An Examination of the Influence of Landmarks in Human Spatial Navigation Using a Virtual Water Maze

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Thesis submitted in fulfilment of the requirements of the Master of Science (MSc) degree, Department of Psychology, Faculty of Science and Engineering, National University of Ireland, Maynooth

October 2019

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Acknowledgements

Many thanks to my supervisor, Dr. Sean Commins, for the massive amounts of motivation, support and advice he gave throughout the last year. Sean truly has gone above and beyond, not only in the last year, but over the course of my time with the department. It is a massive privilege to work with him, as he is always one of my biggest sources of confidence and inspiration. Here's to another great four years!

I would also like to thank Mr. Derek Walsh for all the support and tech-related chats that really helped with making the project run smoothly. Thanks to Dr. Richard Roche for his advice and for telling me that it'll be grand most of the time.

The entire project would not have been possible without the fantastic help from Rory, Louise, Grainne and Jenny, who devoted a lot of free time to helping with the participants and NavWell. I am forever grateful for their contribution.

Of course, none of this would have ever come about without the encouragement of my parents Teresa and David, who have been incredibly understanding and patient throughout the entire process. Special thanks to my grandparents Patrick and Kathleen, who no matter what the situation, are always interested, supportive and proud.

Finally, I would like to thank Emma for supporting me with everything in relation to this project and beyond. My friends and fellow postgrads, who kept me on track. It is only looking back when you realise all those tea breaks with Keith, really did help.

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Abstract

Research into spatial memory and navigation excelled with the invention of the Morris Water Maze (Morris, 1984). In this task animals are required to find a platform, hidden somewhere in a large circular pool of water (below surface level). As animals cannot see the goal directly, they must use various cues in the environment to locate it and escape. Research has shown that landmarks exert control over an animal's navigation ability. Recently, the Commins Lab has developed a virtual version of the Morris water maze task for use with humans; NavWell. This thesis established that the spatial behaviour of human participants navigating in NavWell is also controlled by virtual landmarks. In Experiment 1, participants trained to navigate with two landmarks, searched inaccurately during a recall trial with no landmarks and landmarks rotated 180°. However, does the visual saliency of these landmarks (e.g. brightness) influence our ability to recall a goal location during navigation? In Experiments 2, 3 & 4, we examined this question. In Experiment 2, participants were trained with a bright landmark near the target and a dim landmark far from the target. Participants were then examined with one cue in isolation or both. The group with the dim landmark searched incorrectly compared to the bright group. In Experiment 3, we controlled for brightness by switching the bright and dim landmark positions. Participants with the bright landmark searched incorrectly, but the dim group searched in the correct quadrant of the pool. In a final experiment, brightness was removed as a feature completely. Participants were trained with two landmarks of equal brightness levels. Here, the group with the landmark nearest the platform searched more accurately. The evidence for an associative learning model of human navigation, as well as the importance of proximity as a nontangible influence for landmark preference were then discussed.

Chapter 1

General Introduction

1.1 Spatial Memory

How our brain formulates, stores and retrieves memories has been a major research area involving the examination of the behavioural and neural underpinnings of this vital cognitive function. For example, memory is not a unitary process, there exists multiple systems that have been developed and described over the years. Memory can be split into short-term and long-term memory, referring to the length of time the memory is stored (Baddeley & Hitch, 1974). The types of memory stored in these timeframes can also be split into declarative (represents everyday events and facts; Cohen & Squire, 1980) and procedural (refers to memories for skills completed without active recall). Declarative memory can be further subdivided into semantic and episodic memory; with semantic being the retention of general knowledge (Tulving, 1972) and episodic being the storage of episodes or events (Tulving, 1972; Tulving, 2001). A particularly interesting form of memory is the memory for spatial locations. Spatial memories are stored in our short and long-term memory and can be episodic or semantic. For example, events occur in a specific place, meaning spatial memory is important for understanding the representation of our autobiographical memory (Spiers & Maguire, 2007). But locations may also be independent of the person (i.e. semantic), such as the knowledge of a buildings particular location. Thus, spatial memories are complex. Further, they are constantly updated and do not neatly fall into the aforementioned dichotomies. One task, intimately related to spatial memory, is spatial navigation.

1.2 Spatial Navigation & Strategies

How do we know to where we are going and how do we know how to get there? The ability to retrieve, formulate and recall a route or location relies on multiple behavioural and neural mechanisms. Animals rely on these mechanisms for survival, they need to forage for food, avoid prey and to safely return home. Much of our knowledge of the cognitive, behavioural and neural mechanisms of navigation stems from animal research (Ekstrom & Isham, 2017).

Path Integration

The ability to constantly update, follow and return via a navigational route is known as path integration (Mittelstaedt & Mittelstaedt, 1982). This process takes on the assumption that distance and direction information are internally updated with each sequential movement along the desired path. For example, Desert Ants (*Cataglyphis*), can locate food large distances away from home, and return incredibly accurately and in a relatively straight trajectory. This suggests that they are constantly updating spatial information whilst travelling (Wehner & Wehner, 1986; Wehner, 2003). Studies involving blind and blindfolded humans have demonstrated that successful homing is achievable, albeit error prone, without external input (e.g. visual input, see Loomis et al., 1993). Manipulating the visual setting prior to blindfold navigation does not improve distance and directional encoding or navigation accuracy (Commins et al., 2013). Therefore, humans seem capable of performing path integration much like animals. Nevertheless, this method can be unreliable (Etienne & Jeffery, 2004) and particularly error-prone over longer-distances (see Heinze, Narendra & Cheung, 2018 for a review). Therefore, perhaps recognition of visual features facilitates the correction of errors that may arise from path integration.

Visual Cues and Landmarks

As well as Path Integration, animals make use of visual (and other) cues in their environment. For example, Biro, Guilford, Dell'Omo & Lipp (2002) demonstrated that pigeons can navigate back to their nest faster if they have been exposed to environmental landmarks prior to the journey. Further research by Biro, Meade & Guilford (2004) has shown that pigeons are reliant on memorised visual landmarks when trying to navigate home from novel positions. The birds may also memorise the directional information about each landmark and use this knowledge when compass information is unreliable (Biro, Freeman, Meade, Roberts & Guilford, 2007). The use of visual landmarks seems to be related to the distance and direction information they can provide. Dyer & Gould (1983) argued that honeybees memorise landmarks in their environment in order to aid navigation when information from the sun is not available (also see Dyer, 1996, 1998). Collett, Cartwright & Smith (1986) similarly demonstrated that gerbils use distal visual cues in order to navigate to a goal location.

Information about visual landmarks is used continuously throughout navigation towards a goal, but successful navigation becomes increasingly difficult when more complex arrays of visual cues are manipulated or unstable (Cartwright & Collett, 1983, 1987). Therefore, landmarks may assist in the correction of path integration errors, but the visual stability of landmarks is important for this correction to be accurate. Though one might learn about unstable visual cues, the most accurate navigation is facilitated when a landmarks distance, direction and appearance all remain constant, particularly in relation to a goal location (see Biegler & Morris, 1996). This concept has been further assessed in humans, firstly revealing preferences for integrating visual knowledge when navigating (Foo et al., 2005). Recent research has revealed that humans use a similar correction procedure when route-following, using mainly stable landmarks in the environment to improve navigation accuracy (Jetzschke, Ernst, Froehlich & Boeddeker, 2017). There are several other factors that may

influence the use of a visual landmark during navigation. For example, should a landmark appear visually contrasting to other available landmarks, it is more likely to be incorporated when navigating (see Chan, Oliver Baumann, Bellgrove & Mattingley, 2012; Farina et al., 2015). Additionally, the location of the landmark and previous experience of the navigator may also influence whether a landmark will be incorporated into a navigation strategy.

Navigation Strategies

To complicate things further, the type of navigation carried out in relation to visual cues can differ depending on the situation. These navigation strategies can be egocentric or allocentric (see Figure 1.1). Egocentric navigation involves the relationship between an individual and other objects or locations (see Figure 1.1. Left). Further, it is also considered to include a simple stimulus-response pattern learning, whether it is following a fixed-route (Morris et al., 1982; Packard & Knowlton, 2002) or responding to single landmark (Sutherland & Dyck, 1984). The encoding and behavioural responding of navigation in an egocentric strategy has been shown to depend on the dorsal striatum in rats and humans (Morris et al., 1982; King, Burgess, Hartley, Vargha-Khadem & O'Keefe, 2002; Doeller, King & Burgess, 2008).

On the other hand, allocentric navigation refers to mnemonic representations of viewpoint-invariant relations among objects (Fidalgo & Martin, 2016), as well as fixed relations between objects or locations independent of the individual (see Figure 1.1. Right). These spatial representations are thought to be stored in memory like a cartographic map (Tolman, 1948; O'Keefe & Nadel, 1978). The complex, recall-dependent allocentric strategies have been demonstrated to rely heavily on the hippocampal region (Morris et al., 1982; Ekstrom et al., 2003). The choice of strategy used may depend on the most convenient solution to the task. Indeed, animals may not be able to readily switch from one strategy to another

(Kealy et al., 2008). Additionally, the recall of large-scale allocentric representations has been shown to be necessary when egocentric information is not readily available (Maguire, Burgess & O'Keefe, 1999; Woollett & Maguire, 2010). Although many animals prefer to use egocentric strategies (Waller & Hodgson, 2006; Burgess, 2006), a combination of both egocentric and allocentric strategies cannot be ruled out. However, the choice of strategy may depend on the environment and availability of information.

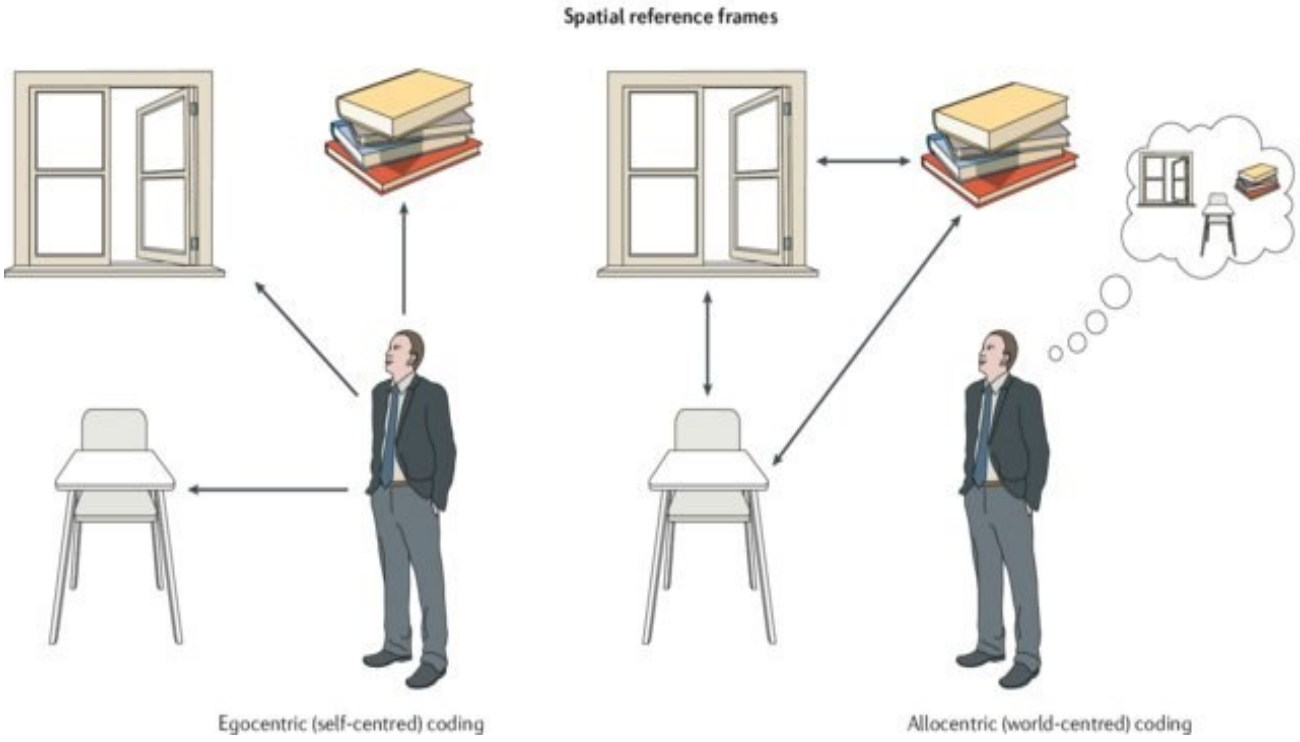


Figure 1.1: A visual representation of egocentric (Left) and allocentric (Right) spatial coding strategies. Egocentric is a self-centred navigation strategy based on the navigators' distance and direction in relation to individual landmarks. Allocentric is an object-centred navigation strategy, based on landmark positions and their spatial relationship with other landmarks or goals. This figure is adapted from Coughlan, Laczó, Hort, Minihane & Hornberger (2018).

Other Influences on Navigation

Whether we choose to use an egocentric or allocentric strategy for navigation seems to depend on the task or visual environment, but these strategies can also be influenced by individual differences. For example, males tend to perform navigation tasks faster than females, but this effect fades with enough training (Perrot-Sinal, Kostenuik, Ossenkopp & Kavaliers, 1996; Iachini, Ruotolo & Ruggiero, 2009). Choice of strategy and accuracy may depend on gender; with females generally preferring the use of allocentric strategies whilst men prefer egocentric strategies (see Dabbs, Chang, Strong & Milun, 1998; Boone, Gong & Hegarty, 2018 for an overview). However, much research indicates that these differences are heavily dependent on the landmarks available (Sandstrom, Kaufman & Huettel, 1998) or on the tool and protocol being employed (Roof & Stein, 1999; Astur, Tropp, Sava, Constable & Markus, 2004). Both males and females navigate accurately when landmarks in the environment are kept constant.

Other individual differences influencing navigation ability and recall include age. Younger human and nonhuman species outperform their older counterparts in navigational tasks (Driscoll, Hamilton, Yeo, Brooks & Sutherland, 2005; Moffat, 2009). Further, the hippocampus, a key brain region in allocentric navigation, not only shrinks as we age but has also demonstrated less activation during navigation tasks with older adults (Moffat, Elkins & Resnick, 2006; Antonova et al., 2009). Specific impairments in allocentric strategy use has been demonstrated in older adults (Gazova et al., 2013) with preferences to use egocentric strategies evident from behaviour and self-report (Newman & Kaszniak, 2000; Driscoll et al., 2005). The impairment of spatial ability has notably been present in very early onset of Alzheimer's disease and pre-clinical dementia (see Coughlan, Laczó, Hort, Minihane & Hornberger, 2018 for an overview). Therefore, understanding learning and recall strategies in older adults could be beneficial for training and improving independence in daily tasks or possibly to monitor at-risk older adults (Lövdén et al., 2012; O'Malley, Innes & Wiener, 2017;

Zygouris et al., 2017). Thus, the individual differences in spatial navigation ability and strategy selection may possess vital insights into age-related brain diseases.

1.3 Neural Networks of Navigation

Should you be faced with the unfortunate situation of being lost in an unknown environment, there are three vital factors that our brains attempt to calculate; "Where am I now?", "Where do I go?" and "How far do I travel?". These elements are at the heart of our basic navigational system; location, heading-direction and distance. Interestingly, these components of successful navigation may also be related to complex neural networks in both the animal and human brain.

Place Cells

The first breakthrough was the discovery of place cells by O'Keefe & Dostrovsky (1971). The researchers carried out extracellular single-cell recordings from the surface of the rat hippocampus (area CA1; see Figure 1.2) as the animal freely roamed through a box looking for food. The researchers noted that all cells had a low firing rate, but particular cells would change to a high firing rate depending on the rats' position. By observing the activation of these newly named *place cells*, researchers could predict the route the rat was travelling. Reversely, they could examine the travelled route and predict which place cells would fire. Certain cell combinations would always be unique for each location, with different cells firing in different locations, known as *place fields* (O'Keefe, 1976). An example of place cell firing patterns can be seen in Figure 1.2. The discovery of place cells led to the understanding that the hippocampus was responsible for place memory and this neural network may facilitate recall. Additionally, it led to the proposal that these hippocampal cells are responsible for "mapping"

an allocentric representation of our environment, described in *The Hippocampus as a Cognitive Map* (O'Keefe & Nadel, 1978). The theory of cognitive mapping is further discussed in section 1.4.

Follow up research demonstrated that place cell firing was controlled by multiple sources, with alterations in activity based on changes in landmark positions (Muller & Kubie, 1987; Knierim, Kudrimoti & McNaughton, 1998), stress (Bostock, Muller & Kubie, 1991) and even age (Wilson, Ikonen, Gallagher, Eichenbaum & Tanila, 2005). More recently, place cells have been discovered to "replay" their firing pattern upon moments of decision-making, sleep and even along the running route of the animal (see Foster & Wilson, 2006; Johnson & Reddish, 2007; Davidson, Kloosterman & Wilson, 2009). Interestingly, place cells have been observed to "preplay" firing sequences of routes the animal intends to follow (see Dragoi & Tonegawa, 2011). Successful recording of place cells in the medial temporal lobe of pre-op epilepsy patients initially designated that a similar cellular system exists in humans (Ekstrom et al., 2003; also see Jacobs, Kahana, Ekstrom, Mollison & Fried, 2010). However, complexity of this spatial cellular network may stretch further than the hippocampal area, with evidence of place cells and other spatial encoding cells found in areas beyond the hippocampal region (O'Mara & Aggleton, 2019). Though it cannot be certain, these discoveries may relate to the neural underpinnings of how the hippocampus *and* surrounding areas help recall spatial memories for navigation. Nevertheless, place cell activity is increasingly complex, and are one of the first neural underpinnings of navigation to support behavioural findings.

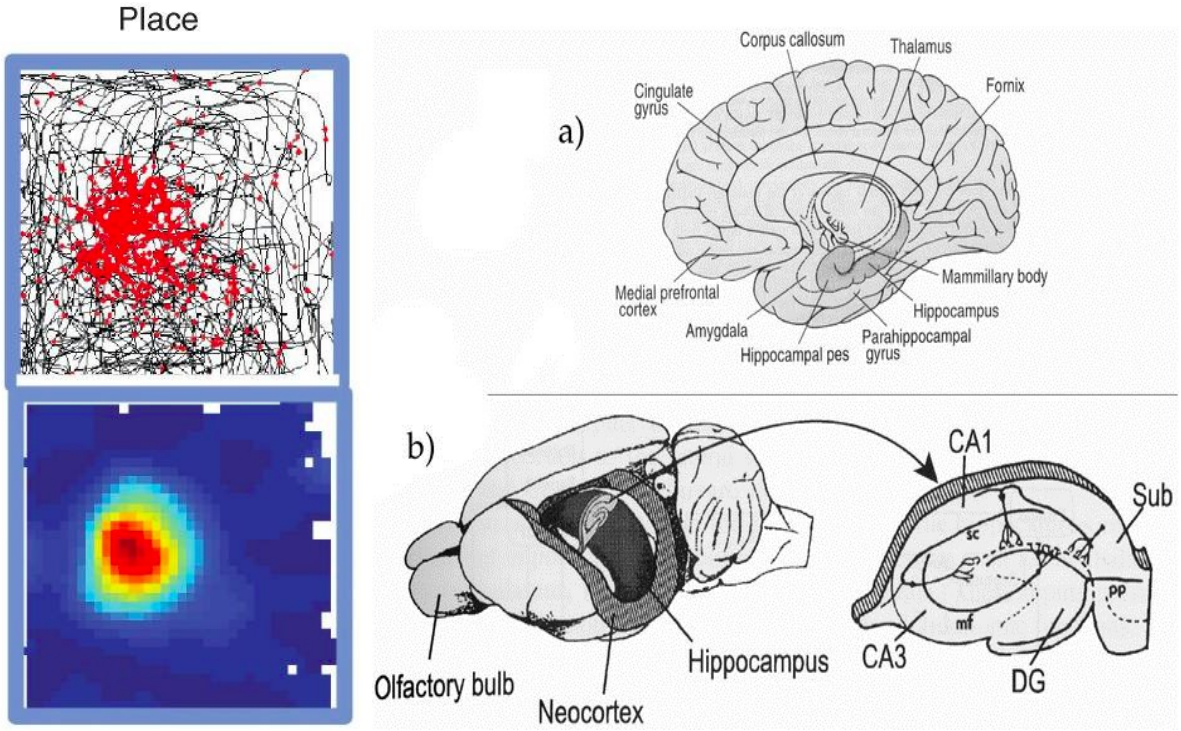


Figure 1.2: (Left) Firing activity of place cells in the rodent hippocampus. The trajectories of the animal with spike locations (high-level activity) can be seen on the top, whereas a colour-coded rate map, with red showing high-activity and blue showing low-activity can be seen at the bottom. This Figure is adapted from Moser, Rowland & Moser (2015). (Top Right; a) Human brain with the hippocampal brain structure labelled. (Bottom Right; b) Rat brain and hippocampal area (CA1) in which Place Cells were discovered in the original study by O'Keefe & Dostrovsky (1971). This figure is adapted from Burgess, Jeffrey & O'Keefe (1999).

Head-Direction and Grid Cells

Though place cells represent location, how does the brain interpret the metrics of the environment and decipher from what direction our route will begin? A sense of direction is essential to understand which "place" will need to be coded for. Extracellular recordings in several areas, including the postsubiculum (PoS) and retrosplenial cortex (RSC) of a freely

moving rat in a landmark-rich environment revealed cells that fired rapidly when the animal was facing a particular direction (see Taube, Muller & Ranck, 1990a; 1990b). The cells stayed virtually silent otherwise (see Figure 1.3). It has since been established that the firing of these *head direction* cells depends on the stability of the environment and its landmarks (see Lozano et al., 2017 for details). These landmark reliant cells have also been observed via fMRI pattern analysis in the human RSC (Jacob et al., 2017; Kim & Maguire, 2019). Further, computational models have supported the idea that certain cells may be landmark dependant, while others deal with orientation only (Page & Jeffery, 2018). The importance of these head direction cells supports the significance of landmarks for navigation in both animals and humans.

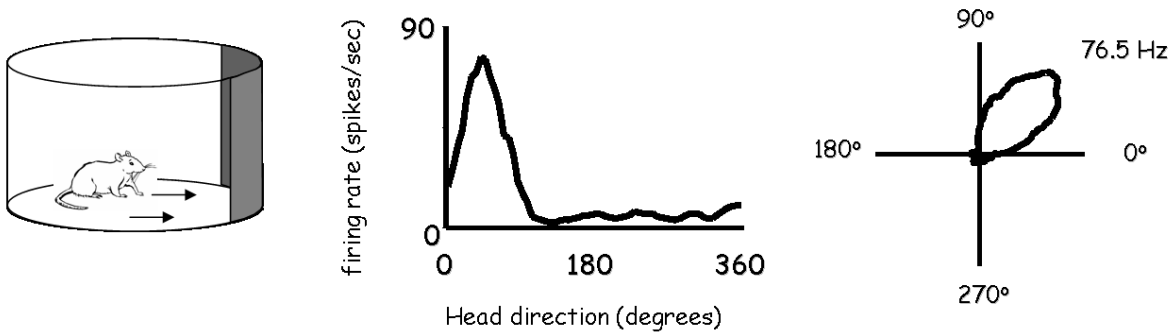


Figure 1.3: Example of a Head Direction cells firing patterns when an animal is facing a specific direction. Image obtained from http://www.memoryspace.mvm.ed.ac.uk/headdirectioncells.html.

More recently, cells recorded in the rat medial entorhinal cortex (MEC; see Hafting, Fyhn, Molden, Moser & Moser, 2005) revealed firing patterns in a grid-like fashion (see Figure 1.4 for an example), which represented the environment in which the rat navigated for food. Though it is not fully known what the purpose is of these *grid cells*, it has been argued they may relate to calculating distance (Moser, Rowland & Moser, 2015). These grid cells have also

been discovered in the human MEC via direct recordings of patients navigating in a virtual world (Jacobs et al., 2013). Doeller, Barry & Burgess (2010) used comparative fMRI pattern analysis with humans and rats, revealing grid-like firing patterns in the MEC when humans were virtually navigating, with a particular overlap in the brain areas responsible for autobiographical memory. The relationship grid and HD cells possess with place cells remains disputed, but their link is essential to understanding the neural underpinnings of spatial cognition.

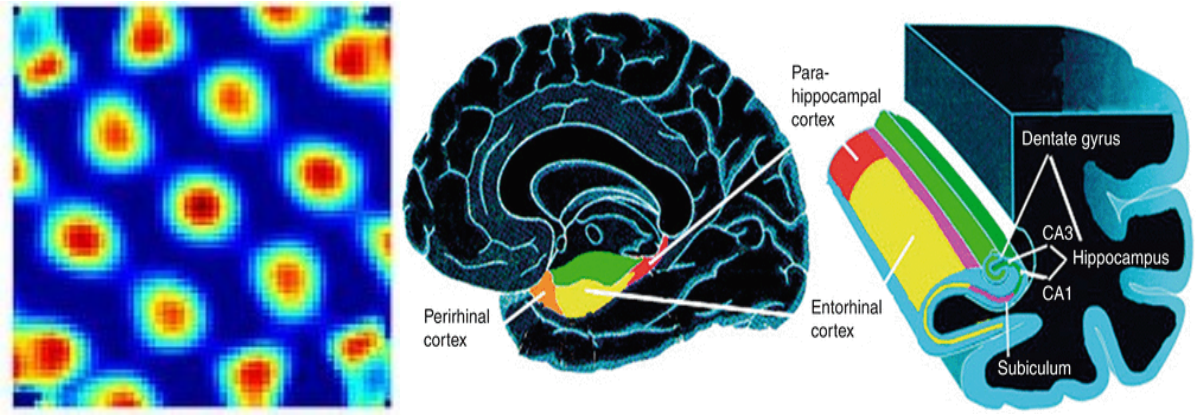


Figure 1.4: (Left) Example of Grid Cell firing patterns when recorded from the MEC. The blue represents very low activity, with yellow indicating average activity levels and red indicating very high levels of cellular activity. (Right) The human brain demonstrating the position of the Entorhinal Cortex (adapted from Tracey & Leknes, 2013).

The Hippocampus and Spatial Cognition

The sea-horse shaped brain region known as the hippocampus, is located bilaterally in the medial temporal lobe (see Figure 1.2). The hippocampus was established to have a role in the memory system, storing information about view-point independent space (see Squire, 1992).

This has mainly derived from lesion studies with rats; who show impairments on spatial tasks such as goal-directed navigation and object location recall (Morris, Garrud, Rawlins, O'Keefe, 1982; Winters, Forwood, Cowell, Saksida & Bussey, 2004). Previous studies have illustrated the dependence placed on the hippocampal region for image recognition during navigation. For example, rats with lesions to the hippocampus fail to recognise a landmark or goal after faultless learning prior to the damage (Morris et al., 1982; Hollup, Kjelstrup, Hoff, Moser & Moser, 2001). Further support for hippocampal involvement in spatial cognition, particularly large-scale navigation comes from the study of expert human navigators. Maguire et al. (2000) examined the posterior hippocampus of London taxi drivers using structural MRI. London taxi drivers are expert navigators, as they are required to have "the knowledge" of all London streets and demonstrate hippocampal activation during recall of complex routes between these streets (Maguire, Frackowiak & Frith, 1997). Comparison of MRI images to that of normal controls (without a career in driving) revealed that taxi drivers had much larger hippocampal regions, indicating stronger plasticity and the possibility that the hippocampus can store complex large-scale representations of space.

Follow up studies by Maguire and colleagues revealed that it is only particularly complex spatial representations that may relate to hippocampal enlargement. London taxi drivers still possess significantly larger hippocampal regions compared to London bus drivers, even though both navigate the city. The nature of the bus drivers constrained route is much less complex than the interchanging, sweeping routes of taxi drivers (Maguire, Woollett & Spiers, 2006). Moreover, the taxi drivers were slower to acquire new visuo-spatial knowledge compared to the bus drivers *and* when compared to matched controls. This may indicate that large-scale, complex spatial representation storage comes at a price, resulting in small-scale deficits in other cognitive domains (Maguire et al., 2006; Woollett & Maguire, 2009). However, this hippocampal volume increase has not been replicated in typical navigators

within the population, even if they would be considered near 'expert' levels, such as individuals with significant driving experience (Weisberg, Newcombe, Chatterjee, 2019). The link between spatial navigation and memory in humans is further supported by a London taxi driver with bilateral hippocampal damage. Patient TT could still navigate through London (virtually), but only when attempting routes that involved major and commonly used roads (Maguire, Nannery & Spiers, 2006). This would imply that the hippocampus is mainly involved in navigating previously learned spatial environments (shown in rats; see Whishaw, 1998 and humans; see Astur, Taylor, Mamelak, Philpott & Sutherland, 2002; Claessen, van Zandvoort, Leijten & van der Ham, 2019). However, the specific site of damage can rarely be determined in patient studies, as it is difficult to specifically pinpoint the impact of damage to current and surrounding connections (see Price & Friston, 2002). Nevertheless, this brain region and its underlying cellular connections play an important role in spatial behaviour, memory and cognition.

1.4 Theoretical Accounts of Navigation

Cognitive Mapping Theory

Previously discussed neural discoveries in navigation research have led to one of the most cited theoretical accounts of spatial behaviour, the 'Cognitive Mapping' theory. Originating from Tolman (1948), it was claimed that spatial behaviour is not a simple set of stimulus-response connections, but instead, that our brain builds up a mental representation of a spatial environment. It was not until the discovery of place cells by O'Keefe & Dostrovsky (1971) that led to the proposal of the theory alongside a related brain area, in: *The Hippocampus as a Cognitive Map* (O'Keefe & Nadel, 1978). In the book, it was proposed that navigation

behaviour has two systems. The first, known as the 'taxon' system, which is a simple stimulus response strategy, in which we respond to landmarks when following a learned route. The second, is the 'locale' system, in which we construct a mental representation of the relationships among landmarks and the environment. It was proposed that these 'maps' are generated by exploration and are composed of allocentric information (see section 1.2). This information is then encoded, stored and retrieved by the neural networks of the hippocampus. These propositions are derived from a large base of research in which lesions to the hippocampus impair navigation (see Morris et al., 1982; Redish, 2001; Claessen & van der Ham, 2017 for a review). Additionally, place field firing is more reliant on extramaze (distal) landmarks (Kubie & Ranck, 1983; Geiller, Fattahi, Choi & Royer, 2017). The later discovery of additional cells, such as head direction cells and grid cells, further supported the concept of a cognitive map in the hippocampus.

The cognitive mapping theory also predicts specific navigation behaviours that should arise from the use of a mental map. Specifically, the theory was proposed to explain the short-cutting behaviour observed in the rat by Tolman's original 1948 study and subsequently, in hamsters (Chapuis et al., 1987) and honeybees (Gould, 1986). However, further studies failed to replicate short-cutting, and found that this behaviour could instead be explained by animals recognising familiar landmarks from a new angle, and moving towards these landmarks along a route (see Cartwright and Collett, 1983; Dyer, 1991; Cruse & Wehner, 2011). Additionally, much short-cutting behaviour derives from experience of using the shorter path during exploration (see Jacobs & Menzel, 2014 for a review of the controversy). Therefore, much criticism of cognitive mapping stems from a failure to replicate shortcutting, with similar results observed in humans. For example, in Tolman's original study (Tolman, Ritchie, and Kalish, 1946), there was a light positioned above the goal location. Recently, this task was replicated virtually with and without the light using humans. Participants failed to demonstrate

accurate shortcutting behaviour without the light present near the goal. But, shortcutting similar to Tolman's original observations was evident when the virtual light was present above the goal location (Wilson & Wilson, 2018). However, this significant yet straightforward reliance on landmarks for navigation has promoted a simpler explanation of this learning and recall behaviour; associative learning (Mackintosh, 1983; McLaren & Mackintosh, 2000).

Associative Learning Theory

Associative theory suggests that navigating animals form representations of available environmental cues and their relationship with the goal-location, another cue or a starting position (Pearce & Bouton, 2001). These learning procedures are based heavily on straightforward conditioning paradigms; with the strength of a stimulus determined by the reliability of the stimulus as a predictor (Rescorla & Wagner 1972; Sutherland & Rudy, 1989; McLaren & Mackintosh, 2000). Cues available in the environment compete with each other for associative strength. The learning of cues for navigation can be explained by the same rules that underlie classical and operant conditioning paradigms (see Pearce, 2009; Jeffrey, 2010 for a review). In the association-based navigation literature, two strategies are considered; elemental and configural.

Elemental learning strategies involve a direct association between an isolated stimulus and the goal (Rudy, 1991). The navigational aid is derived from cue identification, followed by the recall of the formulated spatial relationship, and the goal location to which it is associated (Sutherland et al., 1988; Pearce, 2002; Farina et al., 2015). *Configural* strategies involve associations between multiple cues; establishing one novel cue formation independent of individual cues and features (George & Pearce, 2012; Farina et al., 2015). Thus, the navigational aid derives from the recall of the complete configuration and its spatial

relationship with the goal. This type of learning and recall can explain short-cutting behaviour. Rather than recalling features from a spatial representation and interpreting direction and distance to a goal, the animal merely recognises a familiar landmark that has developed an association with the goal; and navigates towards it (see Bennett, 1996; Pearce, 2001). This theoretical approach can explain most of the shortcutting behaviour seen by golden hamsters (Chapuis, 1987), pigeons (Biro et al., 2007) and even the rats in Tolman's (1948) original experiments.

Associative theory also makes some predictions about behaviour. The learning of a cue can be '**overshadowed'** by the presence of additional cues. For example, a landmark closer to a goal will reduce what is learned about landmarks further from the goal (Chamizo, Aznar-Casanova & Artigas, 2003; Chamizo, Manteiga, Rodrigo, & Mackintosh, 2006; Pearce, 2009). However, information provided by environmental boundaries and geometric cues has demonstrated immunity to overshadowing (McGregor, Horne, Esber, & Pearce, 2009 but see Hébert, Bulla, Vivien & Agin, 2017). Another example, is when one cue (A) is an accurate predictor of location (B). Should a new cue be introduced (C), nothing shall be learned about it as A *already* accurately predicts B. Essentially, learning about C is **blocked** (Kamin, 1969; Hardt, Hupbach & Nadel, 2009). This phenomenon has been demonstrated during navigational learning in rats and humans when new landmarks are introduced (Rodrigo, Chamizo, McLaren & Mackintosh, 1997; Hamilton & Sutherland, 1999; Schoenfeld, Schiffelholz, Leplow & Foreman, 2017). Contrastingly, cognitive mapping theory claims that the spatial maps can be automatically updated, leading to contrasting predictions. Hence, the theoretical debate regarding spatial behaviour is considerably complex and is further discussed in relevant experimental chapters.

1.5 Assessment of Navigation in Animals & Humans

Animal Assessment Tools

There exists multiple tools across animal studies that are used to examine navigation, which include the Radial Maze (Olton & Samuelson, 1976) and the T-Maze (Olton, 1979). The Radial Maze typically has the formation of a centre arena with tunnels or "arms" radiating outwards. The terminus of these tunnels typically contains a well in which a reward (such as food) can be placed. The ability of an animal to recall which identical arm contains the reward, relies heavily on spatial learning, memory and the hippocampus (Bolhuis, Bijlsma & Ansmink, 1986; Crusio, Schwegler & Lipp, 1987). The T-Maze generally takes the formation of a long-stretch of maze with two, hidden turning points at the terminus. Rodents are generally tested for their cognitive ability to recall cue-goal relationships, as each turn has an associated landmark, with only one turn containing a reward. Even when the hippocampus is removed or damaged, rats can still solve simple conditional or alternation reference tasks in the T-Maze (see Deacon, Bannerman & Rawlins, 2001; Deacon & Rawlins, 2006). However, there is difficulty to use or perceive spatial components and cues to locate the goal, but ability may also depend on the location of the damage (Deacon et al., 2001; Trivedi & Coover, 2004).

Though these paradigms have been incredibly influential in exploring animal learning and spatial memory, the "Gold Standard" of these navigational maze tests is the Morris Water Maze (MWM; Morris, 1984). The general layout of the maze (see Figure 1.5) involves a circular pool filled approximately half-way with water. The animal is tasked with locating and recalling the position of an "escape platform", which is submerged below the water surface in a fixed location. The platform is generally camouflaged by colouring the water or making the platform from transparent materials. This facilitates the platform to have a low, if any, visual

presence in the pool, meaning the location of the platform must be found and recalled (see Vorhees & Williams (2006). The animal can be trained with distal landmarks, proximal landmarks or with their trajectory alone (see Nunez, 2008 for an outline of the procedure). The maze provides a highly controlled environment for landmark manipulation, behavioural observation and lesion studies. A highly replicated finding using the MWM, is that damage to the hippocampus results in impaired allocentric (landmark) navigation (Morris et al., 1982; Sutherland & Rudy, 1988). However, trajectory learning, or egocentric search strategies remain preserved (Eichenbaum, Stewart & Morris, 1990; Voorhees & Williams, 2006). Therefore, the flexibility of protocols and procedures provided by the MWM has led to it becoming the most popular test for spatial memory and navigation.

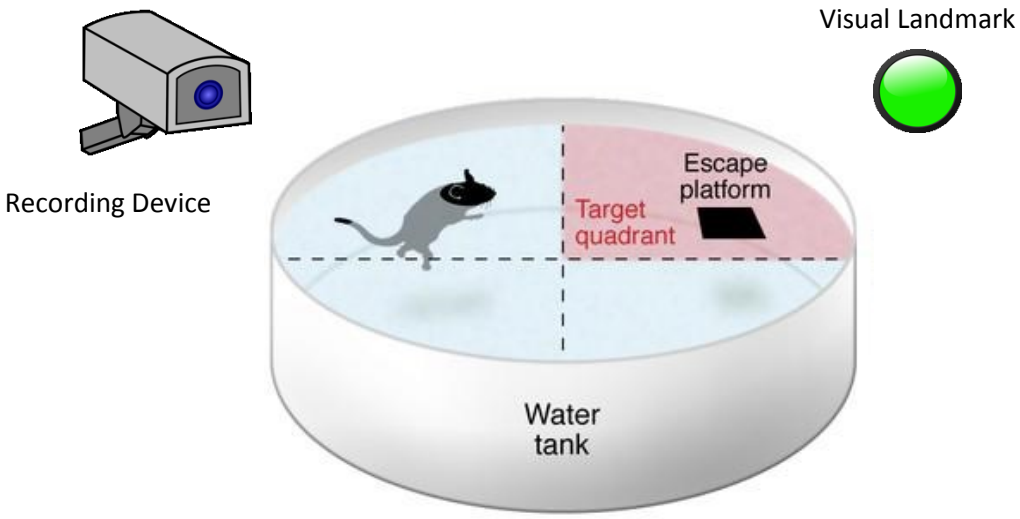


Figure 1.5: A schematic of the Morris Water Maze. The invisible escape platform is submerged in a 'target' quadrant. The circular tank is filled with water and the rat is placed in at one of the compass points. The rats swimming behaviour is recorded by an overhead video camera. Surrounding walls can also display cues/landmarks.

Human Assessment Tools

Human navigation is complex and can sometimes be completely different from animals, as we tend to rely primarily on visual senses. Using a real-world environment, Thorndyke and Hayes-Roth (1982) performed a classic study, in which humans were asked to learn the layout of a building from a map or learn it by free-navigation around the building. Interestingly, there were differences between both groups when asked to estimate routes and straight lines. The map group were able to accurately estimate route distances and straight-line distances but could not estimate the location of unseen places. The navigation group were much better at this, as well as being more accurate with route distances than straight-line. Experiments such as this are usually difficult to organise. Natural environments are also not fully controllable. Similar real-world navigation experiments have been useful to understand factors underlying human learning and memory such as distance estimation (Commins et al., 2013), environmental orientation (Kimura et al., 2017) and spatial working memory (see Duff & Hampson, 2001). However, large-scale navigational tasks are difficult to control, standardise and manipulate (see Park, Dudchenko & Donaldson, 2018).

Virtual Reality Applications

Therefore, with the growing popularity of Virtual Reality (VR) in scientific research, behavioural neuroscientists have made use of VR systems to assess spatial memory and navigation in a controlled environment (Maguire et al., 1997; Spiers & Maguire, 2006). There are many concerns as to how translatable virtual environments are to real-life environments, particularly with navigation and learning. However, Richardson, Montello & Hegarty (1999) demonstrated that learning an environment via simplistic desktop VR was predictive of learning a real environment (also see Santos et al., 2009). Researchers have also virtually

replicated real-world experiments such as those by Thorndyke and Hayes-Roth (1982). These virtual environment replications have demonstrated similar results to their real-world counterparts (Ruddle, Payne & Jones, 1997; Lloyd, Persaud & Powell, 2009). Thus, the translatability of VR as a research tool has been shown to be reasonably reliable, but this would depend on how reasonably realistic the virtual environment, with increased immersion showing increased translatability (see Hoffman, 1998; but see Nunez, 2004). It would also depend on the level of physical locomotion conducted by participants during exposure to a VR task, which should be considered when interpreting findings (Taube, Valerio & Yoder, 2013). However, the aspects of a virtual environment that make it realistic are a matter of debate (see Hoorn, Konijn & van der Veer, 2003). For example, in certain situations, locomotor feedback during virtual navigation increases immersion (Slater, Usoh & Steed, 1995), but may not impact performance (Darken, Allard & Achille, 1998) and only rotations may be an entirely necessary element of locomotor feedback during VR navigation (see Riecke et al., 2010). Nevertheless, VR has proven useful in human navigational research.

Several virtual applications and assessment procedures have shown promising results in detecting cognitive deficits in individuals with mild cognitive impairment (MCI) or psychotic conditions (Weniger & Irle, 2008; Weniger, Ruhleder, Lange, Wolf & Irle, 2011; Veling, Moritz & van der Gaag, 2014). Furthermore, multiple studies have utilised VR in combination with a neurological measure (such as fMRI, electroencephalography (EEG) or electrophysiological recording of place/grid cells) to examine the neural basis of spatial memory and navigation (Ekstrom et al., 2003; Bischof & Boulanger, 2003; Maguire et al., 2006; Jacobs et al., 2013). Thus, from basic navigational research to clinical applications and examination of neural underpinnings, VR has proven vital for the successful, cost-effective and controllable investigation of spatial learning and memory in humans.

Virtual Morris Water Maze

Though there exists a "gold-standard" heavily replicated test for animal navigation, there also exists the need for a standardised testing procedure for *human* spatial memory and navigation. As previously illustrated, the growing popularity and possibilities of VR tools for human navigation research have become apparent. To examine whether animal models of navigation translate to human subjects, researchers have developed an obvious translatable tool; a virtual analogue of the water maze (Virtual Water Maze; VWM). This tool has been demonstrated to be capable of measuring human navigation and spatial memory, revealing similarities seen in the rodent version, such as sex-differences and alternative strategy selection (Astur, Ortiz & Sutherland, 1998; Daugherty et al., 2014). The basic procedure and look of a VWM should remain the same as the original, with a hidden platform, pool walls and landmarks. Nonetheless, several factors that influence navigation in the rodent version of the task are removed when made virtual, such as motivation and physical locomotion (Devan, Parente, Coppola, Hendricks & Johnson, 2018). Despite this, spatial performance was similar across rodents and humans when directly compared on a real and VWM respectively (Schoenfeld, Schiffelholz, Beyer, Leplow & Foreman, 2017). Furthermore, spatial information learned by humans in a virtual maze (*without movement*) can be used later for navigation in comparable real environments (Foreman et al., 2000).

Many researchers and companies design novel versions of the water maze to make them more 'immersive' or realistic (see Figure 1.6 for examples). Some incorporate landmarks from everyday life such as furniture (Folley, Astur, Jagannathan, Calhoun & Pearlson, 2010), whilst in others, the original pool of the water maze is instead a circular desert island, in which participants must search for hidden treasure (Schoenfeld, Moenich, Mueller, Lehmann, Leplow, 2010; Piper, Acevedo, Craytor, Murray & Raber, 2010 see Figure 1.6). Additionally, some high-end VWM's can be expensive, designing original editions can be time-consuming

and many versions have limited protocols (see Commins et al., 2019). Most of these and procedurally similar VWM's have been used successfully to examine spatial memory difference between older and younger adults (Moffat, Zonderman & Resnick, 2001); to record place cells in human participants (Ekstrom et al., 2003; Jacobs et al., 2013) as well as to examine the impairments of psychiatric or neurodevelopmental conditions such as autism on navigation and spatial memory ability (Hanlon et al., 2006; Lind, Williams, Raber, Peel & Bowler, 2013). Though many studies may use different versions, landmark types and protocols, the VWM has been used throughout the literature as a standard testing procedure for human spatial navigation.

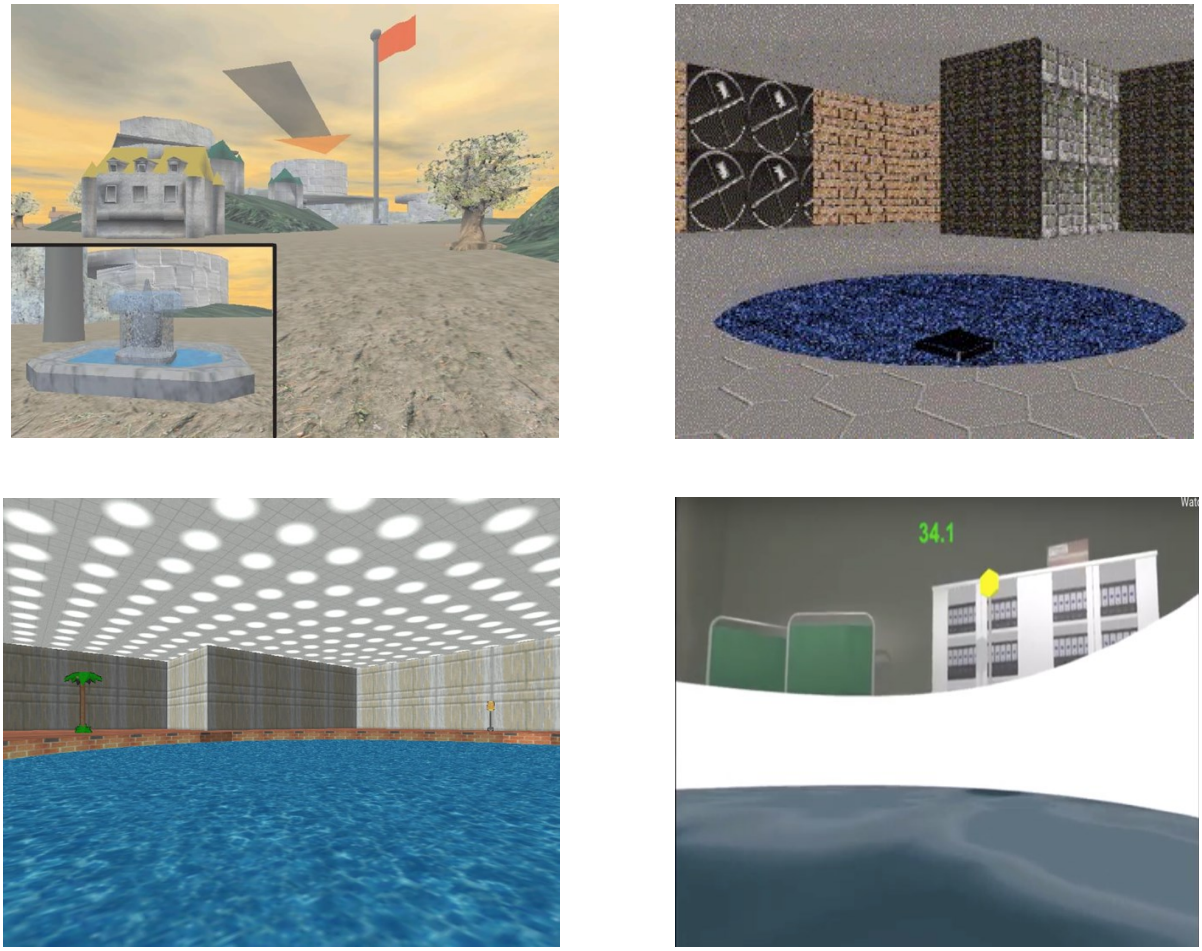


Figure 1.6: Examples of Virtual Morris Water Mazes used in the literature: The "Memory Island" analogue of the VWM (adapted from Piper et al., 2010; Top Left). An original VWM adapted from Astur, Tropp, Sava, Constable & Markus (2004; Top Right). Another original VWM design using real-world landmarks around the pool (Adapted from: http://www.moffatlab.gatech.edu/research/virtual-navigation/; Bottom Left). Commercial high-end version of the VWM by HVS (adapted from https://hvsimage.com/virtual-reality/morris-water-maze/; Bottom Right).

1.6 Thesis Objectives

As previously mentioned, landmarks are a vital factor for navigation in both humans and animals. One major question not addressed by the literature; is how we choose *which* landmarks

to integrate into our navigation strategies. Previous animal literature has manipulated landmarks available in the environment; such as Farina et al. (2015); who demonstrated that rats encode distal landmark information better than proximal when searching for a goal location in the water maze. Interestingly, manipulating a landmarks distance from the goal will reduce searching accuracy and also impair learning about other landmarks positioned further away (Chamizo & Rodrigo, 2004; Chamizo, Manteiga, Rodrigo, Mackintosh, 2006). But, training animals with brighter or bigger landmarks will improve searching accuracy (Chamizo, Rodrigo, Peris & Grau, 2006; Farina et al., 2015; Commins & Fey, 2019). It is apparent that landmarks carry different *salience*. They possess relatively distinct, prominent or obvious features compared to other features, which cause them to be learned, recognised and recalled more than others (see Caduff & Timpf, 2008 for an overview). Similar influence of landmark distances and sizes has been to some degree, explored in humans, demonstrating the same reliance on landmark salience when learning to navigate an environment (Artigas, Aznar-Casanova & Chamizo, 2005; Chamizo, Artigas, Sansa & Banterla, 2011; see Chapter 3 and 4 for an expansion of these studies, but these have been limited). The goal of this project was to expand on the above literature as follows:

1. To examine whether the environmental landmarks present in our VWM are capable of controlling navigation like those presented in the rodent version and other VWM's in the literature.

2. To examine the influence of *landmark salience* on human spatial navigation ability; with a particular focus on cue brightness and proximity.

Chapter 2

General Methodology

The current chapter will address the overall methodological approach to the project. This chapter will provide a descriptive and in-depth report of the experimental design utilised for all experimental chapters. The design used throughout this project is based on the typical procedure for testing using a Morris Water Maze (see Voorhees & Williams, 2006; 2014). This involved an acquisition phase consisting of a 12 Trials for all participants, with independent variables of (i) Escape Latency and (ii) Path Length. This was followed by a single retention trial, with the independent variable of (iii) Percentage Time Spent in Quadrants. The procedure and design are explained in more detail below.

2.1 Participants

Power statistics were used to calculate the minimum number of participants required for each experiment. The software G*Power 3 (http://www.gpower.hhu.de/; see Faul, Erdfelder, Lang & Buchner, 2007) was used to run the required sample size calculation. The overall analysis is a multivariate ANOVA with within subjects and between groups comparisons for 3 related dependent variables (time taken to navigate to goal, distance travelled, percentage of time spent in quadrants). The maximum number of groups in any experiment will be 3. We have indicated a high power (0.9) as it has recently been shown that many studies have been underpowered (Maxwell, 2004; Young, Clarke, Goffus & Hoane, 2009), which contributes to the lack of replications. Similar to other studies (Maei, Zaslavsky, Teixeira & Frankland, 2009; Palejaa, Girarda & Christensen, 2011) we have specified a moderate effect size (0.3). This results in the calculation of 30 as the total sample size required. As there were an intended 3 experiments excluding a control experiment (Experiment 1), a *minimum* of n = 10 per experimental group was required (see Figure 2.1). Participants were recruited via convenience sampling, including

Maynooth University students, friends, family members and members of the public. The precise number and relevant statistics regarding participants in each of the experiments is outlined in the relevant experimental chapters.

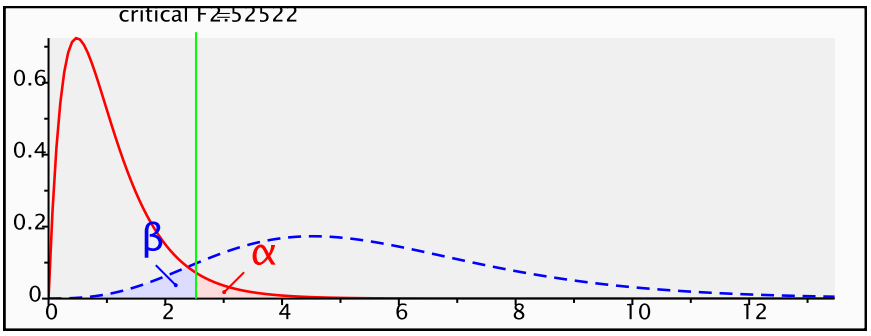


*Figure 2.1: Graphical representation of power analysis run in the statistical computing software G*Power 3.*

Specific inclusion and exclusion criteria were employed during participant recruitment:

Inclusion Criteria: Participants were required to be between the ages of 18 – 55 and be cognitively healthy and/or have no history of neurological/psychological trauma. They must have no medical/psychiatric difficulties preventing them from carrying out a computerised task (see Appendix I).

Exclusion Criteria: Individuals known to suffer from severe motion sickness from computerised simulated movement or with known poor cognitive and/or physical health were excluded from taking part. The classification of 'cognitively healthy' was made by the participants themselves. This being that they have no known medically diagnosed issues related to cognition. Should any participant be concerned about their memory ability in any of the standard tests used in the experiment, they were directed to contact their GP with these concerns. No issues arose whilst carrying out all experiments.

2.2 Materials and Apparatus

2.2.1 Control Tasks

Participants completed a set of baseline neuropsychological tests in an attempt to ensure that all were matched in general cognitive ability. As we wished to examine spatial navigation and memory, we included control tasks that specifically examined general IQ, visuospatial ability and short-term memory, which make up the basic mechanisms of overall spatial cognition (Duncan et al., 2000; Hubbard, 2005). The control tasks were only used in Experiment 2, 3 and 4. The first task was the National Adults Reading Test (NART; Nelson, 1982), which is a widely used vocabulary-based measure of intellectual ability. Participants were required to read a list of 50 phonetically irregular English words from a sheet of paper. Responses were recorded as being correct or incorrect. The number of errors (out of 50) was recorded and was used to estimate full scale IQ according to a conversion table. Secondly, the Trail Making Test (TMT; Army Individual Test Battery, 1944; Reitan, 1992) is widely used to examine visuospatial ability and motor functioning. Part A of the task is a simple visual scanning task that requires the participant to draw a line connecting consecutive numbers from 1 to 25. Part B of the task requires participants to draw a line between consecutive numbers and letters. For example, the participants must connect '1' with 'A', 'A' with '2' and '2' with 'B' and so on. The time taken in seconds to complete each part of the task is recorded by the experimenter. The time calculated from Part B minus Part A was used, which is the most accurate measure of overall executive function and control (see Sanchez-Cubillo et al., 2009).

The last test used was the Rey Auditory Verbal Learning Task (RAVLT; Rey, 1941). This is designed to test immediate learning and recall ability. The test consists of 15 nouns (List A) read out loud for five consecutive trials (A1 – A5). After each trial the participant was

asked to recall as many words as possible. Following these trials, a new set of 15 nouns (List B) was read out loud once only (B1). The participant was then asked to recall as many words as possible from List B. Finally, the participant was asked to recall as many words from List A as possible, without the experimenter reading aloud (A6). The scores for each trial were calculated by counting the amount of successfully recalled words. Performance is assessed by a normative learning curve between trials A1 and A5, a lower performance in the interference trial (B1) and an increase again during the post-interference recall trial (A6). For further information see de Sousa Magalhães, Malloy-Diniz & Hamdan (2012). All of these tasks were presented in a random order for each participant.

2.2.2 Virtual Morris Water Maze

The experiment was carried out on a computer-based program known as NavWell, created in collaboration with Maynooth University Department of Computer Science. The NavWell software can design virtual environments comparable to the Morris Water Maze (MWM; Morris, 1984) in which humans can navigate. The software is based on the standard MWM protocols, with various arena sizes, cues and procedures that can be designed and manipulated by researchers (see Commins et al., *in press*). A 2-D version of NavWell was used for all of the experiments carried out in this project. The NavWell software was presented on a 13.3-inch Apple MacBook Air laptop with a resolution of 2560 x 1600. The participants could look around the environment using a wireless mouse to control their virtual head-direction, capable of a full 360˚ rotation. To move, participants used the corresponding arrow keys; up for forward and down for backwards. Alternatively, the W, A, S and D keys could also be used if preferred. The virtual water maze generated by NavWell was consistent throughout all experiments, with the exception of different environmental cues. The general layout of the environment consisted

of grey pool walls with a clear white coloured ground representing water. The participants viewed the arena in a first-person perspective (see Figure 2.2).

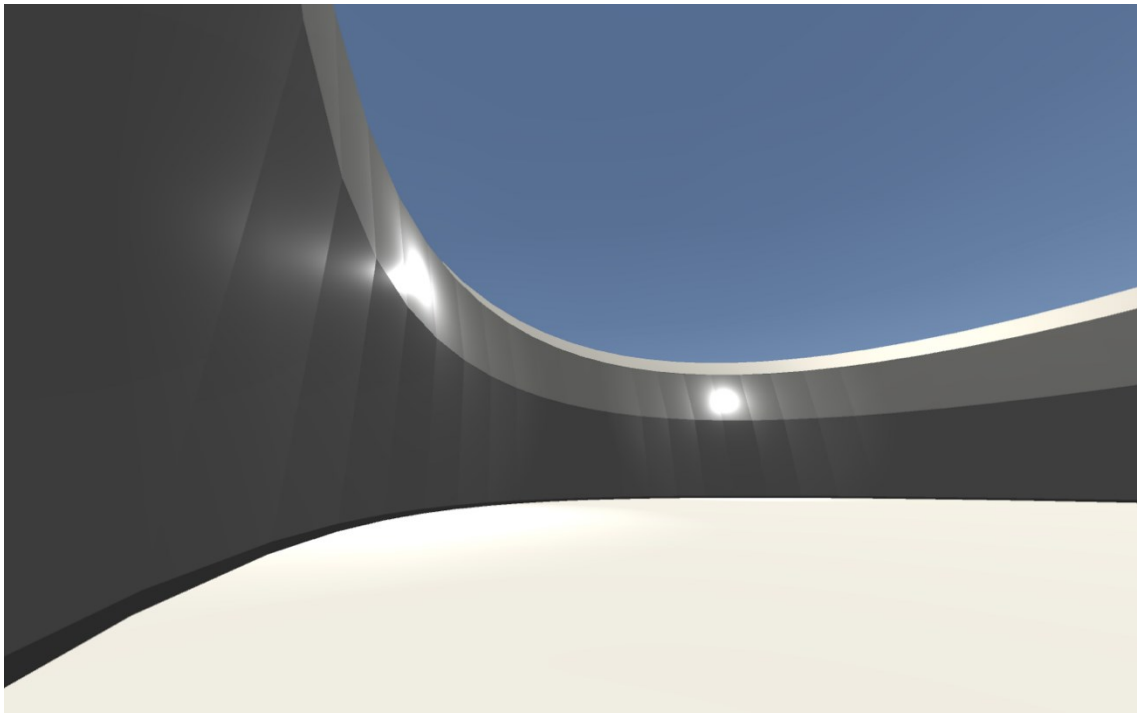


Figure 2.2: The NavWell arena from the view of a participant. The white lights on the wall represent the landmarks that can be manipulated by the researcher.

The goal of the standard MWM is to locate an invisible platform in a circular pool and to recall its location, examining an animal's spatial navigation and memory (see Morris, 1984; Voorhees & Williams, 2006). The open pool is filled half with water, which is then filled with opacifying materials to hide the escape platform (essentially making it invisible). The maze is divided into four quadrants, with 4 cardinal points; North, East, South and West (N, E, S and W). The platform is placed in the middle of one of these quadrants. NavWell requires participants to locate and recall the location of an invisible platform in a virtual translation of a typical water maze pool. The NavWell environment was also split into four quadrants for the

purpose of analysis (see Figure 2.3). The virtual escape platform (target) is approximately 15% of the chosen arena size. Upon traversing the target, it would illuminate blue and present the message:

"Congratulations, you have located the goal platform!".

This would disable movement for the participant, but still permitted them to look around using the mouse (see Figure 2.4). The arena size used for all experiments was a medium circular pool, which took 15.75 seconds to traverse the arena, calculated at 22.05 virtual metres (Vm). The escape latency (in seconds) and path distance (calculated by NavWell in virtual metres) were recorded for each trial. These data were stored on an administrator cloud system and could be downloaded as a .csv file upon completion of the experiment. NavWell also developed a tracked heatmap and path sketch for each trial, as well as, a time percentage spent in each of the four quadrants of the arena. For this project, an invisible platform was placed in the NE quadrant on all occasions.

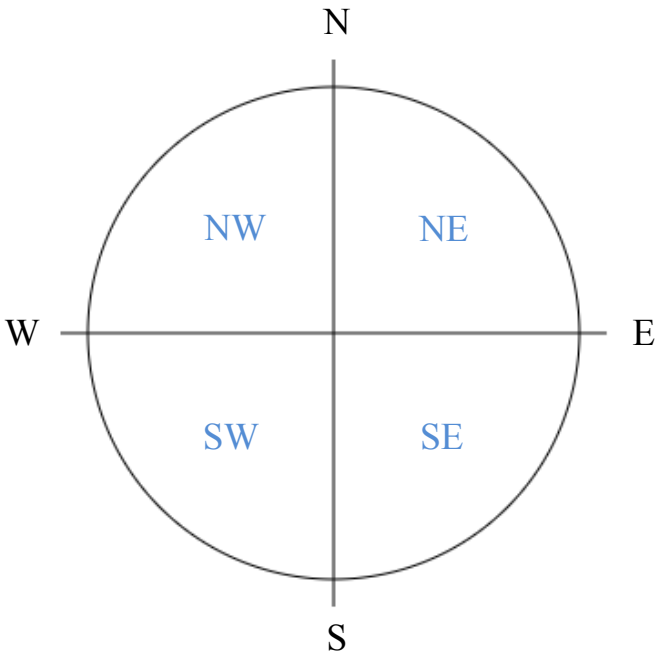


Figure 2.3: How NavWell divides up a circular arena into four quadrants with cardinal points (N, E, S and W). The quadrants are then referred to by their compass point position, as labelled (NW, NE, SE and SW).

Landmarks facilitate an animal's allocentric navigation ability in the Morris water maze. Much of the animal literature has involved a standard water maze, with landmarks presented in the room or in the pool (Chamizo, 2002; Voorhees & Williams, 2006). The landmarks available for participants in all NavWell experiments were circular lights. The luminosity level of the lights could be manipulated, ranging from 0% to 100%. These cues can be placed on the middle of an area of pool wall selected by the experimenter. A detailed version of where these lights were positioned, and their level of luminance is outlined for each experiment in its corresponding methods section. When the environment and experiment was designed, participants were assigned a participant code number for the experiment and randomly assigned to an experimental group. Participants data were translated and anonymised. All GDPR requirements were strictly adhered to with regards to data anonymization and storage. The starting positions were selected pseudo-randomly, consisting of a combination of each compass point (N, S, E and W). The starting positions were altered across the twelve trials.

A single retention trial was given some time following completion of the training trials and the control tasks. In the standard Morris Water Maze procedure, a retention trial is carried out following the acquisition trials to verify learning and examine recall (Morris, 1984; Voorhees & Williams, 2006; Nunez, 2008). The platform is removed from the pool and the search strategy of the animal is examined. For this project, our participants had to recall the targets location during a single retention trial, however, the target did not illuminate blue if it was traversed (i.e. remained invisible). All participants started from the South West (SW) position, a novel starting point (see Figure 2.5). The percentage time spent searching in the target quadrant (NE) was used to measure recall.

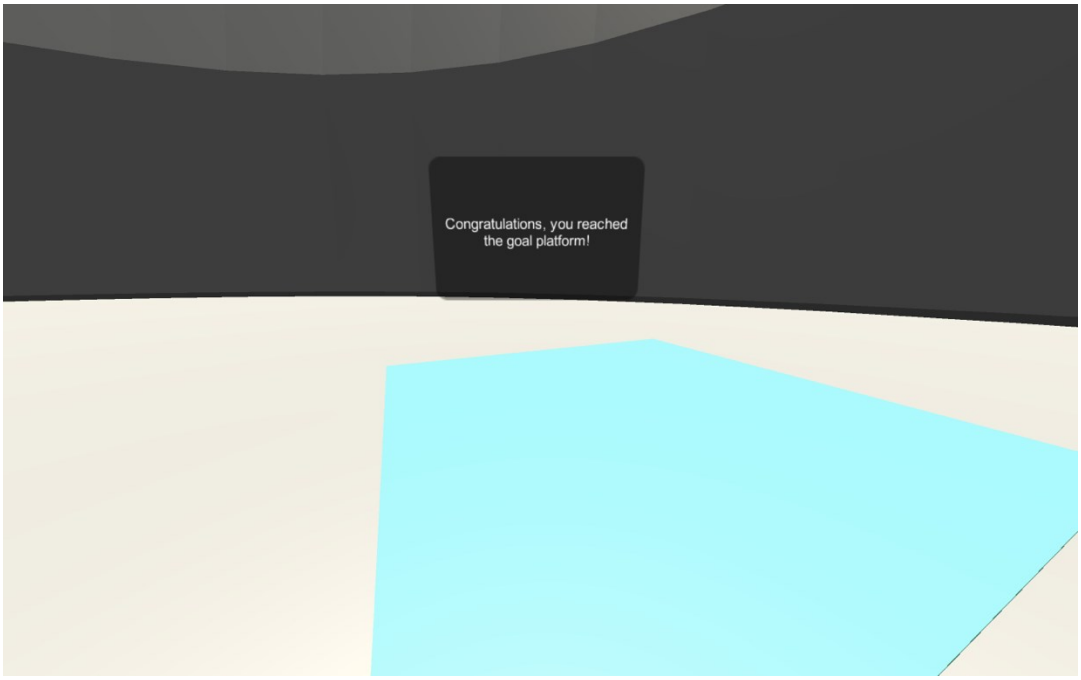


Figure 2.4: The message displayed by NavWell when the platform is traversed by a participant. The platform illuminates blue and the participant is unable to move but can still rotate their head 360˚.

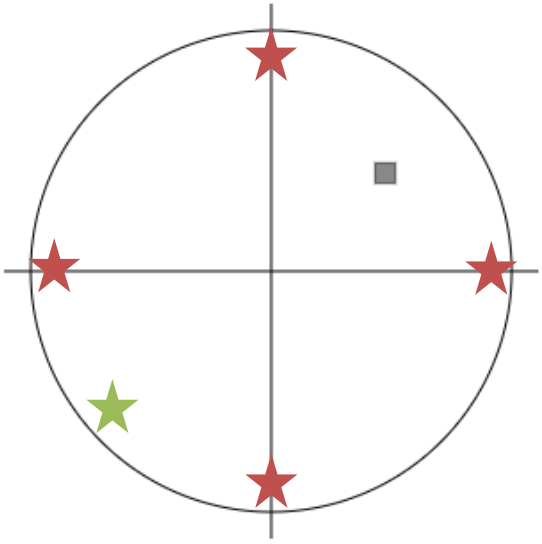


Figure 2.5: NavWell generated image of the arena used and the pseudorandomly chosen starting positions for all participants during acquisition trials (red stars). The novel starting point for retention trials is also visible (SW; marked with green star). The platform position is marked by the grey square.

2.2.3 Self-Report Questionnaire

The importance of qualitative data is often underestimated and is a format of data that cannot be collected from rodents, which make up the majority of MWM participants. As an attempt to further support our behavioural data, a simple questionnaire was designed (Appendix III) to assess the subjective search strategy being employed by participants during retention (see Lawton, 1994; Laurance, Learmonth, Nadel & Jacobs, 2003 for examples). Our questionnaire consisted of an open-ended question that followed two general questions. The two general questions sought feedback about the participants experience using NavWell. These opinion-based questions measured:

a) A Participants ability to use NavWell on a scale of 1 (Very Difficult) to 5 (Very Easy)
b) Whether a participant had suffered motion sickness during testing (Yes or No).

The open-ended, strategy related question was phrased as follows:

In relation to your final trial, please describe the strategy you used to locate the goal. What parts of the environment did you use, if any; how did you start searching etc.

Participants completed the questionnaire following their retention trial. Only after describing their strategy, they were told that the platform had been removed in the final retention trial. It was explained that this was to examine recall ability. Any further questions were answered, and participants were asked that they understood the nature of the experiment to ensure they had been properly debriefed.

2.3 Procedure

All participants were presented with an information sheet explaining the rationale of the experiment and its design (see Appendix I). They were then presented with an informed consent form (Appendix II) outlining their rights to withdraw from the study at any time and how their data would be stored and used. Any questions about the study were answered by the experimenter during this time. All experiments were carried out in a quiet, distraction-free environment. Participants were seated in front of the laptop approximately 60 cm away, and the navigation controls were explained. They were informed that there would be an invisible target for them to locate within 60 seconds. They would only be made aware of its location when it was traversed. There would be a block of 12 trials of 60 seconds each, with a 10 second inter-trial interval (ITI). Following this, they would complete cognitive control tasks to measure standard memory and executive function. They would then undergo a retention test, to examine recall using NavWell, for one 60 second trial.

2.3.1 Practice Phase

Participants were to complete a series of three training trials before commencing the twelve experimental trials. During these practice trials, participants were instructed to move to a blue visible platform. The purpose of these trials was for participants to familiarise themselves with the NavWell interface and the controls. They were also used to control for potential motor, visual or motivational issues. The training maze contained no landmarks, only a blue platform visible from the participants starting position. The arena was a medium circular pool, as explained above. Each trial was 60 seconds in length or ended when the platform had been reached.

2.3.1 Acquisition Phase

All participants, regardless of which experimental group they are assigned to, underwent the same learning/acquisition phase. This environment consists of all available landmarks depending on the experiment, which is outlined in the relevant chapters. Participants were instructed to actively explore the maze and learn its general layout. They were instructed that they were required to locate the target hidden somewhere in the pool, that would reveal itself upon walking over it. They were told that the platform would remain in the same location for all trials and that only their starting position would change. The platform was always located in the centre of the NE quadrant. During acquisition participants started from one of four starting positions as outlined above. All acquisition phases consisted of one block of twelve trials, each lasting 60 seconds. Upon starting the experiment, participants were presented with the following message:

"Welcome Participant. Your experiment is about to start. Your goal is to find the platform within the pool. Use the cues in the environment in order to locate yourself. The experiment consists of 12 total trials"

The first trial begun after 10 seconds, and presented the following message on screen:

"Your trial #1 is about to start. You will have 60 seconds to find the goal."

Participants were then instructed that their sixty seconds will begin when this message disappears. There was a 10 second Inter Trial Interval (ITI), which facilitated participants to look around and attempt to remember the targets location.

When the target was located and illuminated blue, the following message appeared:

"Congratulations. You reached the goal platform!"

"You can rest for 10 seconds. Look around the environment to learn this location."

If participants were unsuccessful in locating the target on any of the trials, NavWell relocated them to the platform position during this ITI. They were then prompted to learn the current location and the surrounding environment by presenting the message:

"You have been moved to the platform location. You can rest for 10 seconds. Look around the environment to learn this location."

The time taken to find the platform (escape latency measured in seconds) and the distance travelled (path length measured in Vm) were used as the dependent measures for this phase.

2.3.2 Retention Phase

Following completion of the three control tasks outlined in section 2.2.1, participants were asked to complete a final retention trial using NavWell. As outlined above, this trial contained no platform and is a common protocol in the standard MWM to examine spatial memory and navigation strategy retention (see D'Hooge & Deyn, 2001 for a review). Participants are told that the platform was in the same location and to attempt to recall its location. This phase consists of a single sixty-second trial with all participants starting from a novel starting position that was not used during acquisition. This was the midpoint of the SW quadrant (see Figure 2.5). During this phase, the platform does not illuminate when traversed and will provide no feedback to participants.

When completed, the participants are presented with the message:

"Your experiment has finished. Thank You!"

Percentage time (of a total 60 seconds) spent in each quadrant and particularly the quadrant containing the target (NE) was used as the dependent measure during the probe trial. Following the above message, participants were asked to fill out the self-report questionnaire. They were then debriefed regarding the probe trial, thanked for participation and any questions regarding the experiment were answered.

2.4 Data Analysis

2.4.1 Quantitative Data

All quantitative data were initially analysed using Microsoft Excel, and later transferred to IBM SPSS Version 25. Graphical representations of the data were constructed using Microsoft Excel. Mixed between-within ANOVAs and One-Way ANOVAs and were run as appropriate, to compare the dependent variables across groups and for further exploration within groups. *Post-hoc* analysis was conducted using Tukey's honestly significant difference (HSD). Bonferroni corrected t-tests were also used where appropriate. A significance level of $p < 0.05$ was adopted for all statistical tests; although full p-values and partial eta squared (referred to as "effect sizes" throughout) are reported. Heatmaps and path tracks (Figure 2.6) of participant navigation were generated by NavWell, based on the data recorded. Percentage time spent in each of the four quadrants was also recorded through NavWell (Figure 2.6). All of these data

were accessed using the NavWell admin console, a cloud-storage database accessible only by the experimenters (see Commins et al., *in press* for further information).

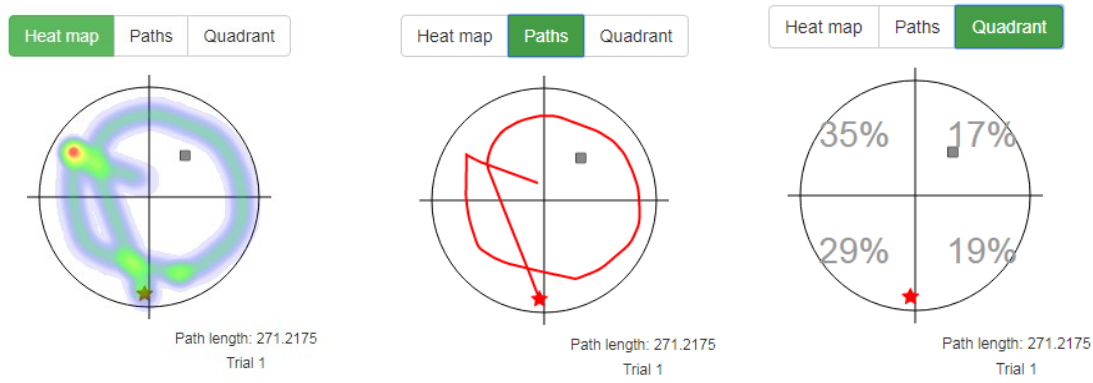


Figure 2.6: Screen captures of the data recorded and reported by NavWell. From left to right are heatmaps and tracked paths of participant navigation, and the percentage of total time spent in each quadrant of an environment.

2.4.2 Qualitative Data

Data retrieved from the questionnaire (see Appendix III) were assessed as a standard likert scale for question one and question two. Data from the open-ended question were analysed using a simple word frequency count based on content analysis (see Chambers & Chiang, 2012; Jacob, McKenna & D'Amorem, 2014). Content analysis is a technique of studying responses to open-ended questions by coding written words into categories. Content analysis involves word frequency counts to determine common themes emerging from the data (Chambers & Chiang, 2012; Jacob et al., 2015). In brief, key words identified were coded to identify environmental landmarks or other elements involved in a participants search strategy. The percentage of participants that identified as using these strategies was calculated by dividing the number of participants coded for a key word by the total number of participants who responded to question three and multiplying the answer by 100. This provided us with the

number of participants from a specific group or from the overall sample that utilised one object or search strategy during the retention trial.

Repeated codes were not recorded, only one code or sub-code is essential to classify a participant as being part of an overarching category. For example, should a participant mention the word "light" this code would be recorded under the category "Light Cue". Should they provide an additional mention of the word "light" elsewhere in their answer, these additional codes would not be counted. This is because we wished to sort participants by a particular object utilised in their search strategy. However, should the same participant also mention using the "shape of the pool" for example, they would also be coded under an alternative category, such as "Geometric Cue". The coding categories differed depending on the experiment and are outlined in the methods section for each. For examples of post-maze strategy questionnaire use in other VMWMs see Head & Isom (2010) and Nowak, Murali & Driscoll (2015). All experiments followed the described analysis in this chapter for the questionnaire data.

2.5 Ethical Considerations

The current project was approved by the Maynooth University Ethics Committee under the Biomedical & Life Sciences Research Ethics Subcommittee (Reference Number: BRESC-2018-016). Informed consent was sought prior to experimentation and following verbal explanation about the contents of the experiment. All data storage, collection and usage were conducted in accordance with the General Data Protection Regulation (EU) 2016/679 (GDPR). Participants were informed about the minor risk of motion sickness and were excluded if known to suffer from severe motion sickness in the past. It was communicated to all participants that the tests used are *not* diagnostic and individual results could not be obtained.

Participants demonstrating concerns regarding their performance on any of the tasks used in the project, were directed to consult with their general practitioner or a medical professional.

Chapter 3

An Examination of Landmark Controlled Navigation in a Virtual Water Maze Task.

3.1 Introduction

Many animals rely on the use of environmental landmarks to navigate through their environment and locate food, water or other resources. Much research has focused on the behavioural learning and navigational strategies of rodents in the Morris water maze (Morris et al., 1984). This research has revealed that there is an important incorporation of environmental landmarks during spatial learning and navigation. The theoretical understanding of how landmarks are utilised in spatial navigation strategies is strongly debated. As previously discussed, Cognitive Mapping Theory (Tolman, 1948; O'Keefe and Nadel, 1976) would argue that landmarks are incorporated into a spatial map. This map can provide a detailed and flexible allocentric layout of the environment, from which the animal can learn, navigate and successfully recall specific place locations. The alternative understanding of cue-based navigation has been developed through Associative Learning Theory (Mackintosh, 1975; Pearce, 2002). This theory would predict that landmarks form associative conditioning relationships between each other and specific environmental goal locations. These cue-goal relationships can be formed elementally or configurally (discussed in detail in Chapter 1) and are strengthened with repeated training (Rodrigo et al., 2014). Regardless, both theoretical accounts suggest that environmental landmarks (or 'cues') are an essential component of spatial navigation, learning and recall.

However, much of the supporting research for landmark-based navigation is focused on rodent behaviour from the Morris water maze (Morris, 1981, 1984). When landmarks are mentioned in the context of spatial navigation, they commonly refer to distal cues. Distal landmarks are objects in the environment that are not directly positioned on or act as the perceived goal (see Rodrigo, 2002 for a review). Consequently, numerous studies have shown

the ability of rats to successfully navigate to the goal platform using landmarks, even when the goal location is not directly visible (Morris, 1981; Chamizo et al., 2006). Performance deteriorates should any of the landmarks be altered (Rodrigo, Chamizo, McLaren & Mackintosh. 1997; Farina et al., 2015), and it is clear that the chosen navigational strategies involve complex relationships between these landmarks. Nevertheless, similar strategy selection, recall ability and landmark use has been reported in humans (Spetch, 1995; Foo, Warren, Duchon & Tarr, 2005; de Condappa & Wiener, 2016).

The introduction of virtual reality (VR) in navigational research has led to a controlled and safe methodology to examine humans during navigation. Wayfinding in virtual environments is no different than wayfinding in real-life environments, in relation to feelings of immersion, performance and decision-making (Coutrot et al., 2019). Interestingly, even rats perform no different in a virtual navigation task compared to real-life environments (see Youngstrom & Strowbridge, 2012). The impact of virtual environments for navigation research has been discussed in greater detail in Chapter 1. The virtual water maze (VWM) has become a popular method of examining navigational behaviour, allowing for translatability and comparison to animal research (Bohil, Alicea & Biocca, 2011).

The general understanding from the navigation literature has been that distal landmarks, are used for successful recall of spatial locations (Sandstrom, Kaufman & Huettel, 1998; Astur, Tropp, Sava, Constable & Markus, 2004; Redhead & Hamilton, 2009). However, their usage is not mutually exclusive, and distal landmarks may be only one of the many elements used to recall a spatial location or to navigate towards a goal. Hamilton, Rosenfelt & Whishaw (2004) demonstrated that rats navigating in a water maze will rely on distal landmarks in order to determine the correct heading direction towards a goal. However, the rats would then switch to using a cue closer to the goal (a beacon) to navigate accurately. Nevertheless, this illustrates the vital control distal landmarks possess over navigation behaviour. Similar cue control has

been replicated with humans in a VWM; along with supporting eye-tracking data (Hamilton, Johnson, Redhead & Verney, 2009; Redhead, Hamilton, Parker, Chan & Allison, 2013). Still, the exact distal cues utilised can vary between sexes and species (Sandstrom et al., 1998; Saucier et al., 2002). The involvement of geometric environmental cues is also important, particularly to establish the reliability or overshadowing of a particular distal landmark (see Cheng & Newcombe, 2005; Hébert, Bulla, Vivien & Agin, 2017). Consequently, navigation and successful learning with the landmarks available (distal or proximal) results in the most accurate recall. Evidence from rats (Rodrigo, Gimeno, Ayguasanosa & Chamizo, 2014) and humans (Foo, Warren, Duchon & Tarr, 2005) demonstrates preference for integrating landmarks into their search and recall strategy, performing better depending on the reliability and salience of these available cues.

3.2 Experiment 1

Experiment 1 attempts to explore whether our virtual water maze software, NavWell (see general methods), is capable of demonstrating similar cue-controlled navigational behaviour that is presented in the current animal and VWM literature. Classic behavioural studies involving rats in water maze, such as Morris (1981), demonstrate that landmarks are essential guides for learning and navigation. This has been established repeatedly in various animals, with the removal of landmarks causing reduced or almost impaired performance (Fenton, Pia Arolfo, Bures, 1994; Strasser, Bingman, Ioalé, Casini & Bagnoli, 1998; Young, Choleris & Kirkland, 2006; Farina et al., 2015). The same impact of landmarks controlling navigation has been demonstrated in other VWM's both with rats (Youngstrom & Strowbridge, 2012) and with humans (Jansen-Osmann, 2002).

Therefore, all participants will be trained to locate a target location in an environment with two similar landmarks. Following learning, they will then be tested with no target and either: the same two landmarks (Control Group), the landmarks rotated 180˚ (Rotated Group) or with no landmarks present (No Landmark Group). The aims of this experiment are to demonstrate that humans use distal cues to navigate (confirming other animal and human findings). Additionally, we will demonstrate that these cues are the only cues available in the environment, i.e. that our NavWell software doesn't contain other features that aid navigation (unknown to us). Thus, if humans do use distal cues it would be hypothesised that the Control group will search accurately, similar to rats and humans in other VWMs, as their landmarks have not been manipulated. The Rotated group will search in the opposite end of the pool beside the landmarks, as if the platform position had also been rotated (see Commins, Cunningham, Harvey & Walsh, 2003); and for the No Landmarks group to have impaired searching behaviour, due to the removal of the previously learned landmarks. It would also be hypothesised that a large majority of self-report measures demonstrate a strategy choice involving a landmark that is intended to act as one. Additionally, should humans be using any other features in NavWell as landmarks, manipulating these cues should reveal no change in navigational accuracy.

3.3 Methods

3.3.1 Participants

All participants (n = 30) were recruited from the population at Maynooth University using the recruitment procedures outlined in Chapter 2. The sample for this experiment was composed of fourteen females and sixteen males with a mean age of 26.2 +/- 1.74. Prior to beginning the experiment, each participant was randomly assigned to one of three landmark conditions (n = 10 per group): Control (male = 5, female = 5), Rotated Landmarks (male = 7, female = 3) or No Landmarks (male = 4, female = 6). These conditions are described below. All participants had normal or corrected-to-normal vision and were comfortable using a computer. Participants also aligned with our inclusion criteria and were asked to be excluded upon reporting severe motion sickness prior to the start of the experiment.

3.3.2 Apparatus

NavWell software was employed on an Apple MacBook laptop computer (see general methods chapter for further information). The self-report questionnaire (also outlined in the general methods chapter) was used for this experiment.

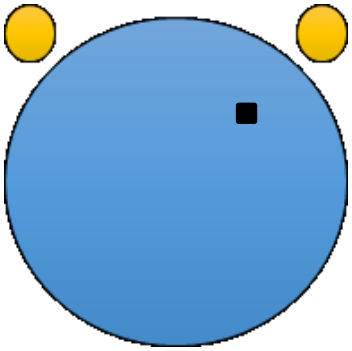
3.3.3 Virtual Environment

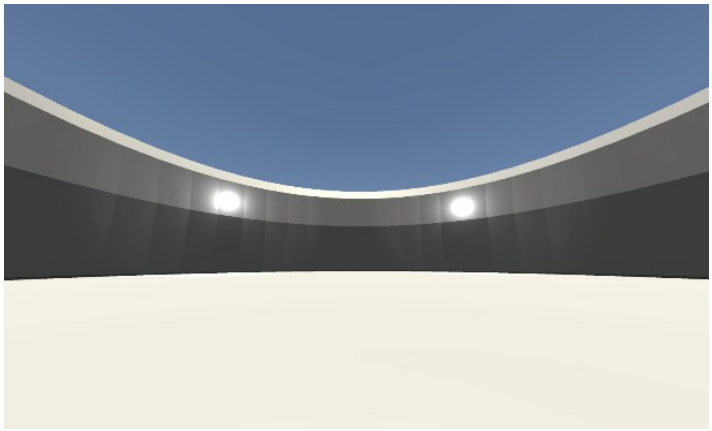
The environment designed for this experiment was kept constant for acquisition and retention trials. The only difference was the layout of the landmarks for each condition during the retention trial. All groups were trained during acquisition with the same landmark layout. NavWell attempts to replicate the layout of a typical Morris water maze (Morris, 1981; 1984).

Therefore, the environment consisted of a medium circular arena (taking 15.75 seconds to traverse the arena, calculated at 22.05 Vm). The four quadrants of a circular pool in NavWell are denoted the North West (NW), North East (NE), South East (SE) and South West). This is further discussed in the General Methods chapter. Two medium-sized circular virtual lights of 50% luminescence acted as landmarks. These were positioned on the NW and NE walls for the acquisition phase (see Figure 3.1). Participants could move freely within the pool, with a first-person viewpoint. Hidden under the surface of the pool was a square platform (which was 15% of the total arena size) that, when walked over, stopped the participant moving and illuminated blue, presenting a message on screen letting participants know that they have found the platform, and that they should attempt to recall its location (see General Methods chapter). The platform for the current experiment was located in the NE quadrant, as displayed in Figure 3.1(a).

The retention phase environmental layout is the same as above, but the landmark positions differ depending on the group allocated to the participant. The position of landmarks during the retention trial for each group are schematically represented in Figure 3.1(b). For the Control group landmarks are in the exact same location as they were during acquisition. The Rotated Landmark group had the lights rotated a full 180° on the walls of the arena. This means that the lights were then located on the SE and SW walls of the pool. There were no lights present for the No Landmarks group, only the bare walls of the arena.

3.1(a)





3.1(b)

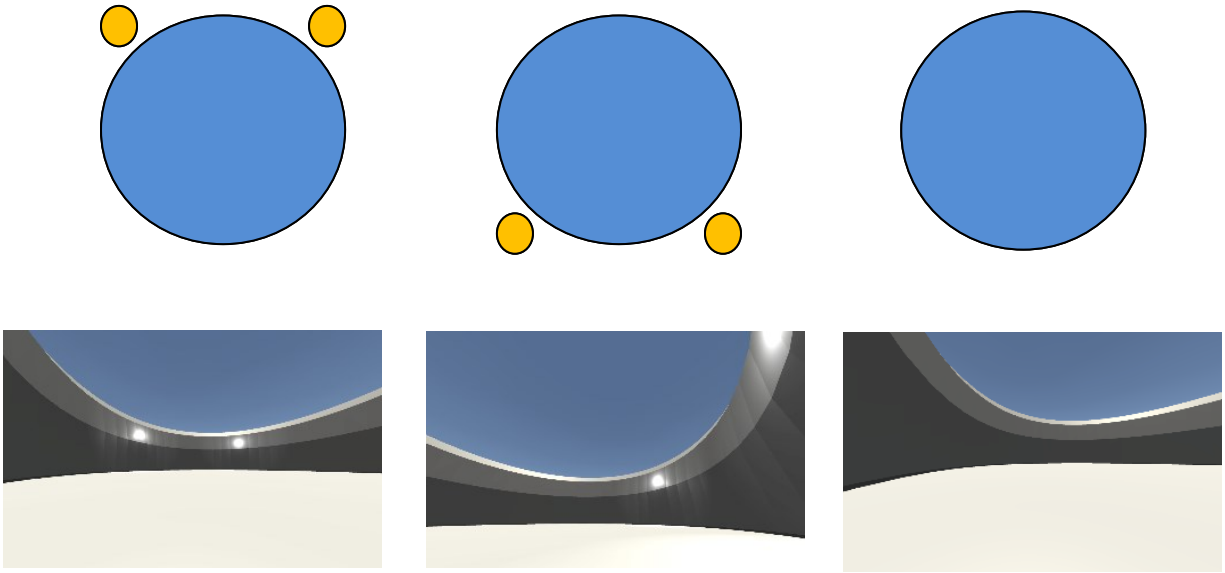


Figure 3.1(a): A schematic representation and screenshot of the environment and landmark layout for the acquisition trials in Experiment 1. The lights (50% brightness level) are illustrated by the yellow circles. The platform location is denoted by the black square (in the NE quadrant). *(b)*: A schematic representation and screenshots of the virtual environment and the landmark positions for each group during the retention trial; Control (Left), Rotated (Middle) and No Landmark (Right) in Experiment 1. The lights (50% brightness) are represented by the yellow circles. The platform position is not marked as it has been removed for the retention trial.

3.3.4 Procedure

Participants were presented with an information sheet (Appendix I) and informed consent was obtained via an attached consent form (Appendix II). The controls of the software were explained to participants, as well as, the general structure of the experiment. Any questions were answered by the experimenter. The general procedure was similar to that outlined in the general methods section. The acquisition phase was the same as outlined and was carried out by all participants. This consisted of 1 block of 12 invisible platform learning trials. Participants started from pseudorandomly assigned starting positions (N, S, E and W) around the edge of the pool. Upon the completion of these twelve trials, all participants took a three-minute break. There were no cognitive tasks for this experiment, as we were only interested in the behavioural performance of participants in NavWell. This experiments sole purpose was to examine whether landmarks in NavWell are being used by participants and acted as a control experiment for future experiments.

Following the break, the participants underwent a Retention Trial using NavWell once again. This was a single sixty-second trial with no platform present. All participants started from a novel start position, at the midpoint of the SE pool wall. As previously described, this trial had different landmark manipulations depending on group allocation (outlined in section 3.2.3). Following the completion of the retention trial, participants were then requested to fill out a self-report questionnaire (see Appendix III). Finally, the participants were debriefed. The experimenter explained the purpose of the study and why there was no platform present in the retention trial. Following this, participants were thanked for their participation.

3.3.5 Data Analysis

All behavioural data was automatically collected from NavWell during each trial. These data were stored on an online cloud-storage database, labelled by experiment and participant codes. NavWell records the escape latency (time in seconds taken to locate the platform), path length (distance travelled in virtual metres before locating the platform) and the percentage of time spent in each quadrant. All data was imported into a Microsoft Excel spreadsheet. Graphical representations of the data were constructed using Microsoft Excel. The data was then exported into IBM SPSS version 25 for analysis. A significance level of $p < 0.05$ was adopted for statistical tests. For graphical representations, $p \leq 0.05$ is represented by a single asterisk (*) and $p \leq 0.001$ is represented by two asterisks (**).

Data retrieved from the questionnaire were assessed as a standard likert scale for question one (difficulty rating) and question two (motion sickness). The open-ended question data were analysed using a form of qualitative content analysis (see Hsieh & Shannon, 2005). Content analysis is a technique of studying responses to open-ended questions by coding written words into categories. Content analysis involved word frequency counts to determine common themes emerging from the data (Chambers & Chiang, 2012; Jacob, McKenna & D'Amorem, 2014). The specific methodological approach to content analysis for the current project is outlined in the general methods chapter (section 2.4.2). The number of participants from each of the groups that utilised specific environmental features when searching and recalling could be established. Additionally, the specific environmental features used most frequently could be identified.

3.4 Results

3.4.1 Acquisition Phase

The escape latency of participants during the acquisition phase was analysed using a 3 (Group) x 12 (Trial) mixed-factorial repeated measures ANOVA. Escape latency can be defined by the amount of time it takes a participant to find the target (with a maximum of sixty seconds). There was an overall significant decrease in escape latency across the twelve trials ($F_{11, 297}$ = 27.497, p < 0.001, effect size = 0.505). Bonferroni-corrected t-tests revealed that participants were significantly faster ($p < 0.001$) at locating the target on Trial 11 (Mean = 13.5s, SEM = +/- 2.9s) and Trial 12 (17.7 +/- 2.5s) compared to the first trial (50.3 +/- 3s; see Figure 3.2). As expected, all participants trained in a similar fashion and successfully learned the task, reducing their escape times across trials (see Figure 3.3). Therefore, there was no difference in escape latency between the groups ($F_{2, 27} = 0.93$, $p = 0.91$, effect size = 0.007). Likewise, there was no Trial X Group interaction effect ($F_{22, 297} = 0.99$, $p = 0.480$, effect size = 0.68).

The path length of participants during the acquisition phase was analysed using the same statistical test. The path lengths were measured by NavWell in Virtual Metres (Vm) and are a measure of the total distance travelled by a participant throughout each sixty second trial. There was a significant decrease in path length across the twelve trials ($F_{11, 297} = 39.9$, $p < 0.001$, effect size = 0.596). Bonferroni corrected t-tests revealed that participants travelled significantly shorter distances ($p < 0.001$) in Trial 11 (42.9 +/- 8Vm) and Trial 12 (69.2 +/- 7.3Vm) compared to Trial 1 (215.8 +/- 15Vm; see Figure 3.4). Again, all participants successfully learned the target location, reducing their path length across trials and taking a more direct route (see Figure 3.5). Thus, there was no difference in path length between the groups ($F_{2, 27} = 0.781$, $p = 0.47$, effect size = 0.055) and there was no Group X Trial interaction

($F_{22, 297} = 0.98$, $p = 0.49$, effect size = 0.068). Conclusively, all participants learned the location of the platform during acquisition, reducing their completion time and path length, regardless to which group they were allocated.

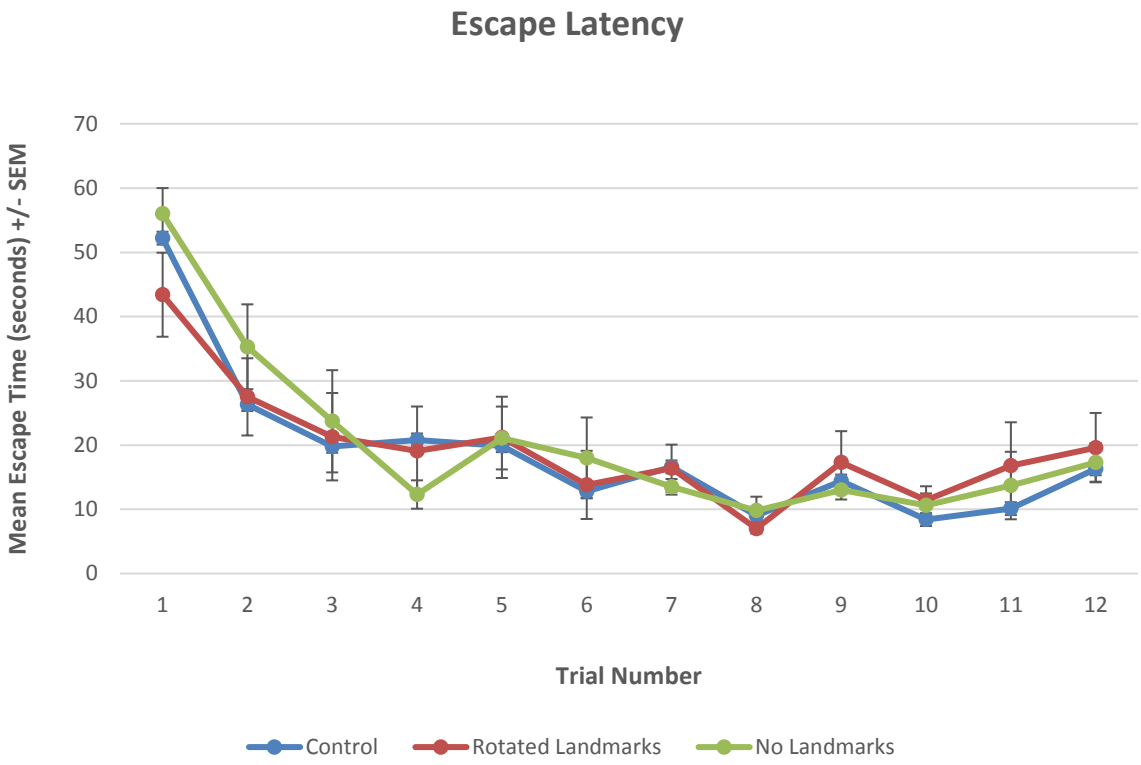


Figure 3.2: Mean time taken to locate the target (escape latency) for all participants in each group. All participants show a similar learning curve, with a reduction in escape times across multiple trials.

Figure 3.3: Example movement time heatmaps of a selected participants Trial 5 compared to Trial 12 during the acquisition phase of Experiment 1. There is a quicker and more direct navigation time and strategy in Trial 12, compared to a more dispersed search time and strategy in an earlier trial; Trial 5.

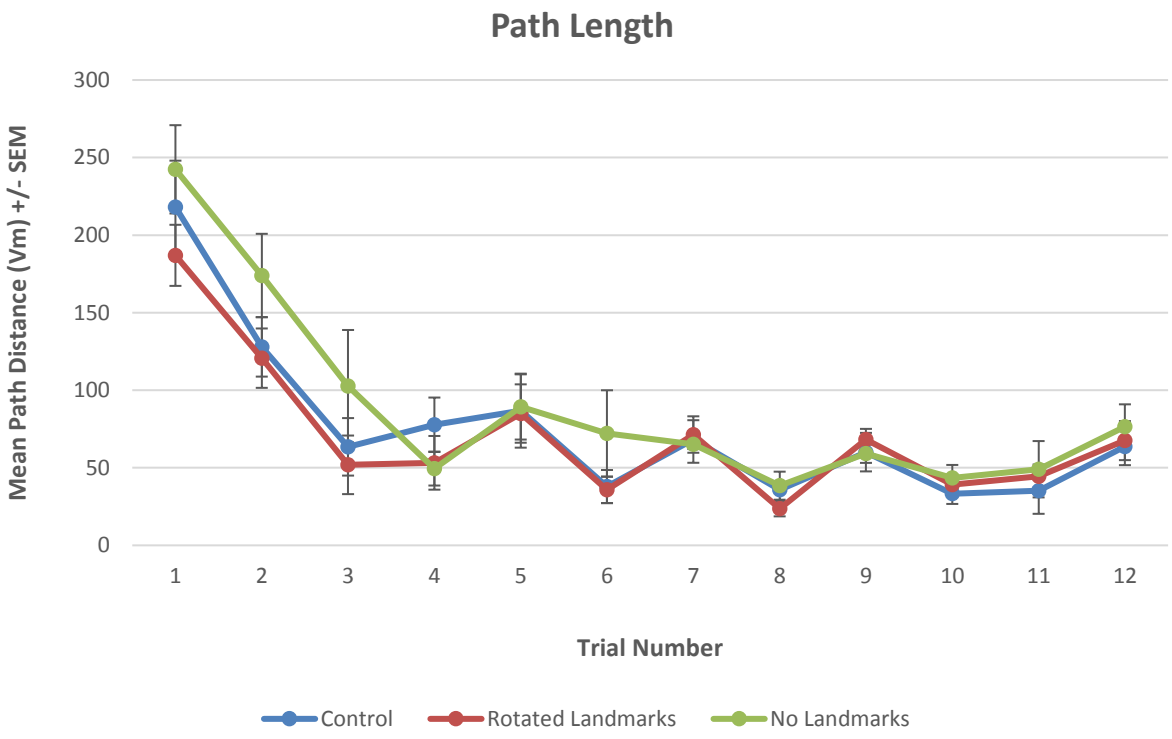


Figure 3.4: Mean Path distances for all participants in each group in Experiment 1. All participants demonstrate a similar learning curve, showing a decrease in route length across multiple trials.

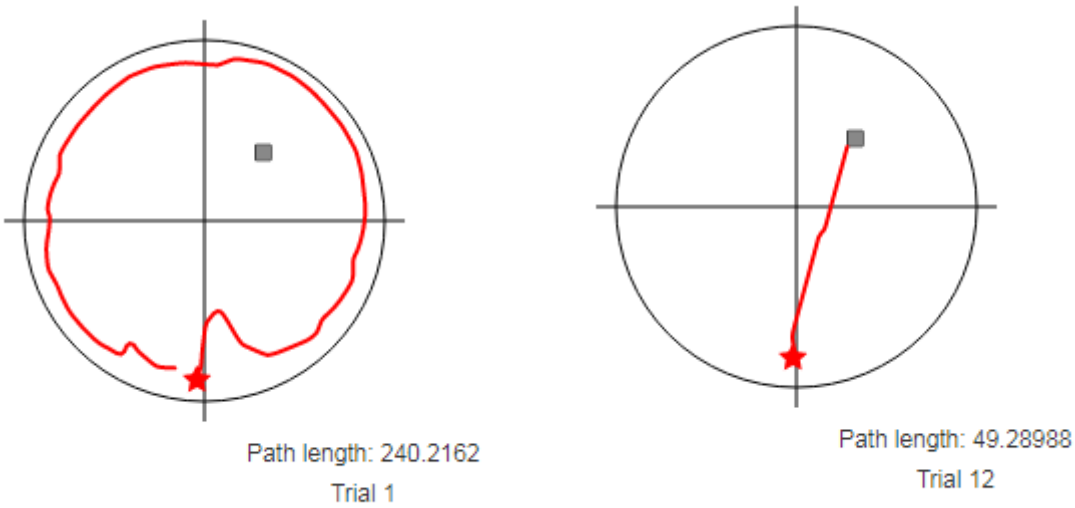


Figure 3.5: Example movement paths for a selected participant during Experiment 1 showing a decrease in path length from Trial 1 compared to Trial 12. The route taken to the target location also becomes more direct by Trial 12.

3.4.2 Retention Phase

To determine that participants trained with the two lights remained reliant on them as part of their navigation to the platform, we examined whether the Control and Rotated groups searched in the target quadrant. For this, the percentage of time spent in each quadrant was recorded for all three groups. `The data was analysed using a 3 (Group) X 4 (Quadrant) repeated-measures ANOVA. There was a main effect for quadrant ($F_{3, 81} = 20.71$, $p < 0.001$, effect size = 0.434). Although there was no significant group effect ($F_{2, 27} = 1.4$, $p = 0.26$, effect size = 0.094) there was a large significant interaction effect between group and quadrant ($F_{6, 81} = 30.05$, $p < 0.001$, effect size = 0.69). This would indicate that specific groups spent more time in specific quadrants.

This interaction effect was explored by a series of one-way ANOVA's on each quadrant of the arena. The Control group spent significantly more time ($p < 0.001$) in the NE target quadrant (69.3%) compared to the Rotated (1.5%) and No Landmark (25.5%) groups. The Rotated group spent significantly less time than the Control and No Landmark groups in the NE quadrant ($p < 0.001$). The No Landmarks group spent significantly more time in the NE than the Rotated, but significantly less time than the Control group ($p < 0.001$ respectively). These results are displayed in Figure 3.6. As predicted, the Rotated Landmark group spent significantly more time in the SW quadrant than the other two groups ($p < 0.001$). This would be where the platform would have been located, should the arena be rotated along with the landmarks.

Each group was then analysed for a quadrant preference using a repeated-measures ANOVA. There was a large overall significant effect found for quadrant within the Control group ($F_{3, 27} = 66.2$, $p < 0.001$, effect size = 0.88). Bonferroni corrected t-tests revealed that this group spent significantly more time in the NE quadrant than any other ($p \leq 0.001$ for NW, SE

and SW). There was also a large significant effect found for quadrant for the Rotated Landmarks group ($F_{3, 27} = 21.1$, $p < 0.001$, effect size = 0.7). Bonferroni corrected t-tests revealed that the group spent significantly more time in the SW quadrant over both northern quadrants ($p = 0.001$ for NW and NE). The SW quadrant is where the platform would have been located if it had also been rotated alongside the landmarks. Though the group did not prefer the SW (76.2% +/- 10.1%) quadrant over the SE (20.5% +/- 8.3%); the result is reasonably close to significance ($p = 0.082$) and the clear mean differences were noted (also see Figure 3.6). There was a small significant effect for quadrant for the No Landmarks group ($F_{3, 27} = 4.9$, $p = 0.08$, effect size = 0.35). However, Bonferroni corrected t-tests only revealed that there was significantly more amount of time spent ($p = 0.009$) in the SW (31.9% +/- 3.2%) quadrant than the NW (16.1% +/- 1.7%). The No Landmark group seemed to display no specifically strong quadrant preference, particularly not one over all others. There seemed to be a more evenly distributed searching pattern (see Figure 3.6). These results indicate that humans, much like animals, rely on landmarks to successfully navigate an environment.

3.6 (a)

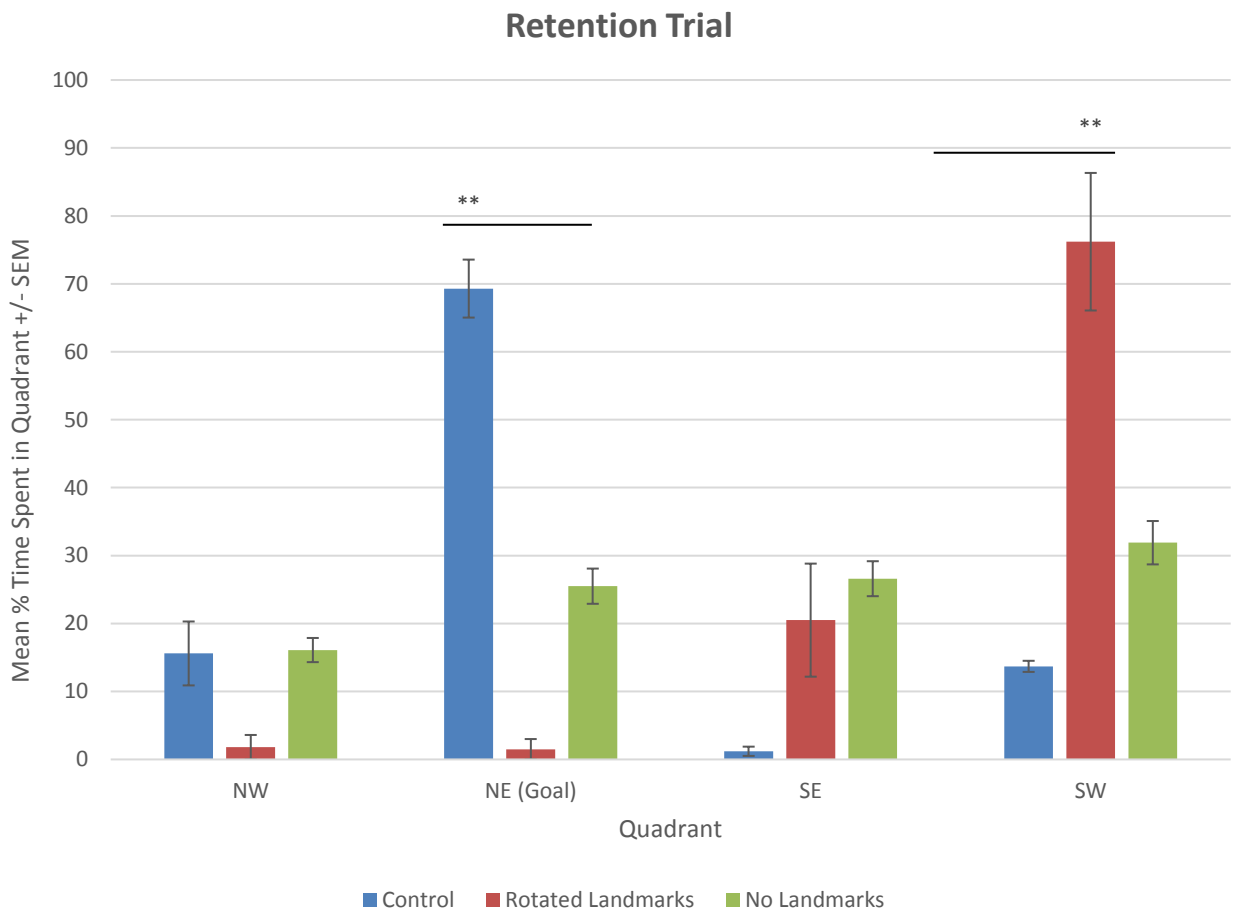
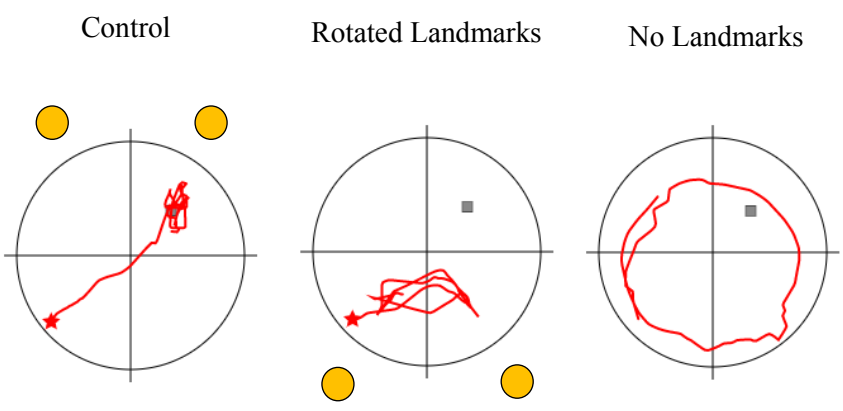


Figure 3.6(a): (Above) Bar chart displaying the mean percentage time and standard error of the mean spent in each quadrant (NW, NE (invisible target), SE and SW) by each group (Control, Rotated Landmark, and No Landmark) in Experiment 1. *(b):* (Below) Displayed are tracks recorded from a selected participant from each group, to reflect the path taken by each group in Experiment 1. Note there was no target present duing this phase.

3.6 (b)



3.4.3 Self-Reported Feedback & Strategy

As the current experiment was a control experiment, it was useful to examine how easy or difficult participants found NavWell to use. Participants responded to a standard Likert scale question as outlined in the general methods chapter. The total number of participants in this experiment was thirty, with all responding to the feedback questionnaire. The percentage of each reported difficulty level is displayed in Figure 3.7.

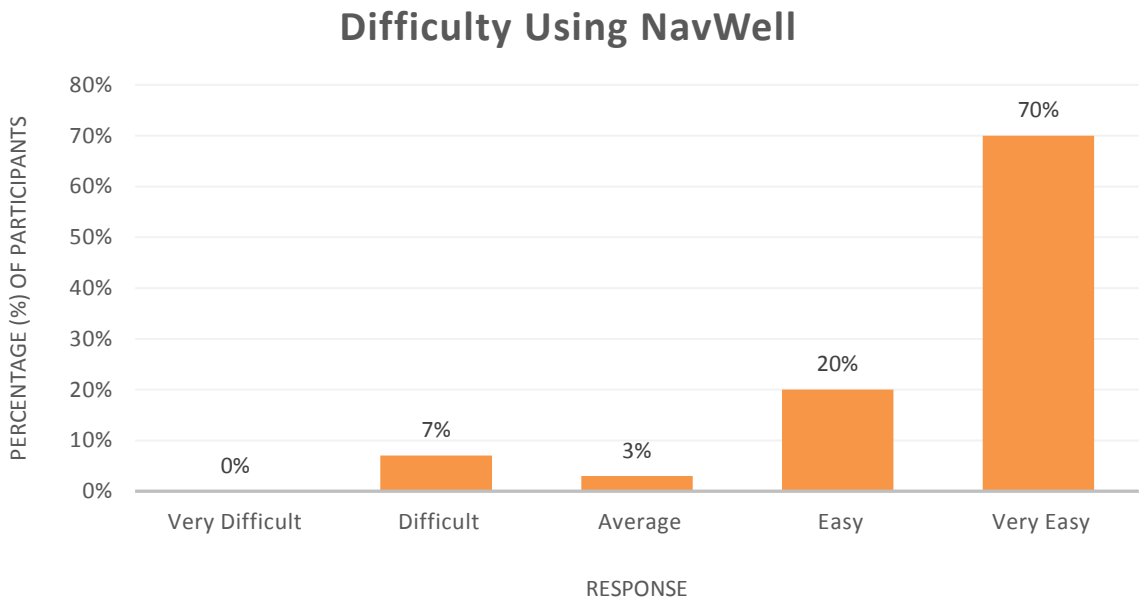


Figure 3.7: Percentage of total participants (n = 30) for each self-reported difficulty level available on the Likert scale.

As displayed in the above figure, approximately 97% of participants rated the software as easy or very easy to use. This provides good feedback for the further development of NavWell, but also indicates that the large majority of behavioural data are derived from intentional and motivated navigation. Any impairments or inability to navigate when using NavWell can be explained by the environment, and not a participant's difficulty learning the motion controls or

understanding the task. However, this may only be applicable to those within this experimental samples mean age and may differ if the average age is increased.

All thirty participants also responded to the open-ended question following their retention trial. A frequency count was carried out on each of the participants' responses. Words that were being searched for were coded and defined before conducting the frequency counts. The first frequency count was to examine whether individuals with the landmarks present during retention, were using the light as part of their search strategy (twenty participants in total). The category "light cue" was coded under several words stemming from the broad definition of a "circular light cue" and from a general overview of the responses made (see Figure 3.8 for codes). Repeated codes were not counted, only one code/sub-code was necessary in a single response to be considered as contributing to the category. Analysis revealed that of twenty total participants who could use the lights, 95% mentioned using the lights when describing their strategy (see Table 3.1). This would demonstrate that the searching behaviour appearing to be controlled by the landmarks present in NavWell, is in fact the intended strategy selected by participants. Therefore, when available, landmarks will be readily incorporated into ones navigational strategy.

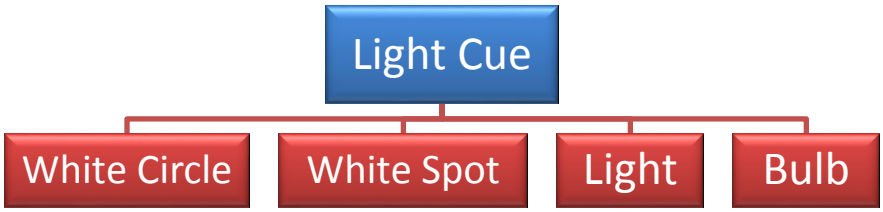


Figure 3.8: Word codes used for frequency analysis of cue utilisation in retention trial search strategy. Main theme word is **Light** and word/word strings coded under Light are "Light, White Circle, White Spot, and Bulb".

Table 3.1: Results from the frequency analysis on the use of cues/landmarks in a search strategy during the retention trial in Experiment 1.

Category	Total Participants Included	Code Count	Percentage	Theme
Mentioning the use of lights as a strategy	20	19	95%	Light Cue

Further analysis was completed on the dataset containing the No Landmarks group. Frequency analysis was carried out on the total of 10 participants. An emerging theme was "Distance Estimation" which was defined by reoccurring words relating to estimating distance using the pool wall. The coded words for the theme of Distance Estimation are displayed in Figure 3.9. The results would indicate that 50% of participants with no landmarks (see Table 3.2) present in their environment attempted to use the other stable features in NavWell to estimate a reliable position of the platform, e.g. "*Tried to use the distance the original platform was from the wall and go around the pool in a circle*". Interestingly, 60% of the participants in this group mentioned attempting to incorporate the lights into their strategy (see Table 3.3), even though the lights were not present, e.g. "*On previous trials there were two lights on upper rim – the platform was near the one on the right. I had the feeling I was placed in maze at the far end, between where the lights were. When this failed, I swam in the following pattern*". This participant sketched the search pattern they followed during their retention trial, which is displayed in Figure 3.10.

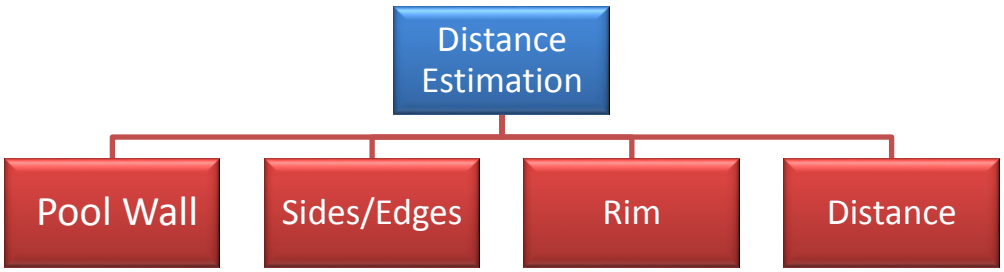


Figure 3.9: Word codes used for frequency analysis of No Landmark group during retention trial. Main theme is **Distance Estimation** and word/word strings coded under this are "Pool Wall, Sides/Edges, Rim, and Distance".

Table 3.2: Results from the frequency analysis of participants mentioning an alternative search strategy when previously stable landmarks (lights) are not available in Experiment 1.

Category	Code Count	Percentage	Theme
What strategy was used when lights not available	10	50%	Distance Estimation

Table 3.3: Results from the frequency analysis of participants mentioning an alternative search strategy involving recall or use of the lights when they are not available in Experiment 1.

Category	Code Count	Percentage	Theme
What strategy was used when lights not available	10	60%	Light Cue

Figure 3.10: Search pattern sketched by the participant mentioned above demonstrating a randomised searching strategy but containing evidence of an estimation of distance (Left). The participant also sketched where they believed they had started the retention trial from, and the location of the lights (Right).

These results indicate that the behavioural data recorded by NavWell, which represents an impairment in navigation throughout the No Landmark group, can be described by participants struggling to change from their original learning strategy. It is important to highlight that this impairment demonstrated during retention is not due to difficulty understanding the task or using the NavWell motion controls, as 90% of participants found the software "Easy" or "Very Easy" to use. Having associated the platforms location with the position of the landmarks, they did not learn any other specific details about the environment, causing uncertainty regarding their starting position, orientation, distance and direction from the goal. Additionally, the self-report data supports the use of the landmarks available in NavWell. The lights in this experiment, were incorporated into almost all of the participants searching strategies, particularly those in the groups (control and rotated) that searched most accurately.

3.5 Discussion

From the current experiment, it is evident that the virtual landmarks present in NavWell exert the same control over navigational learning and recall as they would do in animal studies (see Morris, 1981, Cheng et al., 1994 & Rodrigo et al., 1997). Groups with landmarks present in this experiment, search in relation to the landmarks, and demonstrating significant preference for a quadrant of the pool. However, the group with no landmarks, have no preference, and do not search in one quadrant more than any other. Thus, illustrating that the removal of previously learned landmarks, impairs the use of an accurate searching strategy. This is an important finding, as it supports the use of NavWell as a successful translation of the Morris Water Maze for use with humans. These results are in line with the current literature of human landmark use (Caduff & Timpf, 2008; Chan et al., 2012) and this experiment was essential, in order to clarify that the landmarks in our software have the same impact. Therefore, this not only infers that NavWell can be used to examine allocentric navigation in humans, but also, can be directly compared to animal studies that utilise the MWM.

By incorporating visual landmarks into a navigational search strategy, rats can gain valuable information about a goals location. Distal landmarks can provide direction, distance and orientation information about the spatial location of an individual and their goal. Reliable landmarks that remain constant have been shown to allow successful learning about a spatial layout (Collet et al., 1986) and largely facilitate accurate wayfinding in honeybees, rats and pigeons (Cartwright & Collet, 1983; Biegler & Morris, 1993; Holland, 2003). From the results of Experiment 1, it is clear that participants could navigate to the platform location in relation to the two stable landmarks available, based on escape latency and path length reductions during learning. During retention, the Control group search in the corresponding NE quadrant

significantly more than any other quadrant of the pool. Additionally, they searched for a significantly larger amount of time compared to the other two groups. The searching behaviour of the Rotated group suggests they altered their strategy to search in line with the 180˚ rotation of the landmarks. This is evident from the significant amount of time spent in the southern quadrants of the maze by the Rotated group. Interestingly, they preferred the corresponding SW quadrant over any of the northern quadrants, which is the quadrant the platform would be in, were it also rotated 180˚ alongside the landmarks. Participants altered their search strategy based on the cues, even when the cues were rotated, similar to rodents (see Morris, 1981, Harvey, Brant & Commins, 2009). Humans also demonstrate that when landmarks are shifted, they search with a different assumed orientation (see Zhao & Warren, 2015). Similar to other human studies, participants based their perceived orientation on the landmark position (Lee, Shusterman, Spelke, 2006; Caffò et al., 2018). We believe this is the case here, as participants were unaware the environment has been manipulated. Therefore, allocentric information retained about the environment is applied to searching as normal and is evidently dependent on the stability of landmarks.

The No Landmark group searched with no pattern and favoured no important quadrant of the pool. The group did, however, spend more time in the SW quadrant (starting position) over the NW. As there is no clear pattern or preference, this difference could be explained by participants lingering in the starting quadrant, in order to devise a new search strategy. The participants in this group demonstrated an impairment in searching, as they have learned the environment in relation to the two landmarks available. As these were removed, there is was orientation, direction or distance information available. This results in a change of searching behaviour, similar to rats navigating in darkness (Maaswinkel and Whishaw 1999; Whishaw, Hines & Wallace, 2001; Stuchlik & Bures, 2002) or humans when landmarks are not stable or available (Tlauka & Wilson, 1994; Byrne & Crawford, 2010). Foo et al. (2005) carried out

similar landmark manipulations during virtual navigation. Participants could only accurately navigate (using a shortcut) if they were guided by learned landmarks. The evidence for a switch in strategy was further supported by the qualitative data, illustrating that 50% of these participants, attempted to switch search strategy. The new strategy involved some form of distance/direction estimation. Therefore, the group demonstrated no clear knowledge of the platform position after a strategy switch could be explained by the need for both (albeit virtual) visual and vestibular information for recall (see McGauran, O'Mara & Commins, 2005; Kealy et al., 2008). The virtual distance and directional information have been learnt in relation to the landmarks, which may be why 60% of participants attempted to recall the positions of the lights. But the lights also provided information on starting position and orientation. Therefore, participants struggled to apply a useful search strategy, as all information and associations have been learned in relation to the landmarks.

The purpose of this chapter was to establish whether humans construct cue-goal associations during navigation and are capable of recalling these associations. Additionally, we set out to establish whether our virtual water maze; NavWell, produces navigational behaviours similar to its non-virtual rodent equivalent. Conclusively, the above is true, humans are heavily reliant on the landmarks in NavWell, similar to the current literature from rodent studies and other VMWMs. However, the complexity of these associations and how they are formed cannot be explored without manipulating individual cues. Thus, in the next chapter, we will attempt to uncover the in-depth features of retention and search strategy implication, following landmark learning. This can now be done following Experiment 1, as we now know that the NavWell landmarks exert the same level of navigational control as they would in any experimental design involving a Morris water maze.

Chapter 4:

An Examination of the Influence of Landmark Salience during Human Virtual Navigation

4.1 Introduction

The term landmark generally refers to any visual stimulus in an environment that stably relates to a specific location (see Chan, Baumann, Bellgrove & Mattingley, 2012; Epstein, Patai, Julian & Spiers, 2017). Landmark-related information is a valuable resource during navigation, and reliance on their stability, recognition and relationships with other landmarks are all essential components for successful navigation. The learning and recall of environmental landmarks comprise an important part of the previously discussed cognitive map theory of navigation (O'Keefe & Nadel, 1978). According to this theory, landmarks are integrated into a topographical representation of the environment, which can then be recalled and manipulated to facilitate navigation. However, associative learning theory would predict that landmarks are not treated equally. According to associative theory, certain landmarks or a configuration of landmarks can become associated with a goal location (Pearce 2002; see section 1.4). It has been argued that landmark *salience* is vital in deciding which landmarks will be integrated into certain learning strategies (Rodrigo et al., 2014; Farina et al., 2015; Commins & Fey, 2019).

Salience can be defined as "relatively distinct, prominent or obvious features compared to other features" of a landmark (Caduff & Timpf, 2008, p. 250). One frequently reported feature of landmark saliency is the *proximity of a landmark to a goal*. It has been shown that landmarks closer to the goal demonstrate greater control over navigation accuracy compared to distal landmarks when rats and humans are tested with one or the other, following training with both sets (Artigas et al., 2005; Chamizo et al., 2006; Commins & Fey, 2019). Human learning strategies differed in a VWM, depending on what distance the landmarks were from the goal (Chamizo et al., 2011). For example, Sansa, Aznar-Casanova, Rodriguez & Chamizo (2019) demonstrated a generalisation decrement across landmark retention performance with

distance. Humans trained with two proximal landmarks in a VWM performed worse when attempting to navigate to a goal location when two additional landmarks (distal) were added; compared to a group tested with the original two landmarks (proximal). Therefore, it is clear proximity elicits greater accuracy when learning about an environment or specific landmark-goal relationships.

Further research on the influence of salience has focused on the featural components of landmarks (such as shape, size and brightness). Chamizo et al. (2006) demonstrated that a combination of large and proximal cue features results in the most accurate navigation from rats in water maze. Interestingly, Farina et al. (2015) illustrated that rats demonstrate a preference for brighter but distal landmarks, over nearer but dimmer landmarks. Conversely, Chamizo et al. (2006) found that brighter or bigger landmarks were preferred over others regardless of their relative distance from the goal. However, when both landmarks possess analogous appearance, but one is closer to the goal than the other, the rats performed best with the distal landmark (Farina et al., 2015). Cue salience is a key feature of associative theory. Featural elements of landmarks (such as size) contribute greater *associative strength* (and in turn, promote a stronger association between the landmark and goal; see Rescorla & Wager, 1972). In contrast to cognitive mapping theory, landmarks are not treated equally, some cues acquire more importance when navigating due to visual features or proximity.

Though similar effects of proximity have been revealed in humans (Redhead & Hamilton, 2007; 2009), the influence of landmark saliency in humans has been relatively unexplored. However, some research from pedestrian navigation has shown that humans prefer to navigate streets with mobile navigation devices using landmarks rather than any other information (such as distance and street names; May, Ross, Bayer & Tarkiainen, 2003). Researchers in the field claim that pedestrian-focused navigation systems should rely on landmarks rather than distance/direction-based instructions like vehicle GPS (Rousell & Zipf,

2017). How these landmarks appear or are relative to the desired route influence how beneficial they are at providing accurate navigational aid (Richter & Duckham, 2008; Rousell & Zipf, 2017). Seemingly, humans prefer landmarks that offer more information about a route and are simply easier to remember. But the visual components of a landmark that humans utilise when navigating is still unclear. How humans choose which landmarks become associated with a goal and whether animal preference is comparable to human landmark preference when learning is still debated and will be a focus of this chapter.

4.2 Experiment 2

Animals show no difference in retention ability when both landmarks remain stable during a probe trial (Commins & Fey, 2019). Manipulating landmark proximity and brightness has been shown to influence navigation ability. Increasing proximity of a landmark to a goal improves search accuracy during retention with animals (Chamizo & Rodrigo, 2004; Rodrigo et al., 2014). This result has been replicated in humans using a virtual water maze (Artigas, et al., 2005; Chamizo et al., 2011). Different cue brightness levels have demonstrated no effect on acquisition for animals (Chamizo et al., 2006; Commins & Fey, 2019). However, when one of the cues were removed for retention, animals searched incorrectly when the bright cue was removed, even after repeated training (Farina et al., 2015).

The previous experiment showed that participants using NavWell rely on the landmarks to find the target; as removal and/or rotation of the cues led to impairment and/or a respective shift in search trajectory (also see Stackman, Lora & Williams, 2012). However, it is unknown what aspect of the landmarks are deemed important and if this reveals something about the theoretical basis of spatial learning. One method used in behavioural neuroscience to understand what is learned regarding cues, is to remove a subset during retrieval. This method has been used previously to explore cue learning strategies in honeybees (Cartwright and Collett 1982), gerbils (Collett, 1987), rats (Rodrigo et al., 2014) and humans (Foo et al., 2005; Redhead & Hamilton, 2009). Therefore, using this methodology, the aim of Experiment 2 was to examine three main questions: Do humans treat all cues equally during learning and can they distinguish between cues? Does one cue demonstrate more control than the other; do they compete for associative strength? We know (from section 4.1 above) that both proximity and

brightness (to be examined here) are important in determining salience. However, which component of cue salience, if any, demonstrates more control over navigation for humans?

4.2.1 Methods

Participants

All participants (n = 4) were recruited from the population at Maynooth University using the recruitment procedures outlined in Chapter 2. The sample for this experiment was composed of fourteen females and sixteen males with a mean age of 28.3 +/- 2.3. Prior to beginning the experiment, each participant was randomly assigned to one of three landmark conditions (n = 14 per group): Control (male = 7; female = 7), Bright (male = 6; female = 8) or Dim (male = 6; female = 8). These conditions are described below.

Apparatus

The NavWell software was employed, following the guidelines set out in the general methods chapter.

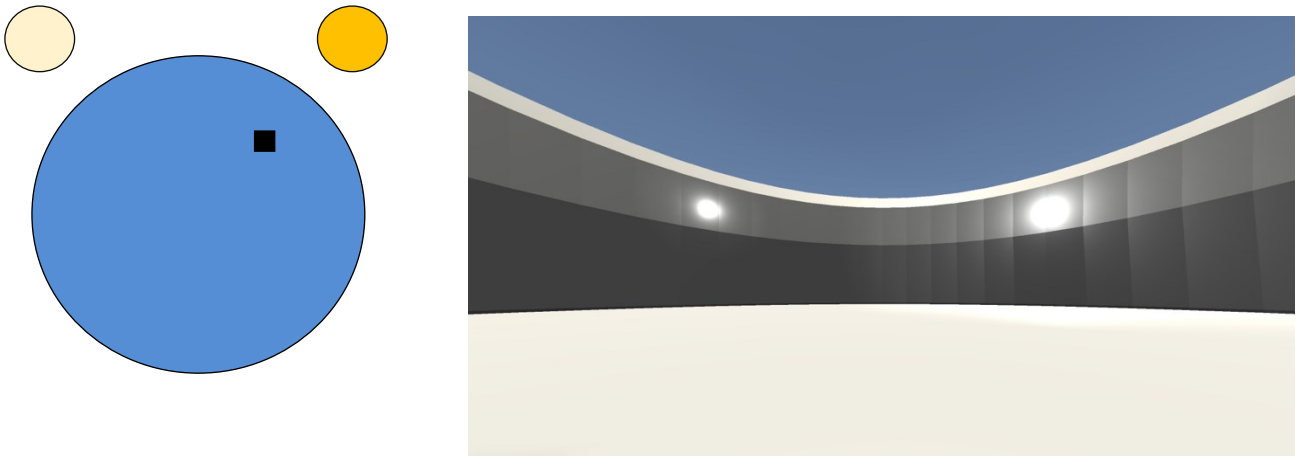
Virtual Environment

The environment designed for this experiment was kept constant for acquisition and retention trials. The only difference was the layout of the landmarks for each condition during the retention trial. The environment was the medium-sized arena as outlined in the Chapter 2. Two medium-sized circular virtual lights of differing luminescence levels acted as landmarks. These

were positioned on the NW and NE walls for the acquisition phase; with the brighter light (80% luminescence level) on the NE wall and the dim light (20% luminescence level) on the NW wall (see Figure 4.1a). Participants could move freely within the pool, with a first-person viewpoint. Hidden under the surface of the pool was the square target which was 15% of the total arena size (see general methods chapter). The target for the current experiment was in the NE quadrant, as displayed in Figure 4.1(a).

The retention phase environmental layout is the same as above, but the landmarks made available differed depending on the group. The availability of landmarks during the retention trial for each group are schematically represented in Figure 4.1(b). For the Control group both the bright and dim landmark were available during retention. The Bright group only had the bright light available. This means that the dim light was missing, and the only landmark was on the NE wall. Reversely, for the Dim group, only the dimmer light was available. This means that the bright light was missing, and the only landmark was on the NW wall.

4.1 (a)



4.1 (b)

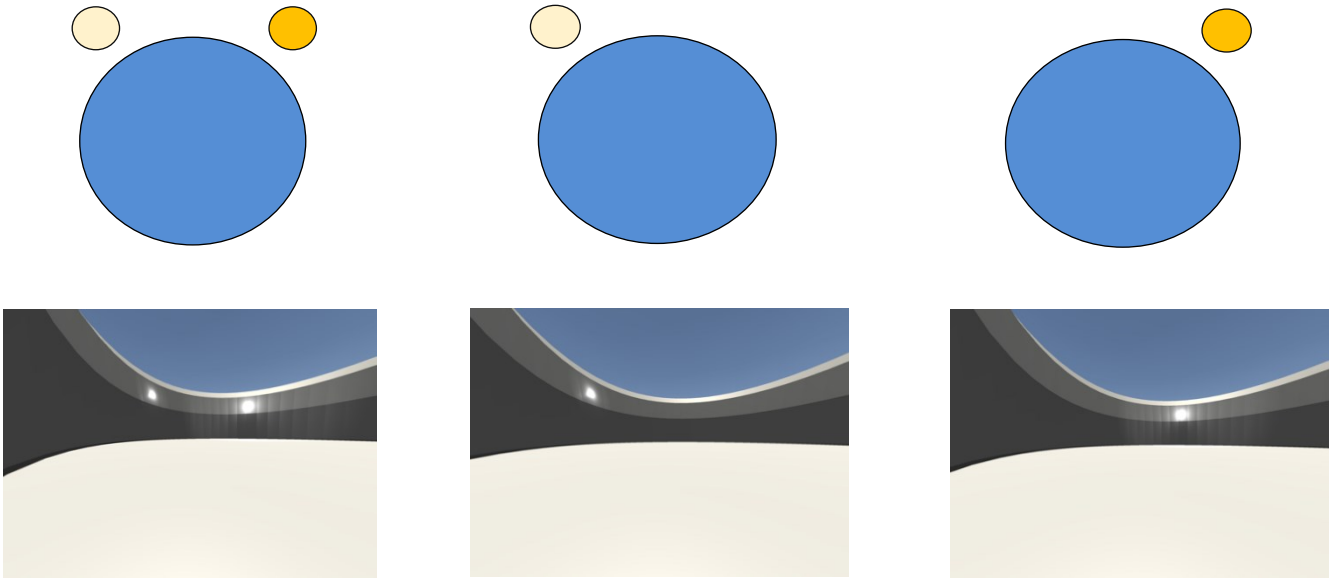


Figure 4.1(a): A schematic representation and screenshot of the environment and landmark layout for the acquisition trials. The left light (20% brightness level) and right light (80% brightness level) are illustrated by the dim and dark yellow circles respectively. The platform location is denoted by the black square (in the NE quadrant). *(b)*: A schematic representation and screenshots of the virtual environment and the landmark positions for each group during the retention trial; Control (Left), Bright (Middle) and Dim (Right). The lights (20% or 80% brightness levels) are represented by the dim and dark yellow circles respectively. The platform position is not marked as it has been removed for the retention trial.

Procedure

Participants were presented with an information sheet (Appendix I) and informed consent was obtained via an attached consent form (Appendix II). The procedure was the same as Experiment 1 (also see General Methods). Following the retention trial, participants filled out the questionnaire outlined in the general methods section (see Appendix III). Finally, the participants were debriefed. The experimenter explained the purpose of the study and why there was no platform present in the retention trial. Following this, participants were thanked for their participation.

Data Analysis

All behavioural data was automatically collected from NavWell during each trial. All data was imported into a Microsoft Excel spreadsheet. Graphical representations of the data were constructed using Microsoft Excel. The data was then exported into IBM SPSS version 25 for analysis. A significance level of $p < 0.05$ was adopted for statistical tests.

Data retrieved from the cognitive tests were scored accordingly. All preliminary analysis and graphical representation of the cognitive tests were completed using Microsoft Excel. Group comparisons were completed using the relevant ANOVA procedures in IBM SPSS version 25. Data retrieved from the open-ended question data were analysed using a form of qualitative content analysis (see Hsieh & Shannon, 2005 and General Methods chapter). This followed the same procedure as Experiment 1. For graphical representations, $p \leq 0.05$ is represented by a single asterisk (*) and $p \leq 0.001$ is represented by two asterisks (**).

4.2.2 Results

Control Tasks

We initially compared the three experimental groups on the various control tasks. A one-way ANOVA was used to examine differences between the groups for the predicted full scale IQ obtained via the NART ($F_{2, 39} = 0.271$, $p = 0.764$) and the time taken to complete TMTb-a test ($F_{2, 39} = 0.179$, $p = 0.837$). Age was also explored with no difference (see Table 4.1). The mean, standard error of the mean (SEM) and corresponding *p*-values are displayed in Table 4.1 below.

Table 4.1: Mean and standard error for age, NART and TMT scores for each group in Experiment 2. The *p*-values are the results of a one-way ANOVA comparing the listed factor between groups.

	Age	*NART*	*TMT a*	*TMT b*	*TMT b-a*
Control	28	91.6	22.6	46	23.4
(SEM)	3.9	2.18	3.97	6.4	3
Bright	28.1	90.3	26.7	48.5	21.9
(SEM)	4.0	2.03	2.9	5.8	3.95
Dim	28.8	89.6	28.3	48.4	20.1
(SEM)	4.2	1.9	3	5.5	4.5
***p*-values**	0.914	0.764	0.461	0.940	0.837

Participant scores on the RAVLT were also comparable, with no difference between the groups on any of the RAVLT trials ($F_{2, 39} = 0.006$, p = 0.994, effect size = 0) with no Trial X Group interaction effect ($F_{12, 234} = 0.806$, p = 0.644, effect size = 0.04). There was a main effect for Trial ($F_{6, 234} = 102.3$, $p < 0.001$, effect size = 0.724). Thus, a typical short-term memory retention and interference curve across groups can be seen in Figure 4.2 below (see methods chapter for further information on the RAVLT). From these results all experimental groups were well-matched for cognitive ability.

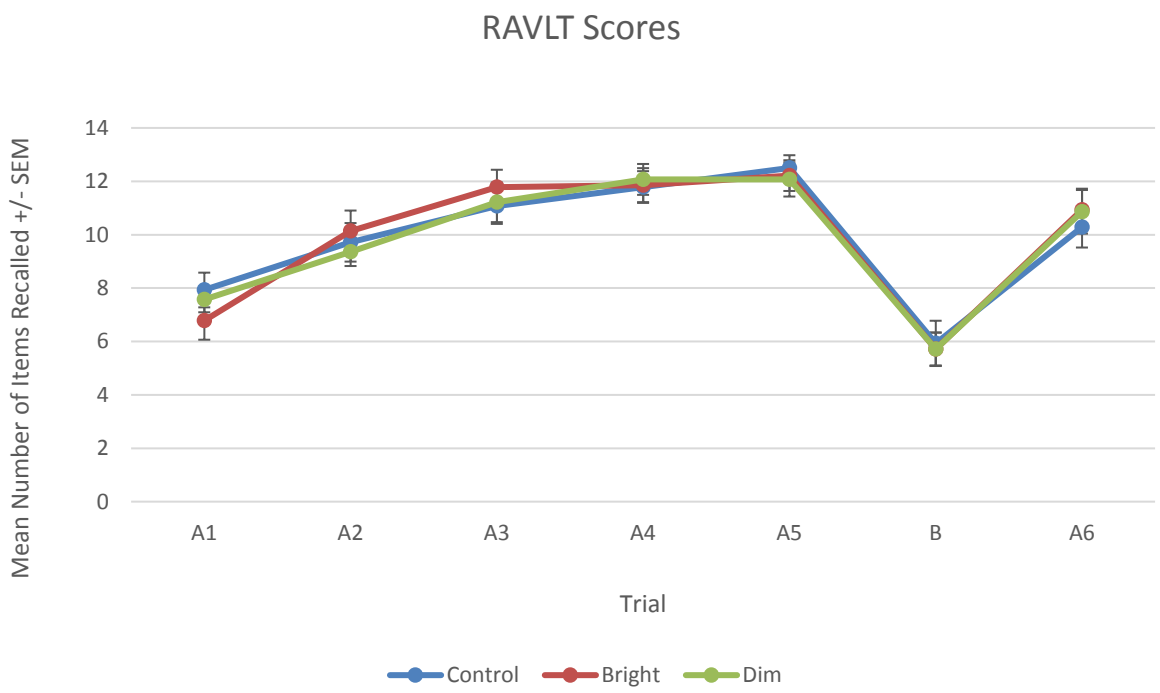


Figure 4.2: Mean number of items recalled on each trial of the RAVLT for all three experimental groups in Experiment 2.

Acquisition Phase

The escape latency of participants during the acquisition phase was analysed using a 3 (Group) x 12 (Trial) mixed-factorial repeated measures ANOVA. Escape latency can be defined by the amount of time it takes a participant to find the target (with a maximum of sixty seconds). There was an overall significant decrease in escape latency across the twelve trials ($F_{11, 429}$ = 34.924, $p < 0.001$, effect size = 0.472; see Figure 4.3). Bonferroni-corrected t-tests revealed that participants were significantly faster ($p < 0.001$) at locating the target on Trial 11 (18 +/- 1.3s) and Trial 12 (17.5 +/- 1.7s) compared to Trial 1 (50.7 +/- 2.4s) and Trial 2 (36.5 +/- 3.2s). As expected, all participants trained in a similar fashion and successfully learned the task, reducing their escape times across trials (see Figure 4.4). There was no difference in escape latency between the groups ($F_{2, 39}$ = 2.002, p = 0.149, effect size = 0.093), there was also no Trial X Group interaction effect ($F_{22, 429}$ = 1.087, p = 0.358, effect size = 0.53).

The path length of participants during the acquisition phase was analysed using the same statistical test. The path lengths were measured by NavWell in Virtual Metres (Vm) and are a measure of the total distance travelled by a participant throughout each sixty second trial. There was a significant effect for Trial across all participants ($F_{11, 429}$ = 36.737, $p < 0.001$, effect size = 0.485; see Figure 4.5). Bonferroni corrected t-tests revealed that participants travelled significantly shorter distances ($p < 0.001$) in Trial 11 (59.3 +/- 1.9 Vm) and Trial 12 (59.4 +/- 2.4 Vm) compared to Trial 1 (146.6 +/- 11.8 Vm) and Trial 2 (121.8 +/- 8.7). Participants successfully learned the target location, reducing their path length and taking a more direct route across trials (see Figure 4.6). Therefore, as would be expected, no difference in path length between the groups was found ($F_{2, 39}$ = 0.784, p = 0.463, effect size = 0.039) and there was no Group X Trial interaction ($F_{22, 429}$ = 0.848, p = 0.665, effect size = 0.042). Therefore, regardless to which group they were allocated, participants reduced their completion time and

path distance across the twelve trials. This would imply that all participants successfully learned the platform location.

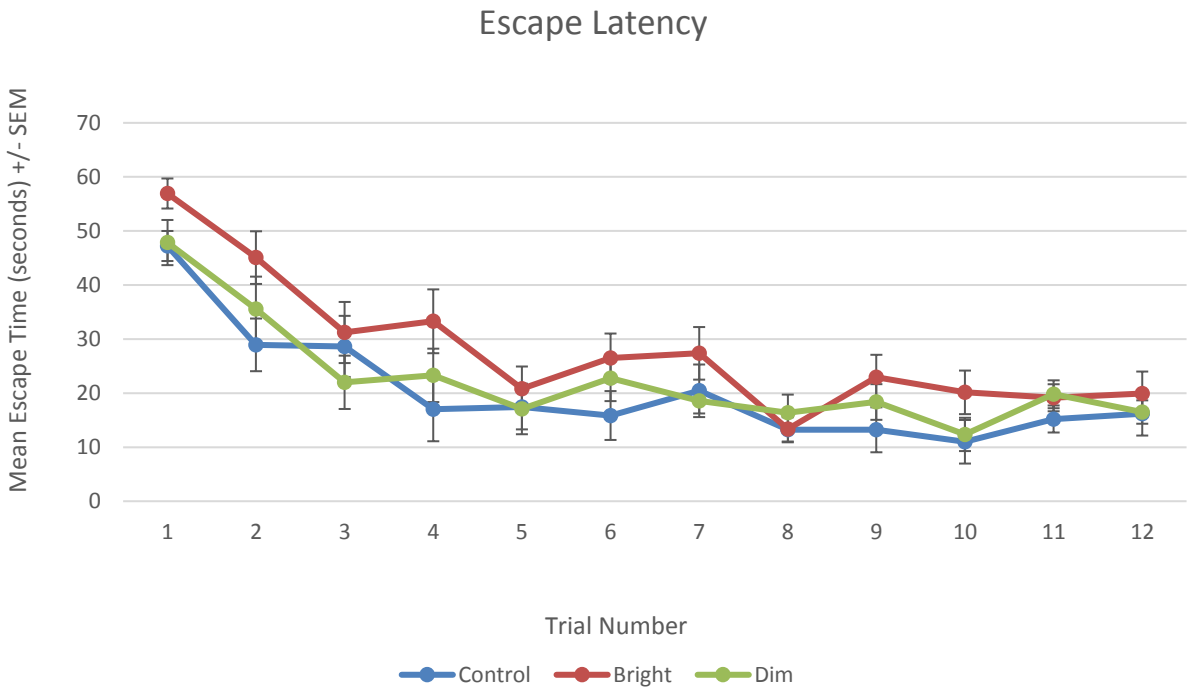


Figure 4.3: Mean time taken to locate the target (escape latency) for all participants in each group. All participant groups show a similar learning curve with a reduction in escape times across trials.

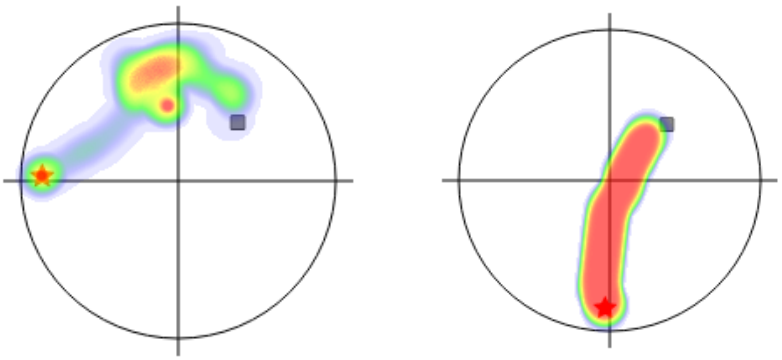


Figure 4.4: An example of movement time heatmaps from a selected participants earlier trial (left) compared to their final trial (right) during the acquisition phase. There is a faster navigation time in the final trial compared to a more dispersed and longer search time in an earlier trial.

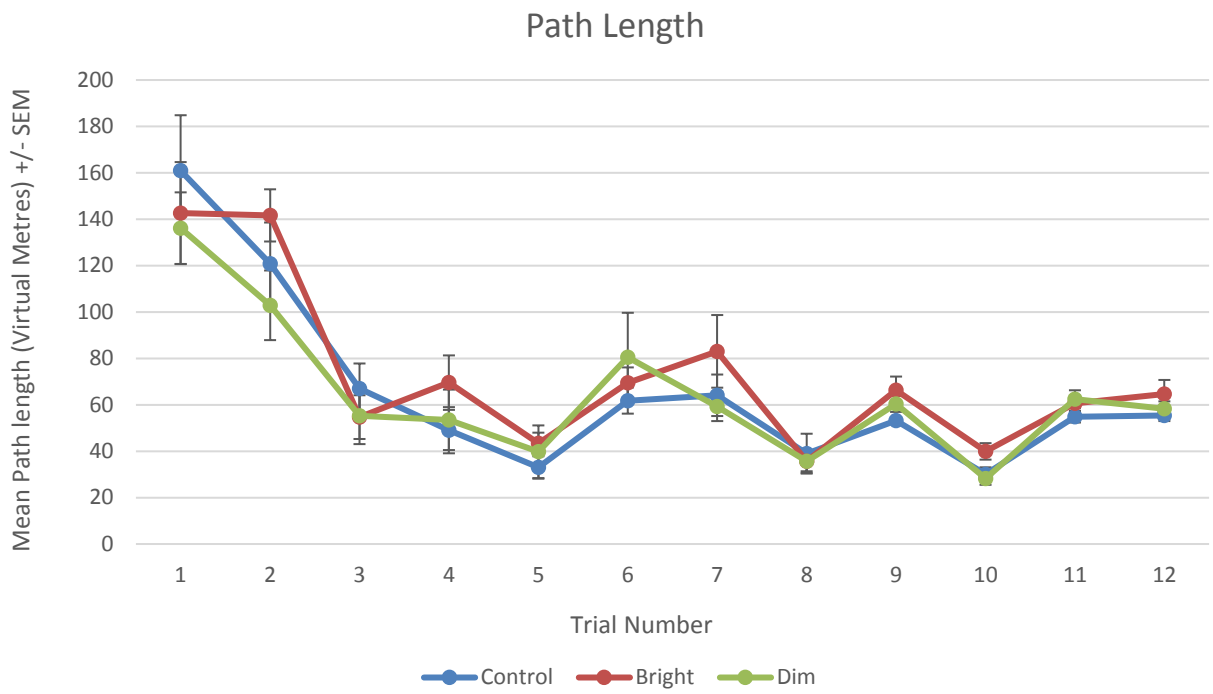


Figure 4.5: Mean path distances for all participants in each group. All participants demonstrate a similar learning curve, showing a decrease in route length across multiple trials.

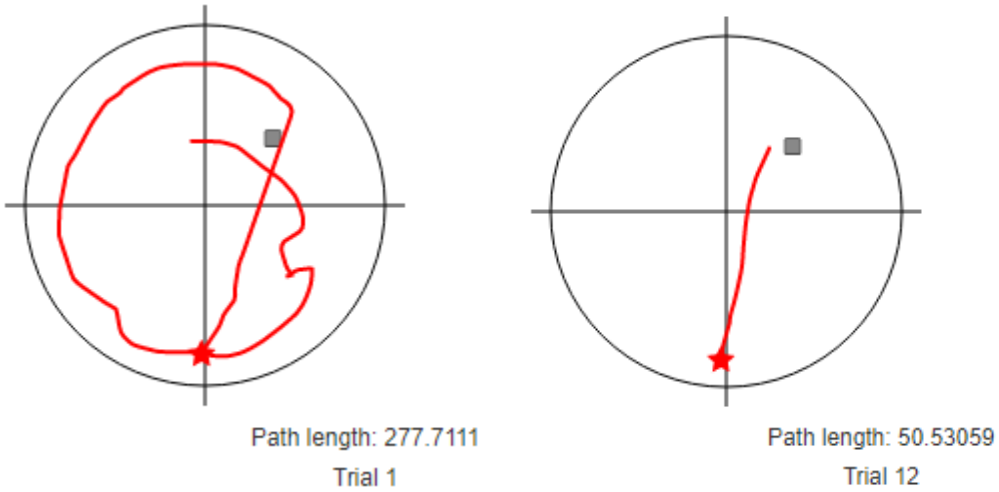


Figure 4.6: An example of movement paths from a selected participant during Experiment 2 showing a decrease in path length from Trial 1 compared to Trial 12. The route taken to the target location also becomes more direct by Trial 12.

Retention Phase

To investigate the effect of cue salience on navigation, we compared how the Bright and Dim groups navigated compared to the Control group and when compared to each other. For this, the percentage of time spent in each quadrant was recorded for all three groups. The data was analysed using a 3 (Group) X 4 (Quadrant) repeated-measures ANOVA. There was a main effect for quadrant ($F_{3, 117} = 47.7$, $p < 0.001$, effect size = 0.55). Although there was no significant group effect ($F_{2, 39} = 0.652$, $p = 0.527$, effect size = 0.032) there was a large significant interaction effect between group and quadrant ($F_{6, 117} = 0.784$, $p < 0.001$, effect size = 0.544).

This interaction effect was explored by a series of one-way ANOVA's on each quadrant of the arena. Focusing on the NE target quadrant, the Dim group spent significantly less time here (15%; $p < 0.001$) compared to the Control (61.8%) and Bright (60%) respectively. Furthermore, the Dim group spent significantly more time (53%) in the NW quadrant ($p < 0.001$) than the Control (18%) and Bright (9%) groups. The NW quadrant is where the only available landmark was positioned for the dim groups. There was no difference between the groups for time spent in the SE ($p = 0.317$) or SW ($p = 0.062$) quadrants. These results are displayed in Figure 4.7.

Each group was then analysed for a quadrant preference using a repeated-measures ANOVA. There was a large overall significant effect found for quadrant for the **Control** group ($F_{3, 39} = 51.22$, $p < 0.001$, effect size = 0.798). Bonferroni corrected t-tests revealed that this group spent significantly more time in the NE quadrant than any other ($p \leq 0.001$ for NW, SE and SW). There was also a large significant effect found for quadrant for the Bright group ($F_{3, 39} = 30.866$, $p < 0.001$, effect size = 0.704). Bonferroni corrected t-tests revealed that the Bright group spent significantly more time in the NE quadrant over the NW ($p < 0.001$), SE ($p <$

0.001) and SW ($p = 0.006$) quadrants. This would imply that the **Bright** group had a significant search preference for the target quadrant. Interestingly, there was a significant effect for quadrant for the **Dim** group ($F_{3, 39} = 20.477$, $p < 0.001$, effect size = 0.612). Bonferroni corrected t-tests revealed that there was significantly more time spent in the NW quadrant (52.85% +/- 5.4%) than the NE, SE and SW quadrants ($p = 0.009$, $p < 0.001$ and $p = 0.028$ respectively). The Dim group showed a significant preference for searching in the NW quadrant rather than the target quadrant. The NW quadrant was the only quadrant with an available visual cue for this group during retention.

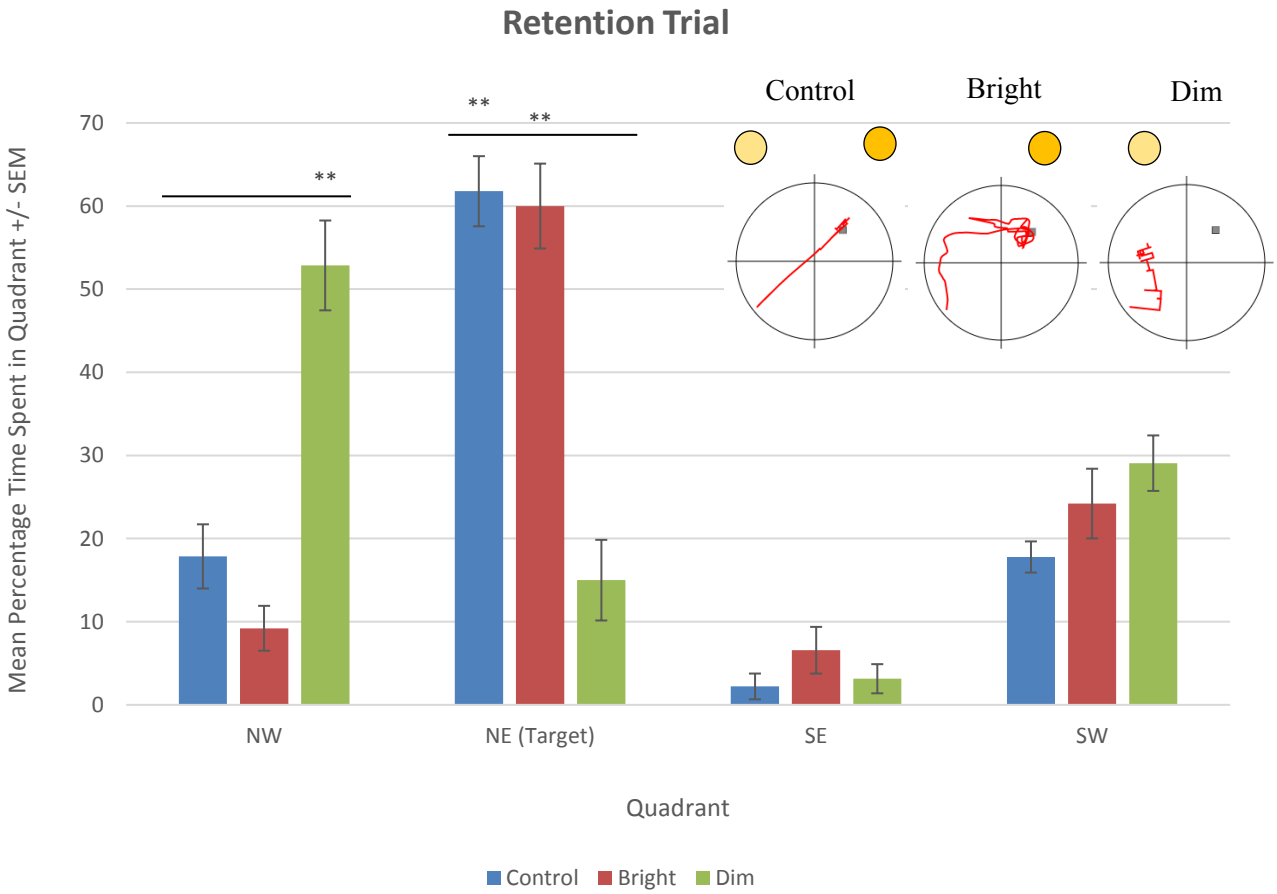


Figure 4.7: Bar chart displaying the mean percentage time and standard error of the mean spent in each quadrant (NW, NE (invisible target), SE and SW) by each group (Control, Bright, and Dim) in Experiment 2. Also displayed are track recording from a selected participant from each group, to display the path travelled by each group.

Self-reported Search Strategy

All forty-two participants responded to the open-ended question following their retention trial (see Appendix III). Frequency counts were carried out as previous for Experiment 1. The frequency counts were assessed as a form of content analysis, which is described in the general methods chapter. The first frequency count was to examine whether participants were using the light cues available during retention (either both, dim only or bright only). The theme "light cue" was coded under several words stemming from the broad definition of a "circular light cue" and from a general overview of the responses made (see Figure 4.8 for codes). Repeated codes were not counted, only one code/sub-code was necessary in a single response to be considered as contributing to the theme. Analysis revealed that of a total 42 participants who had lights present during retention, 85.7% mentioned using the light/lights when describing their strategy (see Table 4.2). This would imply that participants attempted to use any available lights that were in the environment during the retention trial.

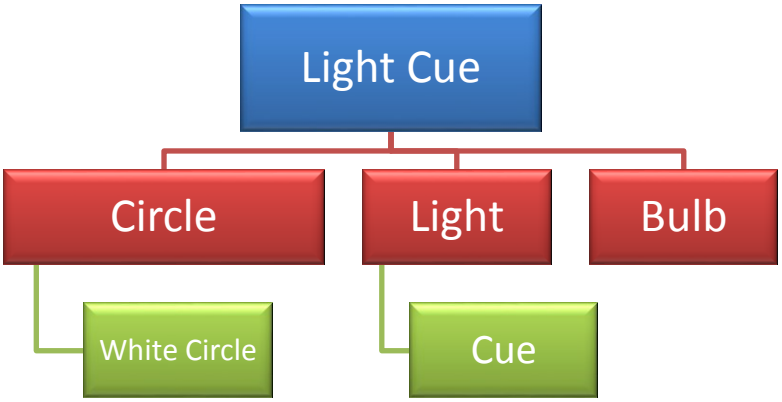


Figure 4.8: Word code used for frequency analysis of cue utilisation in retention trial search strategy. Main theme word is **Light Cue** and word/word strings coded under Light Cue are Light (including cue/light cue), Circle (including white circle/dot) and Bulb (including synonyms).

Table 4.2: Results from the self-report frequency analysis for Experiment 2. It is based on the use of cues/landmarks in a search strategy during the retention trial.

Category	Code Count	Percentage	Theme
Mentioning the use of lights as a strategy	42	85.7%	Light Cue

Further analysis focused on the two groups in which the bright near light was available during retention (Control and Bright). This was to explore whether those who had the bright light, mentioned using that light specifically. Frequency analysis was then carried out on these twenty-eight participants, counting references to the codes under "Bright Light" which are displayed in Figure 4.9. The results indicated that 57% of participants made specific reference to using the bright light in their search strategy (see Table 4.2). Interestingly, of this 57%, a total of 50% made specific reference to its position (mentioning codes such as *right-hand* light and light *in front of* the platform, see Table 4.2). It seems participants had successfully learned to distinguish the bright light from the dim light and incorporated it into their strategy.

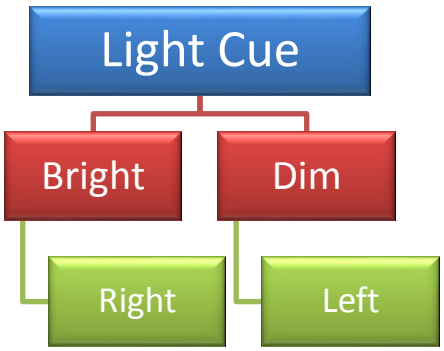


Figure 4.9: Word codes used for frequency analysis of light preference. Coded under the original theme of "Light Cue" the additional themes are "**Bright**" and "**Dim**". Words coded to refer to these themes are: Bright (including bigger/right) and Dim (including smaller/left) as the words refer to specific element that differentiates one light from the other.

Furthermore, another frequency analysis was run on the Dim group, to examine whether participants acknowledged they were using the dim light or not. The words coded under the theme "Dim Light" are also displayed in Figure 4.9. However, the analysis revealed that only 1 participant (7%) acknowledged that the light they were using in their strategy was the dim light. This participant made specific reference to both lights, and how they were attempting to locate the platform: "*I looked for the dim light and then moved to the right of it where I thought the brighter light would be*". A similar strategy by another participant in the Dim group was also described: "*I used the only cue* (dim) *as a start point ... when that was unsuccessful, I moved to the right of the cue where the other cue might have been in the first trials*". It seemed most referred to the dim light as just "*the light*", with over 78% of participants including "*the light*" in their strategy. It seems that the group with the dim light did not learn much about its relation to the platform. Participants may have attempted to incorporate the light into a search strategy but were uncertain of where the target was in relation to this light.

4.2.3 Brief Discussion

All participants successfully learned the platform location over the twelve learning trials. During the retention tests, the Control and Bright groups preferred the target quadrant, while participants in the Dim group favoured the NW quadrant. Unlike the rats in Farina et al. (2015) the group with the dim far cue did not demonstrate impairment, but instead searched in the quadrant that contained the dim light. It may be possible that participants found it difficult to differentiate between the two lights. This is further supported by the low number of participants mentioning the difference in brightness during the self-report measure. Participants seemed to refer to the lights by their directional properties (right and left). Therefore, it is possible that participants misinterpreted their orientation in the environment and mistook what was the dim cue as the bright cue, as they had nothing to compare to its saliency (during retention). This would explain why they search in a similar position, but in a different quadrant.

Furthermore, it may also be possible that the proximity of the bright cue to the target location, caused the bright cue to acquire beacon-like control over navigation. Participants navigated towards the light they *associated* to be nearest to the platform. When the beacon cue was removed, the dim group (having nothing to compare the available cue to) applied the same strategy and navigated towards the only available light. In terms of associative learning, it could be suggested that the strength of the association learned between the bright cue and the target overshadowed learning about the dim cues' relationship with the target. Hence, when presented with the dim cue in isolation, participants struggle to recall how it fed into their overall strategy. This would also indicate presence of an elemental learning strategy over a configural strategy.

Finally, it may be fair to suggest that proximity and not brightness controls what humans learn about landmarks. Though in this experiment the brighter cue is the closest,

therefore we cannot say for definite that brightness acquires greater control. A repetition of this experiment with the cue positions reversed (bright cue further from target) may reveal whether participants are learning more about a cues proximity, rather than featural salience. This will be the main focus of Experiment 3.

4.3 Experiment 3

The aim of experiment 3 is to further demonstrate that humans could learn to navigate using cue proximity rather than brightness, whilst controlling for brightness. In this instance, the position of the dim and bright cue was reversed, meaning the bright light was further (NW) from the target platform (NE). All participants were trained with both cues and then tested with either both or one of the cues. Farina et al. (2015) demonstrated that rats tested with a bright near cue could navigate accurately during retention. The groups tested with the dim far cue showed no quadrant preference above chance level. As human participants in Experiment 2 tested with the bright near cue were most accurate when searching for the hidden target, it would be expected that participants tested here with the *bright* cue further from the target will be the most accurate, should greater salience be acquired by cue brightness. Unexpected results from Experiment 2 also revealed that the group with the dim cue *also* had a quadrant preference, but they were not searching in the correct location. Therefore, it would be expected that the group with the dim near in this experiment, may also develop a search strategy, demonstrating a preference for a specific quadrant. Should the dim group here be more accurate than the bright group, we can confirm that cue proximity acquires greater control over navigation.

4.3.1 Methods

Participants

All participants (n = 40) were recruited from the population at Maynooth University using the recruitment procedures outlined in Chapter 2. The sample for this experiment was composed of twenty-one females and nineteen males with a mean age of 25.7 +/- 1.57. Prior to beginning the experiment, each participant was randomly assigned to one of three landmark conditions: Control (n = 14; male = 7; female = 7), Bright (n = 13; male = 7; female = 6) or Dim (n = 13; male = 5; female = 8).

Apparatus

The NavWell software was employed similar to Experiment 1 & 2 (see General Methods section).

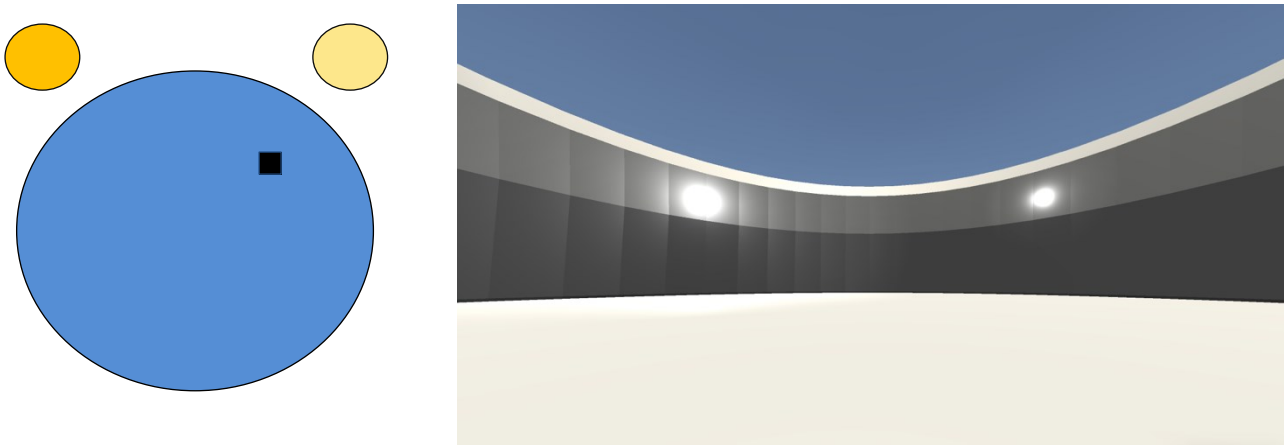
Virtual Environment

The environment designed for this experiment was kept constant for acquisition and retention trials. The only difference was the layout of the landmarks for each condition during the retention trial. The environment was the medium-sized arena as outlined in the Chapter 2. Two medium-sized circular virtual lights of differing luminescence levels acted as landmarks. These were positioned on the NW and NE walls for the acquisition phase; with the brighter light (80% luminescence level) on the NW wall and the dim light (20% luminescence level) on the NE wall (see Figure 4.10). Participants could move freely within the pool, with a first-person viewpoint. Hidden under the surface of the pool was a square target (15% of the pool size; see

General Methods chapter). The platform for the current experiment was in the NE quadrant, as displayed in Figure 4.10(a).

The retention phase environmental layout is the same as above, but the landmarks made available differ depending on the group allocated to the participant. The availability of landmarks during the retention trial for each group are schematically represented in Figure 4.10(b). For the Control group both the bright and dim landmark are available, as they were during acquisition. The Bright group only had the bright light available. This means that the dim light was missing, and the only landmark was on the NW wall. Reversely, for the Dim group, only the dimmer light was available. This means that the bright light was missing, and the only landmark was on the NE wall.

4.10 (a)



4.10 (b)

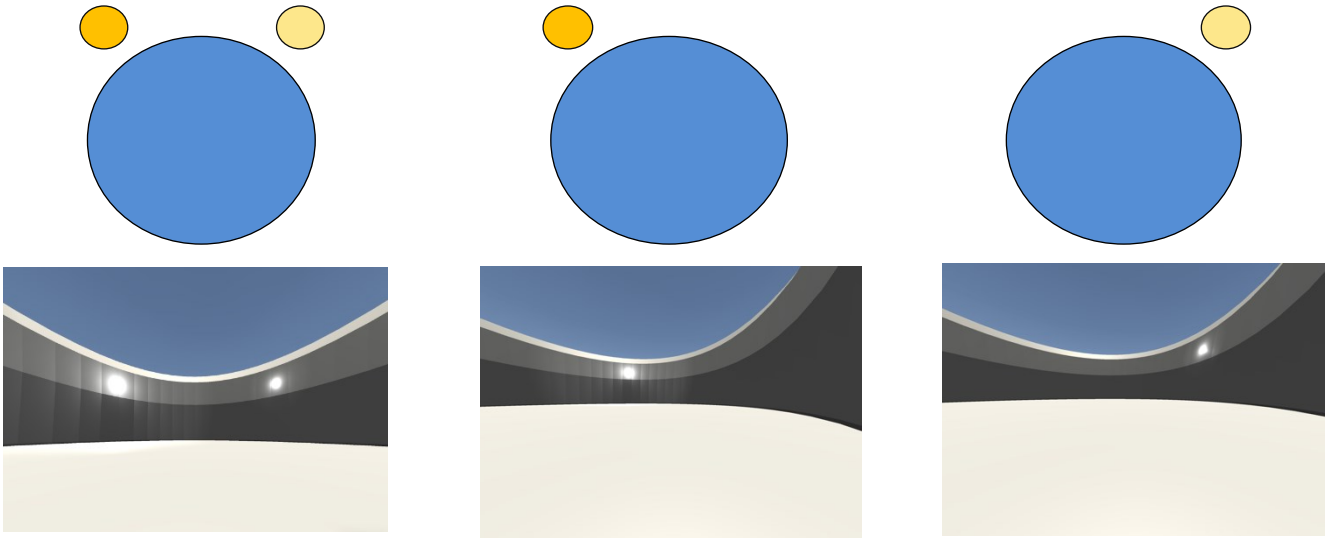


Figure 4.10(a): A schematic representation and screenshot of the environment and landmark layout for the acquisition trials. The bright light (80% brightness level) and dim light (20% brightness level) are illustrated by the dark and dull yellow circles respectively. The target location is denoted by the black square (in the NE quadrant). *(b)*: A schematic representation and screenshots of the virtual environment and the landmark positions for each group during the retention trial; Control (Left), Bright (Middle) and Dim (Right). The lights are represented by the yellow circles. The platform position is not marked as it has been removed for the retention trial.

Procedure

Participants were presented with an information sheet (Appendix I) and informed consent was obtained via an attached consent form (Appendix II). The controls of the software were explained to participants, as well as, the general structure of the experiment. Any questions were answered by the experimenter. The general procedure was the same as outlined in the general methods section. The acquisition phase was the same as outlined and was carried out by all participants. This consisted of 1 block of 12 invisible platform learning trials. Participants started from pseudorandomly assigned starting positions (N, S, E and W) around the edge of the pool. Upon the completion of these twelve trials, all participants were required to participate in some cognitive tests (RAVLT, TMT & NART as outlined in the methods chapter). The purpose of these tests is to ensure there are no cognitive differences between experimental groups. Following the cognitive tests, the participants underwent a retention trial using NavWell once again. This was a single sixty-second trial with no platform present. All participants started from a novel start position, at the midpoint of the SE pool wall. As previously described, this trial had different landmark manipulations depending on group allocation (outlined above under *Virtual Environment*). Finally, the participants were debriefed. The experimenter explained the purpose of the study and why there was no platform present in the retention trial. Following this, participants were thanked for their participation.

Data Analysis

All behavioural data was automatically collected from NavWell during each trial. These data were stored on an online cloud-storage database, labelled by experiment and participant codes. NavWell records the escape latency (time in seconds taken to locate the platform), path length (distance travelled in virtual metres before locating the platform) and the percentage of time

spent in each quadrant. All data was imported into a Microsoft Excel spreadsheet. Graphical representations of the data were constructed using Microsoft Excel. The data was then exported into IBM SPSS version 25 for analysis. A significance level of $p < 0.05$ was adopted for statistical tests. For graphical representations, $p \leq 0.05$ is represented by a single asterisk (*) and $p \leq 0.001$ is represented by two asterisks (**).

Data retrieved from the cognitive tests were scored accordingly. For the Trail Making Test (TMT) the average scores for each section (TMTa and TMTb) were compared across groups. The overall average score (TMT a - b), deemed to be a good determinant of performance (see Bowie & Harvey, 2006) was also compared across groups. For the RAVLT, an average score on each trial for each group was compared. For the NART, the average number of errors were compared across groups. All preliminary analysis and graphical representation of the cognitive tests were completed using Microsoft Excel. Group comparisons were completed using the relevant ANOVA procedures in IBM SPSS version 25.

4.3.2 Results

Control Tasks

We initially compared the three experimental groups on the various control tasks. A one-way ANOVA was used to examine differences between the groups for the predicted full-scale IQ obtained on the NART ($F_{2, 34} = 2.32$, $p = 0.794$) and the time taken to complete TMTb-a test ($F_{2, 34} = 2.43$, $p = 0.104$). No significant difference was found for any measure. We also explored age differences across groups, to which no significant difference was found (see Table 4.3). The mean, standard error of the mean (SEM) and corresponding *p*-values are displayed in Table 4.3 below. RAVLT scores for this experiment were not available due to a technical error.

Table 4.3: Mean and standard error for age, NART and TMT scores for each group in Experiment 3. The *p*-values are the results of a one-way ANOVA comparing the listed factor between groups.

	Age	*NART*	*TMT a*	*TMT b*	*TMT b-a*
Control	23.9	108.8	23.75	39.3	15.55
(SEM)	2.5	1	2	1.2	1.7
Bright	28.8	109.7	23.8	47.5	23.7
(SEM)	2.9	1.2	1.6	4.5	4
Dim	26.4	108.1	21.3	43.1	21.9
(SEM)	2.88	2.5	1.3	5	4.8
p-values	0.731	0.333	0.498	0.302	0.104

Acquisition Phase

The escape latency of participants during the acquisition phase was analysed using a 3 (Group) x 12 (Trial) mixed-factorial repeated measures ANOVA. There was a moderate significant decrease in escape latency across the twelve trials ($F_{11, 407} = 17.9$, $p < 0.001$, effect size = 0.326; see Figure 4.11). Bonferroni-corrected t-tests revealed that participants were significantly faster ($p < 0.001$) at locating the target on Trial 11 (18.25 +/- 2.1s) and Trial 12 (8.8 +/- 1s) compared to Trial 1 (40s +/- 3s). All participants trained in a similar fashion and successfully learned the task, reducing their escape times across trials (see Figure 4.12). There was no difference in escape latency between the groups ($F_{2, 37} = 1.51$, $p = 0.235$, effect size = 0.075), there was also no Trial X Group interaction effect ($F_{22, 407} = 0.957$, $p = 0.519$, effect size = 0.49).

The path length of participants during the acquisition phase was analysed using the same statistical test. There was a significant effect of Trial across all participants ($F_{11, 407} = 18.58$, $p < 0.001$, effect size = 0.334; see Figure 4.13). Bonferroni corrected t-tests revealed that participants travelled significantly shorter distances in Trial 11 (78 +/- 7.2 Vm, $p = 0.004$) and Trial 12 (33.1 +/- 4 Vm, $p < 0.001$) compared to Trial 1 (153.9 +/- 15.1 Vm; see Figure 4.13). Participants successfully learned the target location; their path length reduced and became more direct across trials (see Figure 4.14). There was no difference in path length between the groups ($F_{2, 37} = 0.323$, $p = 0.726$, effect size = 0.017) and there was no Group X Trial interaction ($F_{22, 407} = 0.959$, $p = 0.517$, effect size = 0.049). Therefore, regardless of which group they were allocated, participants reduced their completion time and path distance across the twelve trials, indicating they had learned the targets location.

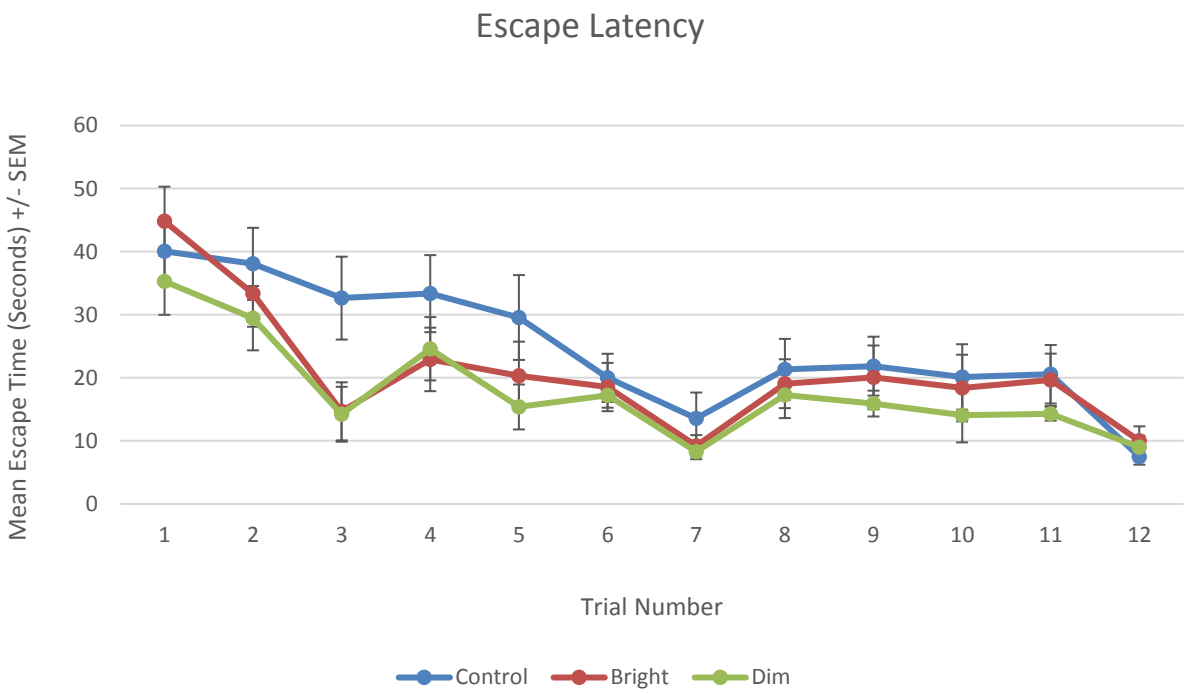


Figure 4.11: Mean time taken to locate the target (escape latency) for all participants in each group. All participant groups show a similar learning curve with a reduction in escape times across trials.

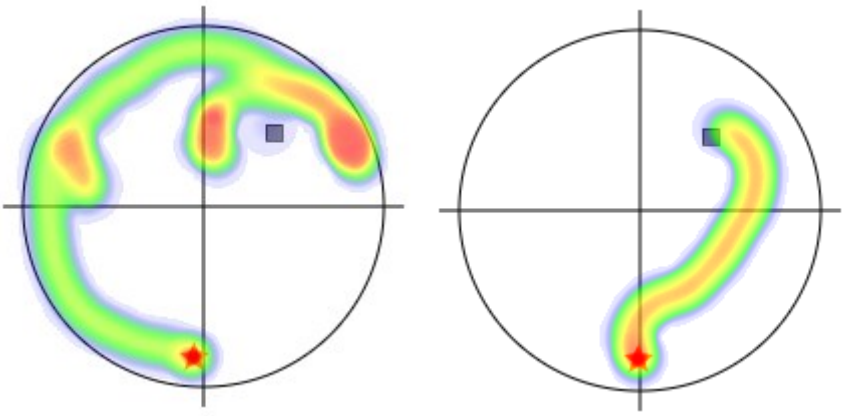


Figure 4.12: Sample movement time heatmaps of a selected participant earlier trial (left) compared to a later trial (right) during the acquisition phase. There is a faster navigation time in the later trial compared to a more dispersed and longer search time in an earlier trial.

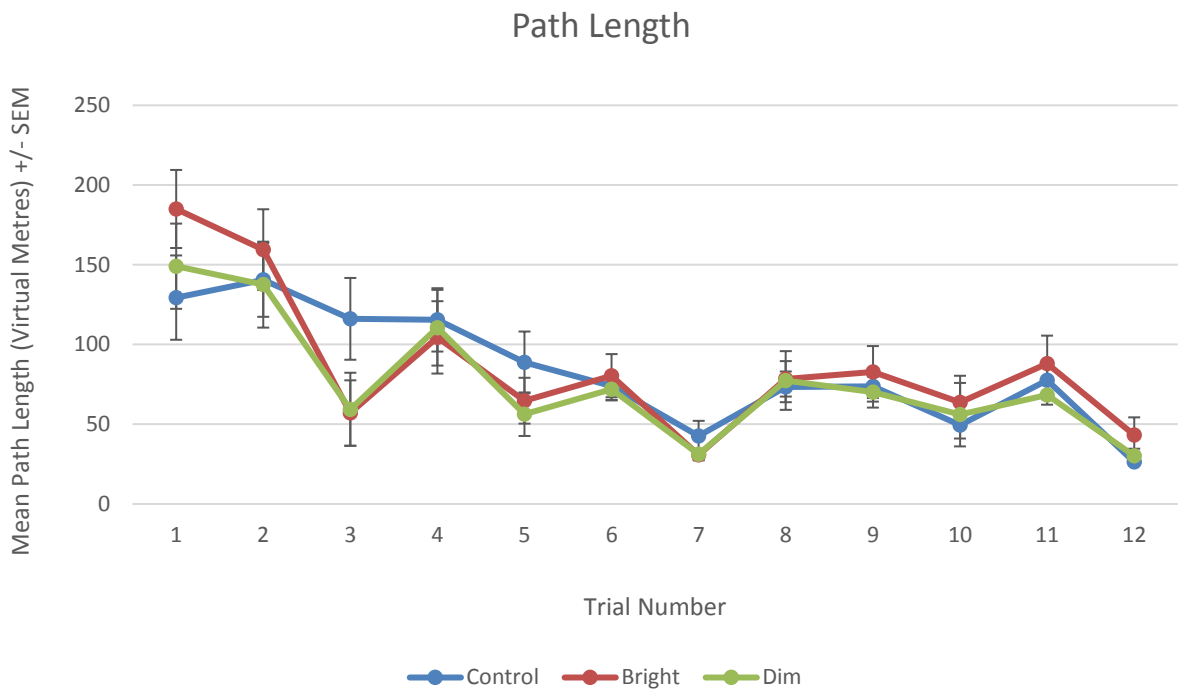


Figure 4.13: Mean path distances for all participants in each group. All participants demonstrate a similar learning curve, showing a decrease in route length across trials.

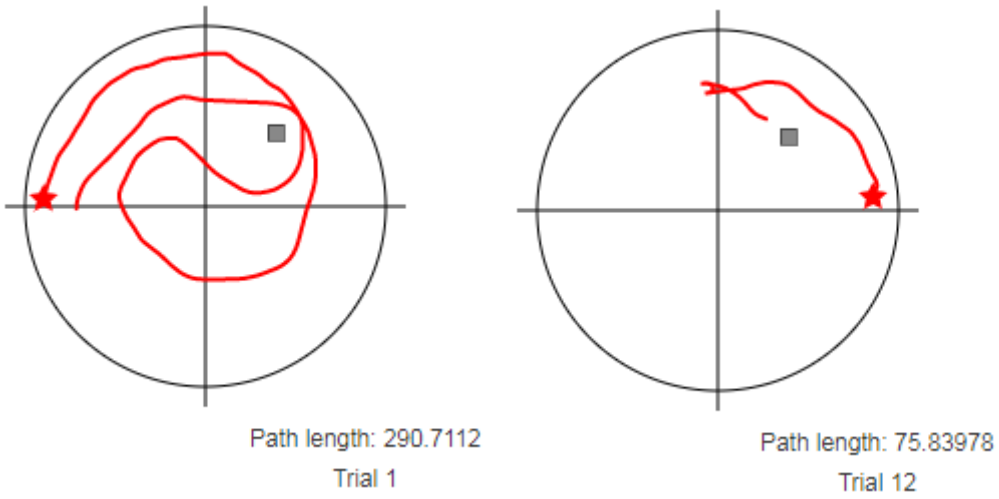


Figure 4.14: Example movement paths for a selected participant showing a decrease in path length from Trial 1 compared to Trial 12. The route taken to the target location also becomes more direct by Trial 12.

Retention Phase

To investigate the effect of cue salience on navigation, we compared how each of the groups navigated with their corresponding landmark(s) compared to each other. For this, the percentage of time spent in each quadrant was recorded for all three groups. The data was analysed using a 3 (Group) X 4 (Quadrant) repeated-measures ANOVA. There was a main effect for quadrant ($F_{3, 111} = 50.72$, $p < 0.001$, effect size = 0.578). There was no significant difference between the groups ($F_{2, 37} = 2.03$, $p = 0.146$, effect size = 0.099), but there was a large significant interaction effect between group and quadrant ($F_{6, 111} = 22.18$, $p < 0.001$, effect size = 0.545).

This interaction effect was explored by a series of one-way ANOVA's on each quadrant of the arena. Focusing on the NE target quadrant, the Control group spent significantly more time here (74.6%; $p < 0.001$) compared to the Bright (23.2%) and Dim (55.3%) groups respectively. The Dim group spent more time in the NE than the Bright group ($p < 0.001$) but spent less time here than the Control group ($p = 0.034$). Furthermore, the Bright group spent significantly more time (55.2%) in the NW quadrant ($p < 0.001$) than the Control (11.6%) and Dim (9.8%) groups. The NW quadrant is where the only available landmark (bright light) was positioned for the Bright group. Additionally, the Dim group spent significantly more time in the SE quadrant than the Control and Bright groups ($p = 0.001$ and $p = 0.004$ respectively). There was no difference between the groups for time spent in the SW ($p = 0.198$) quadrant. These results are displayed in Figure 4.15.

Each group was then analysed for a quadrant preference using a repeated-measures ANOVA. Overall, there was a very large significant effect found for quadrant for the **Control** group ($F_{3, 39} = 121.29$, $p < 0.001$, effect size = 0.903). Bonferroni corrected t-tests revealed that this group spent significantly more time in the NE quadrant than any other ($p \leq 0.001$ for NW,

SE and SW). There was also a moderately significant effect found for quadrant for the **Bright** group ($F_{3, 36} = 17.199$, $p < 0.001$, effect size = 0.589). Bonferroni corrected t-tests revealed that the Bright group spent significantly more time in the NW quadrant over the SE ($p < 0.001$) and SW ($p = 0.007$) quadrants. The mean differences between the NW (55.23% +/- 6.8%) and NE (23.15% +/- 5.2%) are worth noting (see Figure 4.15), though they did not reach statistical significance ($p = 0.101$). There was also a significant effect for quadrant for the **Dim** group ($F_{3, 36} = 14.93$, $p < 0.001$, effect size = 0.554). Bonferroni corrected t-tests revealed that there was significantly more time spent in the NE quadrant than the NW, SE and SW ($p = 0.001$, $p = 0.019$ & $p = 0.013$ respectively). Thus, both the Control and Dim groups preferred the target quadrant (NE) over the other three quadrants. The Bright group preferred the NW over the southern quadrants but not the target quadrant but did spend significantly more time in the NW quadrants than the other two groups.

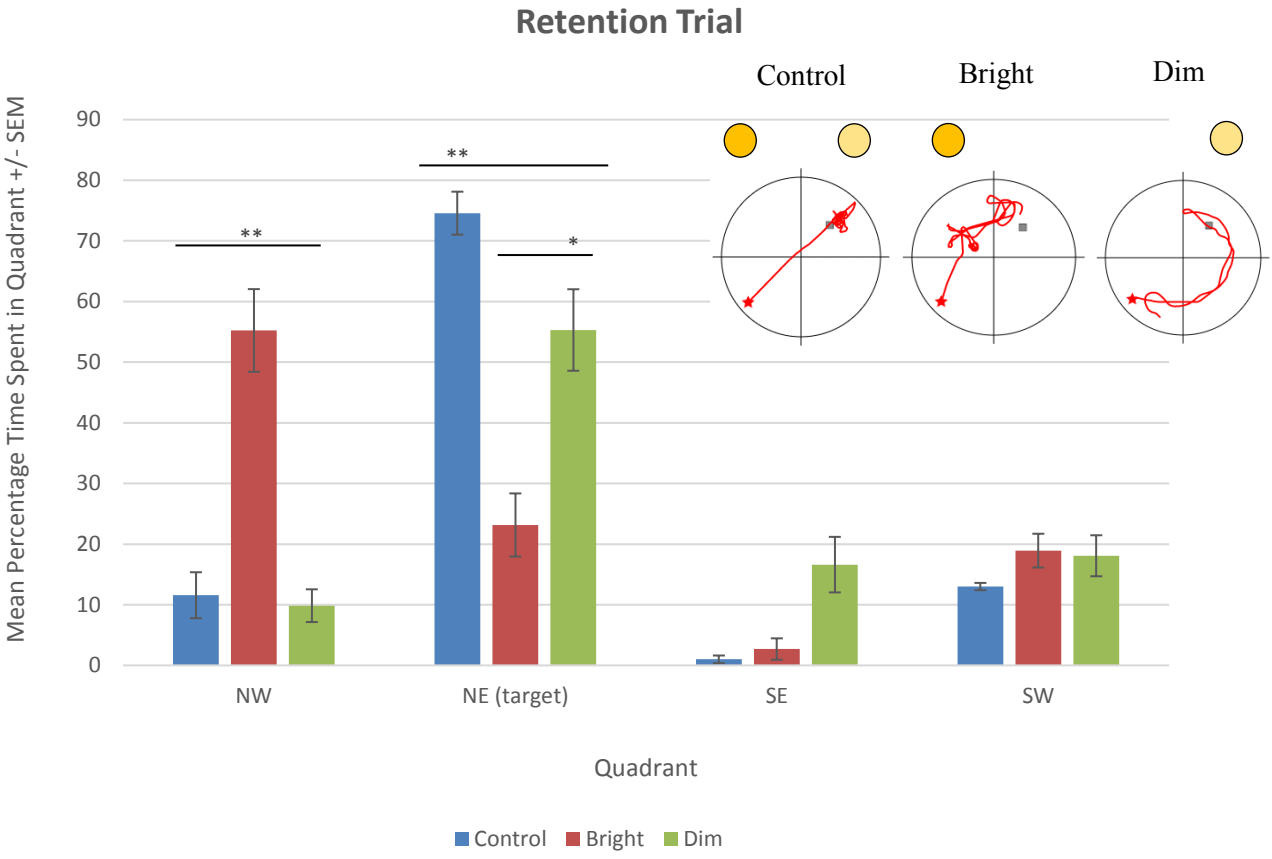


Figure 4.15: Bar chart displaying the mean percentage time and standard error of the mean spent in each quadrant (NW, NE (invisible target), SE and SW) by each group (Control, Bright, and Dim). Also displayed are track recordings from a selected participant from each group, to reflect path taken by each group.

4.3.3 Brief Discussion

The results from the acquisition illustrate that all participants learned the target location during the first twelve trials. During retention, the Control group and the Dim group could successfully recall the target location, demonstrated by their preference to search in the NE quadrant. Interestingly, the Dim group spent significantly less time here than the Control group, even though it was their preferred quadrant. It is possible that participants may have learned the

array of cues (both bright and dim) using a configural strategy, which is why when both cues are present participants are most accurate (i.e. the Control Group). When one of the cues is removed from the array, performance decreased slightly (i.e. the Dim Group). However, it could also be suggested that only the dim (closer) cue was learned (elementally) in relation to the target platform. Therefore, the Controls greater accuracy could be explained by the presence of the second (bright) cue aiding participants' initial orientation in the environment. This would facilitate them to immediately apply their learned search strategy. The Dim group may have taken longer, as they spent some time adjusting their orientation in the environment, before applying their learned elemental strategy. This may explain the greater amount of time spent in the SE quadrant by the Dim group compared to the other two groups, as they adjusted their orientation.

Interestingly, the Bright group searched in the NW quadrant significantly more than the other two groups, spending over half of the sixty-second trial in that quadrant (55.2%). The NW quadrant contained the only cue available in the environment. Perhaps participants did not learn about the visual properties of the landmarks (brightness level) but instead chose to learn about the nearest cue (the dim cue in this experiment). Hence, when this cue was removed, the group applied their search strategy to what they believed was the cue closest to the goal. Perhaps it is not the visual saliency that promotes the use of a beacon-like strategy with the bright cue, but the overall proximity to the goal. When reversed, a similar learning preference for the nearest cue was seen regardless of its brightness. As very little is learned about the other (dim) cue, the same beacon-like strategy is applied when navigating with it in isolation. This suggests that proximity rather than brightness is an essential component of cue salience for humans. Hence, to further explore this idea, it may be vital to explore what occurs in cases of landmarks with equal featural saliency. This will be the key focus point for Experiment 4.

4.4 Experiment 4

The previous two experiments have demonstrated that human participants showed a preference for cues that are nearer to a goal location, ignoring other salient features such as brightness. However, if two cues present with equal visual salience (brightness), is proximity still the overarching factor that determines which cue will be incorporated into their search strategy? As suggested by Farina et al. (2015), rats rely on the most salient cue, rather than the arrangement of cues when navigating. The purpose of Experiment 4 is to closer examine the role of distance in determining a cues salience, and to further support the idea that participants in Experiment 2 and 3 were using the nearest cue to navigate. Participants will be trained with two light cues of equal brightness, one positioned far from the platform (NW) and one positioned near (NE). They will then be tested with either both cues (Control) or one of the two (Near or Far). Should a cues proximity to the goal be the most salient feature, we would expect participants to search under each cue location. If participants are not using a cues proximity to navigate to the target, we would then expect them to be impaired, as there is no defining featural elements to differentiate the two cues. This experiment will reveal whether proximity may play a role in determining a cues salience.

4.4.1 Methods

Participants

A new cohort of participants (n = 42) were recruited from the population at Maynooth University using the recruitment procedures outlined in Chapter 2. The sample for this experiment was composed of 21 males and 21 females with a mean age of 23.07 +/- 1.04. Prior to beginning the experiment, each participant was randomly assigned to one of three landmark conditions (n = 14 per group): Control (male = 7; female = 7), Near (male = 7; female = 7) or Far (male = 7; female = 7). These conditions are described below.

Apparatus

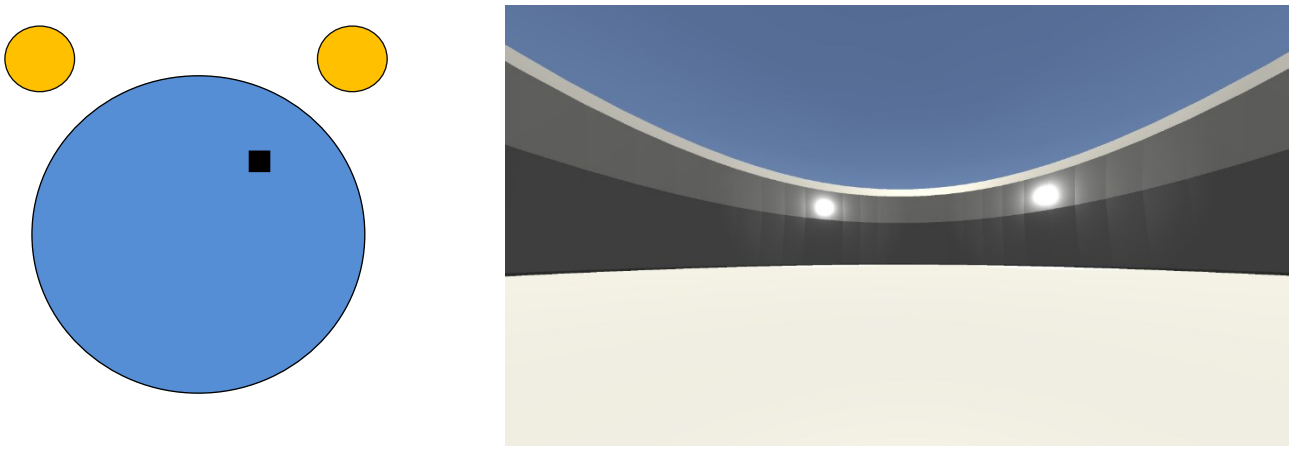
As per previous experiments, the NavWell virtual water maze was employed (see General Methods for details).

Virtual Environment

The environment designed for this experiment was kept constant for acquisition and retention trials. The only difference was the layout of the landmarks for each condition during the retention trial. The environment was the medium-sized arena as outlined in the Chapter 2. Two circular virtual lights of equal luminescence levels (50%), acted as landmarks. These were positioned on the NW (known as 'far') and NE (known as 'near') walls for the acquisition phase (see Figure 4.16). The platform for the current experiment was in the NE quadrant (see general methods), as displayed in Figure 4.16(a).

The retention phase environmental layout is the same as above, but the landmarks made available differed depending on the participants' allocated group. The availability of landmarks during the retention trial for each group are schematically represented in Figure 4.16(b). For the Control group both the near and far landmark are available, as they were during acquisition. The Near group only had the near light available (NE wall light nearest the platform). Reversely, for the Far group, only the far light was available (NW wall light furthest from the platform position).

4.16 (a)



4.16 (b)

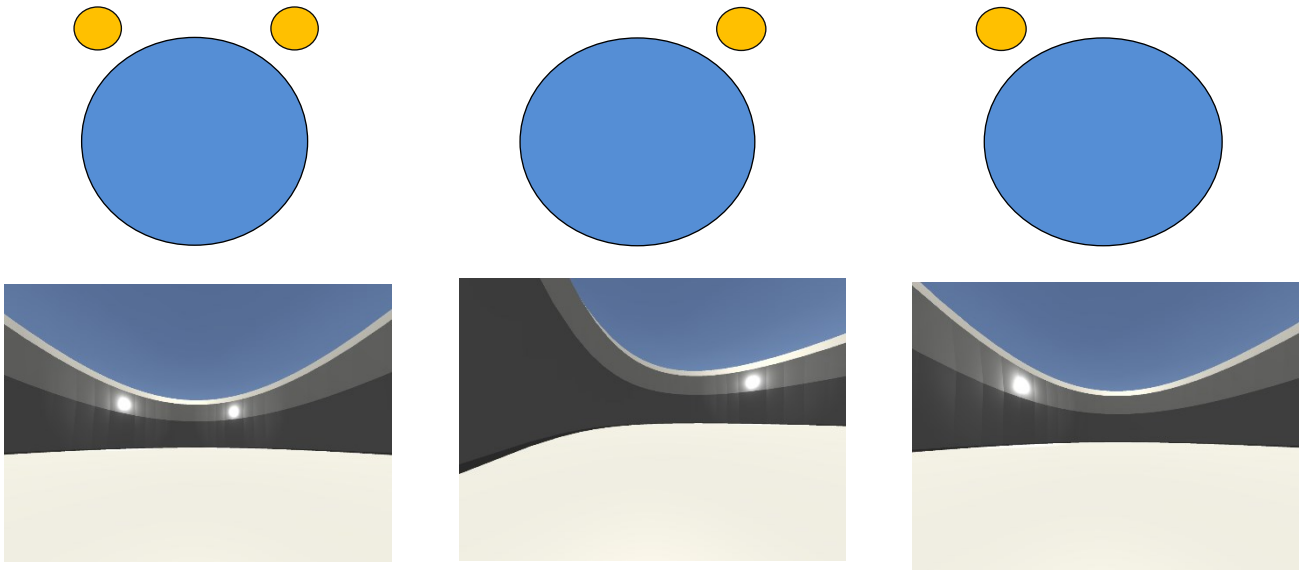


Figure 4.16(a): A schematic representation and screenshot of the environment and landmark layout for the acquisition trials. The two lights (50% brightness level) are illustrated by the dark yellow circles. The platform location is denoted by the black square (in the NE quadrant). *(b)*: A schematic representation and screenshots of the virtual environment and the landmark positions for each group during the retention trial; Control (Left), Near (Middle) and Far (Right). The lights are represented by the dark yellow circles. The platform position is not marked as it has been removed for the retention trial.

Procedure

Participants were presented with an information sheet (Appendix I) and informed consent was obtained via an attached consent form (Appendix II). The general procedure is outlined in the General Methods chapter. The acquisition phase was the same as outlined and was carried out by all participants. This consisted of 1 block of 12 invisible platform learning trials. Participants started from pseudorandomly assigned starting positions (N, S, E and W) around the edge of the pool.

Upon the completion of these twelve trials, all participants were required to participate in a number of cognitive tests (RAVLT, TMT & NART as outlined in the Methods chapter). The purpose of these tests is to ensure there are no cognitive differences between experimental groups. Following the cognitive tests, the participants underwent a retention trial using NavWell once again. This was a single sixty-second trial with no platform present. All participants started from a novel start position, at the midpoint of the SE pool wall. As previously described, this trial had different landmark manipulations depending on group allocation (outlined above under *Virtual Environment*). Finally, the participants were debriefed. The experimenter explained the purpose of the study and why there was no platform present in the retention trial. Following this, participants were thanked for their participation.

Data Analysis

All behavioural data was automatically collected from NavWell during each trial. These data were stored on an online cloud-storage database, labelled by experiment and participant codes. NavWell records the escape latency (time in seconds taken to locate the platform), path length (distance travelled in virtual metres before locating the platform) and the percentage of time spent in each quadrant. All data was imported into a Microsoft Excel spreadsheet. Graphical

representations of the data were constructed using Microsoft Excel. The data was then exported into IBM SPSS version 25 for analysis. A significance level of $p < 0.05$ was adopted for statistical tests. Data retrieved from the cognitive tests were scored as described previously (section 4.2.1). All preliminary analysis and graphical representation of the cognitive tests were also completed using Microsoft Excel. Group comparisons were completed using the relevant ANOVA procedures in IBM SPSS version 25. There was only some data retrieved from the questionnaire for this experiment, which was analysed as described in the General Methods chapter.

4.4.2 Results

Control Tasks

The three experimental groups were compared on the various control tasks. A one-way ANOVA was used to examine differences between the groups for the predicted full-scale IQ score obtained on the NART ($F_{2, 35} = 0.546$, $p = 0.584$) and the time taken to complete TMTb-a test ($F_{2, 39} = 0.343$, $p = 0.712$). No significant difference was found for any measure. We also explored age differences across groups, to which no significant difference was found (see Table 4.4). The mean, standard error of the mean (SEM) and corresponding *p*-values are displayed in Table 4.4 below.

Table 4.4: Mean and standard error for age, NART and TMT scores for each group in Experiment 4. The *p*-values are the results of a one-way ANOVA comparing the listed factor between groups.

	Age	*NART*	*TMT a*	*TMT b*	*TMT b-a*
Control	21.0	104	33.3	58.9	25.7
(SEM)	0.5	1.77	3.5	5.4	2.5
Far	24.0	107	27.2	55.1	28
(SEM)	2.3	1.7	1.9	1.9	4.77
Near	24.0	104	26.6	50.7	24.1
(SEM)	2.0	1.17	1.8	3.2	2.1
***p*-values**	0.305	0.584	0.122	0.449	0.712

Participant scores on the RAVLT were also examined, with no difference between the groups on any of the RAVLT trials ($F_{2, 35} = 1.178$, $p = 0.320$, effect size = 0.063) with no Trial X Group interaction effect ($F_{12, 210} = 0.804$, $p = 0.644$, effect size = 0.044). There was a main effect for Trial (F6, 210 = 128.6, $p < 0.001$, effect size = 0.786). Hence, a typical short-term memory retention and interference curve across groups can be seen in Figure 4.17 below (see methods chapter for further information on the RAVLT). Again, these results would indicate that all experimental groups were well-matched for cognitive ability.

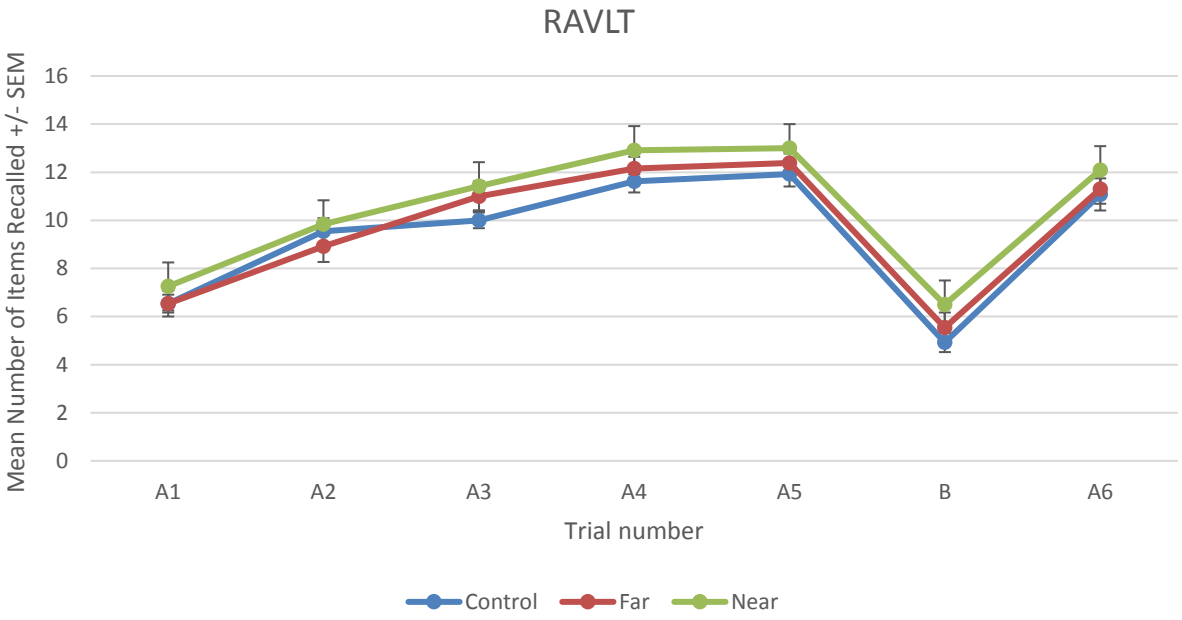


Figure 4.17: Mean number of items recalled on each trial for all three experimental groups in Experiment 4.

Acquisition Phase

The escape latency of participants during the acquisition phase was analysed using a 3 (Group) x 12 (Trial) mixed-factorial repeated measures ANOVA. There was a moderate significant decrease in escape times across the twelve trials ($F_{11, 429} = 19.61$, $p < 0.001$, effect size = 0.335; see Figure 4.18). Bonferroni-corrected t-tests revealed that participants were significantly faster ($p < 0.001$) at locating the target on Trial 11 (14.6 +/- 2.6s) and Trial 12 (18 +/- 2.1s) compared to Trial 1 (48.4s +/- 2.7s) and Trial 2 (40.6 +/- 3.1s). All participants successfully learned the task, reducing their escape times across trials (see Figure 4.19). There was no difference in escape latency between the groups ($F_{2, 39} = 2.224$, $p = 0.122$, effect size = 0.102), there was also no Trial X Group interaction effect ($F_{22, 429} = 1.027$, $p = 0.429$, effect size = 0.05).

The path length of participants was analysed using the same statistical test. There was a significant effect for Trial across all participants ($F_{11, 429} = 21.408$, $p < 0.001$, effect size = 0.354). Bonferroni corrected t-tests revealed that participants travelled significantly shorter distances (all $p < 0.001$) in Trial 11 (51.4 +/- 9.8 Vm) and Trial 12 (72.8 +/- 6.3 Vm) compared to Trial 1 (195.7 +/- 13 Vm) and Trial 2 (179.7 +/- 13.5 Vm; see Figure 4.20). Participants' path length reduced and became more direct across trials (see Figure 4.21). There was no difference in path length between the groups ($F_{2, 39} = 2.943$, $p = 0.064$, effect size = 0.131) and there was no Group X Trial interaction ($F_{22, 429} = 1.15$, $p = 0.29$, effect size = 0.056). Thus, all participants in all groups reduced their completion time and path distance across the twelve trials, indicating they had successfully learned the targets location.

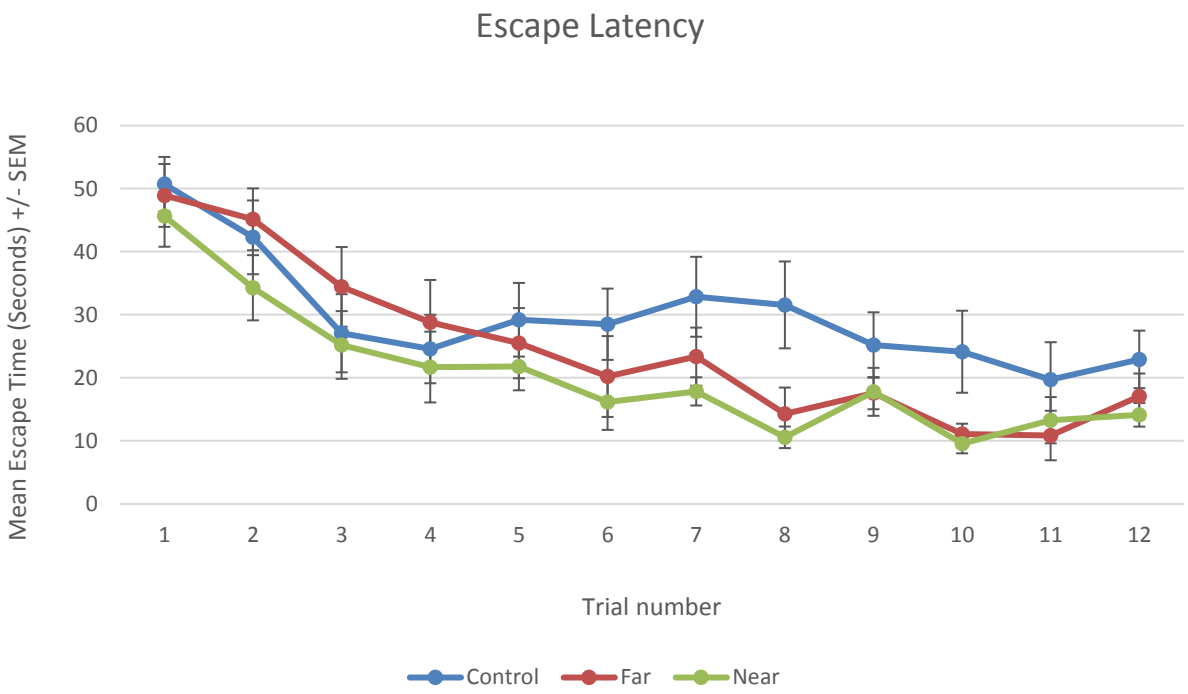


Figure 4.18: Mean time taken to locate the target (escape latency) for all participants in each group of Experiment 4. All participant groups show a similar learning curve with a reduction in escape times across trials.

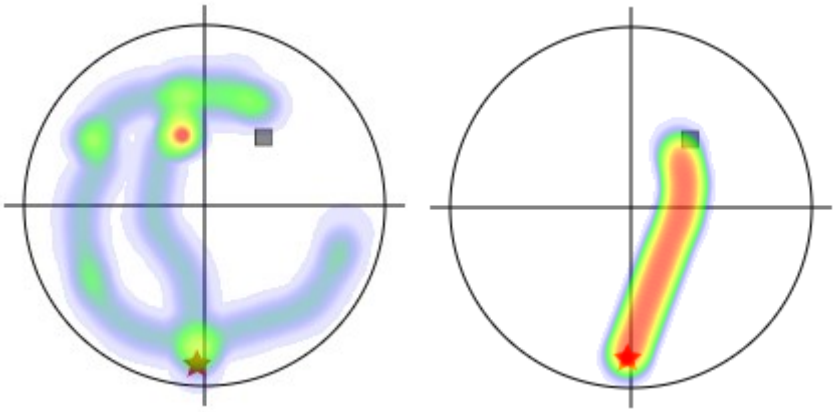


Figure 4.19: Example movement time heatmaps of a selected participant on an earlier trial (left) compared to a later trial (right) during the acquisition phase of Experiment 4. There is a faster navigation time in the later trial compared to a more dispersed and longer search time in an earlier trial.

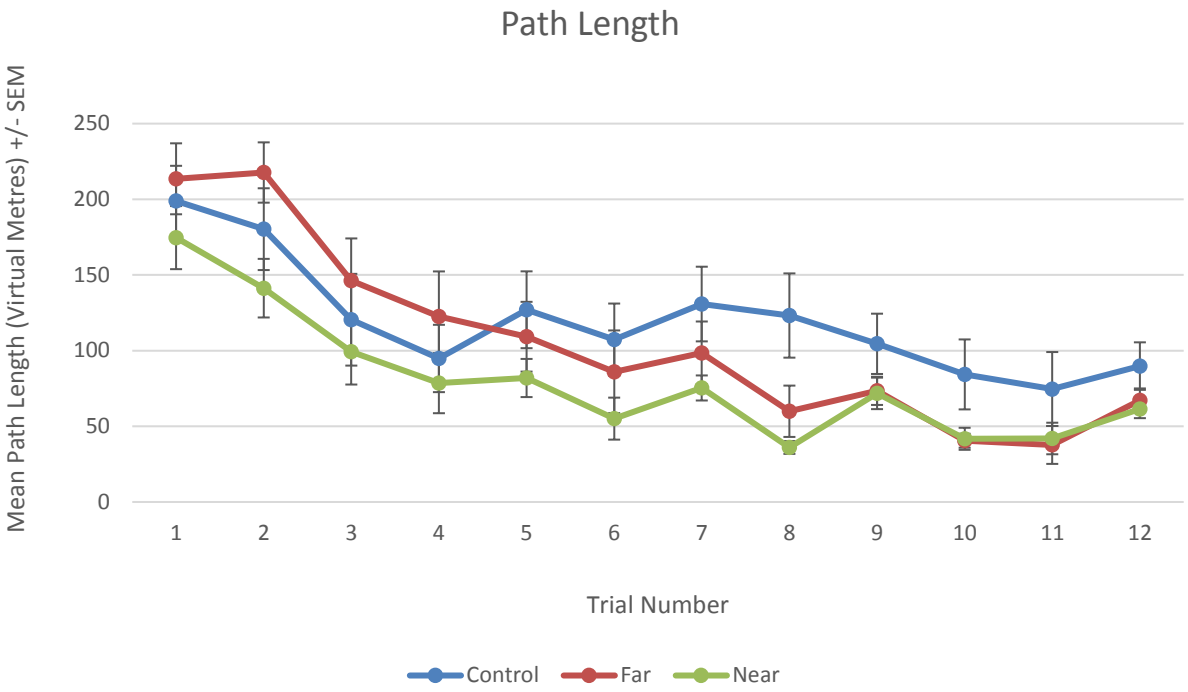


Figure 4.20: Mean path distances for all participants in each group of Experiment 4. All participants demonstrate a similar learning curve, showing a decrease in route length across trials.

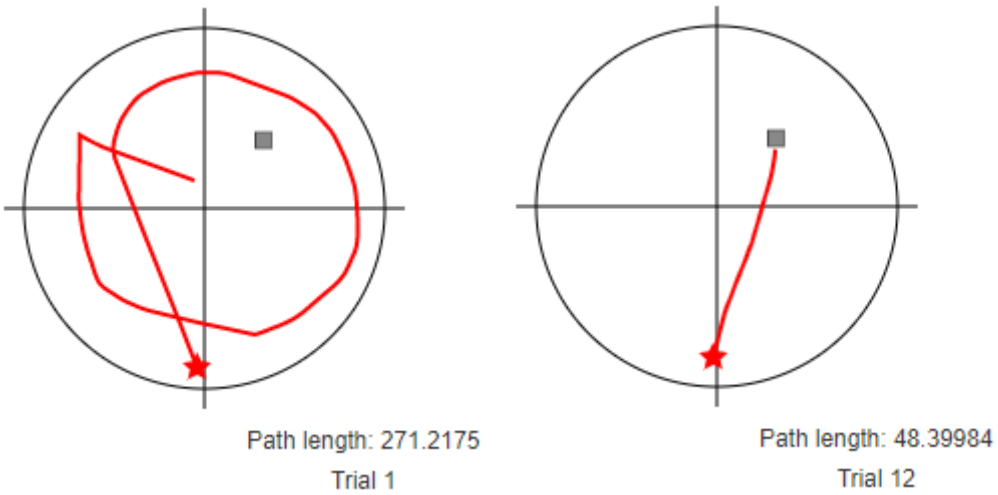


Figure 4.21: Example movement paths for a selected participant showing a decrease in path length from Trial 1 compared to Trial 12 in Experiment 4. The route taken to the target location also becomes more direct by Trial 12. The corresponding path distances (Vm) are displayed below each graph.

Retention Phase

To examine the effect cues with similar visual salience, have on learning and recall during navigation, we compared retention performance of all three groups. For this, the percentage of time spent in each quadrant was recorded. The data was analysed using a 3 (Group) X 4 (Quadrant) repeated-measures ANOVA. There was a main effect for quadrant ($F_{3, 117} = 27.465$, $p < 0.001$, effect size = 0.413). Although there was no significant group effect ($F_{2, 39} = 0.576$, $p = 0.567$, effect size = 0.029) there was a moderately significant interaction effect between group and quadrant ($F_{6, 117} = 0.7399$, $p < 0.001$, effect size = 0.275).

This interaction effect was explored by a series of one-way ANOVA's on each quadrant of the arena. Focusing on the NE target quadrant, the Far group spent significantly less time here (27%) compared to the Control (59.8%; $p < 0.001$) and Near (53.6%; $p = 0.005$). However, the Far group spent significantly more time (40.4%) in the NW quadrant compared to the Control (17.4%; $p = 0.012$) and Bright (9.8%; $p = 0.001$) groups. The NW quadrant is where the only available landmark (far light) was positioned. There was no difference between the groups for time spent in the SE ($p = 0.205$) or SW ($p = 0.221$) quadrants. These results are displayed in Figure 4.22.

Each group was then analysed for a quadrant preference using a repeated-measures ANOVA. There was a large overall significant effect for quadrant within the **Control** group ($F_{3, 39} = 24.147$, $p < 0.001$, effect size = 0.65). Bonferroni corrected t-tests revealed that this group spent significantly more time in the NE quadrant than any other ($p \leq 0.001$ for NW, SE and SW). There was also a moderately significant effect found for quadrant for the **Far** group ($F_{3, 39} = 4.38$, $p = 0.009$, effect size = 0.252). Bonferroni corrected t-tests revealed that this group spent significantly *less* time in the SE quadrant over the NW ($p < 0.036$), NE ($p = 0.022$) and SW ($p = 0.022$) quadrants. However, the Far group did not demonstrate a clear overall

preference (spending more time in one quadrant than any other). Nevertheless, there was a significant effect for quadrant for the **Near** group ($F_{3, 39} = 22.324$, $p < 0.001$, effect size = 0.632). Bonferroni corrected t-tests revealed that there was significantly more time spent in the NE quadrant than the other quadrants: NW ($p < 0.001$), SE ($p = 0.002$) and SW ($p = 0.004$). The Near group showed a significant preference for searching in the NE quadrant, similar to the Control group, despite one of the landmarks being unavailable (see Figure 4.22).

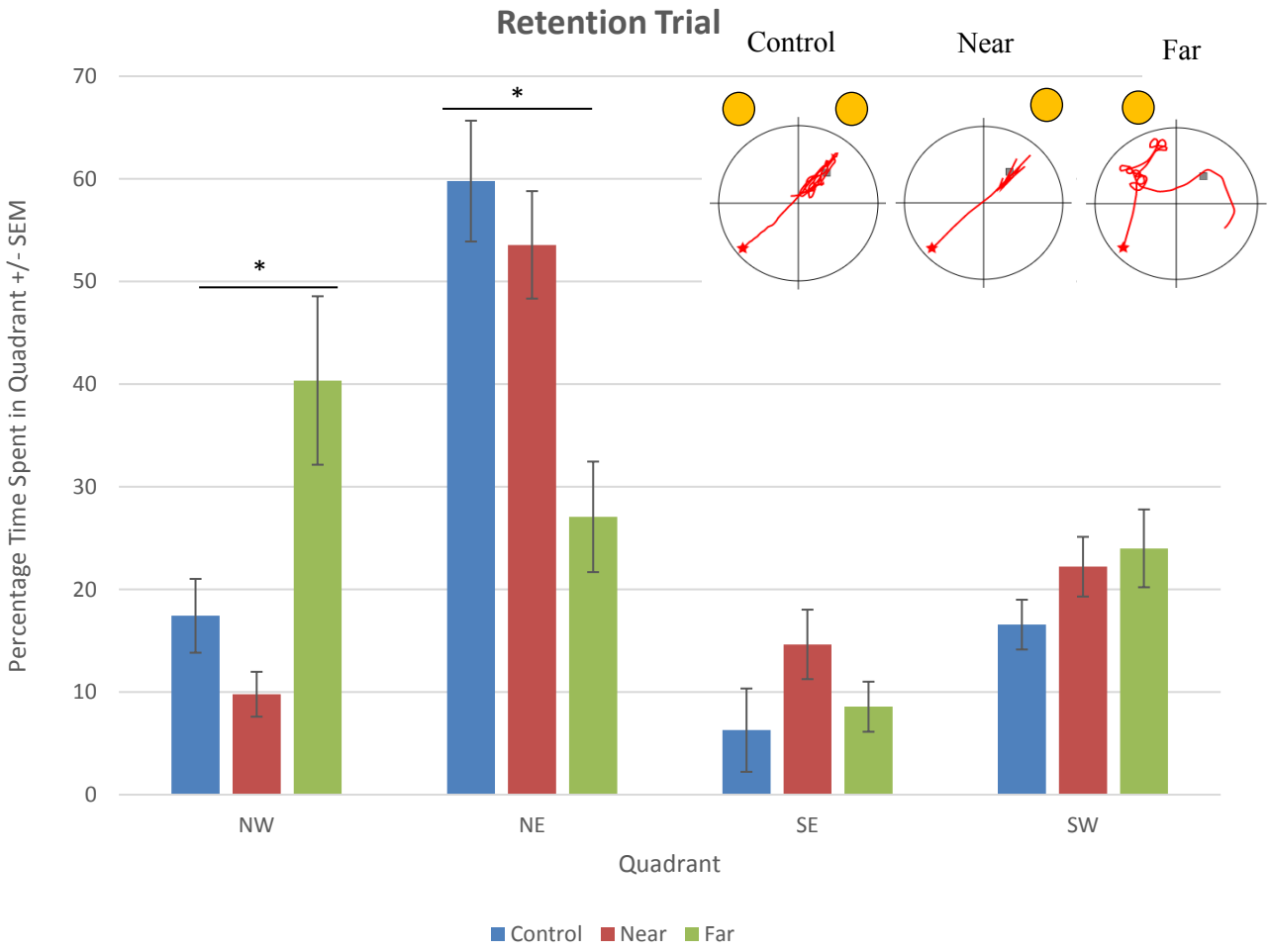


Figure 4.22: Bar chart displaying the mean percentage time and standard error of the mean spent in each quadrant (NW, NE (invisible target), SE and SW) by each group (Control, Far, and Near) in Experiment 4. Also displayed are tracks recorded from a selected participant from each group, to reflect path taken by each group.

Self-reported Search Strategy

A small proportion of participants (n = 7) responded to the open-ended question following their retention trial (see Appendix II). Frequency counts were carried out as previous for Experiment 1, which is fully described in the general methods chapter. The first frequency count was carried out to determine if participants were using the lights available to them. Results demonstrated that of all 7 participants, 100% mentioned the lights as part of their search strategy (analysed under the same codes as Experiment 2; Figure 4.8). As both available light cues were of equal featural salience, further analysis was carried out to determine *how* participants differed between the two lights, if at all. This was done by counting references to the codes under "Light Properties" which is displayed in Figure 4.23 below.

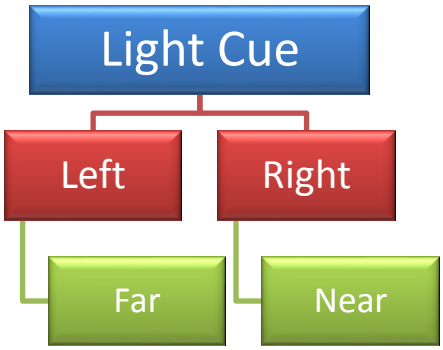


Figure 4.23: Word codes used for frequency analysis of light distinguishing. Coded under the original theme of "Light Cue" the additional themes are "**Left**" and "**Right**". Words coded to refer to these themes are: Left (including far/furthest) and Right (including near/closer) as these words refer to specific element that differentiates one light from the other.

Interestingly, four of the seven in total (57%) defined the lights by their directional properties. Additionally, of these participants, all (100%) of them referred to the near light *only*. This may indicate that very little was learned about the far/left light during learning and

supports the idea that it was not in any way incorporated into their learning strategy. A participant from the Far group explained their strategy during retention as follows: "*I tried to locate the light that was further to the right but it had disappeared, so I couldn't find the platform, as this was the 'cue' I had used previously*". Similar to previous experiments, participants may learn very little about the spatial relationship between a less salient landmark and the goal. For this participant, the right (near) light was the only cue associated with the platform position. However, even some participants from the Near group, were unaware that the light presented in isolation was the light closest to the platform: "*... it was located under the right when both were located ... in the last trial there was only one light I could not find it*". Therefore, perhaps the two lights were useful for orientation, or in fact, some participants learned the targets location using both lights.

4.4.3 Brief Discussion

The results indicate that the Control group navigated the most accurately, spending a significant amount of time in the goal quadrant over any of the other quadrants in the pool. However, the Near group also spent a significant amount of time in the goal quadrant, despite not having the same landmarks available to them as the Control group. This result may illustrate that participants did not learn the cues *configurally*, but instead learned them using an *elemental* strategy. This suggests that participants learned information about each landmark's spatial relationship with the target location separately (see Pearce, 2002). This also may suggest, participants did not need both cues to be present to successfully navigate the environment.

However, an elemental learning strategy cannot fully explain the results demonstrated by the Far group. Were each landmark learned *elementally*, regardless of which landmark was

removed from the configuration during retention, participants should have been able to navigate accurately. However, were they learning *configurally*, they would have searched in both the NW & NE. Nonetheless, the Far group spent more time in the NW quadrant than the other groups (the only quadrant with a landmark available). However, they did not show a strong quadrant preference. Therefore, it is unclear whether the Far group were treating the far cue as the near cue.

The lack of preference displayed by the Far group may illustrate that their performance was impaired due to the absence of the near cue (a reverse of the results by Farina et al., 2015). Therefore, it could be assumed that only the near light was incorporated into spatial learning during acquisition (see self-reported strategies above). This would suggest that for humans, the nearness of a landmark is the most salient feature a landmark can possess. It may also impair learning about other landmarks, regardless of their clear featural saliency (see Experiment 2 and 3). Therefore, when the most reliably salient landmark is removed, humans may attempt to apply the previously learned distance and direction information, to any landmarks available. The overall reliance on cue a cues distance from the goal in human navigation, as well as its theoretical implications are discussed further in Chapter 5.

Chapter 5

General Discussion

It is without doubt, that visual information plays a vital role in defining spatial environments and guiding navigation (Scaplen, Gulati, Heimer-McGinn & Burwell, 2014). Manipulation of visual cues results in an impairment in navigational accuracy and a distortion of place cell firing (Knierim & Rao, 2003; Sansa, Aznar-Casanova, Rodríguez & Chamizo, 2019). Additionally, rotation of environmental landmarks results in concordant navigation strategy and place field rotations (see Fenton, Csizmadia & Muller, 2000; Civile, Chamizo, Artigas & McLaren, 2019). However, what properties of an object promote its use as a cue or landmark? As previously discussed, the salience of a cue promotes its likelihood of being incorporated into a navigation strategy (Carduff & Timpf, 2008). There may be visual or non-visual properties of landmarks that cause these objects to acquire more *saliency* than other available landmarks.

There have been a number of studies demonstrating that associative learning principles exist in human cue-dependent navigation using virtual water maze tasks (Hamilton & Sutherland, 1999; Hamilton et al., 2009). Artigas et al. (2005) demonstrated that a cues proximity to the goal can influence which cue is incorporated into a human's navigation strategy. The strength of this learning and the relative salience of the cue can be manipulated by changing the cues proximity to the goal (Sansa et al., 2019). Additionally, using VR to examine spatial navigation in humans has shown some successful and ecologically valid results (see van der Ham et al., 2015). Virtual versions of the Morris Water Maze (VMWM) have also demonstrated comparative results to its rodent counterpart (see Schoenfeld et al., 2017). Therefore, one of the aims of this thesis was to validate the use of our open-access virtual water maze; NavWell (see Commins et al., *in press*), for examining cue-dependent navigation in humans.

Farina et al. (2015) explored landmark salience in rodents, revealing that visual properties such as cue brightness can control navigation. As a result, more is learned about the platform's location (in a MWM) in relation to brighter landmarks opposed to any other landmarks. Rats navigating with a dimmer landmark in isolation demonstrate an inability to locate the platform; indicating that very little was learned about its spatial relationship to the platform during training (also see Commins & Fey, 2019). Furthermore, featural properties of landmarks (i.e. how a landmark looks) can also cause them to acquire greater associative strength and saliency. Cues that are positioned closer to the platform in a water maze, are more likely to be primarily used (possibly as a beacon) during navigation (see Chamizo et al., 2006; Waller & Lippa, 2007; Rodrigo et al., 2014). Farina et al. (2015) demonstrated that rats may prefer landmarks further from the platform when cues have equal levels of visual salience, suggesting they provide better directional information about the platform (also see Diviney et al., 2013). Though non-visual properties can also contribute to salience for rodents, this thesis has attempted to demonstrate which landmark properties acquire greater salience during *human* learning and navigation.

NavWell as a Virtual Water Maze

From the initial phase of this project, we found that humans rely on the landmarks available in NavWell to navigate successfully, much like rodents in the MWM. This is supported by participants in Experiment 1 with rotated landmarks searching based on the landmark position and nothing else. Several studies with rats in a standard MWM have demonstrated similar navigational control by extramaze cues. Stackman, Lora & Williams (2012) demonstrated that a 90-degree rotation of landmarks was enough to shift searching trajectory. Rotating the entire water maze did not result in a shift in directional responding, illustrating that the cues were

responsible for defining orientation and search strategy (also see Dudchenko, Goodridge, Seiterle & Taube, 1997; Gibson, Shettleworth & McDonald, 2001). Even rats trained over 7 days with landmarks based in the NE and NW quadrant (like Experiment 1) demonstrated a preference for the SW quadrant when tested with a 180-degree rotation of landmarks (Harvey et al., 2009). The authors suggested that these distal cues form part of a view-matching strategy which is then followed by egocentric guidance. The exact effect demonstrated by Harvey et al. (2009) was replicated by participants in Experiment 1.

Participants with the cues rotated in Experiment 1 may have also attempted to match their original learned view at the beginning of the retention trial and apply the correct egocentric strategy to the wrong orientation. The association between the landmarks and goal is retained in memory, but is highly sensitive to change (see McGauran, Harvey, Cunningham, Craig & Commins, 2004). As would be expected, complete removal of landmarks results in impairment, with the No Cue group in Experiment 1 showing no quadrant preference and self-reporting recall difficulties. This would imply that nothing else *but* the landmarks in the environment were used to aid navigation, with a minimum of two necessary in most cases (Prados & Trobalon, 1998; Martin, Walker & Skinner, 2003). The complete removal of landmarks has been repeatedly shown to impair successful navigation (Williams, Barnett & Meck, 1990; Chai & Jacobs, 2010). The rotation of cues causing the shift in directional responding comparable to rats has also been demonstrated in VWM tasks with humans (Newman & Kaszniak, 2000; Fricke & Bock, 2018). Therefore, it seems that landmarks are responsible for controlling orientation during the initial stage of navigation for humans, as well as rats. In turn, this would suggest that the virtual landmarks in NavWell possess the same capabilities that real-life landmarks would for rats. This would support the use of NavWell for examining landmark influence on human navigation and comparing it to research with rodents and other virtual water mazes.

Associative Learning or Cognitive Mapping

The results from the experiments in Chapter 4 have some important theoretical implications. Associative theory would predict that fixed landmarks become associated with a fixed target location, either configurally or elementally (see Pearce, 2002). Rats in the MWM demonstrate configural learning when navigating using four individual landmarks. When tested with two or three during retention, all rats could locate the goal accurately, with no specific landmark necessary (Rodrigo et al., 1997; Chamizo, 2002). All landmarks were learned as a configuration, and any minor manipulation of this learned configuration did not impair navigation. However, rats were trained in a MWM with two sets of three landmarks, with each set sharing a common landmark located near to the goal location. When tested during retention with either two landmarks or the common landmark in isolation, rats demonstrated a preference for the target quadrant. However, without the common landmark, rats were impaired, searching at chance level without a quadrant preference (see Manteinga & Chamizo, 2001; Chamizo, 2002; Rodrigo et al., 2014). Therefore, the closer landmark prevented learning about the configuration of landmarks, resulting in an elemental association between the common landmark and the platform location. Many authors suggest it is the physical appearance of cues in the environment that influences the type of strategy that will be incorporated (see Chamizo, 2002; Farina et al., 2015; Commins & Fey, 2019).

Configural strategies involve associations between multiple cues; establishing one novel cue formation independent of individual cues and features (George & Pearce, 2012). The group of cues is then associated with the goal location. This configural representation can be proportionately activated by any of its original elements (see Pearce, 2002). If this were the case, we would have expected participants in the experiments from Chapter 4 to locate the target quadrant with either cue in isolation. However, in all three experiments, the groups with the farther cue in isolation searched incorrectly. This remaining cue should have prompted the

recall of the learned configuration (Roderigo et al., 2014; Farina et al., 2015). Since it did not, a configural learning strategy can almost entirely be ruled out.

Elemental learning strategies involve a direct association between an isolated stimulus and the goal (Rudy, 1991). The unique spatial relationship between all landmarks and the goal are learned individually, and are therefore recalled individually (see Pearce, 2002; Farina et al., 2015). As in previous animal studies, rodents without a particular landmark in a learned configuration, fail to accurately recall the target location in a MWM (Montienga & Chamizo, 2001; Chamizo, 2002; Rodrigo et al., 2014). Similar learning has been demonstrated with humans in a virtual water maze task (Chamizo, Aznar-Casanova, and Artigas, 2002; Artigas et al., 2005). In our experiments, of the groups navigating with one cue in isolation, only the groups with the near cue (irrespective of brightness level) could accurately locate the target quadrant. The use of an elemental strategy cannot fully explain why the groups with the most distal landmark; i.e. the Bright group in Experiment 2, the Dim group in Experiment 3 and the Far group in Experiment 4, failed to learn about this landmarks spatial association with the target location. Participants should have learned about both elements individually (see Rodrigo et al., 2014; Farina et al., 2015). Therefore, we would have expected them to be impaired or search in two locations equally (see Collett, 1987) when presented with the far cue. Instead, they searched in the quadrant containing the only available landmark.

Interestingly, this disproportionate elemental reliance on one landmark (i.e. the nearest cue) was acquired much faster than the rats in Farina et al. (2015). Therefore, as has been suggested, the relative salience of one landmark compared to others will encourage an elemental strategy (Chamizo et al., 2006; Tommasi, Chiandetti, Pecchia, Sovrano & Vallortigara, 2012). It is possible that the brightness of the available cue could only be judged relatively by our participants, as there was no additional cue present to compare the isolated

one with. Therefore, participant search behaviour could then possibly be explained by some form of partial-elemental strategy, which perhaps is dependent on cue *saliency*. Thus, it may be fair to suggest that participants did not switch from a configural to elemental strategy during acquisition (see Rodrigo et al., 2014). Participants had learned about the near landmark (and seemingly this landmark *only*) in just over half of the trials that the rats learned about it (12 trials in our study vs 56 trials in Rodrigo et al. 2014). It may be safe to suggest that this learning phase is too short for a strategy switch (configural to elemental) to even take place (Hamilton et al., 2004; Rodrigo et al., 2014).

Most importantly, O´Keefe and Nadel (1978) claim that there exist two methods of learning spatial environments; via a locale system and a taxon system. The locale system uses map-based navigation through spatial memories stored in our memory system. The taxon system, uses simple guidance towards a goal, much like beacon navigation (see Chan et al., 2012). This type of learning can block/overshadow learning about other elements in the environment (Diez-Chamizo, Sterio, & Mackintosh, 1985). This behaviour has been demonstrated in humans in virtual navigation tasks (see Hamilton and Sutherland, 1999; Hardt, Hupbach & Nadel, 2009; Redhead et al., 2013). However, O'Keefe & Nadel (1978) also claimed that distal landmarks form a cognitive map – a mental representation of the environment. They consider such learning happens in a non-associative, all-or-nothing way (Chamizo, 2002). Our results seem to adhere to associative conditioning, rather than cognitive mapping

The fact that participants could not accurately recall the target location following removal of one of the landmarks and not another, would suggest that a cognitive map was not recalled or stored by these participants. It would have been expected that regardless of the landmark removed, participants could navigate using their locale system. However, it is important to note that there were only two landmarks available could have made the

environment incapable of being stored as a cognitive map (see Fenton, Arolfo, Nerad, & Bures, 1994). Additionally, the low number of training trials may not have been enough for a stable map to form (see O'Keefe and Nadel 1978, p. 95; Golledge, Gale, Pellegrino & Doherty, 1992; Collett and Graham 2004; Epstein, Patai, Julian & Spiers, 2017). However, as configural associations have been suggested to form the basis of a cognitive map (see Karnik & Gerlai, 2012), and as we found no evidence of configural learning, there was most likely no cognitive mapping. Therefore, though it seems that a cognitive mapping approach was not evident from our results, it cannot be completely ruled out as the overarching navigational strategy.

Cue Salience: Brightness and Proximity

The focus of this thesis was to examine the influence of cue salience on human navigation. Does making a landmark bigger, brighter, nearer etc. improve navigation accuracy? What factors acquire greater salience over others? As previously discussed, it may seem that brightness (visual salience) acquires more control over navigation than proximity (non-visual salience) for rats navigating in a MWM (see Rodrigo et al., 2014; Farina et al., 2015; Commins & Fey, 2019). Rats navigating with a brighter cue far away from the goal perform just as well as rats navigating with a dim near cue (Chamizo et al., 2006). In some circumstances, removal of salient environmental features does not disrupt performance if non-salient features (such as geometric cues) are unchanged (Young et al., 2006). Another element of cue salience that has emerged is cue proximity. Landmarks positioned closer to the goal exert more control (i.e. acquire more salience) over more distal landmarks for rats (Chamizo, 2002; Chamizo & Rodrigo, 2004; Chamizo et al., 2006; Sansa et al., 2019) and humans (Artigas et al., 2005; Livingstone & Skelton, 2007).

Contrary to previous findings in rats (see Farina et al., 2015), cue brightness did not acquire greater control over human navigation behaviour. Though participants in Experiment 3 were presented with a dim near and bright far cue, when navigating in isolation with the far bright cue, they failed to search accurately. Participants with the dim but near cue searched in the correct location. If brightness had exerted behavioural control over navigation (as we originally thought following Experiment 2), we would have expected the bright group to search most accurately. From Experiments 2 and 3, it would be fair to suggest that humans do *not* treat all environmental landmarks equally. Certain landmarks seem to acquire greater associative strength than others; which we believe, is based on a landmark's saliency. Hence, the overreliance on the light closest to target in both experiments, regardless of brightness level, would illustrate that a cues distance from the goal is more important than visual comparative differences (such as brightness). Our data may also suggest that the less salient landmarks are not learned through association at all but instead, are used as visual aid to orientate ourselves in our environment, and to help locate the most salient landmarks.

Experiment 4 revealed some interesting results, when both landmarks were of equal brightness levels. Again, the group navigating with the nearest landmark were most accurate, compared to the group with the far landmark. The far group however, displayed a more dispersed search pattern, searching above chance (though not significantly) near the far cue (NW quadrant) and searching here for significantly longer than the other two groups. Participants in the far group may have applied their original search strategy to what they believed was the landmark closest to the platform. However, some self-report data revealed that participants had been actively aware that the landmark presented in isolation was the far light ("*tried to locate the light that was further to the right but it had disappeared, so I couldn't find the platform"* – see Chapter 4, Experiment 4). Therefore, it may be that participants were impaired without the near cue, which is the only cue that acquired associative properties with

the goal location. The fact that humans seem to only learn about the most salient cue, may be linked to a desire for efficiency when we learn (see Commins, 2018). Learning about too many cues with a lower level of salience may impede what is learned about the target location (see Sansa et al., 2018). Interestingly, the graphical representations of the search behaviour of participants in Experiment 2 (see Figure 4.7) is almost directly comparable to the graph for participants in Experiment 4 (see Figure 4.22). As the cue positions were the same in both experiments, it could be argued that brightness was irrelevant. Perhaps the cues distance from the goal location is the most convenient or reliable information available. Therefore, we attempt to only learn about associations that are the easiest and most consistent, which for humans, may be cues that are nearest to our goal.

When landmarks appear the same, proximity may *still* acquire greater control over navigation than any other feature in the environment. Our results also present different behaviour than that demonstrated by rats in a similar scenario (Rodrigo et al., 2014; Farina et al., 2015). Perhaps, humans navigate accurately or prefer to navigate using landmarks that provide information about a goals distance from an object. The reason proximity acquires greater control over other featural elements of landmarks, may be because proximity provides better distance-related information than would brightness. However, participants also demonstrate a form of beacon navigation throughout all three experiments. Perhaps, with different or additional landmarks a switch of navigation strategy may also bring with it, a switch in which landmarks present as the most salient.

Limitations

One major limitation of this project was the training protocol implemented for all experiments. When animals are tested in the MWM, training is usually completed across several days, with

a block of trials done each day, with a retention trial carried out after all blocks have been completed (see Morris et al., 1984; Vorhees & Williams, 2006; Vorhees & Williams, 2014). Particularly, this was the case for many of the animal studies discussed that also examined cue salience (Chamizo et al., 2006; Rodrigo et al., 2014; Farina et al., 2015). Our participants were tested in one block of twelve trials in one sitting, mainly for convenience. The issue with this is that much research on spatial memory consolidation has demonstrated that we can retain and recall more accurately when learning is spaced (Spreng, Rossier & Schenka, 2002; Commins, Cunningham, Harvey & Walsh, 2003). The effect is particularly strong for place learning in the water maze (see Wingard, Goodman, Leong & Packard, 2015). The support for spacing learning trials, particularly with spatial navigation, stems from research indicating that knowledge about navigation is better learned following sleep (see Noack, Schick, Mallot & Born, 2017). Furthermore, place cells have recently been discovered to retrace learned routes during both sleep and elongated rest states; which results in more accurate spatial learning (see Ólafsdóttir, Bush & Barry, 2018 for a review).

Additionally, the number of learning trials given, was fewer compared to other MWM experiments (Farina et al., 2015: 20 vs 12 in our study), but more than most VWM experiments (Moffat, Kennedy, Rodrigue & Raz, 2006; Daugherty & Raz, 2017: 6 vs 12 in our study). Therefore, the differences in training protocols make our training protocol difficult to accurately compare with previous literature. Several studies have also demonstrated that two-day and even one-day training protocols with rats in the MWM are enough to produce accurate learning and recall, when compared to longer training schedules (Gulinello et al., 2009; Barrientos et al., 2016). Therefore, perhaps increased and/or spaced training may have resulted in more learning about different environmental landmarks or facilitated a more flexible approach to learning strategy by participants.

Some minor limitations worth mentioning are our failure to effectively control for video gaming experience and small sample sizes. The standard NavWell controls accurately reflect that of a first-person computer game (see general methods and Commins et al., *in press*). Multiple studies have shown that video gaming experience can influence performance on similar virtual navigation tools (Richardson, Powers & Bousquet, 2011; Clemenson & Stark, 2015). For example, Richardson & Collaer (2011) demonstrated sex differences in a virtual spatial orientation task. When prior video gaming experience was included as a covariate, sex differences on these tasks disappeared. Our experimental groups contained a mostly equal gender split. If video gaming experience is responsible for sex differences in virtual navigation performance, keeping groups with equal numbers of each gender would be the best way to control for this. Additionally, NavWell performance may rarely be influenced by sex, possibly due to the simplicity of its design (see Commins et al., *in press*).

Though sample sizes could always be improved upon, the relatively low response rate to the self-report measures in Experiment 3 (n = 0) and Experiment 4 (n = 7) could have been increased. It would have been beneficial to have data to further support the behavioural findings and conclusions made, particularly for such key experiments. However, the addition of the self-report questionnaire resulted in a longer experiment time. Though, even with low sample sizes, analysis of escape/search times during virtual navigation usually follows normal distribution (see Ugwitz et al., 2019). Additionally, most animal studies are carried out with very small sample sizes.

Future Directions

NavWell has demonstrated itself as a very convenient, easy to administer tool for examining spatial memory and navigation in humans. As this thesis has revealed, a cues proximity

acquires greater control over navigation for humans when navigating an environment, even when brightness is controlled for. However, there is only two landmarks available in the NavWell environments used throughout this project. Perhaps additional cues may result in different learning strategies. For example, participant search accuracy decreased when more (distal) cues were added to a virtual environment during retention (Sansa et al., 2019). It may also be interesting to control for *both* brightness and proximity, by placing the platform in an equidistant position from two landmarks of equal salience. Perhaps this may result in complete impairment, as humans heavily rely on distance information. On the other hand, this could provoke the use of obscure or geometric cues, such as the pool wall rather than visual landmarks (see Redhead & Hamilton, 2009). For example, when a beacon strategy is made readily available (similar to our experiments), humans have been shown to learn very little about geometric cues. The beacon acquired greater saliency compared to different environment shapes (see Redhead et al., 2013). By controlling for brightness and proximity using NavWell, we may uncover the type of cues that become salient, if any, in these circumstances.

It may be also useful to examine the neural correlates of spatial learning using NavWell. Measuring neural activity using electroencephalography (EEG) could be convenient for researchers and participants when using NavWell. One of the main EEG activities associated with spatial navigation are *theta oscillations*, demonstrated in rats and humans (O'Keefe, & Recce, 1993; Bischof & Boulanger, 2004; Colgin, 2016). It could be interesting to examine neural activity during learning in NavWell, particularly amongst participants with different landmark arrangements. Differences may be seen in theta oscillations (putatively hippocampal rhythms) depending on the landmarks available during learning. This type of neural research has been relatively unexplored, but differences have been found based on participant gender and age (Kober & Neuper, 2011; Lithfous, Dufour, Bouix, Pebayle & Després, 2018). With regards to age; differences in escape latency and recall between older and younger adults has

already been shown using NavWell (Commins et al., *in press*). It may be useful to further explore these age-related deficits using different landmark manipulations.

Broader Implications

The current research project has allowed us to understand how humans learn about our spatial environment when navigating, and what landmarks are considered to be the most salient. This will have implications if examining patients with Mild Cognitive Impairment (MCI) using NavWell. The software itself could reveal the extent of spatial navigation deficits, known to be associated with MCI and early Alzheimer's disease onset (see Allison, Fagan, Morris & Head, 2016). Understanding which cues are the most salient and the type of spatial deficits suffered by these individuals (learning or recall) could be incredibly useful (Davis, Ohman & Weisbeck, 2017; Cogné et al., 2018). This could help us provide visual aids for individuals with AD to navigate throughout hospitals and care homes. Particularly, it could help MCI patients to improve navigation skills, by training with landmarks that are closer, bigger or brighter.

This research could also help us understand degenerative diseases more efficiently. There has been increasing evidence that virtual analogues of the Morris water maze task can detect hippocampus-related memory impairments and predict predementia symptoms during natural aging (Laczó et al., 2009; Verghese, Liptona & Ayersa, 2017). Our research using NavWell may be able to contribute to a possible cost-effective and user-friendly software solution for the prediction of early onset Alzheimer's Disease. Our participants indicate that the software is very easy to use, and it can reveal very specific searching, recall and navigation behaviour. Spatial navigation deficits are emerging as an interesting cognitive biomarker for the disease, which could aid with early treatment and delay of onset (see Coughlan, Laczó, Hort, Minihane & Hornberger, 2018; Coughlan et al., 2019). Salient landmarks have recently

been identified as one of the most helpful navigation aids for those with spatial deficits (see Cogné et al., 2018). Our investigation into human cue salience may help us understand how we use landmarks during everyday navigation. Building upon this information, we may be able to use our understanding of cue salience to provide the best possible method of neurorehabilitation for patients with MCI and AD. This methodology, in conjunction with a cost-effective virtual navigation task (such as NavWell) could have the potential to detect or prevent early-onset dementia and AD in an aging population.

Concluding Remarks

This thesis has identified that during human virtual navigation, landmark proximity acquires more control than brightness. Significant preference for the target quadrant was found in groups navigating with the isolated nearest landmark in all instances; when brightness is both controlled for and eliminated as a factor altogether. Furthermore, we have demonstrated that the NavWell tool is easy to use for participants. It is also fully capable of examining landmark learning and recall with human participants. These findings present as strong evidence towards an 'associative learning' explanation for spatial navigation. They also demonstrate differences in cue saliency between the animal and human literature in spatial navigation. This research is the first step in fully understanding spatial learning and navigation in humans, with NavWell making the journey easier for researchers and participants alike.

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Appendix I: Participant Information Sheet

Maynooth University
National University of Ireland Maynooth

Roinn Síceolaíochta Ollscoil Mhá Nuad
Maynooth University Department of Psychology

Information Sheet:

An Examination of the Behavioural Correlates of Human Spatial Navigation

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Your participation is requested in an experimental study taking place with the Department of Psychology at Maynooth University examining the effects of different landmark and training manipulations on spatial learning and memory. This information sheet will give you an overview of the above study.

What is the study about?

We are interested in how humans navigate an environment and how different landmarks and training schedules can affect successful navigation. The processes involved in human navigation are unexplored and heavily based on animal research. The learning of a spatial location and subsequent recall may be heavily influenced by landmarks and/or training. But, do humans navigate similar to animals? Do we use landmarks differently? How can our memory for spatial locations be reinforced/impaired? We are interested in exploring this further, by examining the navigational behavior of humans in a virtualized water maze task.

What does it involve? What would I have to do?

There would be three parts to your involvement, all of which will take place in a quiet location free from distraction.

Firstly: You will be asked to use the virtual water maze software NavWell on a computer. You will be requested to use the mouse and arrow keys to "swim" around this virtual environment and try to find a hidden platform. You will have a select number of attempts to locate and recall the location of the platform in the environment. This section will last about 15 minutes.

Secondly: You would be asked to complete 3 cognitive tests. The tests consist of the National Adult Reading Test (NART) for general intelligence, the Trail Making Task (TMT) for executive functioning, and the Rey Auditory Verbal Learning Task (RAVLT) for memory. These tests will take about 10 minutes and are only carried out to ensure participants are cognitively matched.

Finally: You will be asked to undergo an additional attempt at recalling and locating the platform location in the NavWell maze. This will last no longer than about one minute. You will then be asked to complete a short paper survey on how you found your experience using NavWell, this should only take another minute.

The specific aims of the study – along with the landmark or training manipulations that were used – will be explained as soon as you have completed the experiment.

Are there any risks to me?

There are no risks associated with this study; all the questionnaires will involve either verbally answering questions or filling in answers with pen and paper. The NavWell software involves the simple mouse and keyboard controlled first-person navigation of a virtual environment, very similar to playing a computer game. In the unlikely event that you experience any distress, discomfort or particularly motion/simulation sickness as a result of using NavWell, or if you have any concerns about any aspect of your performance on these questionnaires, you should feel free to contact me, Dr. Sean Commins or contact your own GP with these concerns.

What happens to my test scores?

The printed data from your participation (i.e. test scores) will be strictly confidential and will be kept in a locked cabinet in the Psychology Department. Your results will be kept confidential by assigning a random number to each participant instead of your name. Aside from your name and age, no other personal data will be recorded. With the exception of the researcher(s) involved in running this study,

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nobody will be allowed to see or discuss any of your data. Your data will be combined with many others and reported in group form – averages etc. – in a scientific paper, but your own data will be available to you at your discretion.

Can I withdraw from the study?

Yes, you may withdraw from the study at any time, or you may withdraw your results up until the time the work is published.

If you are willing to help us by participating in this study, we will ask you to sign a **Letter of Consent**, which accompanies this information sheet. We are very grateful for your participation.

I have some health issues – am I still eligible to take part?

Finally, if you suffer from **any** of the following, you may not be eligible to take part:

- severe visual impairments;
- history of psychological/neurological impairment;
- history of motion or simulator sickness;
- history of epilepsy or memory issues;
- history of drug or alcohol abuse;
- currently taking psychoactive medication;
- other relevant medical conditions;

If you suffer from/have suffered from any of the above, please let us know so that we can determine if you are still eligible to take part.

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Appendix II: Participant Consent Form

INFORMED CONSENT FORM

In agreeing to participate in this research I understand the following:

This research is being conducted by Conor Thornberry, a postgraduate student at the Department of Psychology, Maynooth University. The method proposed for this research project adheres in principle to the Psychological Society of Ireland (PSI) code of professional ethics. It is, however, the above-named student's responsibility to adhere to ethical guidelines in their dealings with participants and the collection and handling of data. If I have any concerns about participation, I understand that I may refuse to participate or withdraw at any stage.

I have been informed as to the general nature of the study and agree voluntarily to participate.

There are no known expected discomforts or risks associated with participation. However, there may be the possibility of developing motion sickness whilst using the software. Should you have previously suffered with motion sickness or develop it during the research you can refuse to participate or withdraw at any stage.

All data from the study will be treated confidentially. The data from all participants will be compiled, analysed, and submitted in a report to the Psychology Department. No participant's data will be identified by name at any stage of the data analysis or in the final report.

At the conclusion of my participation, any questions or concerns I have will be fully addressed.

I may withdraw from this study at any time and may withdraw my data at the conclusion of my participation if I still have concerns.

Signed:

_____ Participant

_____ Researcher

_____ Date

Appendix III: Self-Report Questionnaire

NavWell Participant ID: _____

Question 1

How difficult/easy was your experience using the 2D NavWell software regarding: understanding the software, following instructions and using the mouse and arrow keys?

Very Difficult Difficult Average Easy Very Easy

Question 2

Did you experience any motion or simulator sickness during your use of the 2D NavWell program?

Yes No

Question 3

In relation to your final trial, please describe the strategy you used to locate the goal.

What parts of the environment did you use, if any; how did you start searching etc.

_____

_____

_____

_____

_____