Human place learning is faster than we thought: Evidence from a new procedure in the virtual Morris water maze

by

Dustin van Gerven

B.A., Vancouver Island University, 2010

B.A., Malaspina University-College, 2005

A Thesis Submitted in Partial Fulfillment

of the Requirements for the Degree of

MASTER OF SCIENCE

in the Department of Psychology

University of Victoria

Supervisory Committee

Human place learning is faster than we thought: Evidence from a new procedure in a virtual Morris water maze

by

Dustin van Gerven
B.A., Vancouver Island University, 2010
B.A., Malaspina University-College, 2005

Supervisory Committee

Dr. Ronald Skelton, Department of Psychology
Supervisor

Dr. Mauricio Garcia-Barrera, Department of Psychology
Departmental Member

Dr. Tony Robertson, Department of Psychology
Departmental Member

Abstract

Supervisory Committee

Dr. Ronald Skelton, Department of Psychology
Supervisor

Dr. Mauricio Garcia-Barrera, Department of Psychology
Departmental Member

Dr. Tony Robertson, Department of Psychology
Departmental Member

Research on the neural and cognitive basis of spatial navigation over the last 30 years has been largely guided by cognitive map theory and many of the studies have used a standardized procedure in a single task, the Morris Water Maze (MWM). Although this theory proposes that acquisition of place knowledge should be very rapid, little evidence has been provided to support this point. The present study investigates the possibility that a new procedure for measuring place knowledge in the MWM will show that place learning is faster than previously shown. In a virtual MWM with a fixed goal location, participants were given pairs of standard learning trials plus new explicit probe trials in which they were directed to go to where they found the goal on the immediately preceding trial. The distance between their estimate and the actual location was measured as “Place Error”. Results indicated that Place Errors were surprisingly small after just one learning trial and were equivalent for females and males. These findings provide new evidence for the fast learning proposed by cognitive map theory and demonstrate the value of this new method for measuring place learning.

Table of Contents

List of Tables

List of Figures

Introduction

Spatial navigation is arguably the most important function of the nervous system. In mammals, the ability to move about in the environment, either to find food or water for sustenance or to shelter from threat, is critical to survival. Spatial navigation includes all those processes required for an animal to get from place to place, from sensation and perception, learning and memory, to decision-making and execution. It thus involves a complex, coordinated interplay between many cortical and subcortical brain regions, each of which plays an important role in either understanding where the navigator is or understanding where the navigator should go.

Overview of the neuroanatomy of spatial navigation

Perhaps the first stage in the information processing necessary to spatial navigation is to establish the navigator's real-time position in space relative to objects in the vicinity. To do this, the brain must form an egocentric reference frame (Burgess, Jeffery, & O'Keefe, 1999), or a perceptual model of the immediate environment, and track how it changes with movement. This task is largely performed in tertiary cortex in the parietal lobes. Here, highly refined visual information from the occipital cortex is processed dorsally for relevant spatial information about objects in the immediate vicinity (e.g., orientation, size, depth, motion) (Mishkin, Ungerleider, & Macko, 1983). This information is then integrated with sense information from other modalities (critically proprioception) in the inferior parietal lobule, where the relative spatial position and orientation of body parts (e.g., eyes, trunk, head, limbs) is tracked (Kolb and Whishaw, 2008). From this information, body position with respect to features in the immediate environment, as well as heading vectors to intermediate visible landmarks along a route can be calculated (Maguire et al., 1998; Rodriguez, 2010). Key evidence linking the parietal cortex to spatial navigation comes from spatial deficits resulting from parietal lobe lesions, including apraxias, hemispatial neglect, and topographical disorientation, disorders that can be attributed to an impaired ability to form and maintain complete egocentric reference frames (Aguirre & D'Esposito, 1999; Barrash, 1998).

Once the information has been perceived and schematized, the most important anatomical structure is the temporal lobes, which are known to specialize in information storage (e.g., Nadel & Hardt, 2011). Of particular relevance to spatial navigation are medial temporal lobe structures, specifically the hippocampal formation (the focus of the current work). With respect to spatial navigation, the hippocampus and surrounding structures perform a dual function. First, the hippocampus plays a primary role in translating egocentric (body-centered) spatial information from the parietal lobes into a map-like, allocentric (world-centered) scheme, or *cognitive map* (Burgess et al., 1999; Tolman, 1948). Second, the hippocampal formation is well known for its role in the encoding, consolidation, and recollection of declarative memory, that is, consciously accessible memories of newly acquired facts or recent experiences (episodic) (Richard Morris, 2007). The cognitive map can be viewed as an example of declarative memory, since it is a consciously accessible representation of the spatial relationships between features in the environment (including those beyond the immediate vicinity). Evidence for the hippocampus' role in spatial navigation comes from the well-documented observation that damage to the hippocampus (especially on the right side) typically results in severe allocentric spatial deficits (e.g., Aguirre & D'Esposito, 1999; Barrash, 1998; Burgess, Maguire, & O'Keefe, 2002; Goodrich-Hunsaker, Livingstone, Skelton, & Hopkins, 2009), and the discovery of hippocampal place cells, neurons that fire preferentially when an animal is occupying a specific region in an environment (O'Keefe & Dostrovsky, 1971).

The final step in neuroanatomical processing required for spatial navigation is the translation of spatial knowledge into action. Critical structures involved in this process are the frontal lobes. There is a well-documented role of anterior the frontal regions in top-down executive functions that are important for navigation, such as selecting a destination based on spatial knowledge (planning), holding that destination “on-line” during movement (working memory), or choosing between available strategies to reach it (problem solving) (Mendoza & Foundas, 2007). Processing in these regions (as it relates to spatial navigation) is primarily concerned with *what to do* with spatial information once it has been perceived and schematized in an egocentric or allocentric framework. Once a decision has been made about what to do, posterior portions of the frontal lobes are activated. Processing in these regions is primarily concerned with *how to do* intended actions. Here, primary, secondary and tertiary motor cortex select appropriate actions and sequences of actions to carry out intentions formed in anterior regions of the frontal lobes in response to current circumstances, then execute them through direct connections to skeletal muscles (Koziol & Budding, 2008; Mendoza & Foundas, 2007). Consequently, lesion evidence in both human and non-human studies supports the view that the frontal lobes are critical to both making decisions about navigation and executing motor sequences involved in locomotion (Kessels, Postma, Wijnalda, & de Haan, 2000; Kolb, Sutherland, & Whishaw, 1983; Kolb, 1984).

Place learning and cognitive maps

Another type of hippocampus-dependent declarative memory that is important for spatial navigation is *place learning*. In the context of spatial navigation research, a *place* is a location defined by environmental cues that are close enough to change their orientation, but not their spatial order, as the navigator moves amongst them (O’Keefe and Nadel, 1978, pg 73). *Place* *learning,* then, is the acquisition of consciously accessible knowledge about the location of a biologically significant place in space relative to multiple features in the environment, both near and far (O’Keefe & Nadel, 1978). Through place learning, an animal can learn that a particular place is important so that it may remember its location and return to it when the need arises (e.g., a good place to shelter from predators). By studying place learning, researchers can gain a great deal of insight into neurological and cognitive processes such as neuroplasticity (Skelton, 1998; Skelton, Ross, Nerad, & Livingstone, 2006) and navigational strategy selection (Livingstone-Lee et al., 2011).

Place learning can also be used to investigate cognitive maps. The conceptual and neuroanatomical relationship between cognitive maps and place learning is not well defined in the literature. The result is that, historically, a great deal of attention has been paid to cognitive maps, while comparatively little has been paid to place learning. The cognitive map is an internal representation of the environment that contains the spatial relations between environmental features. The cognitive map provides a holistic framework, constructed rapidly and automatically, within which places can be localized. Place learning thus depends upon the cognitive map. The place-learning animal identifies an important place within the cognitive map, relative to navigationally relevant environmental features, such that the animal can return to that place from any start position in the mapped environment (O’Keefe & Nadel, 1978). Thus, cognitive map construction is an important first step in place learning.

An important but rarely-made distinction in spatial navigation literature is the difference between *knowing where* a place is, and *getting there*. *Knowing where* (i.e., place knowledge) is the end result of place learning: a level of knowledge wherein the location of a navigational goal is known from the outset of the trip, and thus a path can be calculated using the cognitive map.

Getting there, on the other hand, is the knowledge of how to *get to* a location in space. G*etting there* does not require knowledge of the final location, only of a means to reach it. For example, *getting there* can be accomplished through a sequence of simple stimulus-response associations, such as when a navigator follows a route (e.g., turn left on Blanchard, then turn right at the red sign). Evidence from both rat (Whishaw, Cassel, & Jarrad, 1995) and human studies has shown that these two types of knowledge can be behaviourally dissociated, yet few studies do. This lack of distinction has led to a gap in the research on place learning: while some studies assume that place learning, like cognitive mapping, is extremely rapid (e.g., Bast, Wilson, Witter, & Morris, 2009), to date no research has been conducted that truly demonstrates the rate of place learning using measures that are unadulterated by *getting there* components of spatial navigation.

The Morris water maze

Since the early 1980s, place learning, cognitive mapping, and hippocampal function in general have been studied largely using the Morris water maze (MWM) (Morris, 1984). The MWM consists of a uniform, circular pool of opaque water containing a small escape platform hidden just below the surface of the water. By eliminating odor trails and visual cues proximal to the escape platform, the MWM is designed to minimize the contribution of stimulus-response learning to navigational performance. Instead, rats must learn to localize the platform from a variety of different start positions using a constellation of extra-maze cues (i.e., a cognitive map). The MWM has been successfully adapted for human testing using virtual MWM environments presented on computers (e.g., Astur, Ortiz, & Sutherland, 1998; Goodrich-Hunsaker, Livingstone, Skelton, & Hopkins, 2009; Levy, Astur, & Frick, 2005; Livingstone & Skelton, 2007; Sandstrom, Kaufman, & Huettel, 1998; van Gerven, Schneider, Wuitchik, & Skelton, 2012). Learning in the MWM is traditionally assessed by measuring the total distance and latency required to reach an invisible platform (IP) on each trial. Place knowledge is usually measured on a final “probe” trial, where, unbeknownst to the participant, the platform is removed, and the total time spent in a pre-defined area near the platform is measured (probe dwell time).

There are advantages and disadvantages to each of the standard measures usually used in the MWM. The advantage of latency and distance is that they can be measured throughout the learning process, thereby providing some indication of learning rate. However, both of these measures conflate *knowing where* knowledge with *getting there* knowledge. Latency has the added possible disadvantage of including latent constructs, such as confidence or spatial anxiety (Lawton, 1994). The advantage of probe dwell time, on the other hand, is that it is a “purer” measure of place knowledge because it is a measure of proximity to the goal, not a measure of the total path taken, and therefore *getting there* contributions are minimized. The standard probe trial, however, can only be administered after regular learning trials are complete because it has the potential to interfere with place learning (e.g., it could act as an extinction trial). An additional disadvantage of probe trial dwell time is that it fails to represent the full range of place-learning ability (Hardt, Hupback, & Nadel, 2009). Good place learners, who have encoded the platform location in their cognitive map with a high degree of accuracy, may quickly realize that the platform has been removed, and begin searching elsewhere. This, misleadingly, lowers their dwell time percentage, incorrectly indicating a lack of place knowledge.

The current research

The primary purpose of the current research was to discover how fast “pure” place learning occurs in the MWM. To address this question, we paired a new Inter-trial Probe (ITP), an explicit probe trial, with standard virtual MWM invisible platform trials. In previous work, we improved upon the interpretability of the traditional probe trial by introducing a "Drop-the-Seed" trial at the end of the MWM procedure (van Gerven et al., 2012). This trial allowed participants to explicitly reveal their place knowledge by dropping a marker as close as they could to the true platform location. Other researchers have developed similar explicit probe trials (Hardt et al., 2009; Woolley et al., 2010) with common characteristics such as: a) the participants were aware of the purpose and characteristics of the trial (unlike traditional probe trials), b) performance was measured in terms of the difference between the participants' estimate and the actual platform location, and c) the trials were administered at the end of the MWM procedure (that is, after learning was complete). The ITP trial was similar to these precedents, except that it was repeatedly administered between standard learning trials (i.e., invisible platform or IP trials), during the process of learning, rather than after learning was complete. In this way, like typical performance measures derived from standard IP trials (e.g., latency, distance), the ITP trial yielded a measure of learning. Like the traditional implicit probe trial, the ITP trial provided a "pure" measure of place knowledge, without the possible confounding influence of the *getting there* components of navigation. This new procedure thus combined the advantages of standard measures and avoided some of their drawbacks. In accordance with the assumptions made in the literature, we expected that place learning would be extremely rapid, like cognitive mapping.

A subsidiary purpose was to determine whether gender differences are represented in place learning rate. A robust sex difference favouring males has been demonstrated using standard measures of learning in both rats and humans (see Jonasson, 2005, and Lawton, 2010 for reviews). Considerable disagreement exists over the underlying causes for the male advantage, with explanations ranging from hormonal influences (Postma, Winkel, Tuiten, & van Honk, 1999) to cognitive differences driven by evolved sex-roles (e.g., male hunter vs. female gatherer; Silverman, Choi, & Peters, 2007). However, these gender differences, and their explanations, may not depend on the best measures of place learning. Thus, it is of considerable interest to investigate whether the previously seen gender differences remain when a better measure of place learning is used.

The notion of pairing each learning trial with an explicit probe trial in the MWM implies an important question: should the Inter-trial Probes start from the same or different start as the standard learning trial that precedes it? The vast majority of MWM paradigms vary start locations on every trial, which, in principle, should elicit a mode of navigation that is more dependent on the cognitive map (and therefore the hippocampus) (Eichenbaum, Stewart, & Morris, 1990). One rat study arranged same-start learning trials in pairs, but did not directly compare performance to different-start pairs (I. Q. Whishaw, 1985). Moreover, to date, human performance in typical different-start virtual MWM trial procedures has not been compared to performance on a same-start procedure. To investigate this, participants were grouped into two conditions: one in which each trial within a trial pair started from the same place, and a second in which each trial within a trial pair started from a different place.

The next key question was whether holding the start position constant between standard learning trials and Inter-trial Probes would impact males and females differently. Coluccia and Louse (2004) suggest that the magnitude of sex differences in orientation on spatial tasks increases with the difficulty of the task because males have more visuo-spatial working memory resources than females. This would suggest that taxing visuo-spatial working memory less (i.e., by holding the start position constant within trial pairs) might favour female performance. Thus, we expected males to learn the target location faster than females overall, and that gender differences would be larger when task difficulty was increased.

Finally, there is an important question to ask about the new measure that, at this point, can only be addressed indirectly. It is not known whether performance on the ITP trials provides a better measurement of hippocampal function than standard MWM measures do (distance, latency, and probe dwell time). Because facilities to measure hippocampal volumes or function were not available, this question was approached indirectly by examining the relationship between Inter-trial Probe performance and a) tests of cognitive map quality and utility, and b) a test of memory that should reflect hippocampal function. The Room Reconstruction task tests cognitive map quality by requiring participants to “reconstruct” the recently-navigated virtual environment from memory. The “Where’s the Water” task tests immersion or “presence” within the environment, as well as the ability to apply a cognitive map by requiring participants to imagine themselves inside the maze and orient within it. Both tasks have been used to good effect in previous work in the UVic Spatial Lab (Livingstone & Skelton, 2007; van Gerven et al., 2012). The present study added a third, new task to investigate the relationship between paired-associates learning and performance on the Inter-trial Probes. There is a well-established link between verbal paired-associates learning and hippocampal function (e.g., Meltzer & Constable, 2005). More recently, the link has been established between pictorial paired-associates learning and hippocampal function (Yamashita et al., 2009). We examined the relationships between performance on Room Reconstruction, Where’s the Water, and a newly-developed pictorial paired associates task and performance on the Inter-trial Probes. We then contrasted these relationships to those found between traditional MWM measures and the same tests of hippocampal function. We expected that performance on the Inter-trial Probes would predict hippocampal function just as well, if not better, than traditional measures do.

Because this was a new MWM procedure, the present study also addressed two methodological issues. First, it was not known whether the introduction of Inter-trial Probes throughout the process of place learning would change it significantly, thereby reducing the comparability of the current research to other studies. To address this possibility, we measured and compared distance and latency for participants who conducted ITP trials (test conditions) to those who did not (control condition). Because participants were aware of the purpose of the trial and because no feedback was given as to the accuracy of their estimates, we did not expect the ITP trials to significantly change the course of learning. Second, it is possible that performance in the ITP trials was a reflection of participants' ability to judge distances in a virtual environment, rather than of place knowledge. To ensure that performance in the ITP trials reflected only place knowledge, we examined its relationship to performance on a virtual and a real distance-estimation task.

Method

Participants

A healthy sample of 102 participants with equal numbers of males and females were recruited from the University of Victoria undergraduate pool. Using a demographics questionnaire, participants were screened for a history of psychological or neurological problems. Participants were also screened for English fluency to ensure instructions were well understood because some research has shown that task instructions can have an important influence on navigational performance in the MWM (Hardt et al., 2009). Participants were required to provide informed written consent. Ethics approval was obtained from the University of Victoria, Human Research Ethics Committee.

Apparatus

All testing was conducted in a quiet room, free from distraction. Computer-based tasks were displayed on a desktop computer with a 19” LCD monitor set to a resolution of 800 x 600.

Maze Environment

Place learning was investigated using a modified version of the Arena maze (Livingstone & Skelton, 2007), a virtual analogue of the MWM. The virtual environment was designed using the editor supplied by Unreal® (Epic Megagames). Participants experienced the virtual environment from a first-person view, and navigated using a game pad with only forward, left, or right functions activated, analogous to the movements available to a rat in the MWM.

The maze environment consisted of a square room that contained a circular arena. The arena was bound by a wall that prevented participants from exiting the arena during trials without blocking their view of the room beyond. The walls were arbitrarily designated as north, south, east, and west and were featureless except for large windows through which a distinctive outdoor landscape could be seen. Mountains could be seen through the large single window in the north, and a body of water could be seen through the window in the south. The east and west walls each had three smaller windows through which hills that sloped from the mountains to the water could be seen. The navigational target was a circular, solid green platform, approximately 1/6th the diameter of the arena. The platform was positioned in the centre of the southeast quadrant, on a diagonal to the cardinal directions, in line with one of the 4 corners of the room (Figure 1).

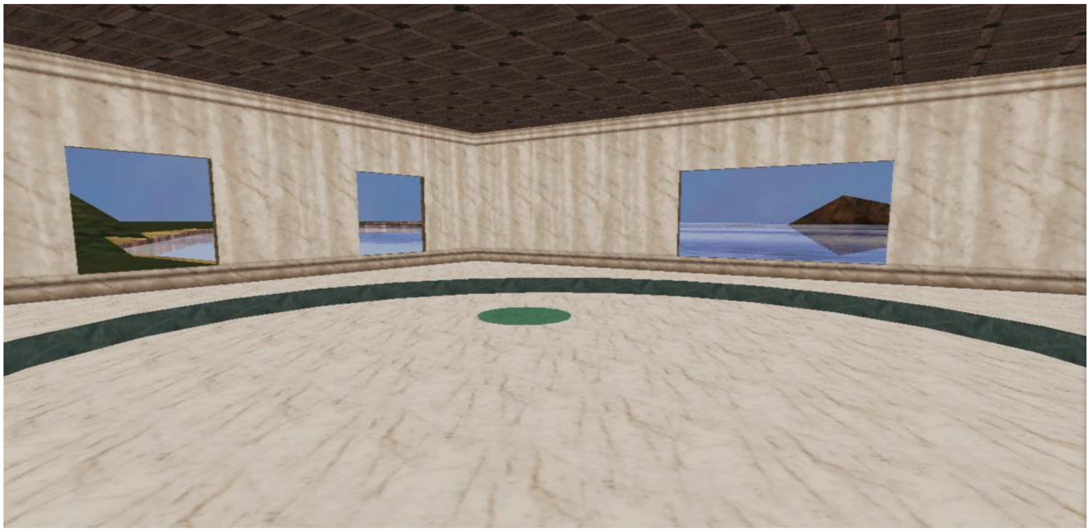

Figure 1. The Arena maze.
This image is taken from an elevated position to highlight room and landscape features visible while navigating in the environment. Note that the green platform shown inside the arena was not visible during testing.

Movement of participants was recorded during navigation using Unreal® "demo" files and extracted using TRAM® software (Skelton et al., 2006). Navigational performance and knowledge of the platform location was assessed using three traditional measures in the MWM: latency (in seconds) and distance (in arbitrary units with 1 platform radius = 12.5 units) to reach the platform, as well as "dwell time" (the percentage of time spent in each quadrant) on probe trials. On Inter-trial Probe trials, place learning and knowledge was assessed using "Place Error", or the distance between the actual and the estimated platform location, measured in platform radii (pr).

Paired Associates Test: Wild Animal Paired Associates

To assess paired associate learning, we used a newly developed computer-based pictorial paired associate task. The Wild Animal Paired Associate task (WAPA) presented moving clip-art images of wild animals superimposed on still nature scenes (Figure 2). Nature scenes were presented for 8 seconds each. During the scene presentation, a wild animal appeared, moved through the scene, and disappeared again. Movement patterns were designed to enhance the ease of identification of the animal images (e.g., a frog hopped, a deer pranced, etc.). Nature scenes were selected to be complex and to not have unique, verbalizable identifiers. Animal-scenes pairs were balanced according to congruency (e.g., congruent: duck + pond, incongruent: skunk + open field).

Figure 2. The Wild Animal Paired Associates task
Image is sampled from one of 14 animal-scene pairs.

Procedure

Design

In order to track the acquisition of knowledge of the platform location over the course of testing we introduced a new trial, the Inter-trial Probe (ITP). On these trials, participants were explicitly directed to indicate where they thought the platform was located. This was equivalent to introducing a Drop-the-Seed trial between each invisible platform (IP) trial. The majority of participants were tested with this procedure. In the “Same-Start” condition, the Same-Start group (*n* = 30) started each ITP trial from the same position as the preceding IP trial. In the “Different-Start” condition, the Different-Start group (*n* = 30) started each ITP trial from a different position than the preceding IP trial. A third “Guess” group (*n* = 12) was asked to indicate the location of the hidden platform before they had seen it. Finally, to determine whether these trials altered the time-course of learning in the paradigm, the “Standard” group (*n* = 30) conducted the traditional MWM procedure, without ITP trials. All groups contained equal numbers of males and females. Table 1 describes the task and trial order for each condition.

Table 1. Trial Order
"X" identifies trials and tasks conducted by participants in a group column. Blank cells indicate tasks or trials not conducted by participants in a group column.

Task and Phase	Group			
	Same Start	Different Start	Standard	Guess
Preliminary Tasks				
1. Demographics Questionnaire	x	x	x	x
2. WAPA (immediate recall)	x	x	x	x
Arena maze Pre-Training				
3. Explore (1 trial)	x	x	x	x
4. Visible Platform (4 trials)	x	x	x	x
Arena maze Testing				
5. Disappearing Platform (1 trial)	x	x	x	
6. Guess (1 trial)				x
7. Invisible Platform 1	x	x		x
8. Inter-trial Probe 1	x	x		x
9. Invisible Platform 2	x	x		x
10. Inter-trial Probe 2	x	x		x
…				
25. Invisible Platform 10	x	x		
26. Inter-trial Probe 10	x	x		
27. Traditional Probe (1 trial)	x	x	x	x
Ancillary Tasks				
28. Room Reconstruction/ Where's the Water	x	x	x	x
29. Distance Estimation	x	x	x	x
30. WAPA Delayed	x	x	x	x
31. Post-test Questionnaire	x	x	x	x

Preliminary tasks

Demographics Questionnaire

Participants completed short, 8 item questionnaire about their age, gender, education, and history of neurological or psychological disorder.

Pictorial Paired Associates Testing (WAPA)

Participants were presented with 14 nature scene-animal pairs for 8 seconds each. Prior to presentation, participants were given complete instructions on how to conduct the WAPA and a short practice-version to ensure that instructions were understood. Participants were asked to name the animal in each scene out loud as it was being presented to ensure that they were paying attention and that their later responses could be scored properly (e.g., if they misidentified the fox as a wolf). Immediately following the presentation, they were given a recall test in which they were presented with 7 of the 14 nature-scenes they had studied, in a different order, and asked to recall the animal that was originally paired with that scene. Approximately 20 minutes later (after the Arena maze testing) participants completed a delayed recall test, in which they were shown all 14 nature-scenes, in a third order, and again asked to recall which animals had been paired with those scenes. Recall accuracy was assessed simply as the number of correctly-recalled animals.

Arena maze pre-training

Participants were first introduced to the Arena maze environment with a set of 5 pre-training trials. These trials were intended to reduce performance variability resulting from lack of experience interacting with computers, perceiving or navigating within 3D environments, competency manipulating the controls, or ability to translate task instructions into action.

Exploration trial

Participants were given an exploration trial in which they were allowed to freely move around in the virtual environment so they could familiarize themselves with the virtual environment and locomotion using the gamepad. The start position was outside the arena, near the east wall, facing inward. Participants were encouraged to look at the landscape through the windows out all sides of the room. Participants explored the room as long as they liked, and the trial ended when they indicated satisfaction with the controls and familiarity with the environment.

Visible platform trials

The purpose of the four visible platform trials was to provide additional practice with the controls and to ensure participants were capable of navigating to a specified target. Participants were asked to walk to a visible platform as quickly and directly as possible. The start position was just inside the arena, facing in, at one of the cardinal points. The platform was visible first in the center of the arena, then pseudo-randomly in the center of each of the 3 quadrants other than southeast (the location of the platform during learning trials). On these and all trials, a bell sounded when participants reached the platform. Once on the platform, participants were instructed to look around the room without stepping off of the platform and inform the experimenter when they were ready to move on to the next trial.

Disappearing platform trial

The purpose of the disappearing platform trial was to familiarize participants with the task of navigating to a target that they could not see and stopping to mark where they thought it was. At the beginning of the trial, the target platform was visible in the center of the arena for approximately 2 s, and then slowly disappeared into the floor. Participants navigated to the platform location, after it had disappeared, and reported when they were where it had been. The experimenter marked the spot for later analysis (though due to technical problems, their placement accuracy on these trials could not be scored). Participants were given instruction regarding this trial immediately before it began.

Guess trial

Participants in the Guess Condition were given a “guess” trial instead of the disappearing platform trial. The purpose of the Guess trial was to determine whether participants could predict the platform location based on any information gathered to this point from the preceding training trials. The trial was identical to the disappearing platform trial in all respects, including start position, except that there was no platform visible at any point in the trial. Participants were instructed to go to the place in the arena where they thought the platform might be found on subsequent testing trials. Participants were told that it was a test of their “intuition”. Once participants had reached their best-guess spot, they alerted the experimenter who marked the spot for later analysis.

Arena maze testing

Two slightly different sets of procedures were used to test those in the standard MWM group and those in the ITP groups. The procedures used for the standard MWM were virtually identical to those used previously in the UVic Spatial lab (e.g., Livingstone & Skelton, 2007; van Gerven, Schneider, Wuitchik, & Skelton, 2012). The procedures for those in the ITP groups were modified only to allow the addition of the ITPs (and the necessary instructions) and are given below.

Instructions

Prior to beginning Arena maze testing trials, participants were informed that they would be tested with 10 pairs of trials and that each trial pair would consist of one conventional invisible platform trial, followed by one Inter-trial Probe (ITP) trial. They were informed that on the first trial in a trial pair, the platform would be invisible, but that it would rise when the participant stepped on it, and they would hear the familiar bell sound. They were advised that on the second trial in a trial pair, the platform would not rise; rather, the participants would have the opportunity to reveal their learning by going to the place where they thought the platform was. It was emphasized that the platform would always be in the same location on all trials, but that the start position may vary. Participants were also informed that they would have only 10 seconds to reach the position where they thought the platform would be. Pilot testing had shown that a time limit was necessary to prevent participants from being overly concerned with minute variations in platform position. To ensure that participants understood these instructions, they were given a short quiz before starting the task. If a participant’s responses were poor, the instructions were reiterated.

Invisible Platform trials (IP)

On the first trial of each pair participants had to find and return to an invisible platform always located in the center of the SE quadrant, as per the usual MWM procedure. The platform remained invisible until stepped on, at which point it became visible and rose out of the floor with the now-familiar bell sound. Start positions varied pseudo-randomly from each of the cardinal points, just inside the arena wall, facing inward. Once the participant discovered the platform, they were encouraged to look around the room from that spot and try to remember where they were, at least on the first 2-3 trials. When the participant was ready, they were reminded that the next trial was a “go to where it was” trial, and then an ITP trial was initiated.

Performance on IP trials was scored as per usual, using the distance and latency required by the participant to reach the platform.

Inter-trial Probe trials (ITP)

On the second trial of each pair participants were required to go to the place in the room where they thought the platform was located on the preceding IP trial. For participants in the Same-Start condition, the ITP trial started from the same start position as the preceding trial, whereas for participants in the Different-Start condition the start position was different in the ITP than it was on the preceding IP trial. So for example, a sequence of start positions in the Same-Start condition would be: West-West, East-East, North-North . . . etc., whereas the trial start sequence in the Different Start condition would be: West-North, East-South, North-West…etc. ITP trials were terminated when the participant indicated that they had reached their estimate of the platform's location or when 10 s had elapsed (whichever came first). At the end of the trial, a virtual curtain was lowered to block the participants' view of the arena and raised to start of the next trial only when they indicated that they were ready for the next trial pair.

Figure 3 illustrates the difference in trial pairs between the Same-Start and Different-Start conditions, and the way in which Place Error was scored.

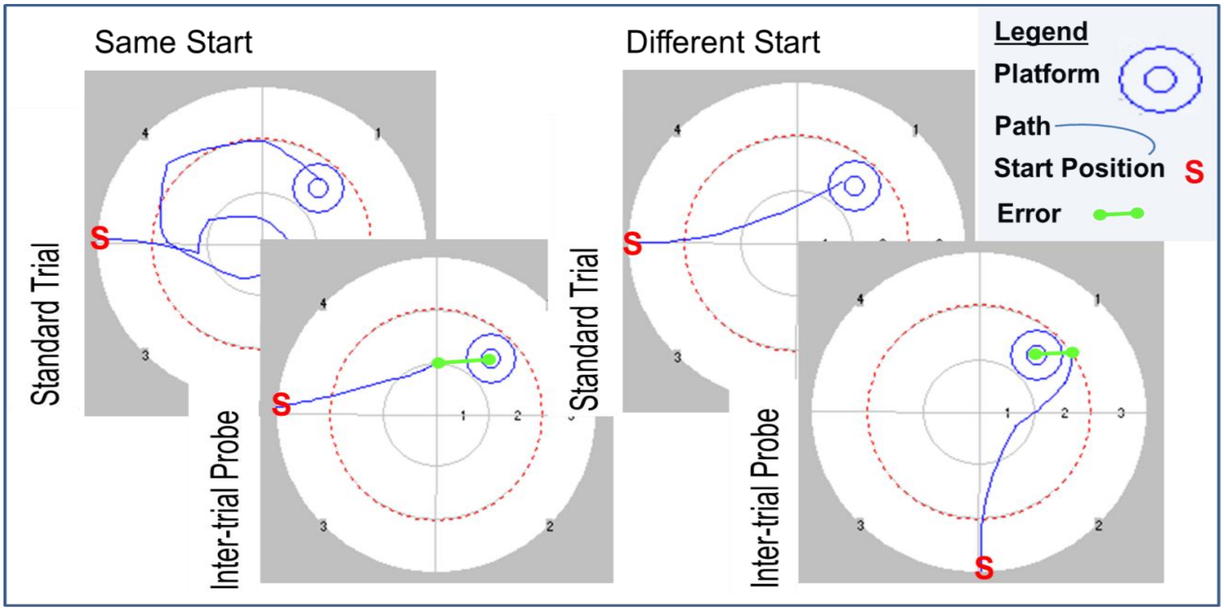

Figure 3. Sample Same-Start and Different-Start Path Trajectories
Images clipped using sample data analysed with TRAM® software. Note that within each image, “north” is depicted on the left, “south” on the right, “east” at the top, and “south” at the bottom. The platform is thus in the center of the southeast quadrant.

Probe trial

For all participants, the final trial in the Arena maze was a traditional probe trial. The purpose of the traditional probe was to provide an implicit measure of place knowledge after learning is complete. This trial was introduced to the participants as if it were simply the next invisible platform trial in the sequence; participants were not given any indication that no platform would be present on this trial. The trial lasted for 50 s at which time the usual bell sounded. Performance in the probe trial was measured as the percent of total trial time spent in the correct quadrant.

Ancillary tests

3D Room Reconstruction and Where's the Water

After Arena maze trials were complete, participants were tested for their knowledge of the virtual environment by "reconstructing" the maze environment and by imagining themselves in the virtual room and pointing towards a salient landmark. Participants were placed in a special Arena maze that had no landscape visible through the windows. From the center of the arena, and facing one of the large single windows (which could have been north or south), participants were asked to select a laminated landscape image that best represented the landscape that would normally be visible through that window, based on what they had learned during Arena maze trials. Once a participant selected an image, the experimenter took note and removed it from view. The experimenter then asked the participant to rotate 90˚ until he or she was facing the center of the next wall (a three-window wall), where the participant was asked to select another image. This process was repeated for the 3rd wall, and then the participant was asked point, from their current "virtual" perspective, in the direction of a specific landmark in the virtual environment (e.g., the water). The participant was then asked to rotate the final 90° and select the appropriate landscape image.

The 3D room reconstruction was scored based on the spatial relationship between the first cardinal image (N, E, S, W) selected by the participant and the other cardinal images they selected. One point was given for each cardinal image in correct relation to the first image (e.g., N opposite S, W clockwise to S). One additional point was given to each cardinal image that was correctly positioned outside the correct type of wall (i.e., N and S for walls with 1 large window, E and W for walls with 3 small windows). In addition, one point was given for a non-cardinal image (e.g., SW) if its edge matched an edge of a correctly positioned cardinal image. The maximum score was 8 (Figure 4). The Where's the Water task was scored on a 3-point scale, where the participant received 2 points for pointing directly at the target landmark, 1 point for missing by up to 45°, and 0 points for pointing anywhere beyond a ±45° range of the target.

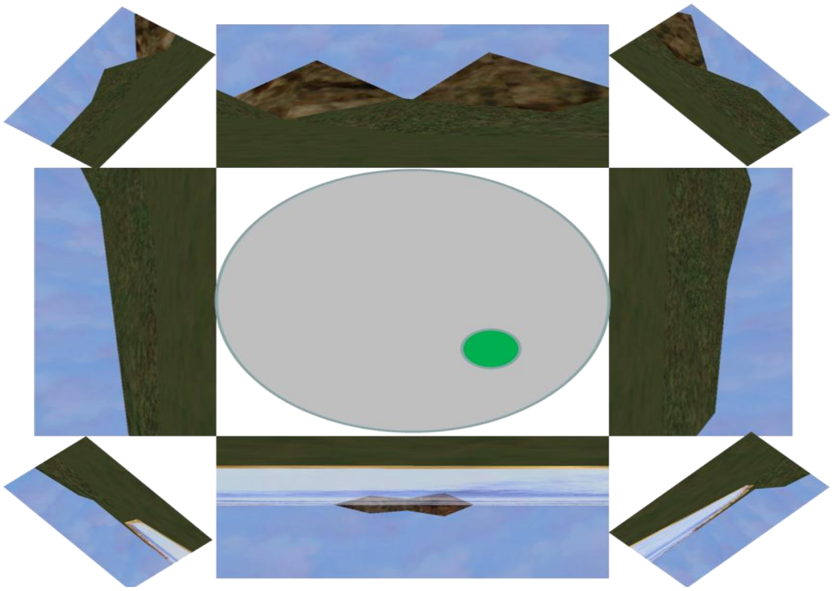

Figure 4. Room Reconstruction Elements.
Landscape elements correctly arranged in relation to each other and the platform (small green circle). Note: figure is not to scale. Landscape images in the task were all the same size; images visible from the center of the arena (grey circle) are shown larger for illustrative purposes.

Virtual and Real World Distance Estimation

Participants were asked to judge distances in both real and virtual space in order to determine whether differences in participants' ability to judge distance were a major factor in determining their scores on the ITPs. In virtual space, participants were asked to estimate distance by estimating the number of platforms that would fit inside the arena, from a position just outside the arena wall. In order to give them a standard metric, a platform was placed first just inside the wall, entirely visible to the participant, and second in the centre of the arena. Thus, the participant was asked first to judge the diameter of the arena and second to judge the distance between an object in the arena and the arena wall. In the real world, participants were moved into the hall and asked to judge the distance between themselves and the end of the hall. In order to give them a standard metric, a 1 m long unmarked stick was placed on the floor in front of them. Participants were asked to estimate how many sticks would be required to span the distance to end of the hall. The distance estimation tasks were scored as the absolute value of the difference between the participants' estimates and the correct number of platforms or sticks (distance estimation error).

Post-Test Questionnaire

To end the session, participants completed a post-test questionnaire. The primary purpose of this was to assess participants' previous experience with video games to control for its possible influence on gender comparisons. Responses to the 5 video-game experience questions, which were ranked on a 6-point scale, were aggregated into a summary "game experience" variable. The secondary purpose of the questionnaire was to gather information about other possible factors that may influence spatial ability, such as childhood experience and environment, for future study.

Data analysis

To examine whether the presence of ITPs changed the course of learning, average latency and distance performance from IP trials 2-10 was compared between participants getting and those not getting ITPs using independent samples *t*-tests. Note: Data from IP trial 1 was excluded from this analysis because on this trial participants are searching for an unknown location, and are thus using different cognitive processes than on subsequent trials, when they are returning to a location.

Acquisition of knowledge of the platform location was assessed by examining changes in Place Error over trials. To assess learning rate, overall Place Error was averaged across participants and over ITP trials 1-10 and compared to performance on the “Guess” trial using independent-samples *t*-tests. In order to determine whether a significant number of participants had learned the platform location in 1 trial, goodness-of-fit Chi Square tests (Zar, 1999) were used to test whether, after the first IP trial, the proportion of participants who estimated the location of the platform as being a) in the correct quadrant and b) within the bounds of the platform itself was higher than chance. In order to compare the accuracy of platform location estimation on ITPs in the present study to the accuracy on single trials given at the end of invisible platform trials in previous studies in this laboratory, average Place Error was also compared to the average accuracy score from Drop-the-Seed trials (van Gerven, Schneider, Wuitchik, & Skelton, 2012). In these trials, participants estimated the platform location and marked their estimate by dropping a virtual seed onto the virtual floor. Their estimates were later scored using a bull’s-eye target with a centre the size of the platform and 6 concentric rings, each with a radius 0.5 platform radii larger. Scores were converted to Place Errors (in platform radii) using the distances of each ring’s outermost limit from the centre of the target.

To test whether gender and varying the start position affected Place Error, a 2x2 factorial ANCOVA was run with video-game experience as the covariate. Gender effects on navigational performance were assessed using independent-samples *t*-tests on Latency, Distance, Probe Dwell time and a summary variable, Spatial Score. This summary variable normalizes distance, latency and probe trial dwell time, and weights them so that performance on invisible platform trials contributes the same as dwell time on the probe trial (Skelton et al., 2006). Spatial Score is calculated according to the following formula:

Spatial Score =(0.5 x Probe Dwell *z*-score) – (0.25 x Latency *z*-score + 0.25 Distance *z*-score)

The strength of the relationships between Place Error, Spatial Score, and measures of hippocampal function (Room Reconstruction, Where's the Water, paired associates), and the ability to judge distance were examined using Pearson or Spearman correlations. Correlations between Place Error and measures of hippocampal function were then compared to correlations between Spatial Score and measures of hippocampal function using t-tests (Field, 2009).

Results

Standard trials

On the visible platform trials, there were small but statistically significant differences between the participants who would be tested in the standard Arena maze and those who were to be tested with Inter-trial Probes (See Figure 5 and 6). Time taken to reach the platform (latency) was not different (ITP *M* = 3.58 s, *SEM* = 0.11; Standard *M* = 3.46 s, *SEM* = 0.12 s; *t*(89) = 0.79, *p* =.43, *d* = 0.16) but distance taken was (ITP *M* = 7.32 pr, *SEM* = 0.03; Standard *M* = 7.18 pr, *SEM* = 0.03; *t*(89) = 2.95, *p* <.001, *d* = 0.59). However, this difference is not meaningful because a) the mean difference was minute (less than 2% of the distance), b) the variances were small due to a floor effect, and c) the difference between the groups was due to sampling error because to that point, both groups had been treated identically.

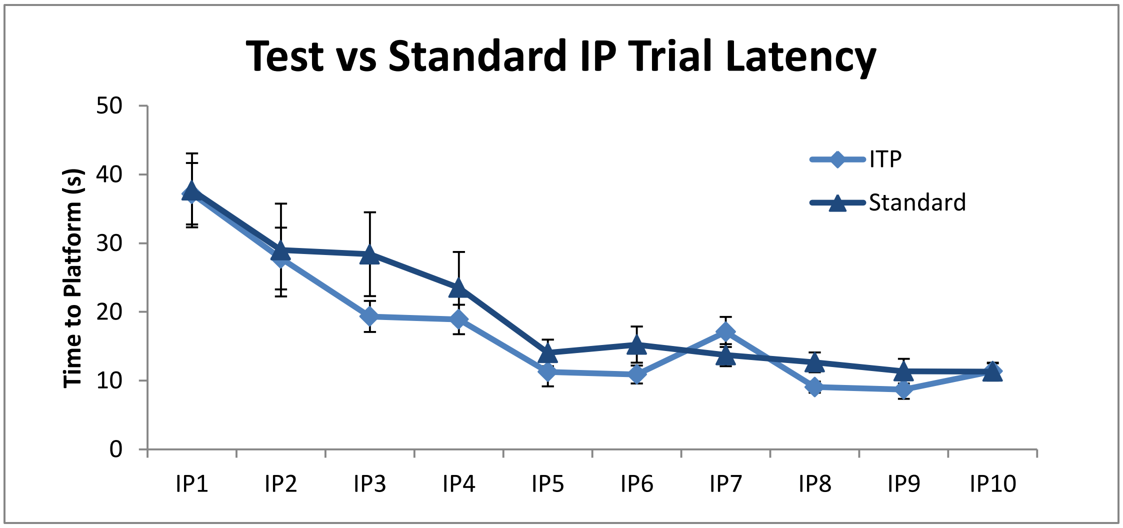

Figure 5. Invisible Platform Latency Over Trials
The X-axis shows the trial number, with Visible trials (V1-4) on the left, and standard Invisible Platform trials (T1-10) on the right. The Y-axis shows time in seconds. Data from the Explore and Disappearing Platform trials not shown.

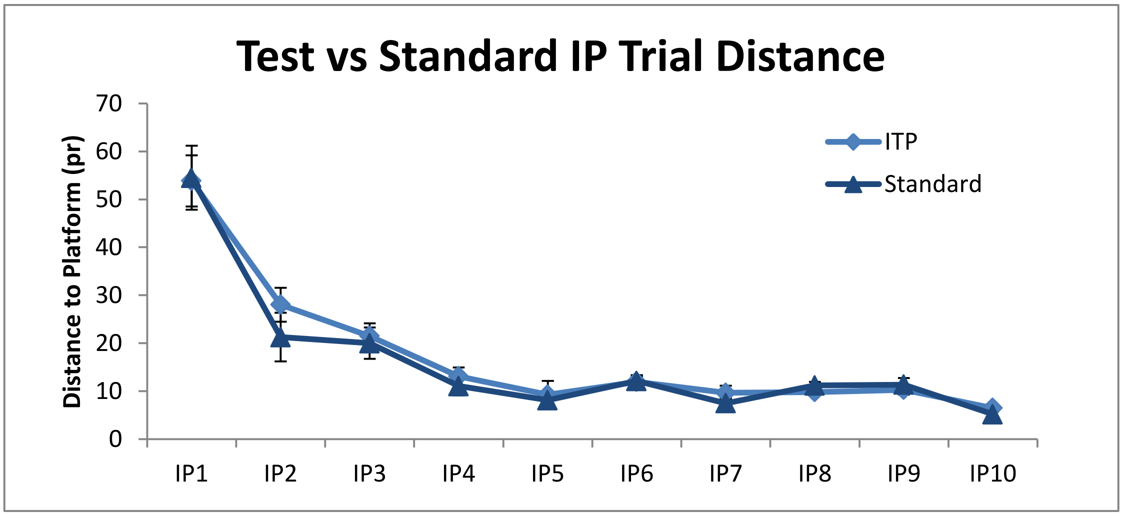

Figure 6. Invisible Platform Distance Over Trials
The X-axis shows the trial number, with Visible trials (V1-4) on the left, and standard Invisible Platform trials (T1-10) on the right. The Y-axis shows time in seconds. Data from the Explore and Disappearing Platform trials not shown

Insertion of Inter-trial Probes did not appear to alter the course of learning in the Arena maze. Standard measures of performance did not reveal any differences in the course of learning during Arena maze testing between participants who received ITP trials and those who did not. There were no differences between Standard and ITP groups in latency on trials 2-10, *t*(89) = 1.31, *p* =.19, *d* = -0.32 (Figure 5 and 7a) or distance on trials 2-10, *t*(89) = 0.59, *p* =.56, *d* = 0.14 (Figure 6 and 7b), or in the percentage of time spent in the correct quadrant on the final traditional probe trial, *t*(89) = 0.50, *p* =.62, *d* = 0.11 (Figure 7c). Furthermore, no differences were found between groups on Spatial Score, *t*(89) = 0.58, *p* =.57, *d* = 0.13 (See Fig**ure** 7d). It

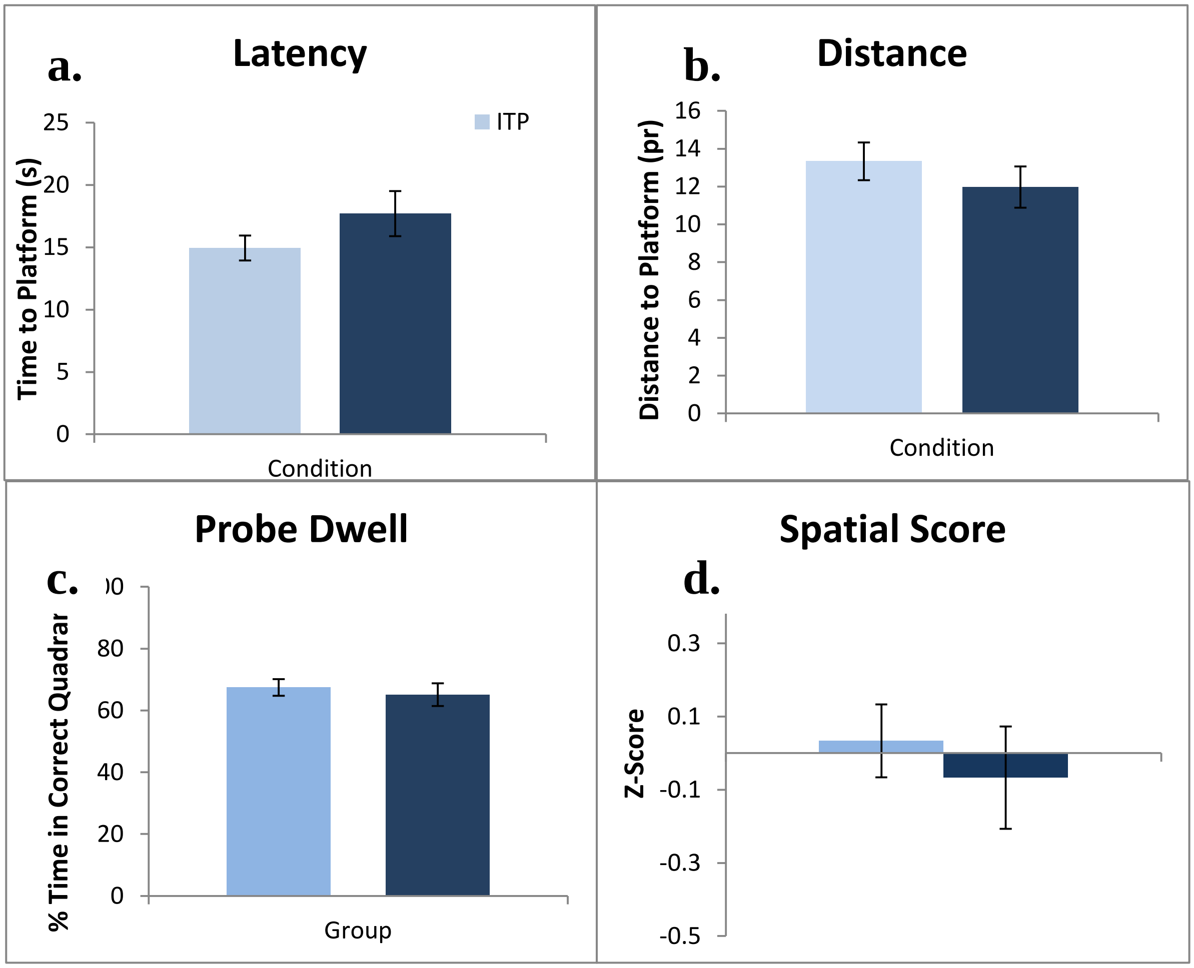

Figure 7. Standard Invisible Platform Trial Performance Measures.
Standard and ITP group performance (X-axis) on a) latency and b) distance to the invisible platform, c) probe trial dwell time, and d) spatial score (Y-axis). Error bars represent standard error of the mean (*SEM*).

should be noted that, although there was a moderate difference in latency on trial 3 between ITP and Standard groups, this difference did not reach significance ($p > .05$).

Inter-trial Probes

The novel measure of trial-by-trial place learning, Place Error on Inter-trial Probes (ITP), confirmed the expectation that place learning occurs very rapidly. Even on the first ITP, after only one learning trial, Place Error was only 2.75 platform radii (*SEM* = 0.31 pr), well inside the boundary of the quadrant that contained the platform during IP trials (3.20 pr) (Figure 8). Over all trials (1-10) Place Error on Inter-trial Probes was very small, less than 1 platform radius (0.88 pr, *SEM* = 0.11 pr) beyond the platform. Another way of viewing the accuracy of the participant's knowledge and the speed of their learning is to examine the number of participants who made estimates that were correct to within the bounds of the quadrant, and the number who were correct to within the bounds of the platform itself. Plots of the positional estimates on Inter-trial Probes 1, 3, and 10 show that even on the first Inter-trial Probe, many participants (60%) had already identified the quadrant in which the platform was located (Figure 9a) Pearson's Chi-Square test for goodness-of-fit revealed that the number of participants who estimated the platform to be in the correct quadrant on the very first Inter-trial Probe was significantly higher than chance level (i.e., 25% of the total area of the pool), $\chi^2(1, N = 60) = 39.20$, $p < .001$. Similarly, the number of participants able to estimate the platform location was significantly higher than would be expected by chance (i.e., the platform was 3 % of the total area of the pool), $\chi^2(1, N = 60) = 70.69$, $p < .001$. The proportion of participants selecting the correct quadrant increased rapidly until trial 3, and remained high on all subsequent trials (Figures 9b, c). Figure 10 shows how the proportion of participants estimating the platform location to be in the correct quadrant rapidly reached an asymptote of about 80% by trial 3.

Figure 11 shows how the proportion of participants able to correctly estimate the exact platform location increased slowly from about 30% on trials 1 and 2 to about 50% on trials 9 and 10. When Place Error estimates were compared to performance on Drop-the-Seed trials given at the end of training in a previous study (Livingstone, 2009), it was clear that the average Place Error at the end of training in the present study was equivalent to estimates at the end of that previous study. Interestingly, accuracy on Inter-Trial Probes reached the level that would be expected from previous work (2.08 pr) on the 3rd trial (Figure 8).

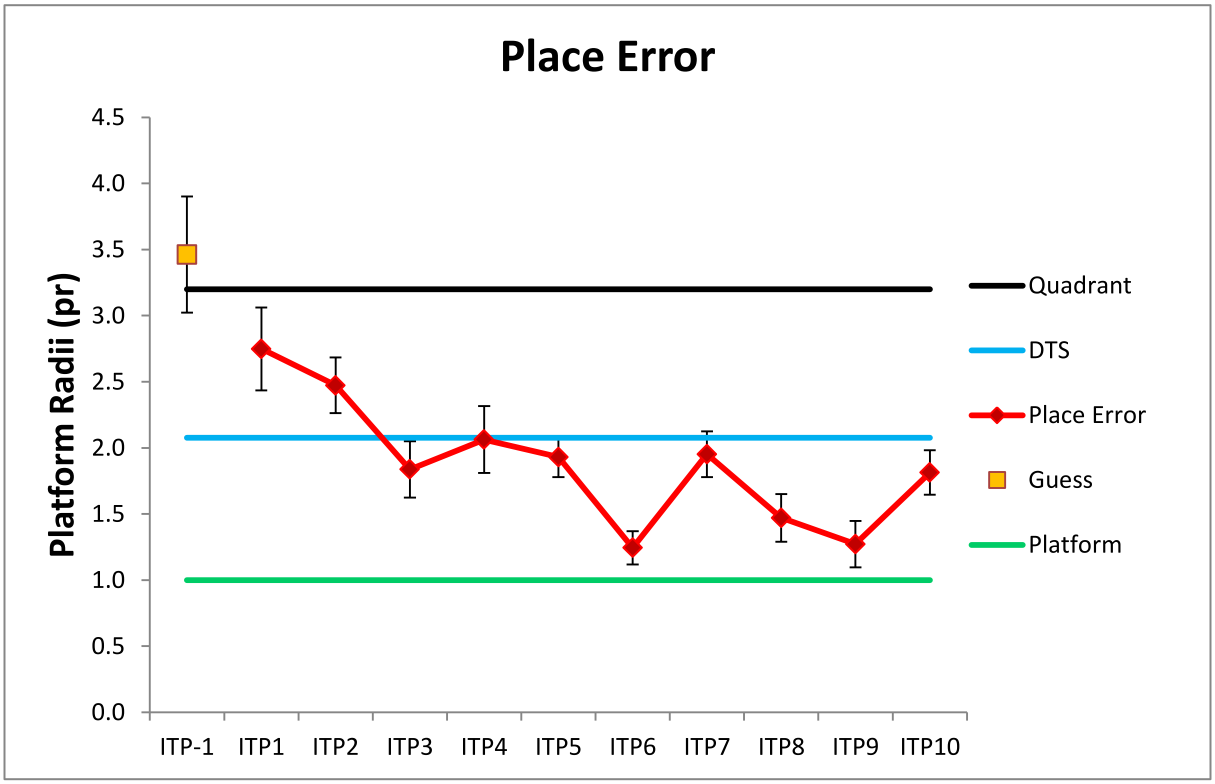

Figure 8. Place Error Over Trials.
Average Place Error (red line) in platform radii (Y-axis) on ITP trials 1-10 (X-axis). For comparison, Guess trial error (yellow), Drop-the-Seed error (light blue), the southeast quadrant boundary (black), and the platform boundary (green) are shown.

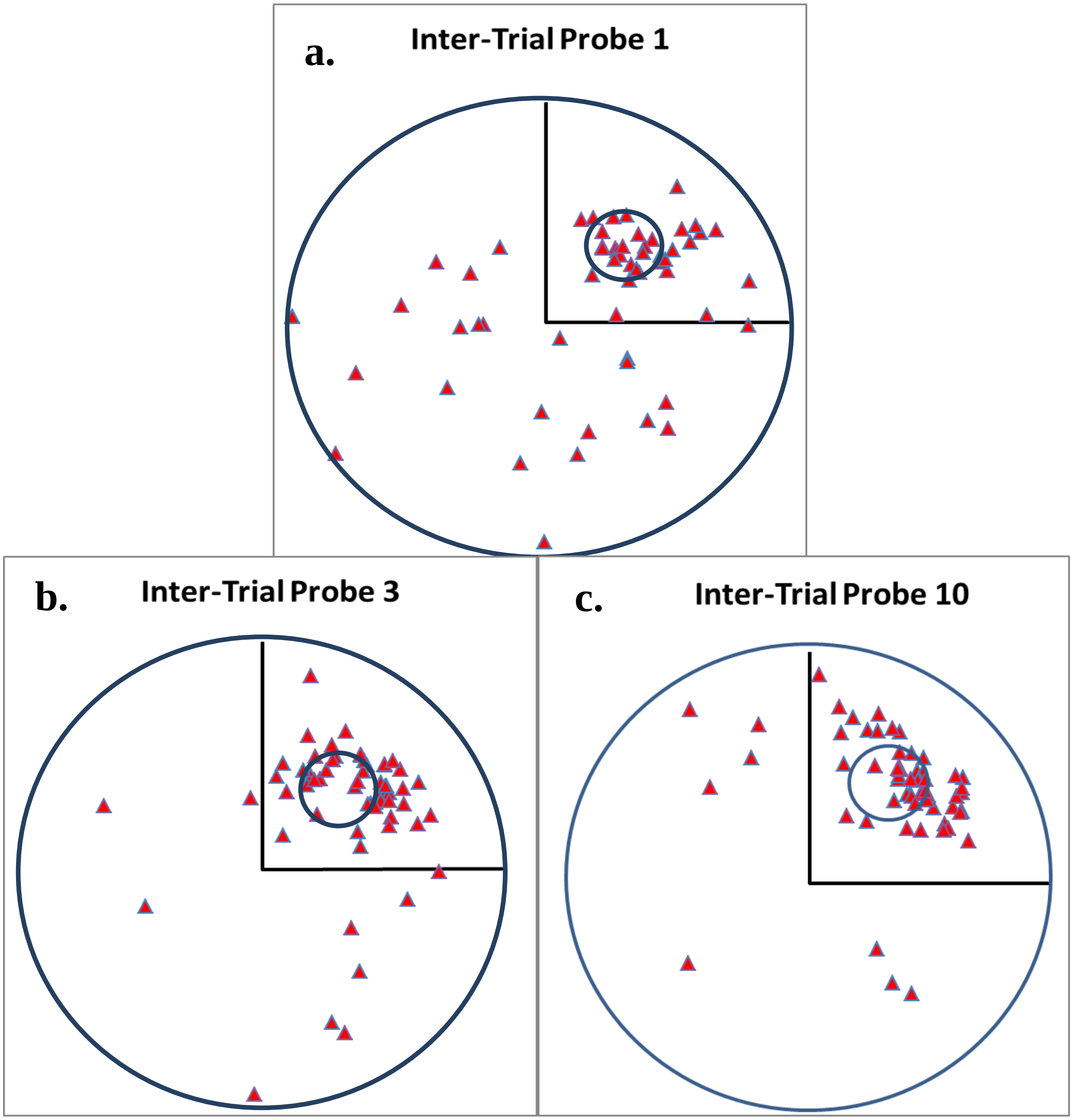

Figure 9. Plots of Inter-Trial Probe Platform Location Estimates.
Individual platform estimates on a) trial 1, b) trial 3, and c) trial 10. The Arena boundary (large circle), platform boundary (small circle), and correct quadrant (black lines) are correctly scaled.

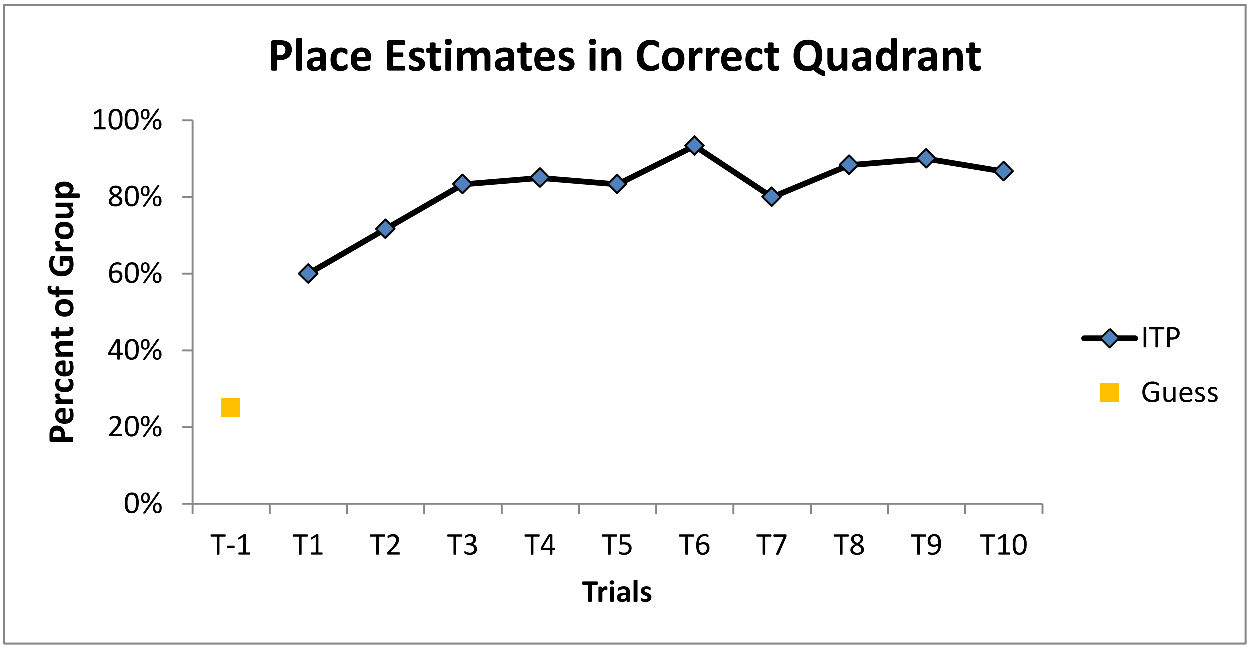

Figure 10. Frequency of Place Estimates in the Correct Quadrant.
Counts of the number of participants who estimated the platform to be in the correct quadrant as a percentage of the group (Y-axis) over trials (X-axis). Guess trial estimates shown (yellow) for comparison.

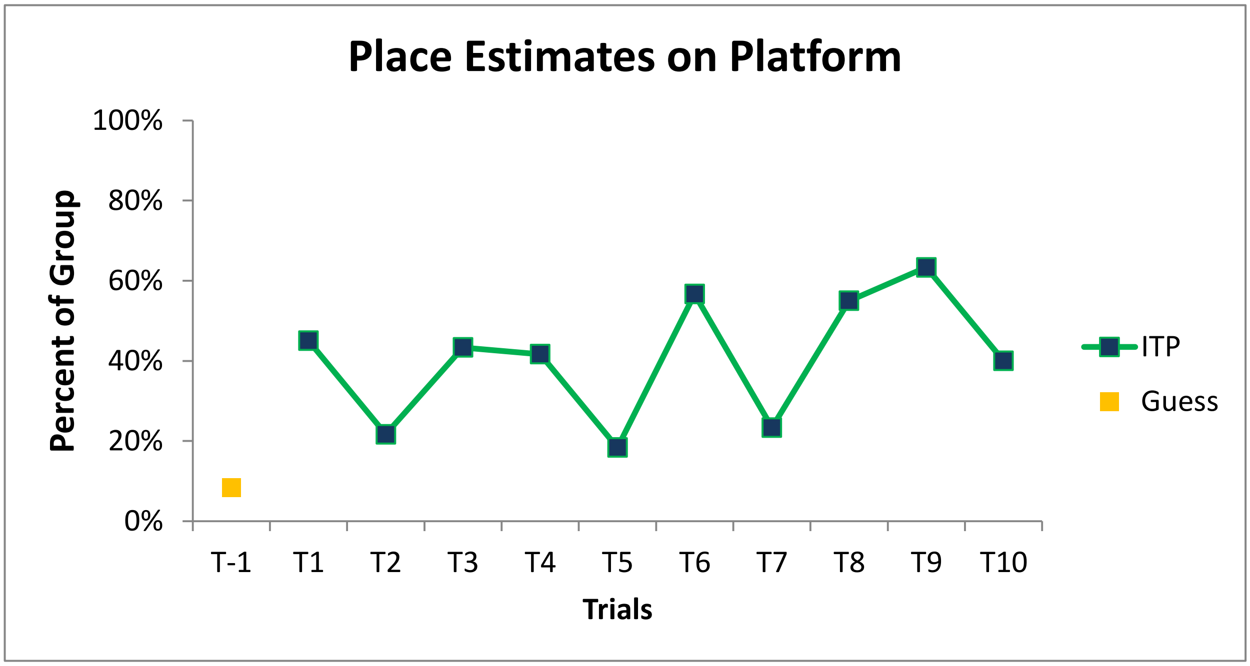

Figure 11. Frequency of Place Estimates on the Platform.
Counts of the number of participants who correctly estimated the platform location as a percentage of the group (Y-axis) over trials (X-axis). Guess trial estimates shown (yellow) for comparison.

Guess trial

Despite the strong performance on the first Inter-trial Probe, it is not entirely clear how much learning can be attributed to the first learning trial and how much learning had happened before that. This high level of performance was not apparent until after most of the data had been collected. At that point it was decided that it would be worth testing participants' ability to estimate the platform location before conducting any learning trials. Accordingly, a relatively small group (*n* = 12, 6 male and 6 female) was asked to guess where the platform would be located on the next trial (after the 4 visible platform trials) based on their "intuition" of where the experimenters were going to put it. Visual inspection of the positions on these Guess trials shows that platform location estimates were distributed equally amongst the 4 quadrants (i.e., 25% each, as expected by chance) and that most guesses tended to be near the locations of the platform on the preceding visible platform trials. Furthermore, 9 of the 12 (75%) were placed at the correct distance from the arena wall to hit the positions of the visible platform on preceding trials and the invisible platform on future trials (Figure 12). Figure 13 shows that this "Guess" group estimated the platform to be, on average, within 3.46 platform radii (*SEM* = 0.44 pr) away from its future location. Although this average distance is beyond the bounds of the correct quadrant, it was not significantly different from the estimates of the ITP group on the first Inter-trial Probe, $t(71) = 1.3$, $p = .20$, $d = 0.27$. Pairwise *t*-tests between the performance of the Guess group and the ITP groups on the first 3 trials showed that the ITP groups were significantly better at estimating the platform location after 3 learning trials, $t(71) = 2.97$, $p < .01$, $d = 0.69$ (Figure 13).

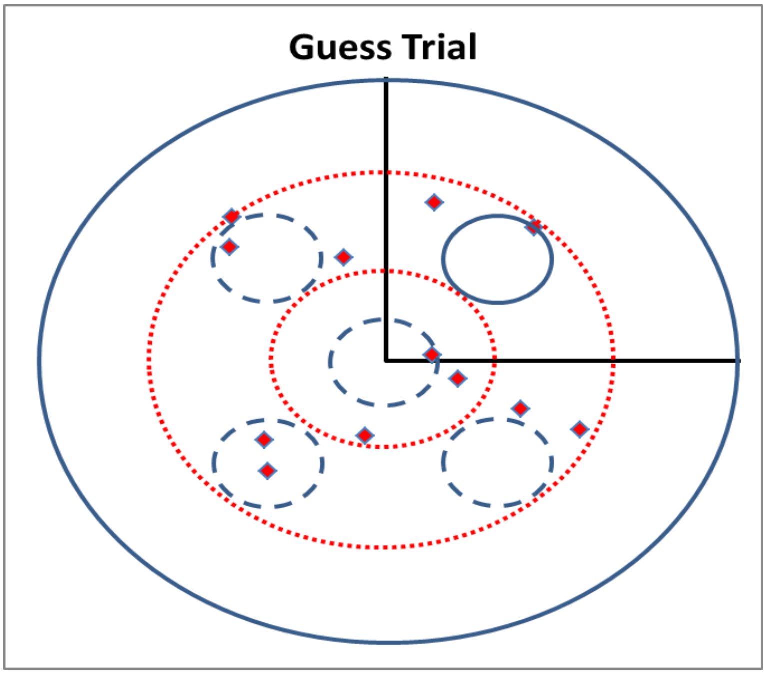

Figure 12. Plot of Guess trial Place Estimates.
Individual estimates of the platform location (small solid circle) on the Guess trial. Dashed circles represent platform locations on the 4 preceding visible platform trials. Red-dotted circles represent a middle annulus, a central ring one platform diameter wide at equal distance from the center of the arena and the arena wall. Platforms and the arena are scaled correctly.

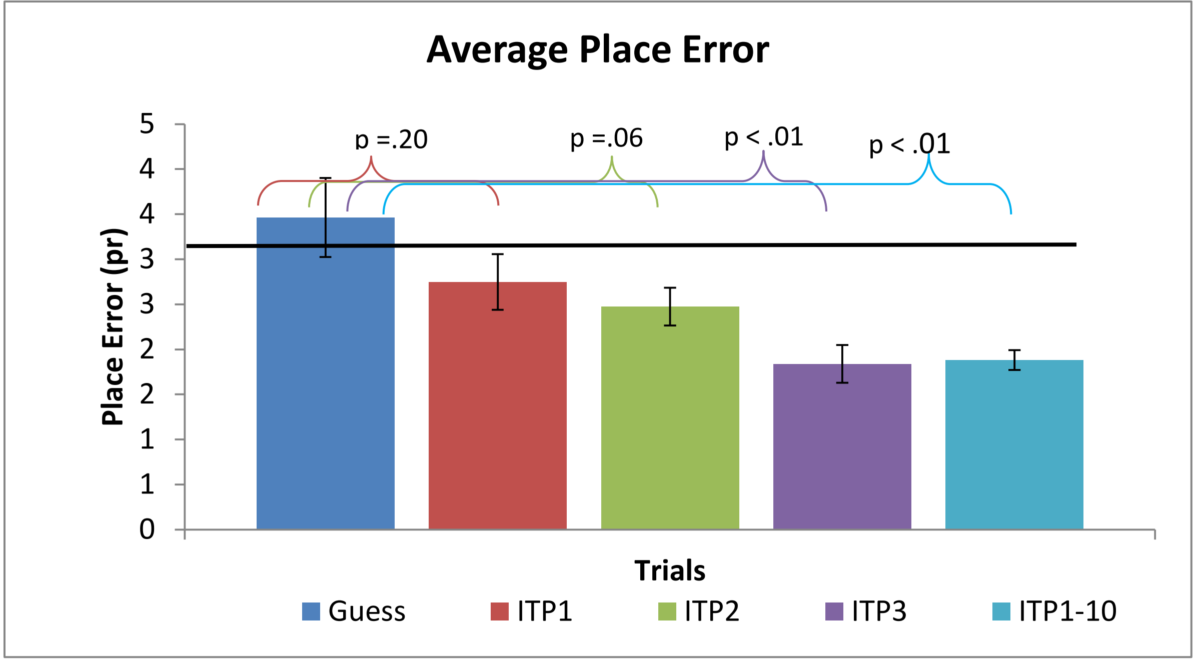

Figure 13. Average Place Error: Guess trial vs. ITP1, 2, 3.
Place Error (Y-axis) for the Guess trial, ITP trials 1, 2, 3, and the mean ITP Place Error over trials 1-10 (X-axis). Significance values are shown for t-test comparisons (curly braces). The horizontal black line represents the southeast quadrant boundary. Error bars represent the standard error of the mean (*SEM*).

Start condition

Comparison of participants in the Same-Start condition to the Different-Start condition indicated that varying the start location between IP and ITP trials reduced the accuracy of place knowledge. Over trials 1-10, the Different-Start group was prone to significantly higher Place Error (*M* = 2.24 pr, *SEM* = 0.18 pr) than the Same-Start group (*M* = 1.53 pr, *SEM* = 0.10 pr), *t*(59) = 3.44, *p* = .001, *d* = .82 (Figure 14). Figure 15 shows that a consistent and stable difference between conditions persisted on most trials. On the first Inter-trial Probe, Place Error scores for Same-Start (*M* = 2.47 pr, *SEM* = 0.32 pr) and Different-Start (*M* = 3.02 pr, *SEM* = 0.32 pr) conditions did not significantly differ (*t*(59) = 0.87, *p* = .39, *d* = -0.22). There were no significant differences between the two conditions in the number of participants who localized the platform to the correct quadrant on the first ITP trial (Same-Start: 20/30, 60%; Different-Start: 16/30, 53%), χ^2 (1, *N* =60) = 2.14, *p* = .14, but both conditions were significantly different from chance, (Same-Start: χ^2 (1, *N* =30) = 27.78, *p* < .001; Different-Start : χ^2 (1, *N* =30) = 12.84 , *p* < .001) (Figure 16).

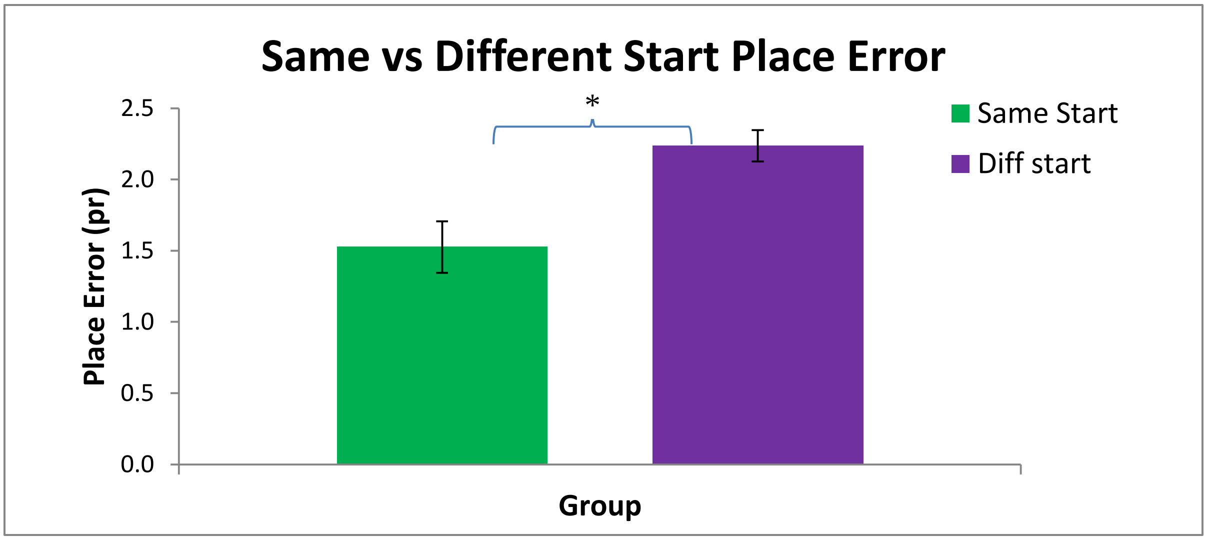

Figure 14. Place Error by Start Condition.
Same- and Different-Start mean Place Error in platform radii (Y-axis) on trials 1-10. Asterisk indicates a significant difference at *p* < .01. Error bars represent the standard error of the mean (*SEM*).

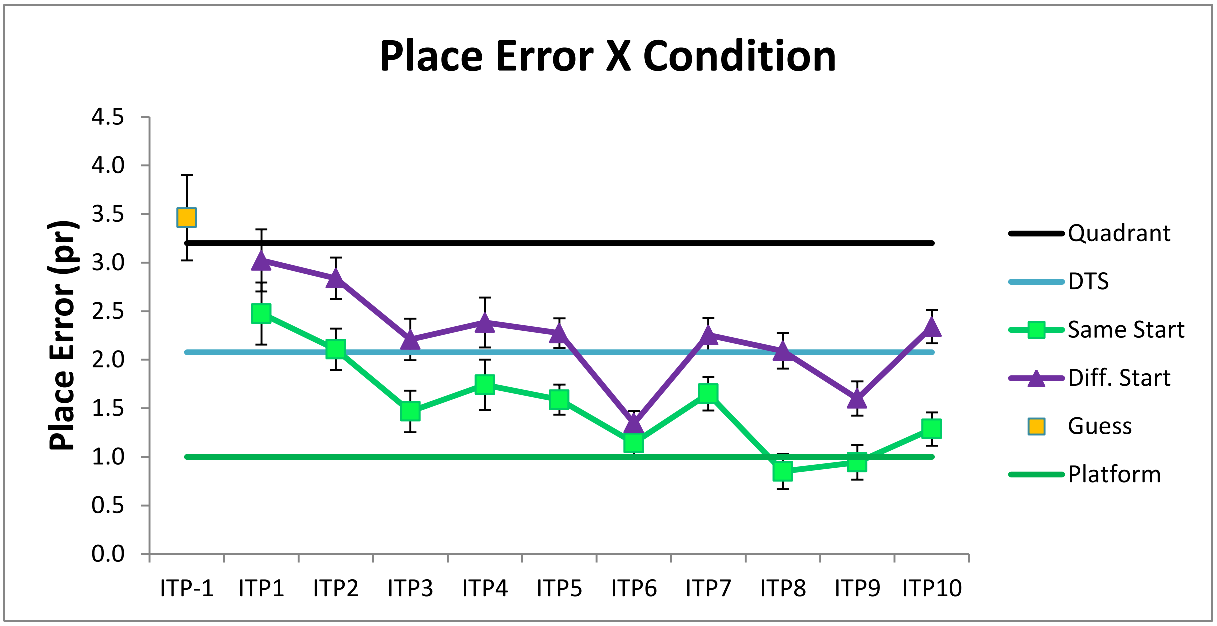

Figure 15. Place Error by Condition Over Trials.
Average Place Error for Same-Start (light green) and Different-Start (purple) in platform radii (Y-axis) on ITP trials 1-10 (X-axis). For comparison, Guess trial error (yellow), Drop-the-Seed error (light blue), the southeast quadrant boundary (black), and the platform boundary (dark green) are shown.

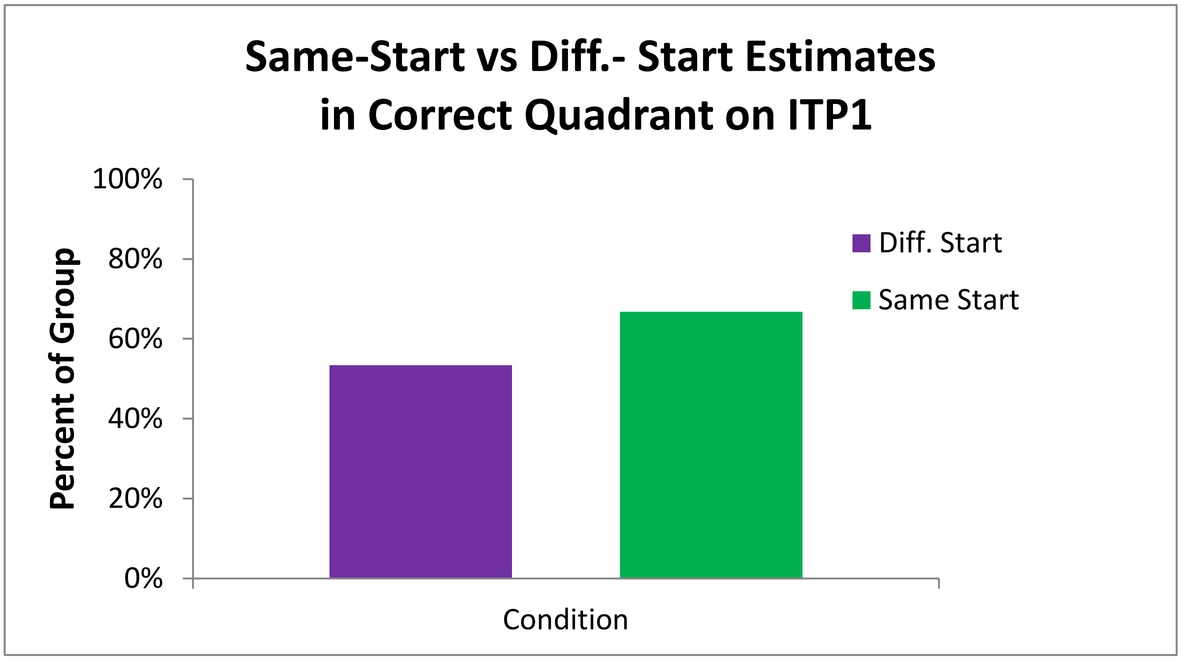

Figure 16. Inter-trial Probe Frequencies in Correct Quadrant by Condition.
Counts of place estimates in the correct quadrant on ITP1 as a percentage of the group (Y-Axis).

Gender

The new measure of place learning was not much different from traditional measures in terms of its ability to reveal gender differences. Gender differences were confined to small differences in latency, and were not present at all in Place Error. On invisible platform trials, there was a significant gender difference in average latency (male $M = 12.60$ s, $SEM = 1.38$; female $M = 17.28$ s, $SEM = 1.36$), $t(59) = 2.40$, $p < .05$, $d = -.60$, but not distance (male $M = 12.43$ pr, $SEM = 1.18$, female $M = 14.25$, $SEM = 1.10$), $t(59) = 1.12$, $p = .26$, $d = -.29$, dwell time in the correct quadrant (male $M = 69.43\%$, $SEM = 3.57\%$, female $M = 65.37\%$, $SEM = 4.21\%$), $t(59) = 0.73$, $p = .46$, $d = .19$) or Spatial Scores (male $M = 0.18$ z, $SEM = 0.13$ z; female $M = -0.12$ z, $SEM = 0.14$ z), $t(59) = 1.57$, $p = .12$, $d = 0.40$. Similarly, there was no gender difference in Place Error on Inter-Trial Probes 1-10 (male $M = 1.67$ pr, $SEM = 0.13$; female $M = 2.09$, $SEM = 0.18$) when the influence of video-game experience was factored out using a 2X2 ANCOVA with gender and condition as independent factors and video game experience as the covariate: $F(1,55) = 0.00$, $p = .97$, partial $\eta^2 = .00$ (Figure 17). Contrary to expectation, Figure 18 illustrates a lack of interaction between gender and condition on Place Error, $F(1,55) = 0.29$, $p = .59$, partial $\eta^2 = .01$. No gender differences were found on the first ITP trial (male $M = 2.46$ pr, $SEM = 0.48$ pr; female $M = 3.03$ pr, $SEM = 0.41$ pr), $t(59) = 1.01$, $p = .32$, $d = -0.26$. Goodness-of-fit Chi-Squared revealed no significant gender difference in the number of males (60%) and females (53%) estimating the platform to be in the correct quadrant on the first ITP trial: $\chi^2\,(1, N = 60) = 2.14$, $p = .14$, but both were significantly different from chance, (male: $\chi^2\,(1, N = 30) = 27.78$, $p < .001$; female: $\chi^2\,(1, N = 30) = 12.84$, $p < .001$) (Figure 19).

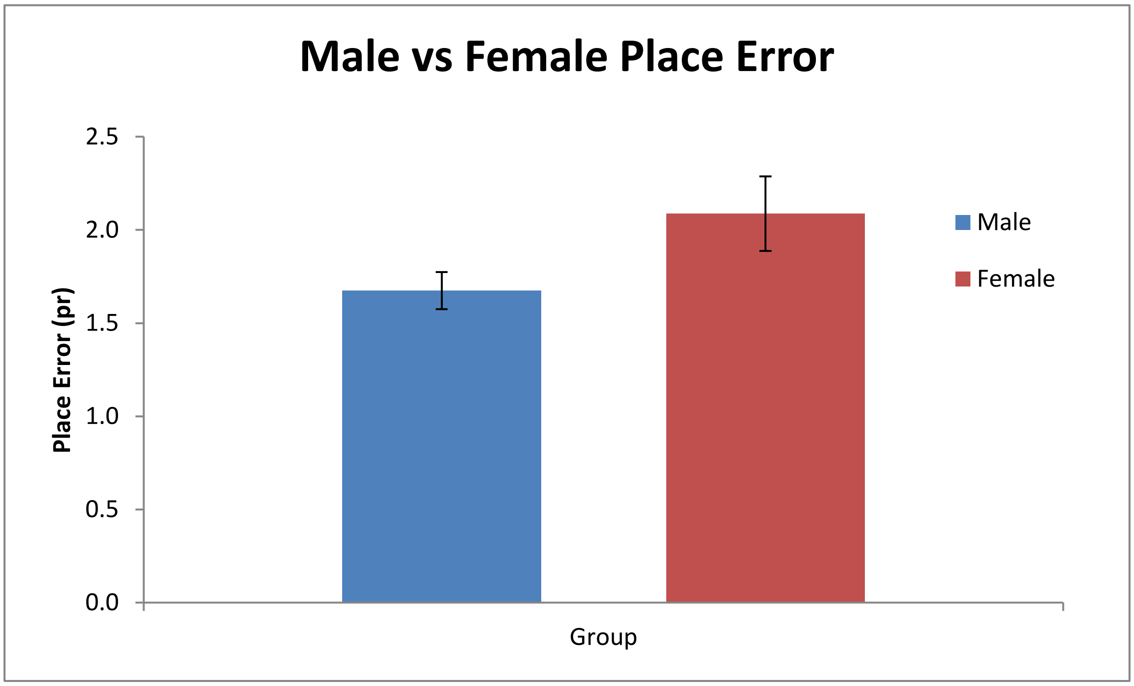

Figure 17. Place Error by Gender.
Mean Male and Female Place Error in platform radii (Y-axis) on ITP trials 1-10. Error bars represent standard error of the mean (*SEM*).

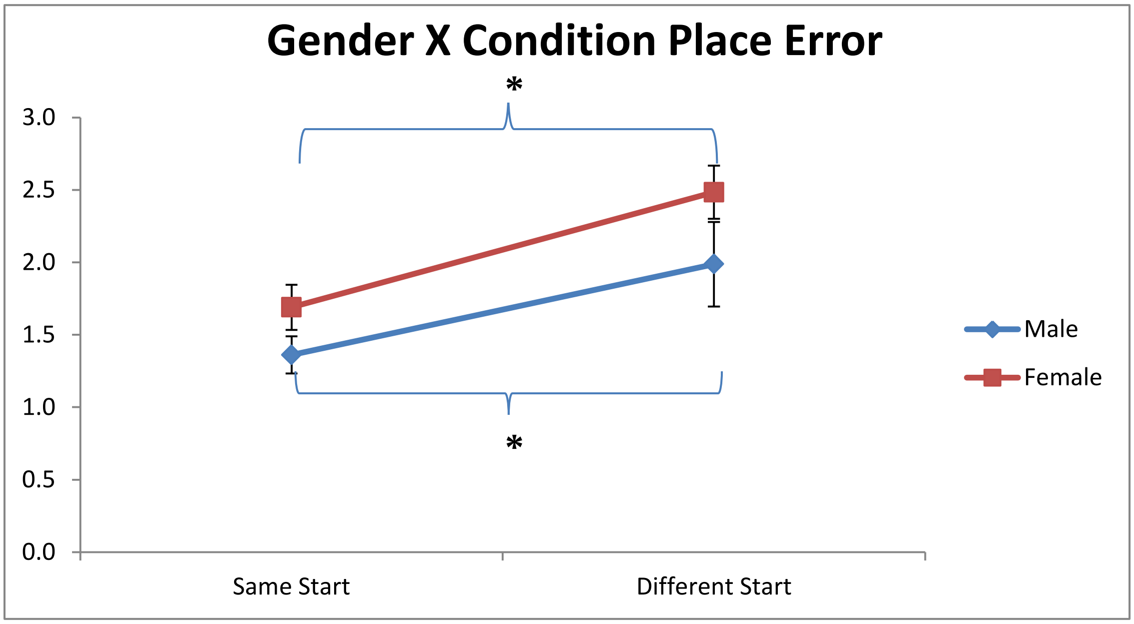

Figure 18. (Lack of) Gender by Condition Interaction.
Same-Start and Different-Start male and female mean Place Errors in platform radii on ITP trials 1-10. Asterisks indicate significant differences between Same- and Different-Start males, and between Same- and Different-Start females.

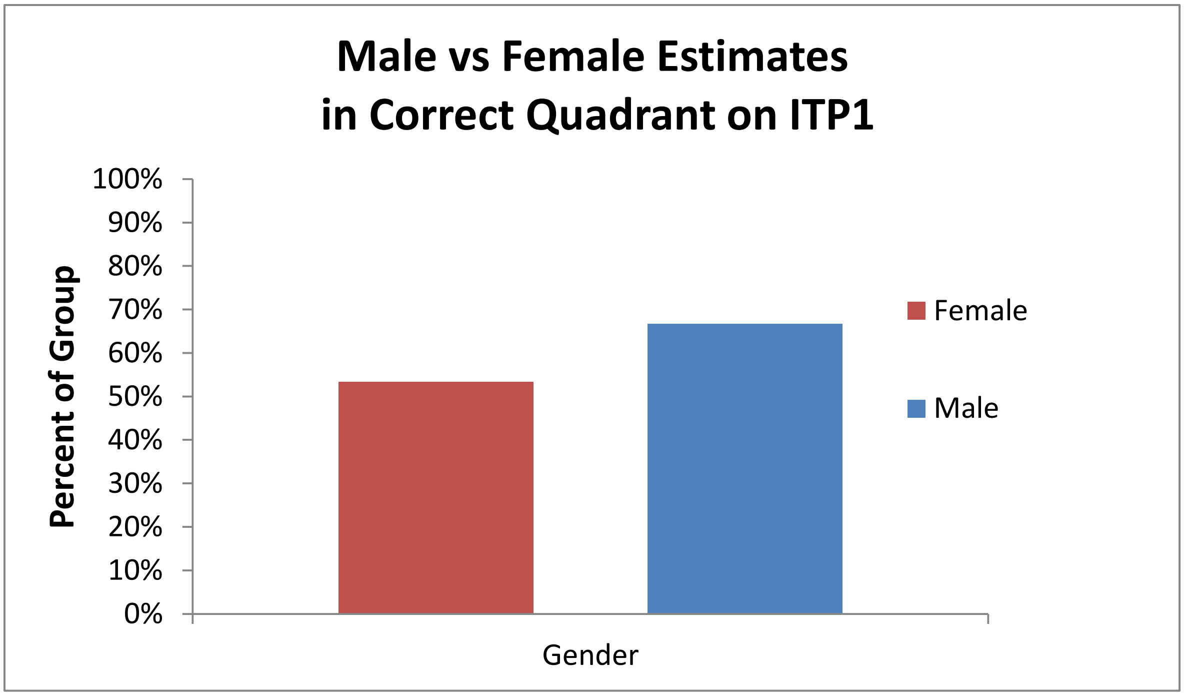

Figure 19. Inter-Trial Probe Frequencies in Correct Quadrant by Gender.
Counts of place estimates in the correct quadrant on ITP1 as a percentage of the group (Y-Axis).

Correlation

Correlations showed that Place Error was related to Spatial Score (*r* (59) = -.41, *p* <.001), and that both were equally good predictors of performance on tests of hippocampal function (Figure 20). Pearson correlations revealed that both Place Error (*r* (59) = -.38, *p* < .01) and Spatial Score (*r* (59) = .29, *p* < .05) were related to performance on the Room Reconstruction task, but there was no difference in the magnitude of these relationships, *t*(59) = 0.73, *p* = .76. Because scores were ordinal, Spearman correlation was used to investigate the relationship between the Where's the Water task and Place Error and Spatial Score. Both correlations were significant, but while the correlation between Place Error and Where's the water was slightly stronger (r_s(59) = -.38, *p* < .01) than that between Spatial Score and Where's the Water (r_s (59) = .25, *p* =.05), the difference was not significant, *t*(59) = 0.98, *p* = .84. Pearson correlation revealed similar relationships between Place Error versus Spatial Score to both immediate and delayed recall paired associate scores (WAPA). The relationship between Place Error and the immediate recall scores failed to reach significance (r (59) = -.25, p =.058), but this was not significantly different from the relationship between Spatial Score and the immediate recall scores (r (59) = .29, p =.02), t(59) = -0.29, p = .38. Finally, Pearson correlation showed that the relationship between Place Error and scores on the delayed recall task (r (59) = -.33, p <.01) and the relationship between Spatial Score and scores on the delayed recall task (r (59) = .36, p <.01) were both significant, but not significantly different from each other (t(59) = -0.22, p = .41) . When the ITP group was split by start condition, the Place Error for the Same-Start group was significantly correlated with performance on Room Reconstruction (r (29)= -.36, p =.05) and Where's the Water (r_s (29) = -.44, p = .01), but not with immediate (r (29) = -.21, p =.27) or delayed (r(29) = -.25, p =.18) WAPA scores. Place Error for the Different-Start group, however, showed the opposite trend, with significant correlations with immediate (r(29) = -.46, p =.01) and delayed (r(29) = -.50, p < .01) WAPA scores, but not with Room Reconstruction (r (29) = -.33, p =.08) or Where's the Water (r_s (29) = -.28, p =.13).

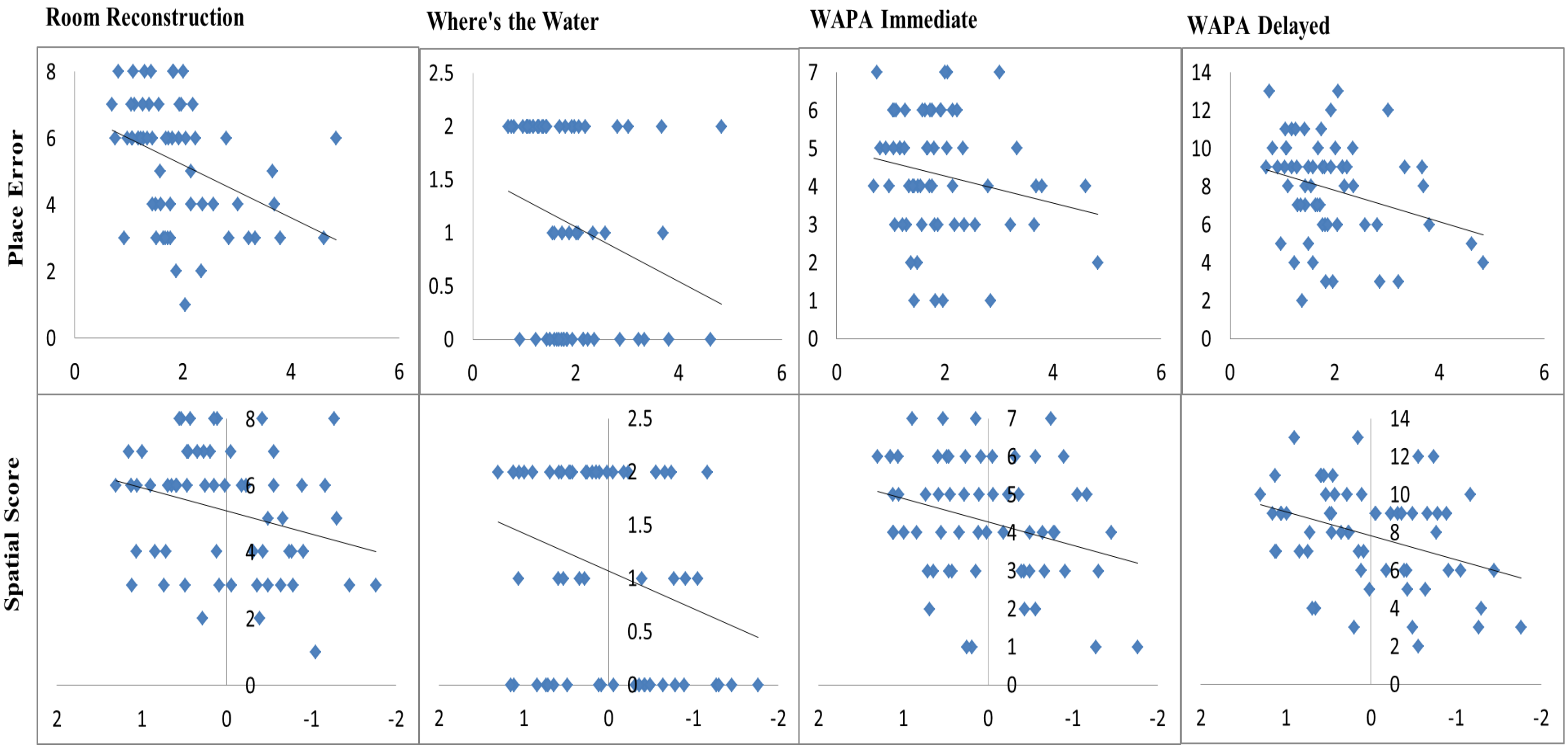

Figure 20. Scatterplot Matrix of Place Error and Spatial Score correlations
Place Error and Spatial Scores are on the X-axes, and scores from tests of hippocampal function are on the Y-axes. Note: because Place Error has an inverse relationship with tests of hippocampal function (lower error is related to better function) the X-axis for Spatial Score has been reversed for easier visual comparison to Place Error.

Analysis of the relationship between Distance Estimation Error and Place Error revealed that scores on the distance estimation task were unrelated to the ability to estimate distance. Figure 21, 22 and 23, respectively, show the lack or correlation between Place Error and participants’ ability to judge the diameter of the arena (*r* = -.01, *p* = .97), ability to judge the distance between an object in the arena and the arena wall (*r* = -.03, *p* = .81), and ability to judge the distance between themselves and the end of the hall in the real world (*r* = .13, *p* = .33).

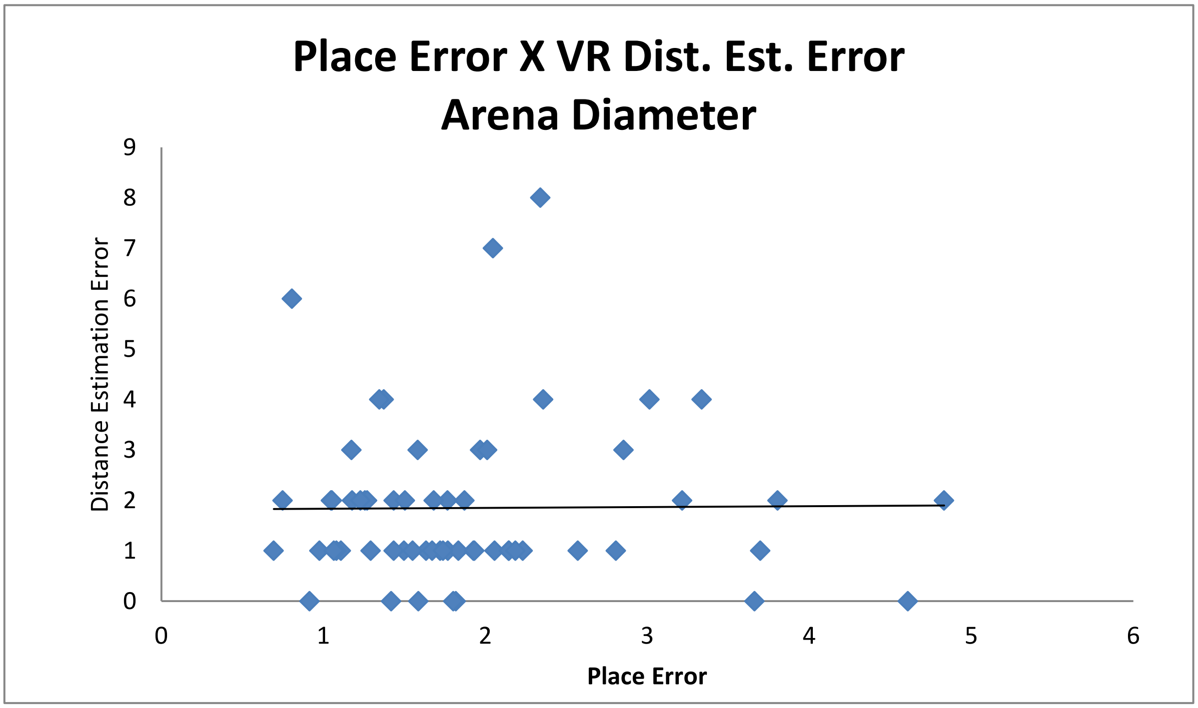

Figure 21. Place Error by Distance Estimation Error Scatterplot: Arena Diameter
The Y-axis is the Distance Estimation Error in platform diameters. The X-axis is Place Error in platform radii.

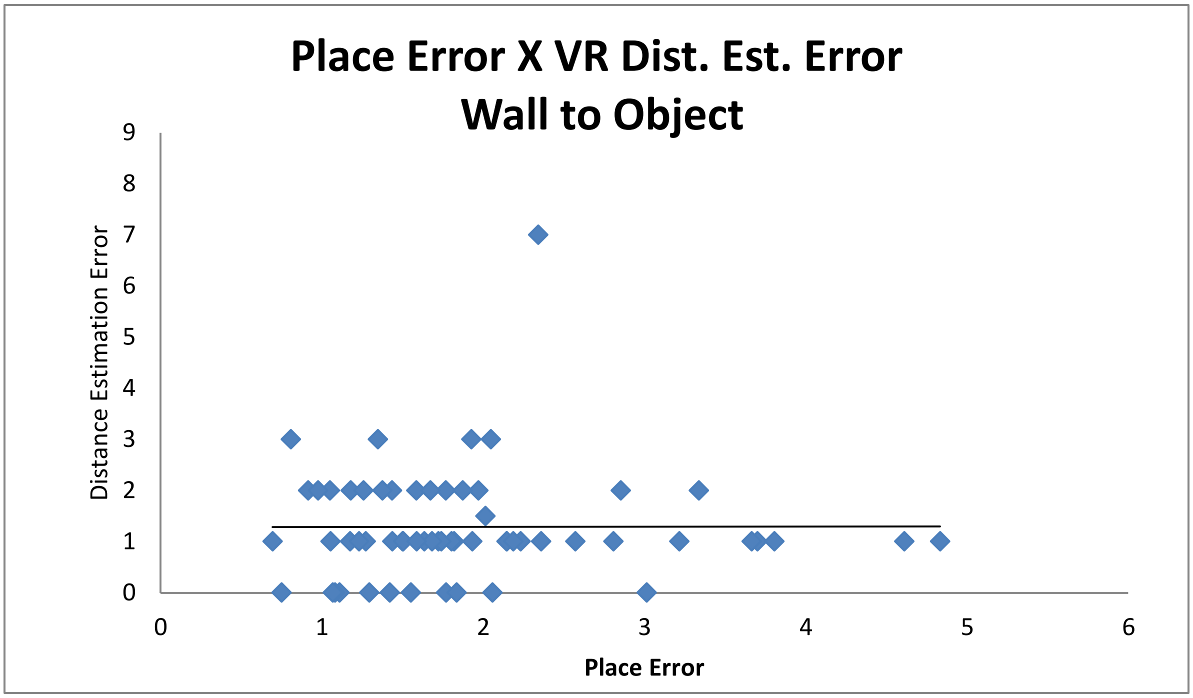

Figure 22. Place Error by Distance Estimation Error Scatterplot: Wall to Object. The Y-axis is the Distance Estimation Error in platform diameters. The X-axis is Place Error in platform radii.

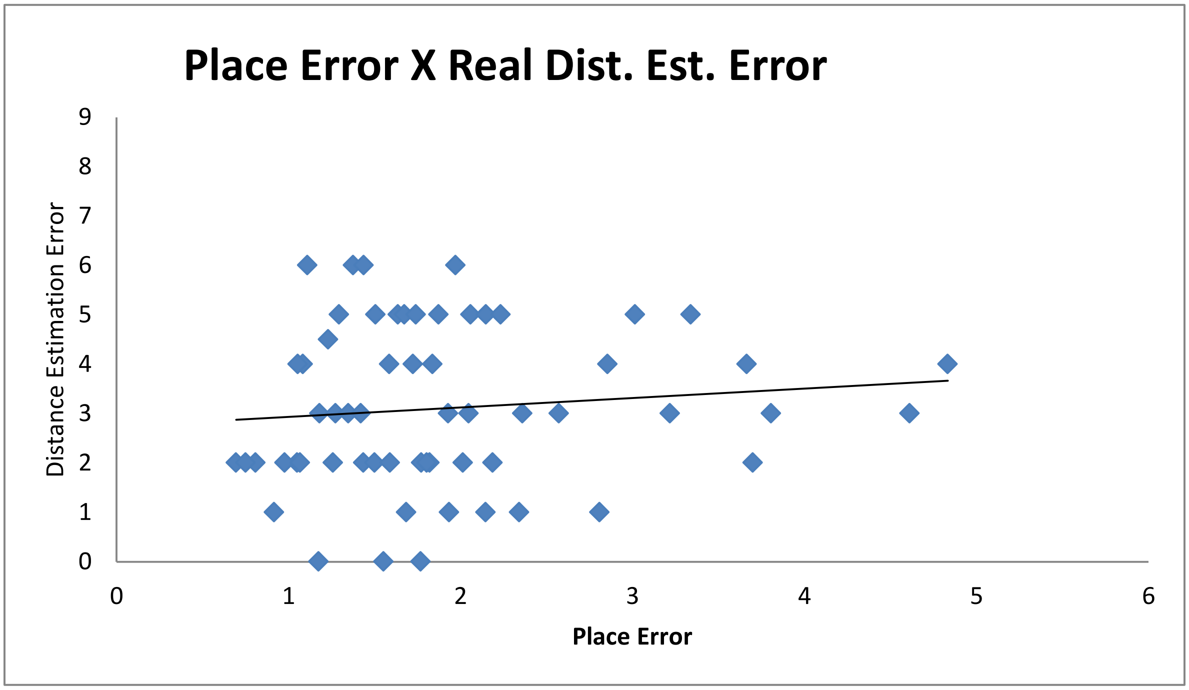

Figure 23. Place Error by Distance Estimation Error Scatterplot: Real World The Y-axis is the Distance Estimation Error in meter sticks. The X-axis is Place Error in platform radii.

Discussion

The present study investigated the course of place learning on a trial-by-trial basis by introducing a new procedure for assessing place learning: explicit probe trials were inserted between standard learning trials. Place Error, a new measure of place knowledge, was derived from these trials. Results indicated that the new procedure did not change place learning, and the new measure provided new insights into place learning. Comparisons of navigational performance between those given and not given the Inter-trial Probe procedure, using standard MWM dependent variables, indicated that the new procedure did not change the course of learning. Comparison of Place Error scores to estimates of distance indicated that this new measure did not merely reflect the participants' ability to judge distance in virtual space. Place Error revealed that place learning appears to be faster than previously thought. After only one learning trial, Place Errors were surprisingly low and counts of estimates localized to the correct quadrant were surprisingly high. Comparisons of Place Errors of participants started from the same versus different locations on the Inter-trial Probes showed that starting from the same location led to smaller errors in localizing the platform, indicating that this small change in procedure led to different assessments of place knowledge. The new measure of place learning, Place Error, did not magnify the gender difference in spatial ability; rather, it tended to minimize it. Finally, the Place Error predicted performance on tests of hippocampal function as well as, but not better than, traditional measures.

This study investigated place learning by using a new MWM trial procedure. Explicit probe trials (i.e., Inter-trial Probes), which in previous studies had only been used after learning was complete, were inserted between standard MWM invisible platform trials. By requiring participants to simply go to the location in the virtual environment where they thought the platform had been on the preceding trial, it was possible to assess the course of place learning in a new way, revealing the accuracy of the participants' knowledge on a trial-by-trial basis. A critical step in evaluating the merit of this new procedure was to investigate whether it significantly changed the course of learning. When navigational efficiency on standard trials was compared between when Inter-trial Probes were present and when they were not, no evidence was found to indicate that the presence of explicit probes interrupted the course of learning in the MWM. This finding was expected because the explicit probe trials did not provide any feedback about the accuracy of the participants' estimates. In addition, participants were not given additional time to visually scan the environment after the (brief) trial ended. This finding shows that it is possible to use the new procedure without changing the place learning that is being measured.

A second important methodological issue regarding the new procedure is whether the dependent variable that resulted from the Inter-trial Probes reflected something much simpler and less interesting than accuracy of place knowledge. To check this, Place Error measures were compared to distance estimates to see if Place Error merely reflected the ability of participants to judge distances in virtual or real space. Importantly, results indicated no such relationship. This was not surprising, however, because previous research has shown that distance estimation in virtual and real environments has little bearing on cognitive-map construction and use (Mellet et al., 2010).

The surprisingly low Place Errors observed from the first Inter-trial Probe onwards indicated that knowledge of place locations in the MWM is acquired faster than previously thought. After just one opportunity to see the platform location, the magnitude of overall Place Error was just slightly larger than the diameter of the platform itself. Further, the small difference between the most accurate (trial 6) and the least accurate (trial 1) trials indicated that little meaningful improvement in accuracy occurred after the first trial. The largest consistent reduction in error occurred between Inter-trial Probe trials 1-3, but this reduction was less than 1 platform radius. Even so, by trial 3 performance on the Inter-trial Probes reached the same level of accuracy that was demonstrated only after 10 trials in previous work from the UVic Spatial Lab (i.e., the Drop-the-Seed trial; Livingstone, 2009). Another indication of the rapid nature of place learning was that after only one learning trial, more than half of the participants correctly identified the quadrant of the platform location and 40% of the participants correctly guessed the platform location itself. This indicated a degree of knowledge accuracy that was acquired much earlier in testing than previous research using similar explicit probe trials was able to show (Hardt et al., 2009; Woolley et al., 2009; Livingstone, 2009).

Previous work with humans using virtual MWMs has been unable to show that human place learning occurs so quickly. Most research has used standard measures, such as distance or latency to the hidden target, which typically do not reach asymptotic performance until trial 5 or 6 (e.g., Chai & Jacobs, 2009; Hardt, Hupback, & Nadel, 2009; Thomas, Laurance, Luczak, & Jacobs, 1999). However, the finding that place knowledge is acquired rapidly in humans is consistent with an early rat study, which is possibly the only prior study to give pairs of trials and start the second trial from the same start position as the first ((I. Q. Whishaw, 1985). A sharp reduction in latency and route-deviation errors from within the first two trial pairs led the author to conclude that place learning in rats occurs very rapidly.

The idea that performance on the first Inter-trial Probe only reflected the knowledge acquired on the first learning trial has to be moderated somewhat by comparison between the performance on this probe trial and the Guess trial given prior to any learning trials.

Performance on the Guess trial was surprisingly good. While Place Error on this trial averaged just beyond the bounds of the correct quadrant, it differed from mean Place Error on the first Inter-trial Probe by only one platform radius. Nevertheless, the difference between the Guess trial and the first Inter-trial Probe can reasonably be attributed to knowledge gained on the first learning trial.

Performance on the Guess trial itself was interesting because it was clearly not random. The spatial distribution of platform “predictions” in the Guess trial offers several possibilities as to why performance was so good. One in 3 participants predicted the invisible platform to be where one of the visible platforms had been in pre-training, and there were several near-misses. A possible explanation for this is that participants were simply returning to visible platform locations that they had recently navigated to in pre-training. Three out of 4 participants predicted that the invisible platform would be within a restricted range at a constant distance from the arena wall. It is possible that the good Guess trial performance occurred because participants had simply learned that the platforms were at a predictable distance from the wall. Either of these possibilities would bias predictions away from the outermost area of the arena, thereby reducing average Place Error. Yet another possibility is that average performance was so good because 1 in 4 participants actually predicted the platform to be in the correct quadrant, one that had not been used on previous trials. While these predictions may have been purely accidental, they may also have been the result of sharp spatial reasoning. While it is not clear which of these alternatives, or a combination of them, best accounts for the good Guess trial performance, all of them indicate just how rapid human place learning is.

The present study reveals, for the first time, that human place learning is more accurate when the start position is the same than when it differs. In terms of task demands, the Different-

Start condition is more similar to traditional MWM procedures than the Same-Start condition because, in the absence of Inter-trial Probes, traditional procedures typically require participants to start from a new place on every trial. Although rare, at least two rat studies have used a Same-Start procedure in the MWM. Whishaw (1985) and Eichenbaum et al. (1990) used traditional measures (e.g., latency to a submerged platform) to assess place learning in rats. While Whishaw's paradigm was similar to the present paradigm in many ways, there are several important differences, apart from the species observed. First, rather than pairing a learning trial with an explicit probe trial, it compared performance on two paired learning trials that started from the same position. Second, Wishaw did not directly compare performance between same- and different-start trial pairs. Eichenbaum et al. (1990), unlike Wishaw, did directly compare a same-start condition with a different-start condition, and found that, similar to the present results, overall latencies were shorter for rats in the same-start condition. However, in Eichenbaum et al.'s procedure, rats were trained to a criterion level of performance using a visible platform, and the start position always remained in the same place on both visible and invisible same-start trials. Thus, it is unclear when place learning occurred.

The underlying reasons for this performance difference between same and different starts are not entirely clear. One (less interesting) possible explanation for this might be that, rather than reflecting more accurate place knowledge, the performance demands (e.g., the number of turns, the minimum required distances from start to platform, etc.) were easier in the Same- than in the Different-Start condition. This does not seem likely, however, because perfect path trajectories from each start position to the platform were mirrored between conditions: they were the same length and required the same angular deviation from the start position. A more likely explanation is that the Same-Start condition reduces cognitive demands. One possibility is that starting from the same place between learning and explicit probe trials makes it easier to orient (i.e., decide where one is in space) at the start. If this was the case, it would be expected that orientation would take less time and therefore the Same-Start condition would result in fewer "failures" to complete the trial (that is, fewer trials ending after 10 s, rather than at the participants' signal). While latencies to start and frequency of Inter-trial Probe failures have yet to be analysed, these dependent variables might provide further insight into this issue. A second possibility is that starting from a different location requires the participant to compute a new and different trajectory to the target location. This is consistent with the results showing that the difference in Place Error between Same- and Different-start conditions was consistent throughout most of the testing.

It is somewhat surprising that no gender differences were found in the rate of place learning or final place knowledge in the virtual MWM given the prevailing assertion that males are superior when it comes to spatial tasks (e.g., Coluccia & Louse, 2004; Lawton, 2010; Voyer, Voyer, & Bryden, 1995). However, this result is consistent with two previous studies that gave explicit probe trials at the end of their trial procedures (Hardt et al., 2009; Woolley et al., 2009) which found no gender differences in final place knowledge.

The correlations between Place Errors on the Inter-trial Probes and performance on tests of hippocampal function were difficult to interpret. They were no better than traditional measures, indicating that either the new measure was not a better indicator of hippocampal function, or that the other (non-maze) measures were not particularly good. When the relationships between performance in the Same-Start and Different-Start conditions and these tests of hippocampal function were examined, it was found that they related differently. Performance in the Same-Start condition was related to scores on the Room Reconstruction and Where's the Water task, but not to scores on the WAPA. On the other hand, performance in the Different-Start condition was related to scores on the WAPA, but not to scores on the Room Reconstruction or Where's the Water tasks. This suggests that the Same-Start condition, Room Reconstruction and Where's the Water measure something different from what the Different-Start condition and the WAPA do. The question remains as to which of these is the best measure of hippocampal function.

Methodological implications and applications

The current approach represents a methodological advance over previous research studying humans using virtual MWMs. The key innovation was the insight that explicit probe trials could be paired with individual learning trials without changing the course of learning in the MWM, and could thereby provide a finer-grained temporal analysis of place learning. While explicit probe trials themselves are not new, in the past researchers have treated them the same way as they do traditional probes and given them only after learning is complete (Hardt et al., 2009; Woolley et al., 2009). Indeed, apart from these exceptions, most research using virtual MWMs has tended to treat humans the same way it has rats, without taking into account uniquely human abilities such as language (which makes explicit probe trials possible). While rat research in the MWM has been and continues to be an immensely rich source of data for spatial navigation research, there are limits to its comparability to human navigation. Rat studies that have used same-start conditions, for example, were limited to traditional measures and unable to demonstrate "pure" spatial learning (Howard Eichenbaum, Stewart, & Morris, 1990; I. Q. Whishaw, 1985). The present study demonstrates how knowledge gained from rat research can be integrated into paradigms that take advantage of human abilities to gain better insight into human learning and memory.

There are a number of practical benefits to the method used in the current study. First, it provides a valuable tool for investigating human deficits in place learning by eliminating a number of confounding factors in the measurement of place knowledge. For example, the hippocampus is known to be particularly vulnerable to insult through sudden impact (a.k.a., traumatic brain injury). Researchers have used virtual MWMs to assess spatial deficits resulting from traumatic brain injury (Skelton, Bukach, Laurance, Thomas, & Jacobs, 2000; Skelton et al., 2006). The MWM has also been used to investigate other sources of deficits, such as age (Driscoll, Hamilton, Yeo, Brooks, & Sutherland, 2005). The method used in the present research and the novel measure of learning derived from it, Place Error, may improve the sensitivity of the MWM to detect spatial deficits, and help to further investigate the nature of these deficits by better dissociating the ability to get to a place from the knowledge of where it is.Second, the novel approach used in this paradigm makes it an ideal candidate for combination with functional imaging techniques. The explicit probe trials put the navigator in a relatively "pure" state of cognition – that is, they are entirely focussed on a place in space for the duration of the trial. As a result, it may yield a "cleaner" signal for functional magnetic resonance imaging (fMRI) or electroencephalography (EEG), techniques that are notoriously sensitive to artifacts, than the signal derived from standard trials. This is a promising area of future investigation.

There are a number of areas in which the present method could be improved upon for future research. First, pilot testing revealed a sub-population of "step-by-steppers" on the Inter-trial Probes: participants who attempted to localize the target area with extremely high precision by making fine, line-of-sight adjustments to their final position and orientation. Since this behaviour did not likely reflect hippocampus-dependent place knowledge, but rather post-hippocampus dependent positional adjustments using single cues (as opposed to a constellation of cues), the Inter-trial Probes were limited to 10 s. While this eliminated the undesired behaviour, this time limit may have been too short, as the frequency of “failures” – trials on which 10 s expired before the participant signaled that they had reached the platform location – was relatively high. To rectify this, we plan to increase the Inter-trial Probe time limit to 15 s in future work. Second, a small portion (4/60) of participants failed to recognise how much time is required to make a full 360° rotation in the Arena maze and did not initiate movement during the first Inter-trial Probe. These participants had high Place Error on the first trial (i.e., the distance between the start position and the platform), and thus slightly increased the average Place Error for that trial. In addition to increasing the time limit, we plan to improve the instructions to avoid this. Third, recent work in our lab has successfully employed novel eye tracking technology to demonstrate that eye movements are reliable indicators of attention during navigation in a similar virtual Morris water maze. We showed that the analysis of gaze and pupil dilation during navigation can reveal sex differences in attention (Mueller, Jackson, & Skelton, 2008) as well as the spatial strategy in use (i.e., allocentric, “knowing where” or egocentric “getting there”) (Livingstone-Lee et al., 2011). By combining similar eye-tracking technology with ITP trials, it may be possible to further dissociate “getting there” contributions to navigation, such as those derived from attention control (an executive function associated with the prefrontal cortex and anterior cingulate gyrus (e.g., Posner & Petersen, 1989)), from the contributions of pure place learning. Fourth, in future studies, it might be interesting to ask participants, how many trials it took them to feel confident that they know where the platform was located, and compare this to the trial at which they asymptoted. This would give an indication of the relation between performance and conscious recollection of performance.

Theoretical implications

The results of this study have interesting implications for spatial navigation theory. The present study demonstrates a new way to study “pure” place knowledge. That is, the approach and methodology used here more clearly distinguished between *knowing where* something is (place knowledge) and *getting there* than most other human MWM research has. “Knowing where” is knowing the location of a navigational goal from the outset of the trip. “Getting there” is a catch-all term that describes all of the behaviours (e.g., locomotion, stimulus-sampling, etc.) that are directed towards reaching a location in space. Thus, *knowing where* cognition is necessarily translated into *getting there* behaviours. However, the problem for spatial navigation research is that *getting there* behaviours can also be derived from other, non-spatial sources of knowledge (e.g., stimulus-response route-following). Furthermore, there are factors that can affect *getting there* aspects of navigation and not *knowing where*, and vice-versa. A concrete example is that, using Place Error, a near-miss of the platform can be interpreted as being based on fairly accurate place knowledge. In contrast, a near-miss based on the same accuracy of knowledge might result in a dramatic increase in total latency and distance because the navigator, surprised at not intercepting the platform where they thought was, may subsequently wander about, checking other locations. Thus, the present method provides a clearer picture of place learning by making a tighter link between the knowledge of a place in space and the behaviour from which that knowledge is inferred.

The picture of place learning that has emerged in the present thesis depicts a mode of learning that is extremely fast. This is an important advance over previous demonstrations and conceptualizations of place learning. It is consistent with predictions made in the most comprehensive and well-supported cognitive-mapping theory to date (O’Keefe and Nadel, 1978) and with more recent updates that conceptualize the cognitive map as an important system amongst a complex of many interacting memory systems that contribute to spatial navigation (e.g., Jacobs & Schenk, 2003). “Pure” place learning, like cognitive map construction, appears to be all-or-none. That is, place learning appears to occur after just one exposure to the stimulus, after which there is little refinement of the spatial knowledge acquired. This is not only different from how previous research has characterized place learning (e.g., asymptotic performance by trial 5), but it is also qualitatively different from other forms of learning, such as stimulus-response (SR), which is known to be slow and progressive and to require many repetitions

Interestingly, even though the main point of the present results was that place learning was rapid, it also showed that it had limitations in terms of how precisely it could be used to find a specific location. The present results showed that while there was rapid coarse-grained place localization to the correct quadrant, improvement in fine-grained localization to the exact location of the platform was minimal. A likely explanation for this is that there are not enough local cues to resolve the platform location as a distinct “place” within the quadrant.

The distinction between *knowing where* and *getting there* helps to shed some light on the nature of gender differences in the MWM. In the present study, latency was the only one of the seven dependent variables (including frequency of place estimates in the correct quadrant and on the platform) that did reflect a difference between males and females. Upon closer inspection, the difference in time taken to reach the platform that appeared on the learning trials appeared to be the result of the tendency for females to pause en route or to pause near the platform after a near-miss. One possible explanation for this is that females are less confident or more anxious about their spatial knowledge than males, and thus take more time to reassure themselves about their location in space. This is consistent with Lawton’s (1994) finding that females suffer from more "spatial anxiety", or anxiety about spatial navigation, than males do. Confidence (or lack of it) is one example of a *getting there* factor largely avoided by the Inter-trial Probes. For example, on standard trials, females may require more time than males to re-orient after a near-miss. It follows that the gender difference in spatial cognition may not be as great as was once thought, and might be driven (at least in part) by factors affecting *getting there* abilities, but not the ability to form and use cognitive maps or acquire place knowledge.

One of the most interesting findings in this study was unexpected: the translocation of the start position within trial pairs reduced the accuracy of place knowledge, or at least reduced the ability of participants to use place knowledge to accurately reposition themselves in the maze. One possible explanation is that, rather than a degradation of knowledge from Same-Start to Different-Start, starting from the same place may allow the recruitment and integration of contributions from other, non-hippocampal learning systems, thus enhancing place knowledge under those conditions. For example, the dorsal striatum is thought to contribute to simple forms of navigation involving spatial stimulus-response (SR) associations (Iaria, Petrides, Dagher, Pike, & Bohbot, 2003), and previous authors have suggested that this accounts for improved performance in same-start situations (Eichenbaum et al., 1990). However, SR learning is known to be comparatively slow and progressive (McDonald & White, 1994). It thus seems questionable that SR learning could account for the large difference between Same-Start and Different-Start conditions, especially since, in the present study, start positions were only held constant for one trial within same-start pairs.

Another possible explanation for the difference in performance between Same- and Different-Start conditions is that the Different-Start condition increases visuo-spatial working memory load because participants were not able to orient using cues that were immediately available from the start of the previous trial (possible in the Same-Start condition). In the case of the Different-Start condition, the navigator's orientation with respect to the environment needs to be re-calculated on every trial, as does a vector to the platform. The hippocampus is implicated in both of these processes (e.g., Maguire et al., 1998; Rodriguez, 2010). In contrast, in the Same-Start condition, orientation and the goal-vector has already been calculated in the preceding trial, and thus recall is all that may be required. The persistent difference between Same- and Different-start conditions may reflect the additional processing time required for the hippocampus to perform the additional operations in the Different-Start condition. The Different-Start condition may thus be more taxing on the hippocampus, and therefore a better measure of hippocampal function.

A third, more prosaic interpretation of the difference between Same- and Different-start performance, already discussed in the methodological implications section, is that participants in the Different-Start condition simply needed more time to orient themselves at the beginning of the trial. If this was the case, it is reasonable to suggest that the additional time may have caused more participants in the Different-Start condition to fail to reach their intended location before their 10-second time-limit elapsed. The data will be examined in more detail to see if this confound might account for the difference.

It is somewhat surprising that no gender-by-start-condition interaction was found Place Error. Coluccia and Louse' (2004) hypothesized that gender differences increase with the difficulty of a task as a result of an increased visuo-spatial working memory load. If this were the case, a differential performance by males and females depending on whether they were in the Same-Start (easier) or Different-Start (harder) conditions would be expected. However, in the present study, there was no differential influence of shifting the start position on gender. This suggests that either differences in visuo-spatial working memory do not explain gender differences in spatial orientation, or that there were no meaningful differences in visuo-spatial working memory or hippocampal function in place learning between genders.

While it is difficult to draw any concrete conclusions from the relationships established between performance on the Inter-trial Probes and the tests of hippocampal function, it is important to note the implicit assumption that the whole hippocampus is devoted to a singular function: cognitive mapping. Of course, this is not the case; a range of mnemonic functions have been attributed to the hippocampus, with different functions supported by different regions and not others (Bast et al., 2009), or even lateralized to one side and not the other (Neil Burgess, 2002). It is altogether possible that the tasks in the present paradigm are engaging different hippocampal regions, thus generating the patterns of correlation found. Another possibility is that these tasks are engaging other, non-hippocampal brain regions, such as the frontal lobes, which have been shown to play a (poorly understood) role in spatial navigation (Kessels et al., 2000). Nevertheless, it is not clear why the Room Reconstruction and Where's the Water tests, which, presumably, require participants to utilize their stored representations of the Arena maze (i.e., their cognitive maps) were correlated with the Same-Start condition, and not the Different-Start condition. Likewise, it is not clear why the WAPA task, which is not dependent on a cognitive map, was related to the Different-Start condition, but not the Same-Start condition. Indeed, given the difference in task demands between the MWM and the WAPA, it is somewhat surprising that the relationship between the Different-Start condition and the WAPA was so strong. In any case, the use of indirect measures of hippocampal function has left open the question of whether Same-Start or Different-Start conditions are better tests of hippocampal function. This suggests the value of using direct measures, such as structural or functional magnetic resonance imaging, to further investigate this issue.

Conclusion

The present study adopted a novel Morris water maze procedure that enabled a trial-by-trial analysis of place learning using explicit probe trials. Place Error, a measure that has never before been used throughout trials, provided a “pure” measure of place learning – that is, one that dissociated it from potential confounding factors inherent in standard MWM measures such as distance and latency. Results indicated that place learning, when assessed using more precise measurements, is surprisingly rapid, requiring only one or two trials to achieve near-maximum accuracy. Interestingly, this new measure did not suggest any gender difference in the ability to construct and use a cognitive map, leaving open the possibility that gender differences in human spatial navigation may be attributed to differences in *getting there* abilities, rather than *knowing where*. The present study also, for the first time, compared a different-start condition (similar to what would be encountered on traditional MWMs) to a same-start condition. Interestingly, this manipulation had a strong effect. It seems that changing the starting location on every trial inhibits place learning. It is not yet clear whether this effect was driven by contributions from other learning systems, easier orientation, or some other unexplored possibility, nor is it clear whether starting from the same or different place more strongly activates the hippocampus. The use of direct measures of hippocampal function is warranted to investigate these curious results more deeply in future research. Despite this ambiguity, the present research has challenged previous assumptions and shed new light on the nature of human place learning in the virtual Morris water maze.

Bibliography

Aguirre, G. K., & D’Esposito, M. (1999). Topographical disorientation: a synthesis and taxonomy. Brain, 122(9), 1613.

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

Barrash, J. (1998). A Historical Review of Topographical Disorientation and Its Neuroanatomical Correlates. Journal of Clinical and Experimental Neuropsychology, 20(6), 807–827. doi:10.1076/jcen.20.6.807.1114

Bast, T., Wilson, I. A., Witter, M. P., & Morris, R. G. M. (2009). From rapid place learning to behavioral performance: a key role for the intermediate hippocampus. PLoS biology, 7(4), e1000089.

Burgess, N., Jeffery, K. J., & O’Keefe, J. (1999). Integrating hippocampal and parietal functions: a spatial point of view. The hippocampal and parietal foundations of spatial cognition (pp. 3–29). Oxford: Oxford University Press.

Burgess, N. (2002). The hippocampus, space, and viewpoints in episodic memory. Quarterly Journal of Experimental Psychology: Human Experimental Psychology, 55(4), 1057.

Burgess, N., Maguire, E. A., & O’Keefe, J. (2002). The Human Hippocampus and Spatial and Episodic Memory. Neuron, 35(4), 625–641. doi:10.1016/S0896-6273(02)00830-9

Chai, X. J., & Jacobs, L. F. (2009). Sex differences in directional cue use in a virtual landscape. Behavioral neuroscience, 123(2), 276–283.

Coluccia, E., & Louse, G. (2004). Gender differences in spatial orientation: A review. Journal of Environmental Psychology, 24(3), 329–340.

Driscoll, I., Hamilton, D. A., Yeo, R. A., Brooks, W. M., & Sutherland, R. J. (2005). Virtual navigation in humans: the impact of age, sex, and hormones on place learning. Hormones and Behavior, 47(3), 326–335.

Eichenbaum, H., Stewart, C., & Morris, R. G. (1990). Hippocampal representation in place learning. The Journal of neuroscience, 10(11), 3531–3542.

Field, A. P. (2009). Discovering statistics using SPSS: (and sex and drugs and rock ‘n’ roll). SAGE Publications.

Goodrich-Hunsaker, N., Livingstone, S. A., Skelton, R. W., & Hopkins, R. O. (2009). Spatial deficits in a virtual water maze in amnesic participants with hippocampal damage. Hippocampus, 20(4), 481–491.

Hardt, O., Hupback, A., & Nadel, L. (2009). Factors moderating blocking in human place learning: The role of task instructions. Learn Behav., 37(1), 42–59.

Iaria, G., Petrides, M., Dagher, A., Pike, B., & Bohbot, V. D. (2003). Cognitive Strategies Dependent on the Hippocampus and Caudate Nucleus in Human Navigation: Variability and Change with Practice. J. Neurosci., 23(13), 5945–5952.

Jacobs, L. F., & Schenk, F. (2003). Unpacking the cognitive map: The parallel map theory of hippocampal function. Psychological review, 110(2), 285–315.

Jonasson, Z. (2005). Meta-analysis of sex differences in rodent models of learning and memory: a review of behavioral and biological data. Neuroscience & Biobehavioral Reviews, 28(8), 811–825.

Kessels, R. P., Postma, A., Wijnalda, E. M., & de Haan, E. H. (2000). Frontal-lobe involvement in spatial memory: evidence from PET, fMRI, and lesion studies. Neuropsychology Review, 10(2), 101–113.

Kolb, B., Sutherland, R. J., & Whishaw, I. Q. (1983). A comparison of the contributions of the frontal and parietal association cortex to spatial localization in rats. Behavioral neuroscience, 97(1), 13–27.

Kolb, Bryan. (1984). Functions of the frontal cortex of the rat: A comparative review. Brain Research Reviews, 8(1), 65–98. doi:10.1016/0165-0173(84)90018-3

Koziol, L. F., & Budding, D. E. (2008). Subcortical Structures and Cognition: Implications for Neuropsychological Assessment. Springer.

Lawton, C. (1994). Gender differences in way-finding strategies: Relationship to spatial ability and spatial anxiety. Sex Roles, 30(11-12), 765–779.

Lawton, C. (2010). Gender, Spatial Abilities, and Wayfinding. Handbook of Gender Research in Psychology, 317–341.

Levy, L. J., Astur, R. S., & Frick, K. M. (2005). Men and Women Differ in Object Memory but Not Performance of a Virtual Radial Maze. Behavioral neuroscience, 119(4), 853–862.

Livingstone, S. (2009, May). Eye movement measurement confirms the effects of experience on strategy selection in virtual Morris Water Maze tasks. Presented at the Northwest Memory and Cognition (NOWCAM) Conference, University of Victoria, Victoria, BC.

Livingstone, S., & Skelton, R. W. (2007). Virtual environment navigation tasks and the assessment of cognitive deficits in individuals with brain injury. Behavioural brain research, 185(1), 21–31.

Livingstone-Lee, S., Murchison, S., Zeman, P. M., Gandhi, M., van Gerven, D., Stewart, L., Livingston, N. J., et al. (2011). Simple gaze analysis and special design of a virtual Morris water maze provides a new method for differentiating egocentric and allocentric navigational strategy choice. Behavioural Brain Research, 225(1), 117–125. doi:16/j.bbr.2011.07.005

Maguire, E. A., Burgess, N., Donnett, J. G., Frackowiak, R. S. ., Frith, C. D., & O’Keefe, J. (1998). Knowing where and getting there: a human navigation network. Science, 280(5365), 921.

McDonald, R. J., & White, N. M. (1994). Parallel information processing in the water maze: Evidence for independent memory systems involving dorsal striatum and hippocampus. Behavioral and neural biology, 61(3), 260–270.

Mellet, E., Laou, L., Petit, L., Zago, L., Mazoyer, B., & Tzourio-Mazoyer, N. (2010). Impact of the virtual reality on the neural representation of an environment. Human brain mapping, 31(7), 1065–1075.

Meltzer, J. A., & Constable, R. T. (2005). Activation of human hippocampal formation reflects success in both encoding and cued recall of paired associates. Neuroimage, 24(2), 384–397.

Mendoza, J., & Foundas, A. (2007). Clinical Neuroanatomy: A Neurobehavioral Approach. Springer.

Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: two cortical pathways. Trends in Neurosciences, 6(0), 414–417. doi:10.1016/0166-2236(83)90190-X

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

Morris, Richard. (2007). Theories of hippocampal function. In P. Andersen, R. Morris, & D. Amaral (Eds.), The hippocampus book (pp. 581–714). New York, NY, US: Oxford University Press.

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

Nadel, L., & Hardt, O. (2011). Update on Memory Systems and Processes. Neuropsychopharmacology, 36(1), 251–273. doi:10.1038/npp.2010.169

O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map: Preliminary evidence from unit acitivity in the freely-moving rat. Brain research, 34, 171–175.

O'Keefe, J., & Nadel, L. (1978). The hippocampus as a cognitive map. Oxford: Oxford University Press.

Posner, M. I., & Petersen, S. E. (1989). The Attention System of the Human Brain. Retrieved from http://stinet.dtic.mil/oai/oai?&verb=getRecord&metadataPrefix=html&identifier=ADA206157

Postma, A., Winkel, J., Tuiten, A., & van Honk, J. (1999). Sex differences and menstrual cycle effects in human spatial memory. Psychoneuroendocrinology, 24(2), 175–192.

Rodriguez, P. F. (2010). Human navigation that requires calculating heading vectors recruits parietal cortex in a virtual and visually sparse water maze task in fMRI. Behavioral Neuroscience, 124(4), 532–540. doi:10.1037/a0020231

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

Silverman, I., Choi, J., & Peters, M. (2007). The Hunter-Gatherer Theory of Sex Differences in Spatial Abilities: Data from 40 Countries. Archives of Sexual Behavior, 36(2), 261–268. doi:10.1007/s10508-006-9168-6

Skelton, R. W. (1998). Modelling recovery of cognitive function after traumatic brain injury: spatial navigation in the Morris water maze after complete or partial transections of the perforant path in rats. Behavioural brain research, 96(1-2), 13–35.

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

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

Thomas, K. G. F., Laurance, H. E., Luczak, M. A., & Jacobs, W. J. (1999). Age-related changes in a human cognitive mapping system: data from a computer-generated environment. CyperPsychology and Behaviour, 2(6), 545–565.

Tolman, E. C. (1948). Cognitive maps in rats and men. Psychological Review, 55(4), 189–208. doi:10.1037/h0061626

van Gerven, D. J. H., Schneider, A. N., Wuitchik, D. M., & Skelton, R. W. (2012). Direct measurement of spontaneous strategy selection in a virtual Morris water maze shows females choose an allocentric strategy at least as often as males do. Behavioral Neuroscience, 126 (3)465-478.

Voyer, D., Voyer, S., & Bryden, M. P. (1995). Magnitude of sex differences in spatial abilities: A meta-analysis and consideration of critical variables. Psychological bulletin, 117(2), 250.

Whishaw, I.Q. & Kolb, B., (2008). Fundamentals of Human Neuropsychology (6th Revised ed.). Worth Publishers Incorporated.

Whishaw, I. Q.(1985). Formation of a place learning-set by the rat: a new paradigm for neurobehavioral studies. Physiology & Behavior; Physiology & Behavior. Retrieved from http://psycnet.apa.org/psycinfo/1986-19233-001

Whishaw, I. Q., Cassel, J. C., & Jarrad, L. E. (1995). Rats with fimbria-fornix lesions display a place response in a swimming pool: a dissociation between getting there and knowing where. The Journal of neuroscience, 15(8), 5779–5788.

Woolley, D. G., Vermaercke, B., de Beeck, H. O., Wagemans, J., Gantois, I., D'Hooge, R., Swinnen, S. P., et al. (2009). Sex differences in human virtual water maze performance: Novel measures reveal the relative contribution of directional responding and spatial knowledge. Behavioural brain research.

Yamashita, K., Hirose, S., Kunimatsu, A., Aoki, S., Chikazoe, J., Jimura, K., Masutani, Y., et al. (2009). Formation of long-term memory representation in human temporal cortex related to pictorial paired associates. The Journal of Neuroscience, 29(33), 10335–10340.

Zar, J. H. (1999). Biostatistical analysis (Vol. 564). Prentice hall Upper Saddle River, NJ.

Appendix A
Background information questionnaire

1. Date of Birth (day, month, year):_________________
2. Education (Last grade or year of university completed, please specify which) :

____

3. Handedness (Right/Left):____________
4. First Language:______________________
5. Do you have any problems with dizziness? (Yes/No)______________
6. Have you ever sustained a brain injury (i.e. been hospitalized overnight for a head injury)?

   (Yes/No)_____________
   If yes, please explain:____

7. Do you suffer from any neurological disorders (eg. epilepsy, MS)? (Yes/No)__________

   If yes, which disorder? ____

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

   (Yes/No)_____________

   If yes, which disorder?____

9. Are you currently taking any medications? (Yes/No)______________

   If yes, please specify:____

Appendix B
Post-test questionnaire

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

1. How well do you think you performed on this task?

   Very Poorly - Poor - Average - Moderately Well - Extremely Well

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

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

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

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

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

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

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

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

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

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

7. Between the ages of 2 and 7, most of my childhood was spent in or around a landscape that allowed me to see
   a) Great distances (e.g. by the ocean or on a farm).
   b) Moderate distances (e.g. in a small town).
   c) Limited distances (e.g. in a large metropolis, in a heavily forested area).
   d) Mixed Please indicate_________
   e) None of the above describes the typical landscape of my childhood.

8. Between the ages of 7 and 14, most of my childhood was spent in or around a landscape that allowed me to see
   a) Great distances (e.g. by the ocean or on a farm).
   b) Moderate distances (e.g. in a small town).
   c) Limited distances (e.g. in a large metropolis, in a heavily forested area).
   d) Mixed Please indicate_________

   e) None of the above describes the typical landscape of my childhood.

9. I grew up in
   a) A large, metropolitan city (e.g., Toronto)
   b) A moderately sized city (e.g., Victoria)
   c) A larger town (e.g., Duncan)
   d) A smaller town (e.g., Mill Bay)
   e) “The country”

10. I tend to think of regions in my hometown in terms of
   a) Directionality (i.e., North, South, etc.)
   b) Landmarks (i.e., the coffee shop across from the big church)
   c) Street names
   d) A combination of the above (Please specify______)
   e) None of the above

11. I was mostly raised by
   a) female caregivers (i.e. mothers, grandmothers, elder sisters, etc.)
   b) male caregivers (i.e. fathers, grandfathers, elder brothers, etc.)
   c) both female and male caregivers, relatively balanced.
   d) None of the above.

12. My siblings are
   a) All male
   b) All female
   c) Mixed
   d) I don’t have siblings

13. I would say that my biggest influences growing up were
   a) Mostly male
   b) Mostly female
   c) Both, fairly equal
   d) Not sure

14. ________ …sports was a significant part of my upbringing.
   a) Both watching and playing
   b) Playing, but not watching
   c) Watching, but not playing

- d) Sports were never a significant part of my upbringing.
    - a. If A, B, or C, which ones?

15. I participated in woodworking, repair or maintenance projects with my parents, siblings, extended family or family friends when I was growing up.
    - a) Often
    - b) Sometimes
    - c) Seldom
    - d) Never

16. I participated in woodworking, repair or maintenance projects at school (including projects related to elective woodworking or metalworking classes)
    - a) Often (whenever there was an opportunity)
    - b) Sometimes
    - c) Seldom
    - d) Never

17. Indicate how often you eat meat (0 = never, 7 = daily)

    Circle: 0 - 1 - 2 - 3 - 4 - 5 - 6 - 7

18. Indicate how often you smoke (cigarettes, or other) (0 = never, 7 = daily):

    Circle: 0 - 1 - 2 - 3 - 4 - 5 - 6 – 7

    How many cigarettes (or other) per day? __________

19. Indicate how often you drink alcohol (0= never, 7 = daily)

    Circle: 0 - 1 - 2 - 3 - 4 - 5 - 6 - 7

    How many glasses/bottles each time? _________

20. Indicate how often you drink coffee (0 = never, 7 = daily)

    Circle: 0 - 1 - 2 - 3 - 4 - 5 - 6 - 7

    How many cups per day? __________

21. How many hours of sleep do you get per night on average? __________

22. How many hours of sleep do you require per night to function best? ___________

23. Do you take any medications or supplements? Circle: YES / NO. If yes, specify:

____

24. Indicate beside each training activity the number of hours per week you engaged in each activity. If you did not engage in the activity write ‘0’. Also indicate the intensity of activity on a scale from 0 to 9 (0= “my grandmother’s pace”, 9= “I worked so hard I thought my heart would explode”).

ACTIVITY	**HOURS PER WEEK**	**INTENSITY**
Bicycling		
Hiking		
Running		
Swimming		
Weight lifting		
Walking		
Other		

25. In a few words, can you explain how you were able to find the invisible platform in the Arena maze?-

____

____

26. In a few words, can you explain how you were able to remember the animals that were associated with the landscape scenes?

____

____

27. Can you think of any activities (i.e., hobbies, sports, etc.), training, occupation or other experience that you are involved in now or in the past that may give you an advantage in spatial navigation, perception or cognition? If yes, please describe it briefly:

____

____

____