windows that may be more relevant for detecting the effects of experience. These could include gaze while on the platform at the end of trials, during exploration or while orienting in the DTS trial. The sample size (n = 37) in the experiments on strategy and experience was generally adequate for the proposed research as confirmed by a priori power analyses. However some secondary Chi-square analyses suggested by the main findings could not be

conducted. For example, some gender effects could not be analyzed and nor could the three-way interaction of training x strategy x environmental awareness.

The limitations of the brain injury study were described in detail in the experiment discussion. They include the same problems encountered in the strategy and experience experiments along with some others related to brain injury. Several of these limitations have practical solutions. For example, in future studies TBI survivors should be screened for possible limiting factors including motor deficits, reaction time deficits, contralateral neglect and memory deficits. TBI survivors should also be allowed sufficient time to explore the environment and to practice using the joystick or gamepad. When interpreting the results of future navigation studies with TBI survivors it will also be important to consider the pre-injury navigational experiences of the individual. A further limitation of the TBI feasibility study was the small sample size which prevented the use of inferential statistics. However, the data sets that were derived from the study of this small sample provided a good foundation for testing feasibility. A full scale study of this type should be conducted with a larger sample (>10 if possible).

Contributions to Research Methodology and Potential Applications

The research program described in this dissertation was able to contribute several methodological improvements and suggests a number of research applications. Key contributions include the development of new virtual environment navigation tasks, the combination of eye tracking with virtual navigation and the extension of experimental findings to the study of navigation deficits in survivors of TBI.

New Virtual Environment Navigation Tasks

The virtual environment tasks designed for the experiments on exploration,

strategy and experience were all new and successful adaptations of the vMWM task. Each was useful for testing navigation behaviour and for eliciting different types of navigational strategies. The research in this dissertation shows how valuable these tasks can be for revealing the cognitive basis of navigation.

The cue-based adaptations of the MWM task developed for the present experiments are important because they allow for comparisons that separate allocentric from egocentric navigation. There have been only a few other studies or behavioural paradigms which have purposefully differentiated allocentric from egocentric cue-based strategy use (e.g., Chai & Jacobs, 2010; Hamilton, Kodituwakku, Sutherland, & Savage, 2003; Hurlebaus, Basten, Mallot, & Wiener, 2008; Parslow et al., 2004) but with the exception of one study (Hurlebaus et al., 2008) most were concerned primarily with group differences in allocentric navigation. A few studies have dissociated allocentric from egocentric response-based navigation by using virtual radial arm maze environments (Andersen et al., 2012; Bohbot, Iaria, & Petrides, 2004; Hardt et al., 2009; Iaria et al., 2003), virtual tunnel environments (Gramann et al., 2010) or virtual towns (Head & Isom, 2010). However, these paradigms were not designed to test cue-based egocentric navigation. The tasks employed in this dissertation thus allowed for important comparisons of allocentric navigation and cue-based egocentric navigation.

The Cue-based vMWM tasks developed for the present experiments are also important because they may allow for improved discrimination of egocentric strategies. For example the visible platform trials tested the ability of participants to use a guidance strategy for travel to a single strong cue visible in the environment. A different type of egocentric strategy should be elicited by the Floor Cue maze because the platform is not

visible from the start and because participants are required to discriminate between two similar cues, one of which marks the platform location. Different strategies might also be elicited by navigation to a single guidance cue that is located on the (invisible) platform or the association of a single cue with an (invisible) platform that is located a short distance from the cue. The Cue maze employed in the experiments on strategy and experience is a variant of this type of task that requires participants to identify an important cue from among a set of similar cues in the environment. Together, these cue-based tasks, along with future adaptations, may provide the basis for studies that better discriminate egocentric strategies and thereby more accurately describe navigation deficits. However, it is worth remembering that the Cue maze provided participants with cues that changed location from trial to trial, presenting them with a situation that may have been somewhat more puzzle-like than normal navigation. Normally, proximal cues for navigation are congruent with spatial features, rather than discordant with them. In this sense, the Dual-strategy maze may have been a more realistic environment than the other two mazes.

The Dual-strategy maze task was designed to elicit either a cue-based egocentric strategy or a place-based allocentric strategy with participants being free to select either way of navigating. This task did not achieve the goal of differentiating gaze position and thereby strategies used at the start of trials. However, when combined with a probe trial it was successful in demonstrating a delayed effect of experience on strategy selection. Future adaptations of the task are also possible such that it could be applied to the study of spontaneous strategy selection or to the study of strategy selection in different time windows of the behavioural trials.

Combining Eye Tracking with Virtual Morris Water Maze Paradigms

Another important research contribution is the efficient combination of eye tracking with virtual environment navigation tasks in the strategy and experience experiments. On a practical level the eye tracking method was low cost and relatively easy to implement, thereby improving on more expensive methods (e.g., fMRI or PET) of testing navigational cognition. The method was also able to combine refined control of environmental stimuli with an objective measure of navigational cognition, at least in environments with a strong bias toward the use of either an egocentric or allocentric strategy. This represents an advance because there are few studies employing such objective measures to study navigational cognition and strategy selection.

The combination of eye tracking with specially designed virtual environments also improves on navigation studies using fMRI or PET by increasing temporal sensitivity. The difficulty with most current brain imaging methods is that time windows for study are usually on the order of a few seconds. However, the eye tracking method described in the present experiments allows for a more sensitive measure of navigational cognitions within the first second of the orientation process. This is important because navigational cognition and attention are likely to be fast and dynamic processes. That is, the formation of cognitive maps and the decisions to attend to particular stimuli or to engage in particular strategies are made very quickly and may change very frequently. The potential to observe these decisions and changes is likely to be improved by the use of appropriate time windows of analysis.

The combination of vMWM tasks with eye tracking also creates a flexible method for examining strategy use and selection at any point during navigation trial. Eye

movements can be used to study navigational strategies in different time windows both within trials and across trials. This is important because navigational strategies may change within trials as the participant changes position and observes the environment from different vantage points. The extent of these rapid changes has not been fully investigated but the methods described in the present experiments appear to be promising for studying the dynamic processes that support spatial navigation. Further, they can be applied within the context of group comparisons or the study of cognitive strategies in individual participants.

The Study of Navigational Cognition

In the study of strategy use and selection the eye tracking method appears to enable the examination of deeper questions about the cognitions associated with navigation behaviour. For example, the findings of the strategy and experience experiments support the theory that cognition (including navigational cognition) is affected by both bottom-up and top down factors. That is, the selection of a cognitive navigational strategy may depend on bottom-up (stimulus) factors like the structure and features of the environment as well as top-down factors such as plastic changes resulting from experience with the environment (e.g., search set). However, the relative influence of these factors on strategy use and selection seems to depend on the nature of the environment and navigational task. In the strategy experiment, orientation in the maze environments differed significantly for the Place and Cue mazes, indicating that the environmental stimuli (bottom-up factors) were driving eye movements. However, in the experience experiment other (possibly top-down) factors such as practice effects affected orientation. For example, as participants learned where to look for important stimuli in

the mazes they may have needed less time to orient at the start of trials. This top-down learning factor (experience) might have the effect of reducing the amount of trial time participants spend looking at the environmental stimuli. Thus the top-down influence of experience may reduce or limit the attention of participants toward bottom-up environmental information. Further research will be necessary to test this and other questions but the methods described here represent an important step toward understanding the relative effects of top-down and bottom-up influences on the selection of navigational strategies.

TBI and Navigation Strategy

Another research contribution was a new potential method for the study of navigation deficits and strategy use after brain injury. The application of this method in a small sample of participants with TBI was relatively successful and showed that eye movements can be useful indicators of how TBI survivors orient toward stimuli in the environment. If pursued, this method could be a useful advance because there are few reliable and ecologically valid tests of navigational ability in TBI survivors. Better methods of assessment should lead to the development of rehabilitation tools that are targeted toward specific navigation problems. The vMWM paradigm is also adaptable for errorless learning, an approach that is especially important for the TBI population. Thus it allows for assessment and rehabilitation without the negative feedback that can be associated with many cognitive tests.

Potential Applications

Beyond the current research contributions there are several potential applications of the eye-tracking method described here. The first of these concerns specific

improvements to imaging studies of human navigation. The exploration experiment shows that adequate exploration of the virtual testing environment is necessary for optimal performance, especially on cognitive mapping tasks. Although many navigation studies employ practice trials, these are rarely conducted in the same environment as is used for testing. Adding exploration trials should improve performance on cognitive mapping tasks and potentially lead to a better understanding of the brain regions involved in navigation. Another application that may improve imaging studies is the identification of individual strategy use during navigation. The combination of eye tracking with imaging data could be used to identify whether individual participants are using the anticipated strategy while navigating. This is especially important in environments where participants may be able to use more than one type of strategy to solve the task. Differentiating these strategies could improve accuracy of localization of brain activity corresponding to the anticipated strategy.

Other applications suggested by the strategy and experience experiments concern new approaches to understanding navigation as a dynamic process. For example, gaze positions during navigation in the Place and Cue mazes could be correlated with EEG measures to establish brain activity during navigation with much greater temporal resolution than is possible with other brain imaging methods. Indeed a feasibility study of this type has recently been conducted (P.Zeman, unpublished data). The aim of this research is to identify networks of activity i.e., the activity of the egocentric and allocentric systems that correspond to place-based and cue-based navigation. In addition, the eye tracking method could be further developed to measure the effects of experience on strategy use within trials. The behavioural results of the experience experiment

suggest that this should be possible because participants tended to select behavioural strategies that corresponded to their training. The identification of an appropriate window of analysis will be central to this approach.

The methods described in the present experiments may also be applied to the study of populations with identified hippocampal damage and potentially life altering navigation deficits. It is important to note that being able to confidently find one's way in the environment is a basic ability that when lost, may have a significant and detrimental impact on quality of life. Virtual versions of the MWM task have already identified navigation problems in survivors of carbon monoxide poisoning and people living with dementia (likely Alzheimers disease). In both cases hippocampal damage was associated with deficits in behavioural performance. However, this research has not been extended to the study of residual abilities or strategy use. The combination of virtual navigation tasks with eye movement measures may identify which strategies people are using and therefore identify areas for therapeutic intervention based on individual spatial abilities.

Implications for Cognitive Map Theory

The present results have several interesting implications for cognitive map theory. These are discussed below according to three elements of the theory, environmental influences, exploration and experience effects. As a reminder and to provide a foundation for this discussion, the navigation systems and strategies are described below according to the original cognitive map theory proposed by O'Keefe & Nadel (1978).

Short Review of Navigation Systems

O'Keefe & Nadel (1978) proposed that space and environments can be perceived through two different psychological (cognitive) frameworks each associated with

different types of navigation behaviours. The first framework, which the authors labeled absolute space, is fixed so that when a person moves within it, the framework remains stationary and the relationships of the other objects to the framework do not change. Furthermore, removal of an object from the framework does not change the overall perception as long as there are enough objects remaining to define the space (Jacobs & Schenk, 2003; O'Keefe & Nadel, 1978). As an example, a person can imagine the overall layout (structure) of their neighbourhood and then imagine being in different places in the neighbourhood. The neighbourhood (and its perception) remains stable and as long as most of the buildings and other environmental features remain fixed, the person can maintain knowledge of the neighbourhood layout even if for example, one building is demolished. This way of perceiving the environment is the foundation for the formation of a cognitive map and for allocentric navigation. O'Keefe & Nadel (1978) emphasized this perceptual framework, naming it locale space, and proposed that the hippocampus was the key brain structure responsible for forming cognitive maps.

In contrast, space can also be perceived via a relative framework which is not fixed and consists only of object (feature) positions in relation to the person. Space defined in this way moves with the person so that they have only to make simple turns or guidance manoeuvres to reach a target. For example, it is possible for a person to imagine finding their way around a familiar neighbourhood just by making simple left and right turns (e.g., turn right at the first intersection, and left at the next one). The key point is that it is possible to perceive the environment and navigate within it without referring to a cognitive map. O'Keefe & Nadel (1978) referred to this perceptual framework as taxon space and it is the foundation for egocentric navigation, a type of navigation that these

authors de-emphasized and excluded from their theory. However, in the study of spatial navigation, this framework is important because both locale and taxon systems contribute to navigational behaviour. Indeed cognitive map theory suggests that if an environment contains "extra-maze stimuli" (i.e., features located just beyond the boundaries of the arena in a vMWM) and many directional features, the locale system is likely to be activated whereas a single strong cue will activate the taxon system. The experiments described in this dissertation are based in part on this assumption and add to cognitive map theory by increasing the emphasis on navigation by local cues. In more modern terminology, the locale system of O'Keefe & Nadel (1978) is called allocentric and the taxon and praxis (body based) strategies are considered egocentric.

Addressing Key Elements of Cognitive Map Theory

The present dissertation addressed three key elements of cognitive map theory. These included the effects of the environment, exploration and experience on cognitive mapping and navigational strategy.

Environmental determinants of strategy. Because cognitive maps are proposed to be built through experience with the environment (O'Keefe & Nadel, 1978, p. 94) it follows that the structure and features of the environment should be a key factor in determining what stimuli are attended to and ultimately how the environment is navigated. The size and layout of the environment as well as its features (landmarks or arrangements of these) provide the raw materials from which the cognitive map is constructed. The environment may also be responsible for determining which navigational system is activated and thus which strategies are used. For example, environments containing many stimuli and thus behavioural choices may promote

cognitive mapping and the use of allocentric strategies. In environments in which there is a strong cue indicating the target location, an egocentric strategy should be favoured (although this fact is only briefly discussed in the original cognitive map theory). It follows, then, that it should be possible to manipulate the utility of environmental stimuli and thereby influence the type of internal representation that is formed and, in turn, the type of strategy that is used to orient and navigate. Indeed O'Keefe & Nadel (1978, p.95) proposed that the mapping system can be blocked if the environment is constantly changing (and thus providing no stable structure). In the present experiments the size and layout of the environments was held constant but some features were manipulated in order to promote the use of either allocentric or egocentric strategies.

The strategy experiment supported cognitive map theory by demonstrating that there was a strong effect of environment on attention when people were navigating. Eye movement measures indicated that in cue-based task environments, where nearby objects are the only markers of the target, people orient initially toward these objects more than to other features of the environment. This is consistent with the view that their initial perceptions were represented via the (egocentric) taxon system and that an egocentric strategy was used during orientation. In contrast, in the place-based task environment where there are no nearby objects to mark the target location, people attended mainly to more distal features. Presumably this was because the environment contained a bias that promoted activation of the (allocentric) locale system, the formation of a cognitive map and the use of an allocentric strategy during orientation. As predicted by cognitive map theory, available environmental stimuli appear to influence the way in which people internally represent the environment and ultimately which strategy they use.

Although the structure and features of the environment are key factors in navigation, it is up to the navigator to interpret them and decide whether to use them. Cognitive map theory suggests that animals interpret stimuli using hypothesis tests, that is, by approaching places or stimuli in the environment and learning about them. Because learning requires an interaction (sensory and/or motor) of the animal with the environment it follows that the choice of what strategy to use depends on both environmental factors (availability of stimuli) and on factors within the navigator. The attention paid to particular objects and features in the environment should then depend partly on decisions made about the importance of these stimuli. In turn, decisions made about the importance of stimuli will determine the type of representation (or map) that is formed. Because this representation guides navigation, these earlier decisions about the importance of stimuli will also influence the type of strategy that is used to navigate. In other words, the strategy (egocentric or allocentric) used will be dependent on whether environmental stimuli have 1) been attended to and 2) are judged to be useful. This suggests that accumulated experience with environmental stimuli will also be a key factor in determining the strategy used. This possibility is discussed in later sections.

An important incidental implication of the strategy experiment was that for most people both underlying navigation systems are intact and accessible for navigation. The fact that participants can be 'forced' to use either an allocentric or an egocentric strategy (as in the preceeding expierment) implies that their systems are able to respond flexibly to changes in the structure and features of the environment. This is consistent with cognitive map theory which assumes that the ability to form a cognitive map or to form stimulus-response associations is innate (O'Keefe & Nadel, 1978, p. 62). Eye movements

during orientation suggest that people form representations based on the available and useful stimuli and then continue to orient and use strategies based on these representations. In the strategy experiment participants used similar strategies during orientation across many trials, suggesting that representations were maintained and possibly strengthened over time. However, the cognitive map theory as originally proposed does not specify whether each individual would use the same strategy in an ambiguous environment where either strategy type would lead to navigational success, nor does it specify how a strategy preference might arise.

The necessity of exploration. A second element of cognitive map theory addressed in this dissertation is exploration of the environment. In order to navigate in an environment the navigator first needs to understand its key features and in theory, this understanding is developed via exploration. O'Keefe & Nadel (1978) asserted that cognitive maps are formed during exploration and that in rats at least, exploration is a species-specific behaviour. They suggested that exploratory behaviour is brought on by a mismatch in the cognitive mapping system (i.e., in the hippocampus) between the stimuli that are perceived at a place in the environment and the stimuli that the system expects to be there. Thus exploration is a response to novelty, i.e., new and unexpected stimuli in the environment. Furthermore, when rats are exposed to novel environments, those with hippocampal lesions fail to habituate (i.e., explore longer)(Kimble, 1963) indicating that the hippocampus might provide a signal to the exploration system that the cognitive map has been sufficiently well developed or as O'Keefe & Nadel (1978) put it, that the behaviour of the animal is no longer exploratory. However, it is only recently that the hippocampus has been linked to cognitive mapping in humans and there have

been few direct tests of the human exploratory response and its importance for navigation.

The exploration experiment confirmed the necessity of exploration to optimal place navigation in humans. It showed that human cognitive maps are formed during exploration as predicted by cognitive map theory and much as they appear to be in other animals. When participants were given the freedom to explore an environment before testing, they had formed a cognitive map prior to that testing. Further, this opportunity for mapping was especially important for later performance on place-based tasks that required an allocentric strategy. Participants who explored the environment before testing did much better on a place-based task than did participants who were not permitted to explore. The exploration experiment also showed that exploration is not important for cue-based navigation, i.e., for tasks that can be easily solved without the necessity of forming or using a cognitive map.

The results of the exploration experiment indicate that the theory of cognitive map formation in animals can be applied to humans and importantly provides the first evidence for the assumption that human cognitive maps are formed via exploration of the environment. However, more study is needed to clarify precisely when and how quickly maps are formed as well as the nature of their contents. The exploration experiment showed that after only one exploration trial and four visible platform trials participants were able to indicate good understanding of the room layout. Therefore useful cognitive maps may be formed very early on, and without being demonstrably required by the task (c.f., latent learning, for description see O'Keefe & Nadel, 1978, p.263). However, precisely when they are formed and also their contents remain elusive.

Because cognitive maps are likely to be representations rather than exact copies of the environment (O'Keefe & Nadel, 1978), it can be speculated that they are constructed in stages and importantly, due to interactions (experiences) with the environment. These stages may correspond to exploratory behaviours and interactions with the environment during which information is acquired and added to the map. For example, exploration likely involves learning about the three dimensional nature of the environment including the spatial relationships of its objects and features (O'Keefe & Nadel, 1978). This knowledge of the three dimensional environment may be enhanced by the acquisition of depth information from monocular and binocular cues, some of which contain reliable information about the relative distances of objects or features from one another. The experience accumulated from this learning likely contributes to knowledge about places in the environment and to the formation of a useful cognitive map. Once formed this map becomes a sort of navigational tool that can be used to make new routes and detours without the navigator having to re-explore the entire environment. Thus, cognitive maps are flexible and most useful for navigating to places (rather than objects) in the environment. The findings of the exploration experiment confirmed this by showing that in a place-based task exploration improved performance.

The role of experience and an expanded cognitive map theory. A third element of cognitive map theory addressed in the present dissertation was experience. Cognitive map theory defines experiences as interactions with the environment that are accumulated in the sensory, motor and likely cognitive systems of the animal. These experiences are thought to contribute to the formation and updating of cognitive maps. Early experiences are exploratory and presumably contribute to map formation whereas

later experiences in already familiar environments would contribute to updating of the map. However, according to cognitive map theory, experience can be achieved in several additional ways. The physical exploration of the environment by locomotion or visual scan constitutes experience although there may be no particular navigational goal in mind. Experience may also be gained in a more purposeful manner, where there is a target to find (or find again) or when the navigator intentionally codes features of the environment or the route in the knowledge that this information will be useful later (Golledge, 1999). Experience may also be gained through successful use of a route, or indeed a strategy. Therefore, experience with a navigational strategy should influence later strategy selection based on the corresponding navigation system having been used more frequently and with some success. This last idea has not been tested before, but was the specific issue in the experience experiment.

Cognitive map theory suggests that egocentric and allocentric navigation systems are both activated during navigation but that the nature of the environment determines the type of information that is stored and therefore the experience that is accumulated. For example, extensive exposure to city environments should result in different accumulated experience than extensive exposure to prairie or desert environments. It is also possible that different types of experience could be derived from the same environment. For example, repeatedly traveling the same route to work every day would provide a different experience than would traveling a different route every day. These differing experiences would presumably activate the brain in different ways and influence strategy selection. The experience experiment supports this view by showing that people who select allocentric strategies and who have had experience with a place-based task also develop a

greater awareness of the structure and features of the environment (as measured by verbal report) than do those who have experience with a cue-based task and select egocentric strategies. That is, experience in environments where there were no strong local cues to identify the target location is associated with enhanced environmental awareness. This awareness is presumably related to the formation of a cognitive map. As is consistent with cognitive map theory, experience with egocentric strategies does not appear to promote awareness of the environment.

One way in which the experience experiment expands on cognitive map theory is by demonstrating the importance of egocentric experience effects. Cognitive map theory proposed that animal learning about the environment is facilitated by a hypothesis testing approach which was considered to be the equivalent of strategy use. In the context of cognitive mapping, strategies would consist of either approaching or avoiding places in the environment. O'Keefe & Nadel (1978) also noted that other hypothesis tests could include using different body turns or approaching/avoiding specific environmental features. However, they offered no further explanation of these effects or how either type of hypothesis might dominate. The experience experiment goes beyond cognitive map theory by showing that experience with a single strong cue (the golden urn in the Cue maze environment) led to the later use of an egocentric strategy (as measured by the strategy probe) in an environment where both allocentric and egocentric strategies were useful. In other words experience with a strong cue led to a preference for continued use of strong cues if they were available. Thus experience effects are not exclusive to cognitive mapping, and given the right environmental circumstances egocentric strategies may be preferred over allocentric strategies.

Modern interpretations of the cognitive map theory also suggest that it is possible for one or the other system to become more practiced and therefore more likely to be activated on later navigational tasks (Jacobs & Schenk, 2003).The experience experiment supported this proposition by showing that the effect of environmental features on the navigator endures even when there is a change to the environment. For example, experience with an environment biased toward the use of an allocentric strategy led to the selection of an allocentric strategy on a later and different task, even when an egocentric strategy would have worked equally well. In contrast, experience with an environment containing a strong local cue for navigation, led to the selection of an egocentric strategy on a later navigation task even when an allocentric strategy would have worked equally well. This suggests that experience with the environment (or learning) persists either in the form of either cognitive maps or more automated stimulus-response associations. Consistent with mapping theory, strategies should then be selected according to both the available environmental stimuli and the degree of accumulated experience with the environment.

At this point, some important conclusions can be drawn. The first of these is that in humans, strategy selection results from an interaction of the environment (including its structure and available features) and the person. The person must necessarily interpret information from the environment in order to make a decision about how to get to a target place or object. A second conclusion is that the person will bring to this interaction a set of experiences and competencies. There is a considerable amount of research devoted to the study of navigational competencies which are often labeled as spatial abilities. Unfortunately, these abilities have frequently been interpreted as either fixed or innate

rather than acquired through experience with the environment. This implies that strategies are fixed according to innate (internal) abilities resulting from developmental or other factors such as gender or age. It is worth noting that O'Keefe & Nadel (1978) rejected this view in their original theory, at least in terms of development.

The results of the present experience experiment demonstrated that experience (only 10 trials' worth in this case) can influence the strategies that people select and use regardless of their gender, for example. Thus the experience experiment suggests that navigation research should move beyond the concept of fixed spatial abilities toward the understanding that spatial abilities are flexible and can be learned. By emphasizing that navigational strategies are the result of person/environment interactions it is possible to reframe navigation research as the study of these interactions. This more optimistic approach acknowledges that spatial navigation is a basic human function available to most people and that learning through experience with the environment is possible, even in fully developed adults.

Just as fixed spatial abilities to do not determine navigation strategy, neither does the structure of the environment. In an effort to remove spatial ability as a factor some researchers focus entirely on the environment as the determinant of strategy, i.e., the decision about which strategy is used. But the mere fact that a decision has to be made shows that the environment is not uniquely responsible for strategy selection. Furthermore, ignoring spatial ability also ignores all of the previous experiences of the person and denies the position that information accumulated in the navigation systems can influence which strategy the person selects. The experience experiment shows that experience with the environment does accumulate across trials and that people make

decisions about which strategy to select based on both the available stimuli and the information they have already acquired.

Perhaps the most useful conclusion that can be made is that strategies people use *are* interactions of the environment with the person. These interactions can be mediated by both environmental stimuli and the experiences that people accumulate via the two navigation systems. Logically this suggests that the ability to select a strategy is not fixed but rather is flexible and amenable to change based on both external and internal factors. In other words, people are not inherently prone to use one strategy or another, but rather they select strategies based on the combination of incoming information from the environment and the degree of experience that their navigation systems have with the structure and features of that environment. Opportunities to explore the environment and to gain experience with navigation using different types of environmental stimuli should then allow for more flexibility in strategy selection and ultimately a better navigational outcome.

Beyond the Cognitive Map

A Cognitive-Behavioural Navigational Model

As briefly outlined in Chapter One, the experiments in this dissertation were mainly designed within the framework of a new theoretical cognitive-behavioural model of spatial navigation which contains the cognitive map. The following short discussion relates the results of the experiment back to the model to update it and to suggest places for future adaptations. The model as it stands proposes that navigational cognition is a dynamic process in which the environment is scanned; information is received by the navigation systems, processed by these systems and results in the engagement of a

strategy for finding a target location. The motor system is then activated and the person locomotes through the environment toward the target. The model assumes that while the navigator is moving toward the target, new environmental information becomes available and may be used to update existing representations of the environment. This process is continuous and forms a navigation loop that is repeated until the navigational goal is found or a new goal is selected (for details, see Appendix 6-A). At the heart of the model are two navigation systems, one of them being the cognitive mapping system.

Modelling the importance of the environment. The strategy study supports the premise of the model that environmental features are very important in determining strategy selection. The experiment showed that strategies during orientation were related to the type of environment that participants were presented with. The Place maze elicited an allocentric strategy (indicated by upward gaze) whereas the Cue maze elicited an egocentric strategy (indicated by downward gaze) during the scanning process. The structure of these two mazes was identical but by adding features (proximal cues) in the Cue maze it was possible to change the scanning behaviour of participants. The different gaze positions in the two mazes suggest that the most useful environmental information was responsible for activating one or the other navigation system, resulting in different strategies during orientation. Manipulations of environmental stimuli such as those just described presumably affect navigation at the level of the visual scan. It should be noted at this point that other sensory systems including audition or touch can contribute to map formation but the most important source of information for human navigation is likely the visual system. The cognitive-behavioural navigational model proposes that each of the navigational systems continuously receives information via the visual scan. The model

also predicts that the structure and features of the environment will determine which system is activated and therefore which strategy type is engaged.

The navigational model also proposes that the visual scan can happen very frequently either for the purpose of updating or perhaps confirming knowledge about the environment. Presumably, scanning can occur as the person begins navigating but also at any point along the way toward the target location. The strategy experiment clearly showed that a visual scan of the environment occurred at the very start of each trial. It was not possible to determine whether scanning behaviours during the rest of the trial differed from those observed during orientation. However, strategies during orientation did appear to become more consistent across trials. That is, on successive scans people maintained a pattern of orientation gaze toward the most useful stimuli and presumable continued to activate the same navigational system. Future experiments would be necessary to determine the factors driving updating or frequency of scanning while navigating.

Modelling the Effects of Experience. The model also predicts that experience plays an important role in human navigation. Information is presumably being received by both systems all the time and representations of the environment are then built up in either system via repetitions of the navigation loop. As previously noted, experience is defined as interactions with the environment that occur while the person is navigating or exploring. In the model, every time a new visual scan occurs and one of the two navigation systems is activated, a new interaction (experience) has occurred. An implication of this is that one or the other system may become more practiced (i.e., can be activated more frequently) based on the information that is received from the

environment. If this occurs, then the strategy selected for navigation will likely be associated with that system. This describes the situation observed in the experience experiment where place or cue-training was associated with the selection of allocentric and egocentric strategies, respectively.

Although experience effects can be partially explained by changing activity in the navigation systems, the continuous flow of information to both systems implies that a strategy selector is necessary to mediate which strategy is engaged. Since both systems are continually activated and only one strategy can be activated at a time it follows that a decision must be made about which strategy to engage. This decision will be based partly on experience, i.e., the accumulation of activity in each of the two systems as it relates to current visual scans. The findings of this dissertation, which reveal the dynamic nature of strategy usage, highlight the need for further research on the cognitive and neural bases of strategy selection. Most cognitive or behavioural models of spatial navigation do not include the effects of experience. This is presumably because experience is reflected in changes to brain structure, i.e., plastic effects which are outside of the scope of such models. However, the current model has its foundations in animal models of the anatomical systems associated with navigation. For example, the allocentric cognitive system is presumed to have the hippocampus as its central structure whereas the egocentric system is presumed to be centred on the caudate. Thus it is possible to infer that experience effects such as those observed in the current experience experiment were the result of changes that occurred in the brains of the participants. However to fully model these effects it would be necessary to add computational models of activity in the hippocampus and caudate systems and to describe a location for the strategy selector.

The cognitive behavioural model could not explain why in the Dual-strategy maze participants did not have gaze positions corresponding to the strategies they selected at the end of trials. The model predicts that visual scan during orientation should be toward the stimuli that are most useful for solving the task and that the scan should continue to reflect the importance of these stimuli across trials. Because participants had received training in very specific environments it was expected that this training would be reflected in the visual scan in a similar environment. However, this was not the case. Apart from the explanations already given, there are other possibilities that are reflected in the model and discussed below.

The current model shows that visual scans can occur very frequently and suggests that decisions about which strategy to select can occur equally rapidly. In ambiguous environments such as the Dual-strategy maze, it is possible that no clear strategy emerged because both strategy types were being used interchangeably. This would result in a neutral average gaze position at or near to the horizon because gaze positions above and below the horizon were occurring in relatively equal proportion. O'Keefe & Nadel (1978) noted that in environments with no strong bias, the hypotheses animals make (i.e., the strategies they select) will be weak and observable as apparently random behaviour. This may partially explain gaze positions in the Dual-strategy maze but contradicts the finding that at the end of trials participants consistently selected strategies related to their training experience.

An additional factor that is not well explained by the current model is the (top-down) effect of experience on the visual scan. The navigation loop shows that the navigator could become more practiced at using one system or the other but does not

explain how that practice might affect the visual scan. Presumably, over time experience with particular types of stimuli could affect where in the environment people look on successive scans. This could reflect habit or a preference for these stimuli types. For example in the Dual-strategy maze participants seemed to look mainly in the vicinity of the horizon perhaps because they had learned that the most useful stimuli (allocentric or egocentric) were located nearby. The current model should be adapted to reflect these potential top-down effects.

Exploration and the model. The exploration experiment was focused on the contribution of exploration to the formation of a cognitive map and was therefore not directly based on the navigation model. According to cognitive map theory exploration can occur either while the person is stationary or while they are moving through the environment and is non-goal directed. That is, exploration is not associated with finding any particular object or place and is therefore not part of the navigational cognition loop in the current model. However, exploration must presumably be linked to the model through the cognitive map component in the allocentric system.

Most models of navigation (including the current one) do not acknowledge the role of exploration. However the results of the exploration experiment suggest that a cognitive model of exploration should be linked to any model of navigation. It is clear that cognitive maps are formed via exploration and therefore that exploration underlies the ability to navigate. For example, the exploration experiment showed that exploration happens during very early experiences with the environment and that it appears to be necessary for cognitive mapping and for later navigation in place-based tasks. These findings imply that exploration occurs during early loops that involve the visual

scan, the allocentric system, motor systems and locomotor systems.

An exploration model would show that as the navigator moves through the environment information is sent to the allocentric system (and possibly the egocentric system) with no necessity to select a strategy. This process continues until a cognitive map is formed, at which point it becomes available for the purpose of navigation. A tentative model of exploration is given in Figure 6.1. It shows that after a number of

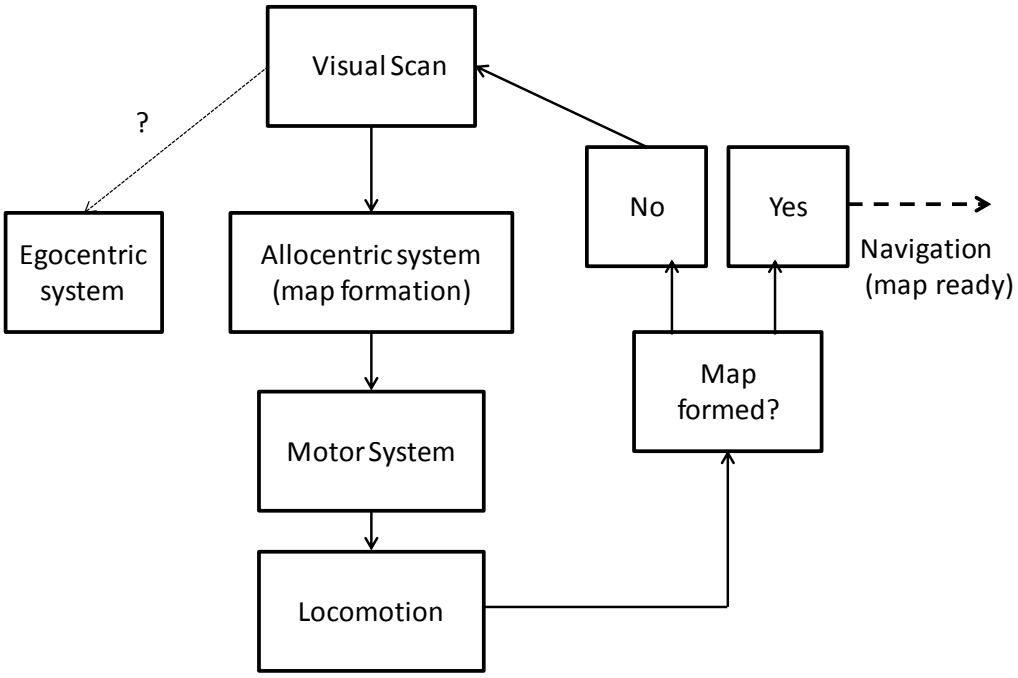

Figure 6.1. A preliminary cognitive-behavioural model of exploration and its link to navigation.

experiences (research has not specified exactly how many and under what circumstances) a map is formed and can be used to navigate. The quality of that map will presumably be affected by the structure and features of the environment and potentially by the prior experiences of the navigator with other environments.

Future Research

The results of the experiments in this dissertation suggest the possibility of a continued research program aimed at better understanding of navigational strategy selection. Such research will also allow for the development of improved models of human spatial navigation and for improved understanding of navigation deficits.

Behavioural studies with healthy participants. Studies with healthy participants could employ eye tracking and virtual MWM tasks to pursue three key lines of research, 1) the study of exploration behaviour and its importance for cognitive mapping, 2) further investigation of the effects of experience on strategy selection and 3) further study of egocentric navigation. For example, experiments could be designed to investigate the relative importance of different types of exploration (free vs. during trials) or to test the amount of exploration that is required to form a useful cognitive map. Furthermore eye tracking could be applied to the study of exploration to discover where people look while exploring the environment and the precise influence of this looking on map formation. As previously discussed new windows of analysis could be investigated for the influences of experience on strategy selection. Another possible line of research involves more study of the differences between cue-based and body-based egocentric strategies. In human navigation studies, little attention has been paid to teasing apart different types of egocentric navigation but this may be important both for the identification of deficits and for developing paradigms that can show different brain activities associated with different types of egocentric navigation.

Advancing the cognitive-behavioural model. The experiments described above and others may also serve the larger purpose of expanding on existing cognitive models

of navigation. New findings about human spatial navigation could contribute to the addition of new components to the model or to adaptations of existing ones. In the current context, the model could not fully explain the findings of the experience and exploration experiments and should therefore be adapted to better explain the results. Also future studies with a focus on the strategy selection could lead to the development of new components to explain the temporal nature of exploration, cognitive mapping and navigation. Most importantly, a working model of navigation will inform new experiments in the field of spatial navigation.

Specifying navigation deficits. Apart from research with healthy participants, another line of work flows naturally from the TBI feasibility study. A research program could be designed to address problems with navigation observed after brain injury. These common problems are presently considered as general memory problems but clearly spatial memory problems and navigation deficits are distinct from verbal memory problems that are frequently the focus of cognitive rehabilitation. Research directed specifically toward navigation problems will be useful for the development of focused assessment and rehabilitation tools.

Concluding Remarks

To conclude, the research program reported on in this dissertation achieved a number of objectives. It was able to show for the first time that exploration is crucial to cognitive mapping and allocentric navigation in humans. The convincing results of the exploration experiment suggested that exploration should be considered as an important component in future navigation experiments and in models of navigation. The research was also successful in combining eye tracking with virtual navigation tasks to distinguish

allocentric from egocentric strategies during orientation. The flexibility of this method was demonstrated in the experience experiment where eye tracking was applied to the study of strategy use in an ambiguous environment. Although results were mixed, this method should prove useful in future studies using different time windows of analysis. Indeed the brain injury feasibility study demonstrated that the method should be useful for discriminating strategy use in populations with navigation problems. The most striking finding in the experience experiment was that strategies used in training corresponded to strategies selected in a strategy probe trial at the end of testing. Thus strategies acquired in training were retained across 10 trials in a new environment, even when other strategies could have been used. Furthermore, allocentric strategies were associated with greater environmental awareness. All of these findings occurred independently of gender. Taken together, the results of the 3 experiments all indicated that strategies are not innate or within the person but rather may be interactions of the person with the environment. As was concluded in the animal literature more than fifty years ago (Restle, 1957):

> ...there is nothing in the nature of a rat which makes it a "place" learner or a "response" learner. A rat in a maze will use all relevant cues, and the importance of any class of cues depends on the amount of relevant stimulation provided as well as the sensory capacities of the animal. (p. 226)

Presumably, the same is true for humans. In this way, the environmental and experiential determinants of strategy encompass both allocentric and egocentric systems and can be seen to depend more on the nature of the environment and the integrity of the sensory systems and not on pre-determined strategies located within the person. Future models and experiments should be able to expand on this point to so that navigation can be

viewed as a balance of bottom up environmental inputs with top-down effects of experience.

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