Examining Overshadowing and Blocking in Human Spatial Learning using a Virtual Water Maze

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Abstract

Spatial navigation and learning have been previously investigated in animal and human studies with two major theories dominating the literature, associative learning theory (Pearce, 2009) and cognitive mapping theory (O Keefe & Nadel, 1978). Cue competition is a key feature of associative learning theory. Overshadowing and blocking are two cue competition effects which have featured in previous animal and human studies. The role of landmarks has been examined in animal studies using the Morris water maze (Morris, 1984). This task requires animals to navigate around a circular pool of water and locate a hidden platform. Animals use cues in the environment to learn the hidden platform's location over a series of trials. NavWell (Commins et al., 2020) is a virtual Morris Water Maze task developed by the Commins Lab to study human spatial behaviour and learning. This thesis examined overshadowing and blocking in healthy young human participants using NavWell. In experiment 1 (overshadowing), landmarks positioned near the goal controlled searching behaviour more than the distal landmarks demonstrating an overshadowing effect. Additionally, distal landmarks appeared to have been ignored suggesting that participants use a strategy requiring the least effort when learning. In experiment 2 (blocking), a single landmark learned in phase 1 did not interfere with learning of a novel landmark introduced in phase 2 and as such, a blocking effect did not occur. As cues were equidistant and proximity was not a factor, all cues were treated equally by participants and integrated into a cognitive map. Evidence for an associative account of learning (experiment 1), support for a cognitive mapping-based approach to learning (experiment 2) and the influence of proximal cues were discussed.

Chapter 1

General Introduction

Finding our way around familiar and unfamiliar environments is a skill crucial for our survival. Many species including birds (Beason, 2005), bats (Toledo et al., 2020) and honeybees (Evangelista et al., 2014) have demonstrated how important navigational ability is for them to locate food, avoid predators and to wayfind. Humans are no exception. Unfamiliar surroundings, poor visibility (Aguirre & D'Esposito, 1999), memory impairments due to age (Puthusseryppady et al., 2024) or age-related disease e.g. Alzheimer's disease (Babcock et al., 2021) can all disrupt our ability to navigate successfully. It is only then that it becomes apparent how important this skill is for the smooth running of our everyday lives and how easily it is taken for granted.

1.1 Mechanisms of Navigation

Two mechanisms are thought to underlie animal and human navigation. The first, termed *path integration* does not require the use of landmarks and can be defined as the ability to use cues produced by the animal's self-motion (egocentric cues) to calculate the position of the animal relative to its starting position or other important locations (Whishaw & Wallace, 2003). Such self-motion cues include vestibular cues (Cheng & Gu, 2018) and proprioception (Han et al., 2016). Path integration implies that an animal continuously updates information about its environment as it travels along its chosen path. As such, when an animal requires to return home, it can do so using a direct home vector without difficulty (Patel et al., 2022). An example of path integration can be found in young rats who were required to navigate to the end of a linear track in darkness, preventing the use of landmarks to navigate and forcing the rodents to find the goal by estimating distance instead (Bjerknes et al., 2018). In humans, path integration has been shown to be influential in both small and large-scale navigation (Klatzy et al., 1998, Anastasiou et al., 2023). Mokrisova et al. (2016) also noted that human participants with conditions such as Alzheimer's disease and mild cognitive impairment have shown impaired accuracy on a path integration task due to degenerative effects in the medial temporal lobes and parietal cortex. Path integration tasks therefore may be useful in identifying early cases of Alzheimer’s disease (Bierbrauer et al., 2020).

A second navigational mechanism depends on an organism’s ability to use environmental cues or landmarks (van Hoogmooed, 2022). These cues may be visual (Holland, 2003), auditory (Rossier et al., 2000) or olfactory (Gire et al., 2016). From these cues, animals may orient themselves to a particular location or direction (Yesiltepe et al., 2021). Landmark use has been studied across a wealth of different species including fish (Odling-Smee & Braithwaite, 2003), birds (Griffiths et al., 2021) and humans (West et al., 2023). It has been noted that not all landmarks hold the same value when it comes to using them to reach a goal or recalling a location. Some cues due to their specific features, may stand out more than others. This is referred to as *cue salience* or the noticeability of a cue due to characteristics such as size, colour, shape or position (Sorrows & Hirtle, 1999, Chamizo et al., 2012). For example, a large landmark positioned near a goal may have better learning outcomes compared to a small one positioned far away (Chamizo et al., 2006). Global landmarks (those visible from many locations) are recalled better than local landmarks (only visible from a short distance away) (Credé et al., 2020). A cue’s salience appears to play a pivotal role in how it is used by the subject to navigate, or indeed whether it is used at all.

1.2 Neural basis of Navigation

A significant early contribution to our understanding of the neural underpinnings of navigation was the discovery of '*place cells'* by O'Keefe & Dostrovsky (1971). Recording of single cells in area CA1 of the rat hippocampus during navigation found that certain cells would change their firing rate in relation to the position of the rat (See Fig 1.1 (a). These cells were termed 'place cells' and when studied closely, could predict which path the rat was travelling (Ainge et al., 2007). The discovery of these cells highlighted the role of the hippocampus in positioning as well as the recall of locations and in turn, it led to the claim by O'Keefe and Nadel (1978) that these particular cells form a mental representation or cognitive map of our environment that we develop through exploration (see section 1.3 below). In addition to place cells, which relate to a specific part of the environment, activity in other cells called *head direction cells* has been observed relating to the direction an animal is facing. Though originally discovered in the postsubiculum by Jim Ranck, (1985) they have been observed in areas such as the thalamus (Hernandez et al., 2024) entorhinal cortex (Giocomo et al., 2014) and the striatum (Mehlman et al., 2019). Head direction cells receive direct input from the vestibular system i.e. path integration system (Yoder & Taube, 2014). In addition, place cells and head direction cells have been shown to respond to manipulations of visual cues in the environment. When distal visual cues are rotated, place cells and head direction cells follow the rotation pattern (Yoganarasimha et al., 2006). The discovery of *grid cells* in 2005 have suggested the basis of a distance metric for navigation (Hafting et al., 2005). These cells along with goal (Nyberg et al., 2022), speed (Kropff et al., 2015) and border cells (Solstadt et al., 2008) have all contributed to the current understanding of the neural basis of navigation.

In humans, a landmark study by Maguire and colleagues (2000) examined a unique group of individuals, taxi drivers, who spent a significant amount of time studying to gain “the knowledge” of London and who earn their living by wayfinding. When the MRI scans of the taxi drivers were compared to those of normal controls, it was discovered that the left and right posterior hippocampal region of the taxi drivers was larger than that of the non- taxi drivers indicating that this area was dedicated to memory related to spatial navigation specifically (see Fig 1.1(b). Further analysis revealed that the length of time taxi drivers had spent working was positively correlated with grey matter volume in posterior hippocampus (Maguire et al., 2000). Recent findings have shown that the human hippocampus also contains a variety of cells relating to navigation including place cells (O Keefe & Dostrovsky, 1971), view-responsive cells (Rolls, 2022), and grid cells (Mosner et al., 2015).

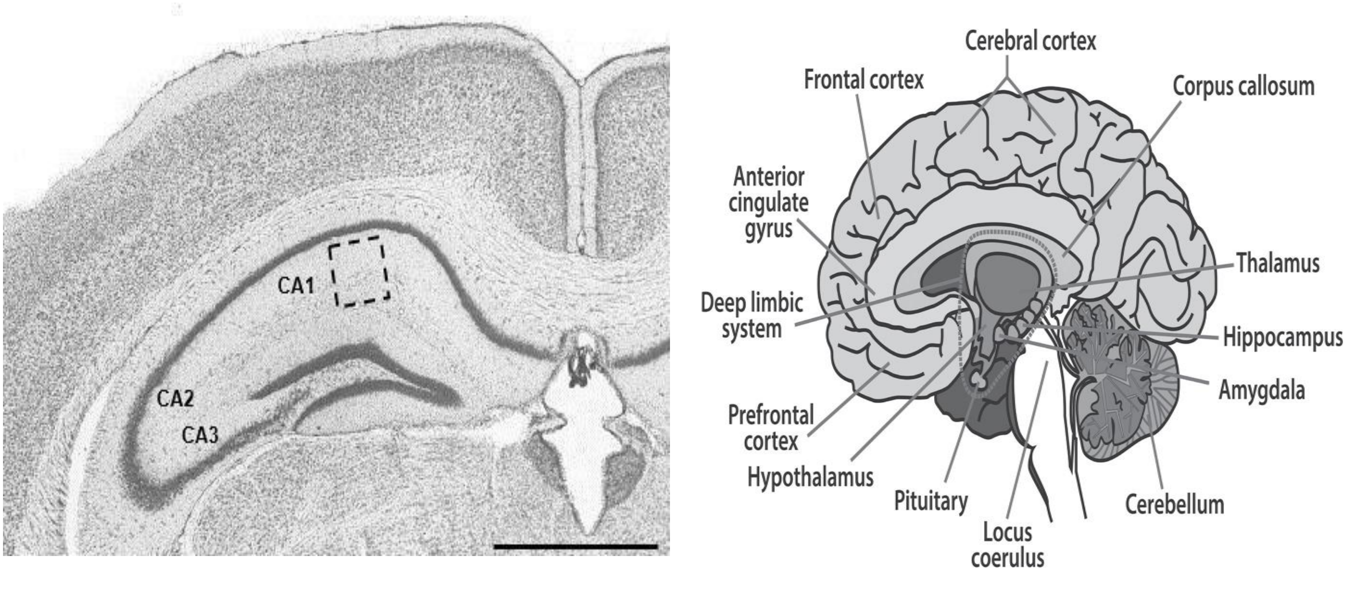

Figure 1.1(a): Area CA1 of the rodent hippocampus where place cells were originally discovered. This figure is adapted from Zabenko & Pivneva, 2016. **(b)** Human brain with the location of the hippocampus structure indicated. This figure is adapted from Valentine et al., 2015.

1.3 Testing Navigation

Studies of rodent navigation have employed a variety of mazes to test behaviour. These include the *T maze* (see Fig 1.2 (a)), in which the rodent is placed at the bottom of the T shape and tasked with locating a food reward placed at the end of one of the top arms. Errors at attempting to find the reward or time taken to find it can be used as a measure of performance (O Keefe & Dostrovsky, 1971). The *radial maze* first presented by Olton & Samuelson (1976) is a slightly more complex maze consisting of a circular platform from which extends 8 arms of equal length and spaced equidistantly (See Fig 1.2(b). Short-term /working memory can be examined by placing a food pellet at the end of each arm and observing rodents collect the food reward. If an animal returns to a previously searched arm for the reward, this can be considered an error. Another influential tool for studying navigation is the *Morris water maze* (Morris, 1984), a maze in which the rodent is placed in a circular pool in which a hidden platform is submerged in water. The rodent is required to navigate to the hidden platform to escape the water, a task it can quickly learn over several trials (See Fig 1.3(a). The rodent must also use cues in its environment to find the hidden platform. Recent studies examining human navigation have used virtual tools including the virtual equivalent of a Morris water maze (Clarke et al.,2015; Korthauer et al., 2017). These virtual environments can be used to conduct behavioural experiments with human participants and can control for environmental distractions which may arise during real world navigation. Typically, the *virtual water maze* design is identical to that of the Morris water maze – a circular pool environment containing a hidden platform, surrounding walls and different landmarks which can be placed in specific positions on the arena walls (see Fig 1.3 (b). The virtual water maze has been used in numerous studies to investigate human navigation including issues such as path complexity (Daughtery et al., 2015), neurodegenerative disorders (Roth et al., 2020) and age (Zhang et al., 2021). NavWell, a virtual water maze developed by the Commins lab has been shown to be an inexpensive and versatile tool with which to study human navigation (Commins et al., 2020). Previously it has investigated the influence of landmarks, spatial learning and memory (Thornberry, 2019; Thornberry et al., 2023; Thornberry & Commins, 2024) and as such will be used in these studies to investigate overshadowing and blocking.

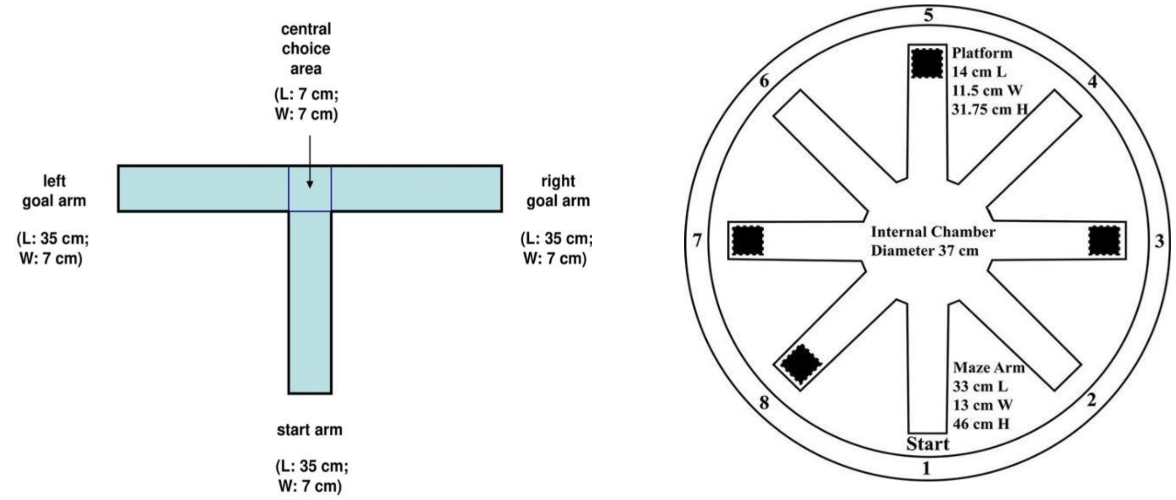

Figure 1.2(a): Schematic of the layout of the T maze and **(b)** the Radial Arm maze apparatus. These figures have been adapted from D’Isa et al., 2021 and Penley et al., 2013.

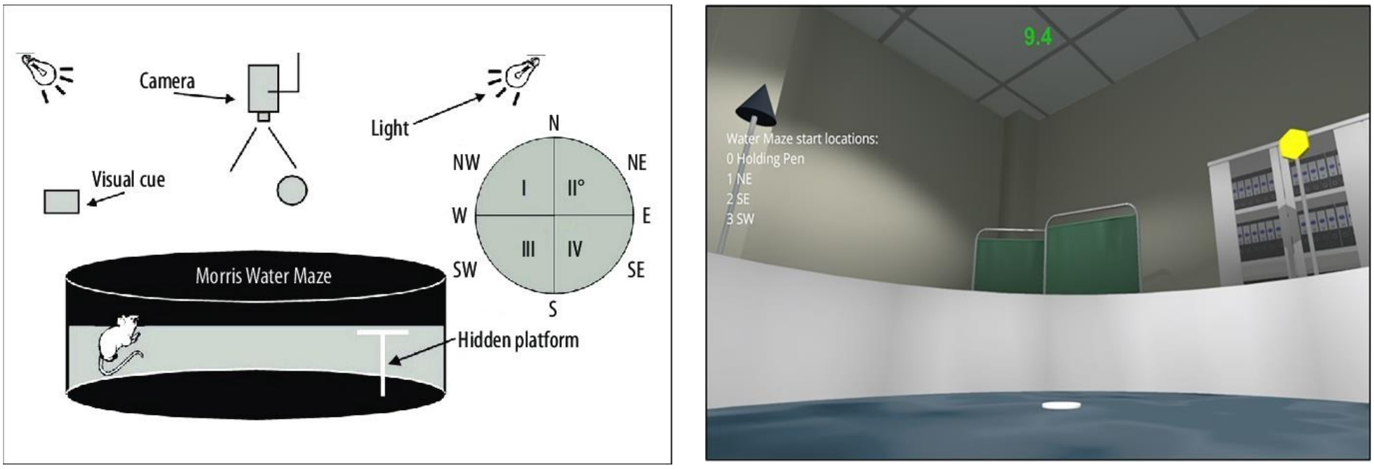

Figure 1.3 (a): Layout of the original Morris water maze and **(b)** an example of a Virtual water maze for use in human research. These figures have been adapted from Wu et al., 2016 and D’Archangel et al., 2022.

1.4 Theories underpinning Navigation.

Cognitive Mapping theory

One of the most influential accounts of spatial navigation, is the cognitive mapping theory which originated from Tolman’s proposal that navigation behaviour relied on the production of a mental representation or ‘map’ of the organism’s environment, which is developed and stored through exploration of that environment (Tolman, 1948). This, Tolman argued, contrasted with a simpler behavioural stimulus-response account of navigation. O’ Keefe and Dostrovsky’s discovery of place cells in the rat hippocampus (1971) provided additional support for the idea of a map-like representation guiding navigation. These cells fired in response to the location of the rodent (Moser et al., 2015).

Their publication of ‘The hippocampus as a cognitive map’ (O’ Keefe & Nadel, 1978) claimed that navigation behaviour operated along two separate systems, the *taxon* system and the *locale* system.

The locale system corresponds to Tolman’s idea of a cognitive map. This flexible system allows an animal to associate various cues in the environment with other cues as well as the goal location. These spatial relationships are independent of the navigator (termed allocentric) and allow for the construction of a *cognitive map* (Peer et al., 2021). The taxon system is more of a route-based system as opposed to a map like system (Cheng, 2012) and relies on path integration or dead reckoning (the continuous updating of an individual’s direction and position relative to a location using internal (proprioceptive and vestibular) cues derived from the motion of the individual’s own body (Anastasiou et al., 2023).

Associative theory

Another way of understanding how we navigate can be found by applying the principles of associative learning (Pearce, 2009) to navigation behaviour. This approach suggests that for the navigator, landmarks become associated with other competing landmarks as well as specific goals or locations in the environment (Waller & Lippa, 2007). In the experimental learning phase, pairing cues and goals repeatedly helps build associative strength over time (Zahn et al., 2018). Additionally, certain cues may have more associative strength than others. According to this approach, learning occurs through *cue-goal* association, not through the development and maintenance of a complex spatial map, which is required by cognitive mapping theory. The navigator simply uses landmarks that have become associated with a goal in order to locate it.

Traditionally, associative theory postulates two distinct strategies for learning, *elemental* and *configural*. Elemental models of learning require the learning and recall of an association between two stimuli, a landmark (conditioned stimulus) and a goal (unconditioned stimulus). In this way, a direct association develops between a goal and landmark, without the need to encode several relationships between cues relative to the goal (Buatois & Gerlai, 2020). In contrast, configural models involve the subject using the relationship between several stimuli to orient themselves toward a goal location. In this case, all stimuli in the configuration are used as a whole to guide the navigator to their goal (Sutherland &Rudy, 1989). If one imagines a tourist navigating around an unfamiliar city with multiple landmarks available - many environmental cues singly or combined may be encoded by the navigator to help them find their goal location (Ghirlanda, 2015).

If there are multiple landmarks in the environment, associative theory posits that *cue competition* will occur (Pavlov, 1927, Kamin,1969). Cue competition refers to the observation that learning about the relationship between a cue and an outcome is influenced by learning about the predictive significance of additional cues that are present at the same time (Packheiser et al., 2020). Two hallmarks of cue competition are '*overshadowing*' and '*blocking*'. Overshadowing is the observation that learning about a particular cue can be reduced by the presence of the multiple cues. For example, a cue positioned near a goal will overshadow or lessen what is learned about a cue positioned far from the goal (Chamizo et al., 2003). This phenomenon has been widely featured in animal studies and to a lesser extent, human studies (see below).

A second 'blocking' phenomenon finds its origins in Kamin's (1968) fear conditioning experiment where rats were presented with a tone (A) paired with a shock to the foot

(A+) for several trials. Following this, the tone was paired with a light (X) and this was repeatedly followed with a shock to the foot (AX+). Rats showed less fear in response to (X) when presented alone compared to a control group who had undergone the same (AX+) training but had not been trained with the (A+) compound. This demonstrated a blocking effect where earlier learning about stimulus (A) blocked learning about stimulus (X) (Kamin, 1968). Later, the Rescorla-Wagner model would explain the blocking effect by claiming that if a CS predicts a US accurately in a conditioning trial, nothing will be learned about a second CS presented with the first CS (Rescorla & Wagner, 1972). This observation again has been noted in animal literature (see later for review) and more recently in human studies (Prados et al., 2013).

1.5 Overshadowing & Blocking

Overshadowing in the non-spatial domain

The overshadowing phenomenon has been observed in many diverse experiments involving different species, domains and areas of investigation. For example, a study investigating whether the principles of associative learning could be applied to learning in a social context found that participants learned more about co-operative behaviours of game partners in a trust game when presented alone as opposed to in a pair (Telga et al., 2023). This effect was observed regardless of variables such as gender category and the manipulation of instructions. Further evidence of overshadowing in humans using a face recognition task showed that a verbal description impaired the identification of faces later presented in both children and adults. It was suggested that the participants' change from processing a description to processing features was the cause of this verbal overshadowing effect (Dehon et al., 2013). While in a fear-learning study, participants showed faster fear learning via higher shock expectancy ratings and skin conductance reactivity to a CS + which was paired with an electrical shock compared to ratings and reactivity resulting from a CS- which was presented without a shock i.e. a single conditioning trial resulted in increased fear learning compared to a non-conditioned stimulus (Haesen et al., 2017). Overshadowing has also featured in animal studies including during horse training, where overshadowing was investigated as a potential desensitization method for certain aversive stimuli. Overshadowing techniques proved effective in lessening fearful reactions from horses across a number of different protocols (Mc Lean, 2017). Other animal research investigating planarian worm learning capabilities demonstrated that planaria are able to show Pavlovian conditioning ie. they show increased response to the light - CS when reliably paired with a US and furthermore planaria trained with a light- vibration compound showed less conditioning to each element when compared to control groups trained with single elements (light or vibration) demonstrating an overshadowing effect (Prados et al., 2013).

Blocking in the non-spatial domain

The blocking effect is probably the most well-known example of a cue competition effect (Kamin, 1968). A typical blocking procedure will involve a schedule where a cue of interest is trained with another cue that predicts an outcome. This is preceded by pairings of one of the cues with the outcome (Boddez et al., 2014). This blocking effect has been demonstrated across many species including (snails (Prados et al., 2013), honeybees (Blaser et al., 2004) and humans (Dickenson et al., 1984)).

In a piece of research investigating the conditions that result in blocking, it was discovered that both the modality of the blocking cue and the sensory experience of it determined the strength of the blocking effect in mice (Sanderson et al., 2016). For example, mice trained for 200 trials with a visual blocking cue to block conditioning to an auditory cue showed evidence of blocking, but this was not the case for mice trained for only 80 trials with the same cue. In a second experiment, mice were trained with an auditory blocking cue to block conditioning to a visual target cue. Mice were trained with 80 and 200 trials and both conditions showed evidence of blocking highlighting that blocking may depend on trial number and cue modality. Further animal research sought to demonstrate the blocking phenomenon in a serial pattern learning experiment. In phase one rats were trained to press levers in a specific pattern. An auditory cue signalled a violation of the pattern. In phase 2 a coinciding spatial cue was added. When tested with just the spatial cues, blocking was apparent, providing evidence for associative theory as an explanation for rodent serial pattern learning (Kundey & Fountain, 2010). Emotional state was shown to affect performance in human participants during a study investigating the impact of stress on the blocking phenomenon. Using a fear learning paradigm, lower unconditioned stimulus expectancy scores for the blocked stimulus versus a non-blocked stimulus were found. This showed that stress impaired preferential processing of predictive stimuli (Kausche & Schwabe., 2020). Furthermore, the influence of cue salience was investigated in a blocking experiment and found that on high salience cues the blocking effect was stronger compared to low salience cues. Lower salience cues were shown to have greater influence on responding, highlighting the likelihood that the cue outcome relations for blocked high salience cues were weaker. Participants identified redundant cues quicker if they were of higher salience (Le Pelley et al., 2014).

The blocking effect, despite its widespread appearance in the literature has at times shown to be elusive. For example, recently a series of 15 aversive and appetitive conditioning experiments with rodents were conducted in a bid to identify a blocking procedure that would consistently produce a robust effect (Maes et al., 2016). Though all procedures used in the first 14 experiments had been previously employed in published studies, there was a failure to demonstrate a blocking effect. It was determined that this was not the result of a lack of power in the studies. A final high powered exact replication of a previously successful blocking study was conducted, and this also failed to produce a blocking effect. It was suggested that the previous successful blocking experiments had poor control conditions and as a result did not allow the study to conclude that the between-groups difference observed is a true blocking effect (Maes et al., 2016).

In response to this work, Soto (2018) argued that the blocking phenomenon is indeed parameter dependent and can predict what parameters are required to produce a small blocking effect or none at all. It was suggested that contemporary learning theory offered an explanation for the failure to replicate the effect in Maes et al (2016) as these experiments had mostly used same modality stimuli which recent (Soto et al., 2015; Kinder & Lachnit, 2003; Wagner, 2003) models of associative learning suggest will produce a weak blocking effect or none at all. In response to Soto's commentary, Maes et al (2018) countered that contemporary associative learning theory cannot be viewed as a single entity. As it consists of such a wide range of theories, many of which use different parameters and would make different predictions – it was impossible to claim that this predicted the failure of Maes et al 2016 to produce a blocking effect in 10 experiments. In addition to weaknesses in Soto's theoretical argument, Maes et al (2018) pointed out that both previous data and statistical evidence did not support Soto's argument. Soto's commentary did, however, highlight the role of moderators (the generalization and salience of stimuli) and the need for investigation into the role of boundary conditions and stimulus modality similarity.

Overshadowing in the spatial domain (animal studies)

The overshadowing phenomenon has also been studied in animals in the spatial domain with studies investigating the factors that aid or hinder successful navigation. The overshadowing phenomenon was first investigated in 1985 by Chamizo, Sterio and Macintosh in experiments investigating if locale learning could be overshadowed by guidance learning (Chamizo et al., 1985). When rats were trained with intramaze and extramaze cues, the extramaze cues overshadowed intramaze cues but not vice versa. Rats also appeared to use the whole set of extramaze cues to locate the goal arm. A comparison between O Keefe & Nadel's (1978) work and Pavlovian learning was drawn, suggesting that place and cue learning interact with each other in a similar manner to pairs of stimuli in a conditioning experiment (Chamizo et al., 1985).

Learning about a goal location using geometric cues (i.e. those provided by the shape of the environment) has been previously shown to remain unaffected by other landmarks present in the environment (Pearce et al., 2001; Hayward et al., 2003; Hayward et al., 2004). For example, when rats were provided with a landmark and geometric cues to learn a goal location there was no evidence of overshadowing between the landmark and geometric cues. This indicated a lack of cue competition occurring between geometric and landmark cues in the environment and raised the possibility that learning about these two types of landmarks does not follow the rules of cue competition (McGregor et al., 2009). Furthermore, sex differences were noted in a study investigating the relationship between landmark learning and geometric shape learning. Male rodents demonstrated an overshadowing of shape learning over landmark learning, but landmark learning didn't overshadow shape learning. The reverse was true for female rodents. This suggested that the different sexes had a preferred source of information that they used to learn, and which overshadowed the least salient source (Rodriguez et al., 2011).

Overshadowing in the spatial domain (human studies)

Although a wealth of information has been gathered from animal navigation studies, and humans and animals have common ground in terms of how they navigate (Zhao, 2018), caution should be used when generalizing findings from animals to humans as there are noted differences between human and animal navigation. The structure of environments humans and animals typically use or are tested in are often different (Srinivasan, 2015; Schoberl et al., 2020). Additionally, the human visual system is superior to that of rodents which would ultimately affect navigational ability profoundly (Ekstrom, 2015).

Within the spatial domain, a variety of experiments have examined overshadowing in human participants. For example, Chamizo et al. (2003) investigated whether landmark based learning could be overshadowed by guidance learning in a Virtual Water Maze task. It was found that participants using landmarks, and a visible platform were faster to find the platform when compared to control participants in a group using landmarks and a hidden platform. Learning of the landmarks was overshadowed by guidance due to the visible nature of the platform (Chamizo et al., 2003). Furthering this evidence of disruption to locale learning by a visible goal platform, a subsequent study used a visible platform and distal cues (both geometric and non-geometric) to investigate if learning a taxon strategy using a visible platform disrupted the learning of other taxon and locale strategies. It was indicated that when participants could use a simpler (taxon) strategy, they did, rather than a more complex locale strategy (Redhead & Hamilton, 2007). In a direct follow up to the animal studies discussed earlier, Redhead et al. (2013) examined the influence of cue salience on overshadowing in a Virtual Water Maze task using geometric cues (provided by the walls of either a triangular or trapezium shaped pool) and a platform with a visual cue (beacon). In the triangular pool no overshadowing by the beacon of the new geometric cue was found. The trapezium shaped pool presented a different result, where learning of the geometric cues was disrupted by the beacon’s presence. Interestingly, the typically observed bias of female participants to favour a beacon and of males to favour geometric cues was not observed in this instance. It was suggested that geometric cues in the triangular pool were more salient and, as a result, were not overshadowed by the beacon (Redhead et al., 2013).

Another factor that appears to influence overshadowing is proximity. Several experiments conducted by Herrera et al. (2022) demonstrated the role of spatial contiguity between landmarks and a goal. Overshadowing of geometry was apparent when proximal landmarks were used. This was not the case when distal landmarks were used (Herrera et al., 2022). In contrast, Sansa et al (2019) found conflicting results with an overshadowing effect found using *both* distal and proximal landmarks. The authors suggested that this was due to generalization decrement (and not associative competition) i.e. participants responded to one established configuration of landmarks, but this didn't transfer to a later configuration (Sansa et al., 2019). These studies are discussed in more detail in Chapter 2.

Blocking in the spatial domain (animal studies)

A review by Chamizo (2003) of animal studies revealed a lack of support for cognitive mapping theory. When a novel landmark was introduced to an already established set of landmarks, rodents did not appear to integrate it into their cognitive map as should be expected (Rodrigo et al., 1997). A later study further demonstrated that rats failed to use a newly introduced landmark to find food, instead relying on their initially learned configuration of landmarks (Biegler & Morris, 1999; Chamizo, 2003). This evidence of landmark competition and blocking in particular supported an associative account of learning as opposed to the suggestion by O'Keefe and Nadel (1978) that locale learning involves the updating of the animal's cognitive map.

Further animal studies required rats to swim to a hidden platform marked with a beacon (without access to any room cues) in phase one. When the rodents were provided with room cues in addition to the beacon, learning about these cues was blocked. In two further experiments, phase one involved rats swimming to a platform marked with a beacon which was moved to a new location in each trial. Again, learning about the room cues in Phase 2 was blocked when the beacon was present. This effect appeared disrupted if the beacon's appearance was altered or the amount of exposure to it was manipulated. The proximity of the beacon compared to the distal room cues appeared to control navigational strategy (Roberts & Pearce 1999). Rats trained initially to locate an invisible platform using three landmarks (ABC) learned less about a fourth landmark (ABCX) in the second phase of training compared to control animals who were trained initially with a different set of landmarks (LMN) and then trained with (ABCX). Prior learning of the (ABC) configuration in the experimental group blocked learning of X in Phase 2. Similar to Roberts & Pearce (1999), when the location of the platform in this study was altered in Phase 2 the blocking effect was eliminated (Rodrigo et al., 2005).

Insects have also demonstrated the blocking effect. Bees were trained to locate sugar water in an initial phase using one landmark. In Phase 2 a second landmark differently coloured to the first was introduced. A second control group of bees underwent identical training except phase 1 was omitted. When tested, the blocking group spent less time searching in the target area than bees in the control group - a demonstration of blocking in honeybees and evidence of associative learning in the species (Cheng & Spetch, 2001). In a more recent study, wasps have demonstrated the blocking effect during foraging behaviour. In an observational study, wasps were presented with a cue paired with food, and then a novel cue was added during their second visit to the food location. When tested (the first cue was removed and the food displaced) the second novel cue appeared to be ignored by the wasps, demonstrating blocking in the species for the first time (Moreya et al., 2021).

Blocking in the spatial domain (human studies)

The blocking phenomena has featured in the human literature with studies investigating what influences are required for it to occur. Factors such as the shape of an enclosure used to train participants in a Virtual Water Maze task have shown to influence whether blocking occurs or not. Participants trained in a circular enclosure demonstrated a blocking effect with learning of local landmarks blocking learning of distal landmarks. When participants were trained in a square environment using the same procedure, blocking did not occur (Wilson & Alexander, 2010). In a further study, learning about non-geometric cues blocked learning about geometric cues providing support for an associative account of learning (Buckley et al., 2016). Evidence of blocking with human participants was apparent when participants were required to use geometric information to learn the location of a goal in a computer task. When participants received initial training with one shape to find the goal this resulted in reduced learning about a second shape introduced in a later phase (Prados, 2011). Expanding on Prados (2011), a similar blocking experiment was conducted, this time using a within-subjects design. When blocking participants received training with a cue in the presence of a cue that already predicted the goal, they showed a reduction in response when compared to the control group extending previous findings of blocking occurring in between-subjects designs (Prados et al., 2013). Further evidence of blocking in human navigation was shown in a study where, using a VWM task participants were initially trained to locate a goal using a set of distal cues. When a second set of cues were introduced later in the training, participants demonstrated impaired learning of the goal with these cues. These results were interpreted as providing support for an associative account of navigation as opposed to that proposed by cognitive mapping theory as the new cues introduced later were not integrated into the spatial map (Hamilton & Sutherland, 1999).

1.6 Thesis objectives

Landmarks are crucial for successful navigation across species. Overshadowing and Blocking have been demonstrated in previous literature; however, it remains unclear how these phenomena translate over to human literature. Previous human studies as outlined above investigating the influence of distal and proximal landmarks have produced conflicting results (overshadowing of geometry by proximal but not distal landmarks (Herrera et al., 2022) and overshadowing of both distal and proximal landmarks (Sansa et al., 2019)). Blocking has previously been shown in spatial learning studies using landmarks with some supporting an associative account of learning (Hamilton &Sutherland, 1999) and some a cognitive mapping approach (Jacobs et al., 1998), however, the results remain inconclusive. The current work aims to add to the literature by investigating what influences these phenomena. In Chapter 2, we aimed to explore overshadowing in humans using the virtual water maze task. Specifically, we examined the role of proximity. Herrera et al. (2022) demonstrated overshadowing of near but not distal landmarks arguing that proximity was important for overshadowing to take place. Sansa et al. (2018) however, reported overshadowing of both distal and proximal landmarks. Both of these studies used cues positioned opposite to the goal, which may not have been considered important or even used by participants. To rule out this possibility, we have reduced the number of landmarks used and have positioned them on the same side of the goal with one positioned nearer and one further away. It was hoped that this will allow for all cues to be available for participants to form an association. We hypothesised that cues located closer to the hidden goal will overshadow distal cues (i.e. those further away) from the goal. In Chapter 3, we investigated blocking in humans again using the virtual water maze task and a paradigm similar to that previously employed by Hamilton & Sutherland (1999). Specifically, we examined the influence of equidistant cues on the blocking effect. To limit the possibility of participants only learning a subset of cues (Hardt et al., 2009) we have reduced the amount of cues used. Secondly, Hardt et al. (2009) found that removing cues nearer the target but not those further away impaired performance. In this study, we have kept cues equidistant, so that this is not an issue. We hypothesised that a similar blocking effect will occur to that reported by Hamilton &Sutherland (1999). Findings from these studies will also add to the cognitive mapping vs. associative learning discussion. If we find both overshadowing and blocking, this suggests that humans learn (at least in this context) via associative learning. If not, and we find that all cues are treated equally i.e. no cue competition or overshadowing, or that novel cues are readily incorporated into an existing schema or map, this suggests that humans learn via the use of a cognitive map.

Chapter 2

An examination of overshadowing using a virtual water maze task

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2.1 Introduction

Navigating to a particular place and subsequently recalling its location is a fundamental life skill. Remembering where food is hidden or how to return to a breeding site in migrating animals is often a matter of life and death. For humans too, recalling places and finding our way is of critical importance. It is only when people become disorientated, as in the case with Alzheimer's disease (Coughlan et al., 2018) or being lost in poor visibility conditions, that we understand the extent of our reliance on spatial memory for everyday activities. One influential account of spatial navigation and memory is the cognitive map theory (Tolman, 1948, O'Keefe & Nadel, 1979). In this model animals can develop a map-like representation through their exploration of an environment via the encoding of relationships between landmarks, between landmarks and the goal, and between the navigator, landmarks and the goal. From this, novel routes and shortcuts to the goal can be then created. While the cognitive map has received widespread attention across a range of species (birds, Casini et al., 1997; insects Bennett, 1996 (but see Dhein, 2023) and mammals, Lisman et al., 2017), an alternative account of spatial learning, based on associative learning theory (e.g. see Miller & Shettleworth, 2007), may provide a better and arguably a simpler explanation. With this model only certain elements of the environment are learned and associated, and the association is formed only when required; as such, there is no need to develop a full map of the environment. All landmarks/cues are therefore not treated equally, with some given more weight or relevance compared to others.

The salience or the "significance or noticeability" of a cue (Chamizo et al., 2006, p. 340) can provide a particular cue with relevance. Specific features of a cue such as its size, shape, luminescence can all contribute to its salience. For example, Farina et al. (2015)

demonstrated that rats trained with brighter cues outperformed those with dimmer cues regardless of how near the cue was to the goal in the Morris water maze. However, proximity to the goal is a very important salient feature, with many studies showing that animals learn and recall locations better when provided with proximal cues compared to distal ones (honeybees: Cheng et al., 1987; birds, Bennett, 1993; rats: Chamizo and Rodrigo, 2004; mice: Hebert et al., 2017; humans: Artigas et al., 2005, Chamizo et al., 2011). Such competition between cues (near vs far; bright vs, dim, large vs small) is a hallmark of associative learning theory and can be tested more formally using blocking and overshadowing designs (Pavlov, 1927; Kamin, 1969). Blocking refers to the observation that pre-training with one cue of a compound subsequently interferes with learning the second cue of the compound. By contrast, overshadowing refers to the idea that individual cues in compound will share the associative value, and therefore learning will be reduced for each component cue, compared to if one of those cues was learned individually (Schmidt & De Houwer, 2019). Overshadowing has been previously observed with human participants across many domains including visual and tactile recognition (Stahlman et al., 2018), verbal learning (Schooler, 2014), geometrical learning (Prados, 2011) and causal learning (Vandorpe & De Houwer, 2005).

Overshadowing has also been observed in the spatial domain across many studies with non-human animals (Spetch, 1995, Sanchez-Moreno et al., 1999, Horne et al., 2002, Hebert et al, 2017, Rodriguez et al., 2011; Farina et al., 2015). However, research with human participants has not been examined to the same extent (Sansa et al., 2018) and this research has tended to focus on the debate on whether cue competition (including overshadowing) can be applied to all spatial elements, particularly with respect to boundaries and the geometry (Cheng, 1986; Cheng et al., 2013) of the testing environment (for example, see Buckley et al., 2021; Redhead et al., 2013; Wilson & Alexander, 2010). Other factors including the role of landmark salience (size, shape, proximity etc) on overshadowing in human participants has received less attention. Indeed, a study by Herrera et al. (2022) has recent emphasised the importance of proximity, by demonstrating overshadowing of geometry by near but not distal landmarks. Importantly the authors suggested that contiguity in space (i.e. closeness) is the key factor, and it is this feature that allows for overshadowing to take place. However, in a study examining competition among landmarks in a virtual water maze task, Sansa et al. (2018) reported an overshadowing effect with both distal and proximal landmarks. This observation is not consistent with Herrera et al.'s suggestion, where you might expect to see overshadowing with proximal cues only and not distal ones. In both these studies the distal cues were located opposite to the goal, therefore participants may not have considered them as being relevant and/or ignored them completely.

To rule out this possibility, we modified Sansa et al.'s (2018) task by making two changes. First, we reduced the number of landmarks from four to two. Second, we placed these two cues on the same side as the hidden target, rather than having cues on the opposite side of arena. However, the proximity of these cues to the target was different, with one cue placed closer to the target compared to the second. By having the two cues relatively close to the target and minimising the number of cues that are available, we hoped that all cues would be readily available to the participant to form an association. We hypothesised that we would see an overshadowing effect, but we asked whether reducing the cue distance would show an overshadowing effect similar to Sansa et al. (i.e. proximal cue still gaining more control over performance compared to the distal one) or would the overshadowing effect be more equal between the two cues (i.e. no effect of proximity).

In the first experiment, we simply wanted to make sure that the two cues used in our overshadowing paradigm were equally salient and that participants could use both to find the target. Then in experiment 2 and following the typical overshadowing paradigm, we used the following groups: the first group was trained with the two cues (proximal and distal) and retested with the distal one; the second group was trained with two cues and retested with the proximal one; the third group was trained and retested with the distal cue only; the fourth group was trained and retested with the proximal cue only. A fifth control group was trained with two cues and retested with the same two cues. We expected an overshadowing effect for both the distal and proximal groups but predicted that this effect be will relatively similar for both groups, given the location of the cues.

2.2 Method

2.2.1. Experiment 1: Testing the salience of the cues.

Participants

Participants (n = 12) with a mean age of 24.8 (range 19 – 46) were recruited using a convenience method of sampling. There were 7 females and 5 males (**See Appendix A**). All were presented with an information sheet outlining the experiment (**See Appendix B**). Participants gave informed consent prior to starting the experiment and were fully debriefed afterwards (**See Appendix C**). Every participant had normal or corrected-tonormal vision. All reported as being healthy and not having any medical or psychological issues.

Spatial Navigation task

The spatial navigation task used in the experiment was the NavWell task (Commins et al., 2020), a human equivalent of the Morris water maze task (Morris, 1984). The task required participants to virtually navigate a circular arena in order to locate an invisible target. Once the target was found participants were required to recall this location and navigate to the target on each of the subsequent trials as quickly as possible. The virtual maze was a circular environment (taking 15.75s to traverse the arena, calculated at 22.05Vm) with an invisible target (15% of the total arena size) located in the middle of the northeast (NE) quadrant. The target remained in the same location for all trials (in the middle of the NE quadrant – see Figure 2.1(a) inset, black broken square) and only became visible when the participant crossed it. Depending on the experimental condition, one cue (either a small circular light or a green square) was placed on the north wall of the arena (Figure 2.1(a) inset, yellow circle and green square, respectively). A mouse and laptop display were used in the experiment which did not have an immersive aspect or involve physical locomotion for the participant.

Procedure

To examine whether the two cues were equally as salient, participants were divided into two groups and were tested with either the circular light (n = 6) or the green square (n = 6), both on the north wall on the arena. All participants underwent 12 training trials on the virtual water maze task. Participants started each trial from one of 4 positions around the arena (N, S, E & W) in a pseudorandom fashion. All participants were required to locate the target within 60 seconds; if they didn't locate the target within this time, they were teleported to the goal location. Participants remained at this location for 10 s and were instructed to look around the environment. Time taken to locate target (seconds) was recorded for each participant for each trial to measure learning.

Following the learning phase, participants were asked to sit quietly for 5 minutes before recall was tested. To test recall, a single probe trial was given. Participants were given a single 60 second trial to navigate towards the goal. However, the goal was no longer present. All participants started from a novel position (SW). The percentage time spent (of the 60 s) in goal quadrant (NE) compared to the other 3 quadrants was used to measure recall.

Ethical considerations & Data Analysis

All experiments were approved by the Maynooth University Ethics Committee (BSRESC-2021-2453422) and were conducted according to the ethical guidelines provided by the Psychological Society of Ireland (PSI). Time to target, path length and percentage of time spent in the target quadrant were extracted from NavWell; these measures were all imported into IBM SPSS (v23) for analysis. Means and standard error of means (SEMS) were calculated for each trial and for each group. Mixed factorial ANOVAs were used to analyse learning and recall phases. Where relevant, Tukey HSD test was used for between group *post-hoc* comparisons and Bonferroni corrected t-tests were used for within-group comparisons. A star-based level of significance was used where $^{*}p < 0.05$, $^{**}p < 0.01$ and $^{***}p < 0.001$.

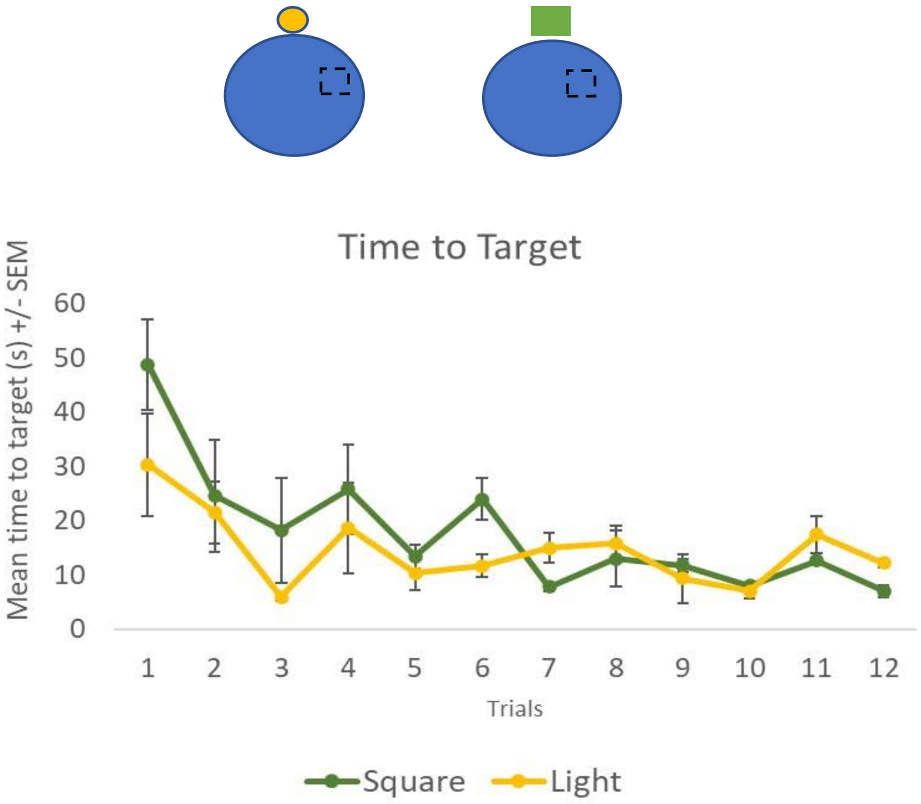
2.3 Results

For the learning phase, a 2 X 12 mixed factorial ANOVA was conducted to compare the time taken to reach the target for both groups across the 12 trials. An overall main effect for Trial was found ($F(11, 99) = 5.778$, $p < 0.001$, $\eta2 = 0.391$). Bonferroni-corrected ttests showed that both groups learned the task, with a significant decrease in time taken to reach the target from Trial 1 (mean = 38.7 s, SD = 22.9) to Trial 12 (mean = 9.8 s, SD = 3.4). There was no main Group effect ($F(1, 9) = 1.2$, $p = 0.302$) and no significant Trial X Group interaction effect ($F(11, 99) = 1.192$, $p = 0.332$) was noted (Figure 2.1a).

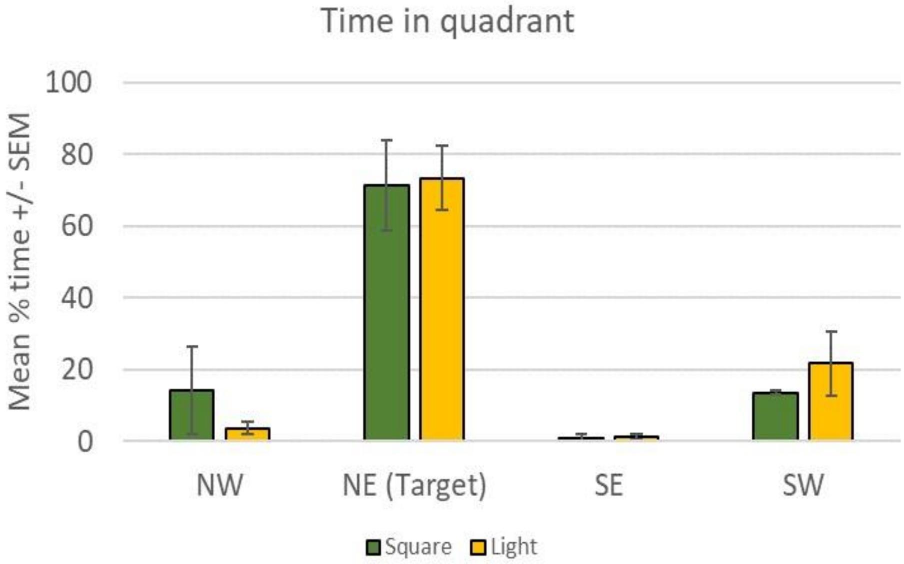
For the recall phase, a 2 X 4 mixed factorial ANOVA was conducted to compare the mean percentage time (of the 60 s) spent by both groups in each of the 4 quadrants. An overall main effect for Quadrant was found (F(3,30) = 26.56, p < 0.001, ɳ2 =0.727). Bonferroni-corrected t-tests showed that both groups spent significantly more time in the target NE quadrant (mean = 72.3%, SD = 22, p < 0.001) compared to the other three quadrants (Figure 2.1(b). No main Group (F(1, 10) = 1.0, p = 0.341) or Quadrant X Group interaction effect (F (3, 30) = 0.384, p = 0.765) was noted. (See Figure 2.1b).

Figure 2.1(a): Mean time (+/- SEM) taken by participants using light (yellow circle) or square (green) to find the hidden target. The hidden target was located on the floor in the NE section of the arena (broken square) with the cue located on the northern wall (see inset for representative diagram). **Figure 2.1 (b):** Mean percentage time (of 60 seconds) +/- SEM spent in all quadrants of the arena (including the target NE) for both groups in the recall trial in experiment 1.

2.1(a)


Time to Target
Mean time to target (s) +/- SEM
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
Trials
Square
Light

2.1(b)


Time in quadrant
Mean % time +/- SEM
100
80
60
40
20
0
NW
NE (Target)
SE
SW
Square
Light

Experiment 2: Testing the overshadowing effect.

Results from experiment 1 suggested that both cues were equally salient and that the two cues acquired the same control of the participants' performance. As such, we were able to move onto the main overshadowing experiment using the same two cues but manipulating the distance of each cue relative to the target.

Participants

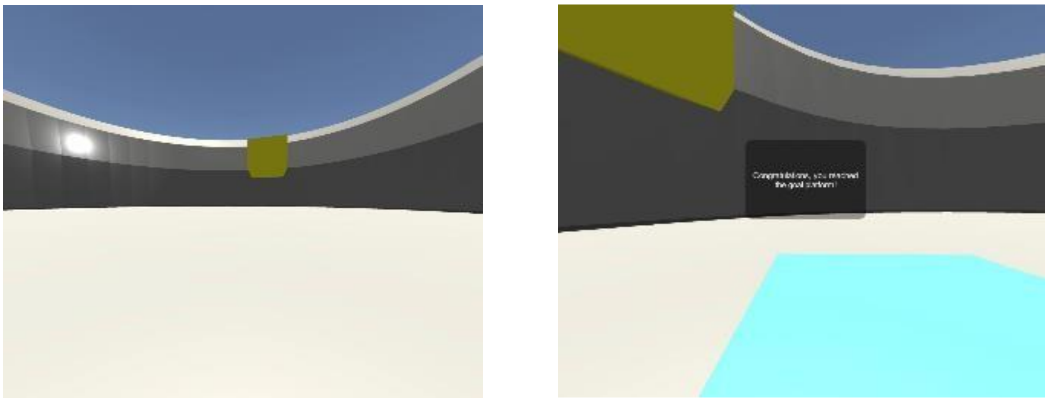
Participants (n = 113) aged 18 - 46 (mean 21.6, SD = 4.4) (**See Appendix A**) were again recruited using convenience and snowball sampling and consisted mainly of Maynooth University students. Participants were again provided with an information sheet outlining the experiment (**See Appendix B**). All participants gave informed consent prior to starting the experiment and were fully de-briefed afterwards (**See Appendix C**). Some participants from Maynooth University received course credit for participation. Every participant had normal or corrected-to-normal vision. Participants that self-reported as having severe visual impairments, a history of psychological/neurological impairment, a history of motion or simulator sickness, epilepsy or memory issues, reported a history of drug or alcohol abuse or were taking psychoactive medication were excluded from the study. *A priori* power calculations were done to estimate the number of participants required to determine a main effect of spacing. Using fixed effects ANOVAs and an effect size of 0.3 (see Strickland-Hughes et al., 2020) with power of 0.9, p = 0.05, and 5 groups (see below) estimated 114 participants. This higher power level of 0.9 was useful in determining a large enough sample to detect a statistically significant result. To ensure participants were generally matched on visual attention, visual-spatial and executive functioning the Trail-Making Test part A and B was administered (Army Individual Test Battery (1944); Reitan and Wolfson (1992)). In part A, the participant was required to connect numbered circles in ascending order as quickly as possible and in part B a letter was introduced (1- A, 2- B, 3-C etc). Participants again had to connect the circles containing these numbers and letters in ascending order whilst they were timed by the experimenter. Lower time scores tend to reflect better performance (Reitan & Wolfson, 1985) (**See Appendix D**).

Spatial Navigation task

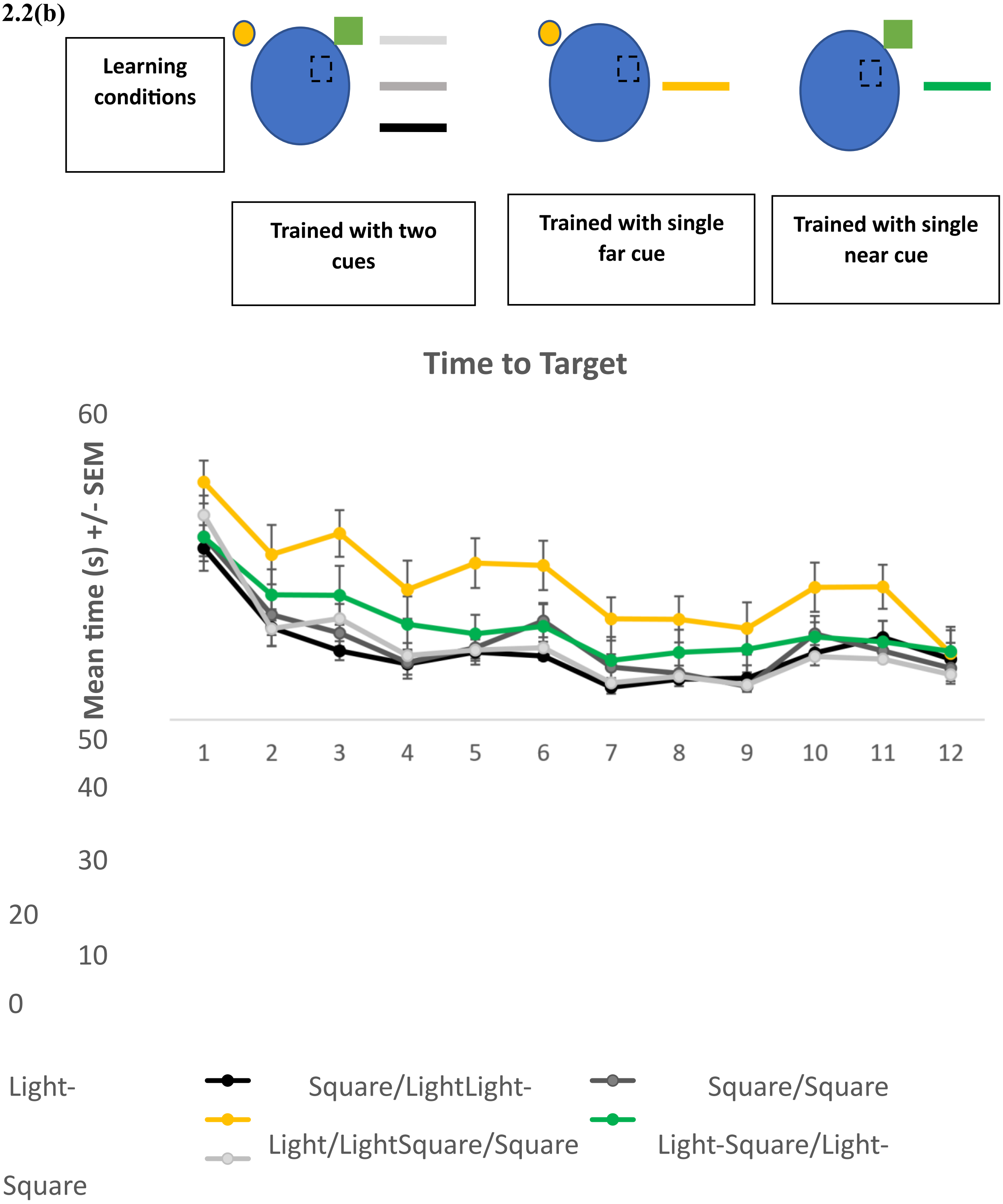
The NavWell task was again employed from this experiment. The setup was exactly as described above. The target remained in the same location for all trials (again, in the middle of the NE quadrant) and only became visible when the participant crossed it (Figure 2.2(a). However, depending on the experimental group (see Procedure below), one or two cues were used. The cues were located on the wall of the arena and consisted of a small circular light (located on the northwest quadrant wall) and a green square (located on the northeast quadrant wall).

Figure 2.2(a): Screenshot of the NavWell environment and location of cues - circular light (NW) and green square (NE) used in experiment 2. The goal platform (light blue square) is visible near the NE cue (green square). **Figure 2.2(b):** Schematic representation of learning conditions and mean time in seconds (s) +/- SEM it took to reach the target for five groups across 12 learning trials in experiment 2.

2.2 (a)



2.2(b)



Procedure

For the learning phase, all participants underwent 12 training trials in the virtual water maze task. Again, participants started each trial from one of 4 positions around the arena (N, S, E & W) in a pseudorandom fashion. All participants were required to locate the target within 60 seconds; if they didn’t locate the target within this time they were teleported to the goal location. Participants remained at this location for 10 s and were instructed to look around the environment. Time taken to locate target (seconds) and path length (distance travelled in virtual metres [Vm]) were recorded for each participant for each trial to measure learning.

Following the learning phase, participants were asked to complete the Trail Making Test (TMT) to ensure a time delay between the learning and recall phases, as well as to examine that our groups were generally matched cognitively. Part A required the participant to connect numbered circles in ascending order as quickly as possible. In part B, a letter was introduced (1- A, 2- B, 3-C etc). Participants were required to connect the circles containing these numbers and letters in ascending order whilst being timed by the experimenter. Lower time scores reflected better performance on the task The time difference between part A and part B of the TMT was used.

To test recall and the overshadowing effect, a single probe trial was given (once the TMT test was completed). Participants were given a single 60 second trial to navigate towards the goal. However, the goal was no longer present. All participants started from a novel position (SW). Depending on the group, the cues either remained the same as the learning phase or a cue was removed (see below and Figure 2.4(a) inset) for the recall trial. The percentage time spent in goal quadrant (NE) was used to measure recall.

To examine the overshadowing effect, participants were randomly assigned to one of 5 different groups. Group 1 (Light-Square/Light, n =21) was trained with two cues (light in NW and green square in NE) and was retested with one cue (light in NW). Group 2 (Light-Square/Square, n =24) was trained with two cues (light in NW and green square in NE) and was retested with one cue (green square in NE). Group 3 (Light/Light, n =23) was trained with one cue (light in NW) and was retested with the same cue (light in NW).

Group 4 (Square/Square, n =23) was trained with one cue (green square in NE) and were retested with the same single cue (green square in NE). Group 5 (Light-Square/LightSquare, n =22) was trained with two cues (light in NW and green square in NE) and was retested with the same two cues (light in NW and green square in NE). See Figure 2.2 (b) for a visual representation.

Mixed factorial ANOVAs were again used to analyse learning. Where relevant, a Tukey HSD test was used for between group *post-hoc* comparisons and Bonferroni corrected t-tests were used for within-group comparisons. A star-based level of significance was used where $^{*}p < 0.05$, $^{**}p < 0.01$ and $^{***}p < 0.001$. One-way ANOVAs were conducted to analyse recall, as well as to compare age and TMT scores across the 5 groups.

2.5 Results

An initial one-way ANOVA was conducted to determine if age differed across the five groups. Although an overall significant difference was noted ($F(4, 104) = 2.920$, $p = 0.025$, $\eta^2 = 0.19$), *post hoc* comparisons tests using the Tukey HSD test failed to indicate where those differences lay. A further one-way ANOVA was used to examine whether the five groups were generally well matched on the TMT task, no overall significant difference was noted between the groups ($F(4, 103) = 1.633$, $p = 0.172$), suggesting that the groups were generally matched for cognitive abilities (see Table 2.1 for details).

Table 2.1

Demographic Information for each Experimental Group in the Overshadowing Experiment (Experiment 2).

Group	N	Age (+/-SEM)	M/F/not reported	TMT b-a (+/-SEM)
Light-Square/Light	21	22.5 (1.6)	4/15	21.1 (2.6)
Light-Square/Square	24	23.2 (1.01)	6/17	21.7 (2.0)
Light/Light	23	22.5 (1.7)	10/13	24.8 (5.9)
Square/Square	23	19.9 (0.35)	4/19	16.2 (2.4)
Light-Square/Light-Square	22	19.9 (0.3)	3/17/2	16.6 (1.7)

Latency

The latency data were not normally distributed (Kolmogorov Smirnov P < .001). Outliers were not removed. The assumption of homogeneity of variances was violated (Levene's test of equality of variances P < .001). The assumption of homogeneity of intercorrelations was violated (Box's test of equality of covariance matrices = P < .001).

A 5 X 12 Mixed Factorial ANOVA was conducted to analyse the time taken to reach the target during the learning phase (See Figure 2.2 b). An overall main effect for Trial was found (F(11, 98) = 33.27, $p < 0.001$, η2 =0.78). Bonferroni-corrected t-tests showed that all groups had learned the task with a significant reduction in time taken to reach the target from Trial 1 (mean = 41.1 s, SD = 19.9) to Trial 12 (mean = 12.26 s, SD = 14.3). There was also a significant Group effect (F(4, 108) = 7.695, $p < 0.001$, η2 =0.22), with Tukey *post-hoc* revealing that Group Light/Light (trained with light in NW position and retested with same) was significantly slower at learning the target location compared to the other groups ($p < 0.01$, Figure 2.2(b). No significant Trial X Group interaction effect (F (44, 404) = 1.436, p = .040) was noted. No significant difference was noted between any group on Trial 12 (F (4, 108) = 0.468, p = 0.759).

Distance Travelled

The path length data were not normally distributed (Kolmogorov Smirnov $P < .001$). Outliers were not removed. The assumption of homogeneity of variances was violated (Levene's test of equality of variances $P < .001$). The assumption of homogeneity of intercorrelations was violated (Box's test of equality of covariance matrices = $P < .001$).

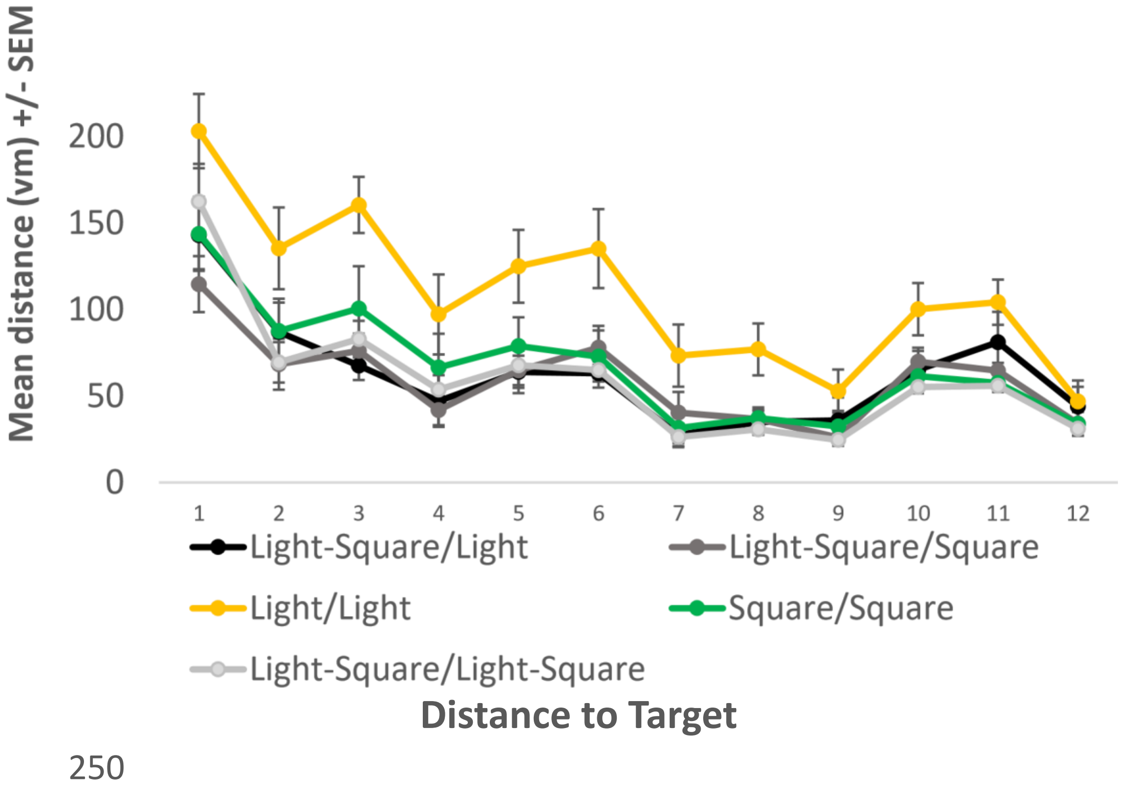
A further 5 X 12 Mixed Factorial ANOVA was conducted to analyse the distance taken to reach the target during the learning phase (See Figure 2.3).

Again, an overall significant effect for Trial (F(11, 98) = 58.48, $p < 0.001$, η2 =0.87) was found with Bonferroni-corrected t-tests revealing that all groups took significantly shorter paths to reach the target on Trial 12 (mean = 37.9 vM, SD = 34.7) compared to Trial 1 (mean = 153.2 vM, SD = 91.5). Again, a significant Group effect (F(4, 108) =

11.91, p < 0.001, η2 =0.306) was found, with Tukey *post-hoc* revealing that Group Light/Light (trained with light in NW position and retested with same) took significantly longer paths compared to the other groups (p < 0.01, Figure 2.3). No significant Trial X Group interaction effect (F (44, 404) = 1.401, p = .052) was noted. To check that all groups were equivalent on Trial 12, a one-way ANOVA was conducted. No significant difference was noted (F (4, 108) = 0.903, p = 0.465).

Figure 2.3: Mean distance to target (path length) in virtual meters (vm) +/- SEM for each of the five groups across 12 learning trials in experiment 2.

2.3



Recall

An overall one-way ANOVA was conducted to compare the mean percentage time spent by each group in the target quadrant (NE, Figure 2.4(b). An overall significant effect (F(4,107) =10.504, p < 0.001, η2 =0.39) was found. Tukey *post-hoc* tests showed that the LightSquare/Light group (trained with two cues (light in NW and green square in NE) and was retested with one cue (light in NW) spent significant less time in the target quadrant compared to all other groups. When we compared each group to chance levels (25%), all groups were significantly different (all p <0.001) except for Light-Square/Light group (t(20) = 0.485, p = 0.316). This suggested that although trained with two cues, this group were unable to use the single cue provided (light in NW) to locate the target.

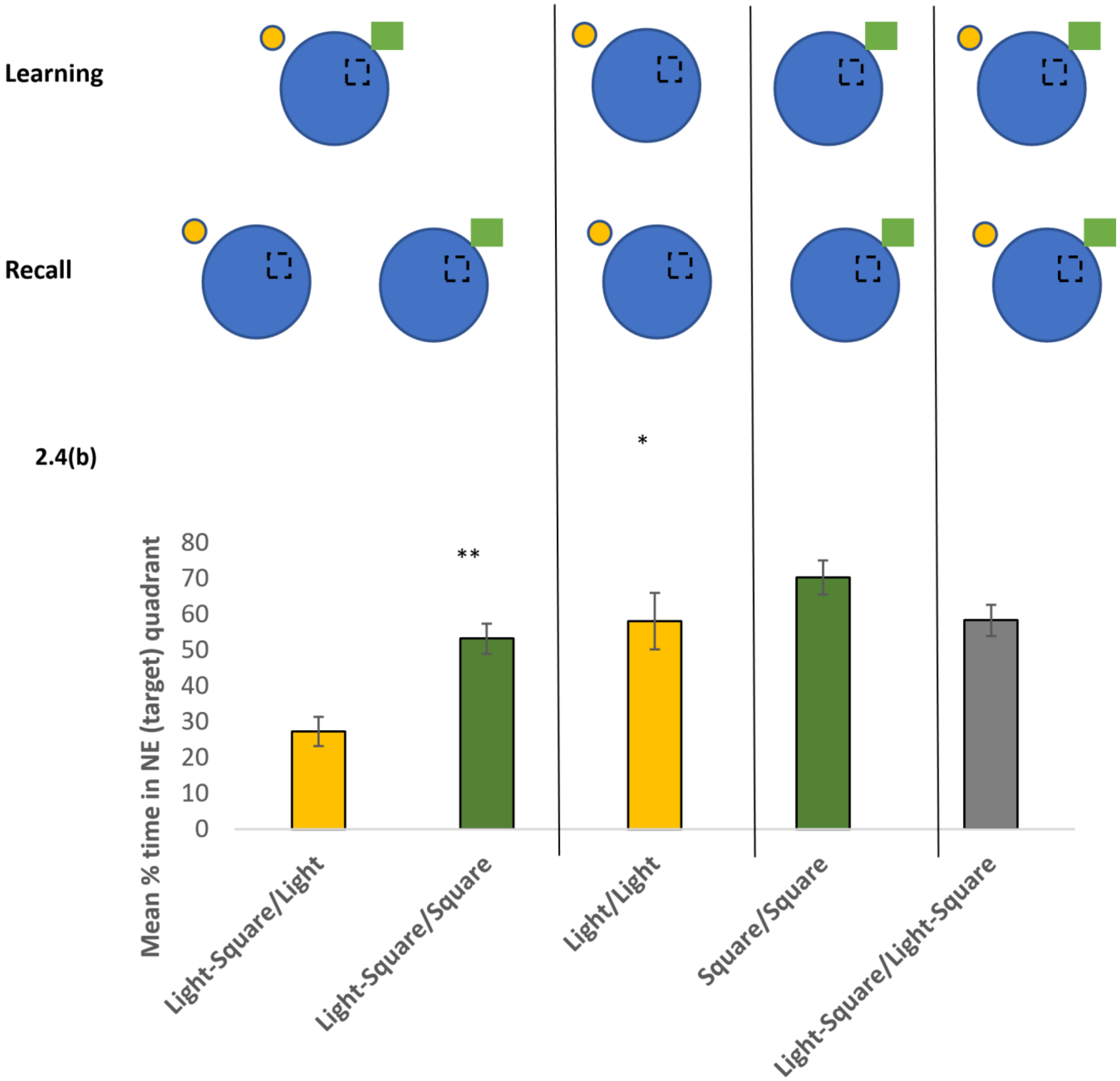
To specifically examine the overshadowing effect, we first compared LightSquare/Light group and Light/Light groups (Figure 2.4(b), yellow bars). A significant main effect was found (F(1,42) =14.08, p < 0.001, η2 = 0.25) suggesting that those trained with the two cues but retested with the light only (Light-Square/Light group) spent significantly less time in the target quadrant (mean = 27.3%, SD = 21.6) compared to the Light/Light group (i.e. those trained and retested with the same light cue, mean = 58.1%, SD = 31.4). This suggests an overshadowing effect. We next compare LightSquare/Square group and Square/Square groups (Figure 2.4(b), green bars). Again a significant main effect was found (F(1,45) = 9.67, p = 0.003, η2 = 0.17) suggesting that those trained with the two cues but retested with the square only (Light-Square/Square group) again spent significantly less time in the target quadrant (mean = 53.2%, SD =

19.8) compared to the Square/Square group (i.e. those trained and retested with the same square cue, mean = 70.3%, SD = 26.3). This again suggests an overshadowing effect.

Finally, an overall significant main effect for proximity was found, whereby the two groups retested with nearer cue (Light-Square/Square group and Square/Square spent significantly longer time (mean = 61.5%, SD = 20) searching in the target area compared to the two groups retested with the far cue (Light-Square/Light and Light/Light, mean = 43.4%, SD = 31, $F(1,87) = 15.207$, $p < 0.001$, $\eta2 = 0.149$).

A further overall one-way ANOVA was conducted to compare the mean percentage time spent by each group in the NW quadrant, (Figure 2.4(b). An overall significant effect ($F(4,104) =5.018$, $p < 0.001$, $\eta2 =0.16$) was found. Tukey *post-hoc* tests showed that the Square/Square group (trained with one cue (green square in NE) and was retested with one cue (green square in NE) spent significantly less time in the NW quadrant (mean = 7.04 %, SD = 6.04) compared to the Light -Square/Light group (trained with two cues (light in NW and green square in NE) and was retested with one cue (light in NW) (mean = 24.10, SD = 18.00). This suggested that the Square/Square group may have been using the only cue available to them to locate the target.

Figure 2.4(a): Schematic representation of learning and recall groups used in experiment 2. **Figure 2.4(b):** Mean % of time (of 60 seconds) +/-SEM spent in target NE quadrant for the recall trial for each of the five groups.



2.6 Discussion

Here we replicated recent findings by Sansa et al. (2018) and show that overshadowing occurs during spatial learning in humans, and that landmarks located closer to the goal control searching behaviour more than those located further away. This was contrary to our prediction where we thought that the location of the cues would allow the overshadowing effect to be more equal and no effect of proximity would be found. This suggests that absolute distance is not a factor. While there are multiple studies demonstrating general overshadowing effects across a range of species including honeybees (Cheng et al.,1987), birds (Bennett, 1993) and other non-human mammals (Chamizo and Rodrigo, 2004; Farina et al., 2015), up until recently there have been few examining this in humans. These results add to the growing literature suggesting associative learning provides a good account for spatial memory rather than the need to evoke a cognitive map. With associative learning theories there is recognition that only certain elements of the environment are used during learning and that all elements are not treated equally. We demonstrated this by showing that the near cue (the most salient one) is used and this cue overshadows the far one through competition.

Sansa et al. explained their overshadowing effects in terms of generalisation decrement (Pearce, 1987, 1994) rather than associative competition, because the authors argued that participants could approach the goal from different directions across the trials; therefore, all of the equally-spaced cues could be learned (see also Rodrigo et al., 1997). However, given that performance was better controlled by the proximal cues compared to the distal ones, cue location may have been a factor in their results. Similarly, Commins et al. (2019) using a virtual water maze task also showed that participants were slower to learn the target and subsequently were not as accurate in recalling the location when cues were placed opposite to the target compared to those that were placed near the target. We tried to rectify this and had the cues more prominently placed (i.e. both were on the same side as the target); despite this, the proximal cue still controlled behaviour significantly more than the distal cue. Although we can not rule out the possibility of generalisation decrement as an explanation - a one cue environment (as during retest) is different to a two cue one (as during training), we offer an alternative explanation. Examination of both our findings and those of Sansa et al. (2018) show that some cues are totally ignored. For example, when retested with just the two distal cues (Sansa et al.) or the far cue (light in NW, current experiment) after being trained with the compound set, participants searched in the target location at chance level (25%) only. This would suggest that during training when both distal and proximal cues were available, participants learned the location relative to the proximal cue(s) and *completely ignored* the distal and less salient one(s). Interestingly, Herrera et al. (2022) ruled out the possibility that participants ignored the distal landmark in their overshadowing experiment, pointing out that their discontiguous group (geometry + distal cue) learned the task better than the control group (geometry only). However, in both the current and Sansa et al.'s (2018) study, participants in the proximal + distal group learned the task equally as well as those in the proximal group only. Therefore, ignoring the less salient distal cue during training is a strong possibility here which led to searching at chance levels during retest.

Although all cues can provide information on the target location (experiment 1), participants seemed to learn about the most salient one only i.e. the nearest one in the current experiment. This perhaps speaks to an idea of 'learning efficiency' (see Commins, 2018), whereby participants use the least effortful way of learning. For example, if two cues are in a compound, they don't learn the location of the target with respect to both cues (as this may be effortful) or indeed the less salient one (as again, this may be effortful), but simply learn with respect to the more salient one. There is good reason to believe that learning the location relative to the distal cue is more effortful because we showed that participants were significantly slower to learn the task when only the distal cue is available (Group Light/Light, Figure 2B & 2C, see also Commins et al., 2019). Similarly in Sansa et al.'s study the group trained with the distal cues only (Group 2-2D, Figure 3) was also significantly slower to learn the target location compared to the other groups. This suggests that although the location of the platform can be learned relative to the distal cue(s), it is more effortful. As such it is ignored, especially when presented alongside a more salient cue. Future experiments should examine whether increasing the salient value of the more distal cues (e.g. having it bigger or brighter) might allow for this cue to be used during learning.

In conclusion, reducing the number of cues and having them both closer to the target location (to ensure that all cues are noticed) resulted in an overshadowing effect whereby the proximal cue-controlled performance more than the distal cue. However, rather than distal cues being simply overshadowed, it seemed to be totally ignored. We suggest that participants use a learning strategy that tries to reduce the amount of effort needed by learning locations relative to only the most salient of cues.

Chapter 3

An examination of blocking using a virtual water maze task

3.1 Introduction

Cognitive map theory (O’Keefe and Nadel, 1978) provides an influential account of spatial navigation and memory, whereby animals can develop a map-like representation of their environment through exploration. Associations between different landmarks and between landmarks and the goal (allocentric relationships), as well as between the navigator, landmarks and/or the goal (egocentric relationships) can be integrated into a cognitive map. An alternative account, based on associative learning theories (e.g. see Miller & Shettleworth, 2007), may also provide an equally valid account of spatial learning. An important feature of associative learning accounts is that an event may be preceded by significant cues which are used by the learner to predict an outcome (Packheiser et al., 2020). This can be applied to spatial learning whereby some landmarks/cues, due to their characteristics e.g. size, shape, colour, brightness and especially proximity, are more salient or noticeable than other cues. These cues compete with each other to gain influence over behaviour (Beesley & Shanks, 2012). Cue competition gives rise to associated effects such as overshadowing (see Chapter 2) and blocking.

Blocking, as originally described by Kamin (1968; 1969b) is observed when rodents were trained to respond to element A and subsequently trained to respond to the same element A with the addition of element B. When tested with element B on its own, rodents failed to respond to it, leading to the conclusion that the prior learning of element A on its own had interfered with or had blocked the learning of element B. Importantly, cognitive map theory and associative learning theory both predict different outcomes with respect to blocking; as such, the phenomenon has been used to test both theories (see

Hardt et al., 2009; Buckley et al., 2021). For example, the cognitive map theory suggests that if an environment has been learned and new spatial information is then provided (e.g. an additional landmark), the internal representation of the environment will be updated automatically through attention and exploration. Specifically, if subjects are initially trained in an environment with a number of landmarks (that can be used to indicate a particular location), then if another landmark is added to the original environment, subjects readily update their cognitive map and can use the new landmark to find the goal, provided that the additional landmark has been noticed. Therefore, cognitive map theory predicts that blocking will not be observed. In contrast, associative learning theories predict that the original landmarks will interfere and block further learning of any additional landmarks.

The blocking effect has been found in non-human animal studies across many learning paradigms (see Chapter 1 for a review). However, the occurrence of blocking in spatial learning has been inconclusive. Some studies have highlighted strong blocking effects. For example, Biegler & Morris (1999) showed that rodents did not integrate novel cues when they were introduced to a previously established configuration. Instead, they relied on the landmarks they first learned. Similar strategies were evident during foraging behaviour in wasps, with novel cues ignored once they were introduced (Moreya et al., 2021). Further evidence of blocking in rodents was found when rats were trained first with one proximal landmark to locate a food reward and subsequently had a second cue added (Stahlman & Blaisdell, 2009). The training of the first landmark impaired learning of the second, demonstrating blocking of a single proximal landmark by another proximal landmark. The effect has also been demonstrated with distal cues using the water maze task (Rodrigo et al., 1997; Chamizo, 2003).

Many studies investigating blocking in human participants in recent years have focused on the role of geometric cues provided by the environment itself. For example, such studies have examined whether geometric cues (e.g. the overall shape of the environment) can block non geometric cues (e.g. landmarks within the environment) (Wilson & Alexander, 2008; 2010; Redhead & Hamilton, 2007; Hayward et al., 2003; Pearce et al., 2001) and these studies have again led to mixed results (Sheynikhovich & Arleo, 2010), with some showing a blocking effect and others not – see Chapter 1 for details. Although there have been relatively few studies that have focused on exploring the blocking effect using landmarks alone, the results of these have also been mixed. For example, using a virtual water maze task Jacobs et al. (1998) showed that removal of a subset of distal cues did not impair performance, suggesting that a cognitive map was formed with all landmarks. In contrast, Hamilton & Sutherland (1999) showed that blocking can occur. Using a traditional blocking paradigm, participants were trained to find a hidden location in a virtual water maze task using 4 distal cues in phase 1 of the experiment. In the second phase, 4 additional cues were provided. Then during the test phase, the original 4 cues were removed. The authors showed that participants were unable to find the hidden target using just the additional cues. This suggests that blocking had occurred and learning with the original cues interfered with learning about any additional cues. Hardt et al. (2009) attempted to explain the difference between these two studies in a number of studies. In one experiment the authors showed that the location of the cues during learning was important. Deletion of a subset of cues close to the target impaired performance, whereas performance was unaffected with removed cues that were further away, suggesting that only a subset of the distal cues were explored and encoded (also see Chapter 2). The authors attributed this to the participants forming an egocentric representation rather than seeing it as a challenge to the cognitive map theory.

In a second experiment the authors highlighted that the provision of instructions may moderate the blocking effect. Combining the results, the authors suggest that blocking in human spatial learning may be a result of poor performance rather than a learning deficit (Hardt et al., 2009).

Given the relative lack of research using landmarks and the inconclusive nature of the results to date with respect to blocking in human spatial learning, we employed a paradigm similar to that previously used Hamilton & Sutherland (1999). Using a VWM task (Commins, 2020), we assigned participants to one of three groups, a blocking group or one of two control groups. In the blocking group, participants were trained on 8 trials to search for a hidden platform with a single cue (X) in phase 1. They were then given an additional 8 learning trials with an additional cue (XY) in phase 2. Participants were then tested with the second cue (Y) only. One control group underwent phase 2 training (XY) only and were re-tested with a single cue (Y). To control for the number of trials, the second control group were given 8 trials with a novel cue (Z) in phase one, trained for a further 8 trials with the combined cue-set (XY) and then re-tested with just one cue (Y). Furthermore, to control for the effect of distance (see Hardt et al., 2009) we used cues at an equidistance from the goal location. We hypothesised that we should observe a similar blocking effect as reported by Hamilton & Sutherland (1999), that performance in the blocking group would be impaired compared to the two control groups. Such a finding would lend support to the associative learning theory of spatial learning rather than the cognitive map.

3.2 Method

Participants and materials

Participants (n = 60) aged 18 – 41 (Mean = 21.28, SD = 3.34) were recruited using convenience and snowball sampling and consisted primarily of Maynooth University students. These included 23 males and 37 females **(See Appendix A)**. Participants were provided with an information sheet outlining the experiment (**See Appendix B**). All participants gave informed consent prior to starting the experiment and were fully debriefed afterwards **(See Appendix C)**. Some of the participants from Maynooth University received course credit for participation. Every participant had normal or corrected-to-normal vision. Participants reporting severe visual impairments, a history of psychological/neurological impairment, a history of motion or simulator sickness, epilepsy or memory issues, reported a history of drug or alcohol abuse or were taking psychoactive medication were excluded from the study. A *priori* power calculations were done to estimate the number of participants required to determine the main effect of blocking. Using fixed effects ANOVAs and an effect size of 0.3 with a power of 0.9, p = 0.05 and three groups, we estimated 60 participants. To match participants on visual attention, visual-spatial and executive functioning the Trail-Making Test (Reitan, 1958) part A and B was administered (**See Appendix D**).

Spatial navigation task

NavWell (Commins et al., 2020), a virtual version of the Morris Water Maze task (Morris, 1984) was again used in this experiment. See chapter 2 for a detailed description. This task required participants to navigate around a virtual arena to locate a hidden target. This target only became visible if the participant traversed it. Participants were then required to recall the target's location in later trials. The hidden target was positioned in the centre of the northeast quadrant of the circular pool for all trials. To aid recall, different configurations of cues were positioned on the arena wall depending on group and phase of learning (see Fig 3.1 (a) below for details).

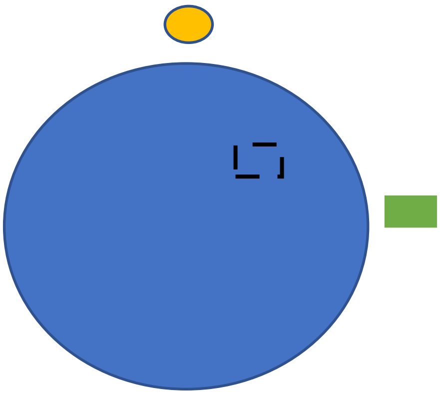
Procedure

Participants took part in two learning phases. They were randomly assigned to one of three groups (n = 20/ group), a Blocking group, a Control 1 and a Control 2 group. Participants in the Blocking group undertook phase 1 which consisted of 8 (60 second) learning trials to find a hidden target using a bright light cue positioned on the north perimeter wall of the arena (Fig 3.1(b). Phase 2 of their learning trials consisted of a further 8 trials of training to find the hidden target, this time with the previous bright light cue and a second cue, a green square, positioned on the east perimeter wall. Both cues were equidistant from the hidden target. Between trials, participants were transported to the target location for 10 seconds and asked to memorise it. Lower time to target and path length scores reflected better performance.

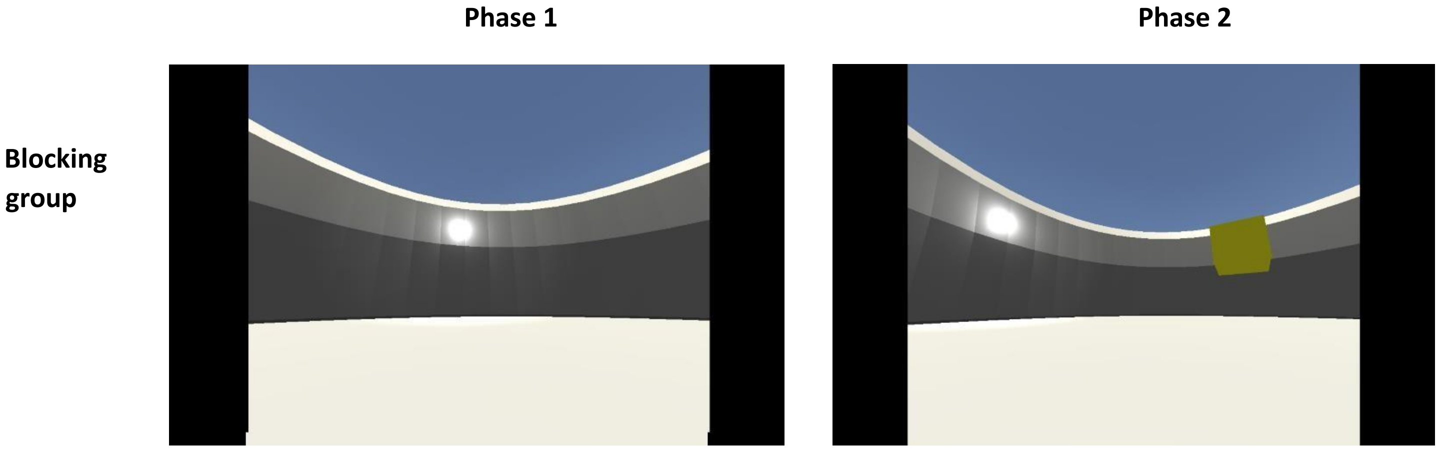
Participants in Control 1 group did not participate in phase 1 but simply undertook 8 Phase 2 learning trials where the two cues were available (bright light in the north and green square in the east) (see Fig 3.1(c), the TMT and final recall trial. Participants in Control group 2 undertook 8 learning trials in phase 1 where they trained to find a hidden target with a novel cue (small green triangle) positioned on the north perimeter wall of the arena. Participants immediately undertook a further 8 trials in phase 2 with the two cues (as above – see Fig 3.1(d). Following the learning phase, all participants from all groups completed the TMT (see description above) and a single 60 second recall trial. For the recall trial, a single cue (green square on the Eastern wall) was used. See Fig 3.1(e). The platform did not become visible to the participant during this trial. Following this, all participants completed a brief questionnaire gathering demographic information and details of their experience of using the NavWell task.

Figure 3.1 (a): Schematic diagram of the NavWell arena. **(b):** Learning phase: Participants in the Blocking group learned using bright light only in phase 1 and bright light and green square in phase 2. **(c):** Participants in the control group 1 had no trials in phase 1 and learned using bright light and green square in phase 2. **(d):** Participants in control group 2 learned using small green triangle in phase 1 and bright light and green square in phase 2.

3.1(a)



3.1(b)



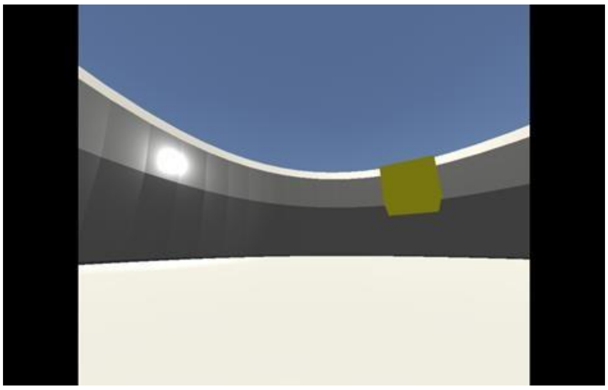
3.1(c)

Phase 1

Phase 2

Control group 1

No trials



3.1(d)

Phase 1

Phase 2

Control group 2

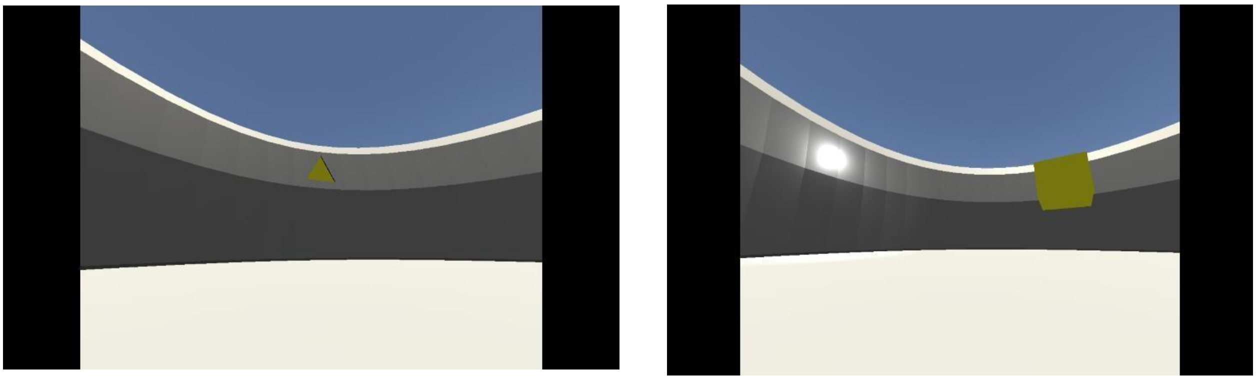
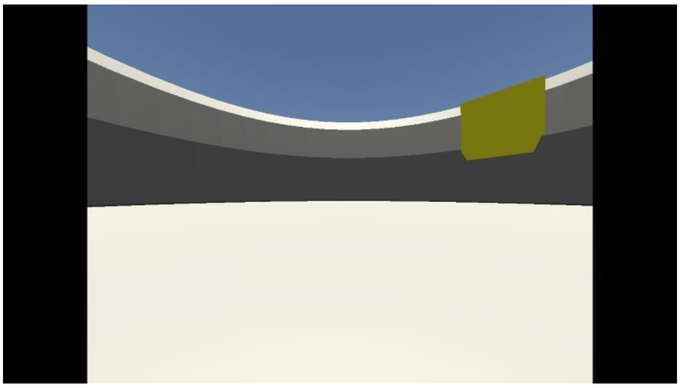


Figure 3.1(e): Recall phase. All groups used a single cue (green square on the Eastern wall) to locate the target.

Recall phase

3.1(e)

All groups



Ethical Considerations and Data Analysis

All experiments were approved by the Maynooth University Ethics Committee (BSRESC- 2021-2453422) and were conducted according to the ethical guidelines provided by the Psychological Society of Ireland (PSI). Time to target, path length and percentage of time spent in the target quadrant were extracted from NavWell and imported into Microsoft Excel. Means and standard error of means (SEMs) were calculated for each trial and for each group. Graphs were created using Microsoft Excel. Scores were then imported into IBM SPSS version 26 for analysis. One-way ANOVAs were used to analyse age and TMT scores across groups. Mixed factorial ANOVAs were used to analyse learning and recall phases. Where relevant, the Tukey HSD test was used for between group *post-hoc* comparisons and Bonferroni corrected t-tests were used for within-group comparisons. A star-based level of significance was used where $*p < 0.05$, $**p < 0.01$ and $***p < 0.001$.

3.3 Results

Demographics

We initially compared the three groups to ensure that they were generally matched on age and cognitive abilities. A one way between groups ANOVA was conducted to determine if Age differed between groups. The assumption of homogeneity of variances was not violated. There was no statistically significant effect found (F (2, 57) = 3.87, p = 0.026). Additionally, a one way between groups ANOVA was conducted to determine if TMT b-a scores differed between groups. The assumption of homogeneity of variances was not violated. There was no statistically significant effect found (F (2, 57) = 0.437, p = 0.648). This suggested that groups were generally matched on both age and cognitive abilities (see Table 3.1).

Table 3.1

Demographic Information for each Experimental Group in the Blocking Experiment.

Group	N	Age (+/-SEM)	M/F	TMT b-a (+/-SEM)
Blocking	20	22.9 (1.1)	10/10	19.6 (1.5)
Control 1	20	20.3 (0.4)	5/15	18.2 (2.0)
Control 2	20	20.6 (0.3)	8/12	20.7 (1.9)

Latency

The latency data were not normally distributed (Kolmogorov Smirnov P < .001). Outliers were not removed. The assumption of homogeneity of variances was violated (Levene's test of equality of variances P < .001). The assumption of homogeneity of intercorrelations was violated (Box's test of equality of covariance matrices = P < .001).

Phase 1

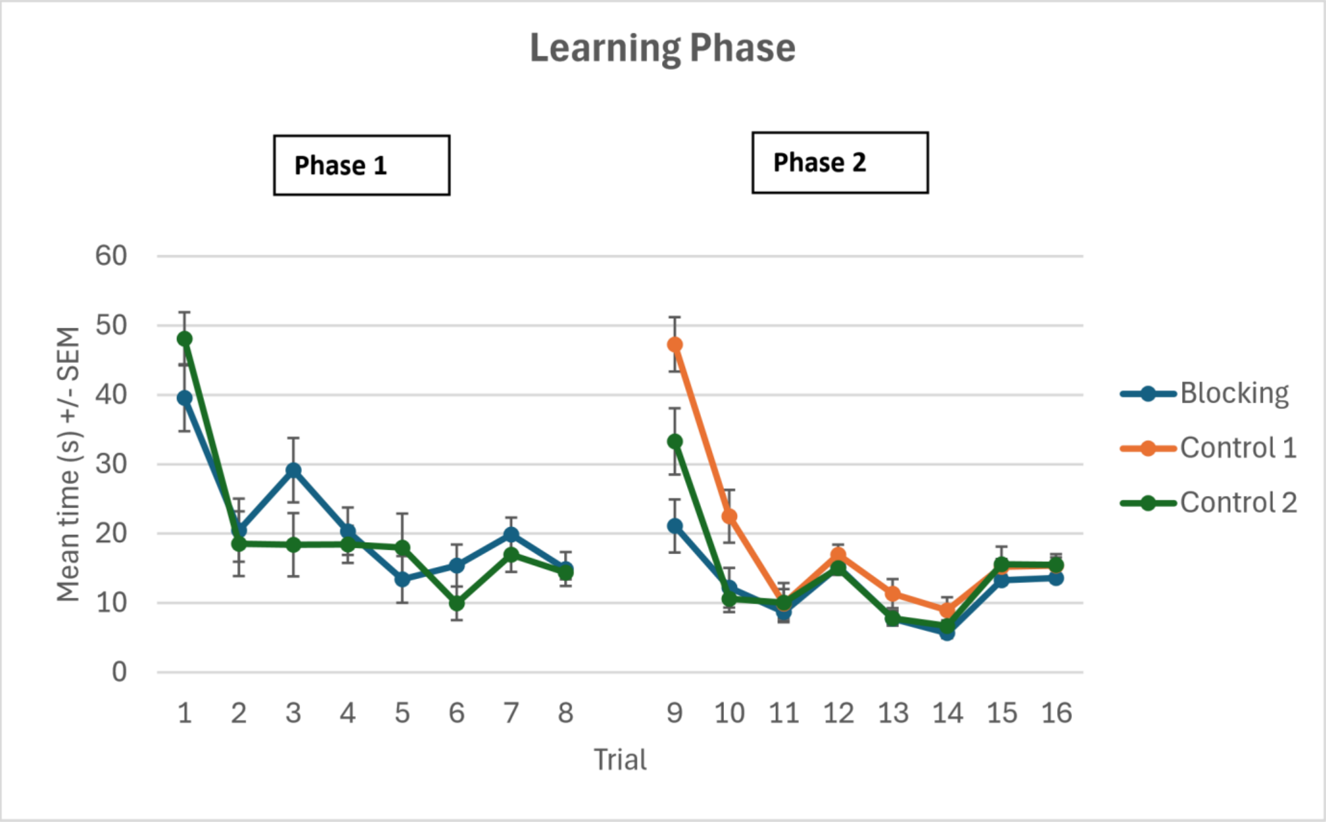
During the first phase, the Blocking group (those with the bright light cue (located in the north position) and the Control 2 group (those with the small green triangle cue located in the north position) were required to find the hidden target across 8 trials. Both groups learned the task well, with the Blocking group reducing their time to target from 39.60 s (+/- 4.82 SEM) on trial 1 to 14.90 s (+/- 2.44 SEM) on trial 8. Similarly, the Control 2 group reduced their time from 48.10 s (+/- 3.82 SEM) on trial 1 to 14.40 s (+/- 0.995 SEM) on trial 8.

A 2X8 mixed factorial ANOVA was conducted to analyse the time taken to reach the target between groups 1 and 3 during Phase 1 learning trials (1-8). There was a significant main effect for trial (F (7,266) = 21.32, p < 0.001, partial eta squared = 0.359). Bonferroni corrected t-tests revealed that participants were quicker to find the target on T8 compared to T1. There was no significant trial X group interaction effect noted (F (7,266) = 1.896, p = 0.070, partial eta squared =0.048) There was no statistically significant effect for group (F (1,38) = 0.162, p = 0.690, partial eta squared = 0.004).

Phase 2

During the second phase, all three groups: Blocking, Control 1 and Control 2 had the bright light cue in the north position and the green square cue in the east position and were again required to find the hidden target across 8 trials. A 3X8 mixed factorial ANOVA was conducted to analyse the time taken to reach the target between groups 1 2 and 3 during Phase 2 of participant's learning trials (9-16). There was a significant main effect for trial (F (7,399) = 45.178, $p < 0.001$, partial eta squared = 0.442). Bonferroni corrected t- tests revealed that participants were quicker to find the target on T16 compared to T9. There was a significant main effect for group (F (2, 57) 10.366, $p < 0.001$, partial eta squared = 0.267) with post hoc Tukey tests revealing that the Blocking group performed significantly better than Control group 1 (p = 0.000) and Control group 1 performed significantly better than Control group 2 (p = 0.013). There was a significant trial X group interaction effect noted (F (14, 399) = 4.462, $p < 0.001$, partial eta squared = 0.135. A further One-way ANOVA was conducted to analyse the differences in time to target between the three groups on trials 9 and 10. There was a statistically significant effect found for trial 9 (F (2, 57) = 9.74, $p < 0.001$) with a post hoc Tukey test revealing that the Blocking group took significantly less time to reach the target (mean = 21.10 , SD = 17.13) compared to Control group 1 (mean = 47.30 , SD = 17.54) and Control group 2 (mean = 33.30, SD = 21.37). There was a statistically significant effect found for trial 10 (F (2, 57) = 4.74, p = 0.012). with a post hoc Tukey test revealing that the Blocking group (mean = 12.20, SD = 12.79) significantly less time to reach the target compared to Control group 1 (mean = 22.50, SD = 17.04) and Control group 2 (mean = 10.60, SD = 8.53 took significantly less time to reach the target compared to Control group 1 (mean = 22.50, SD = 17.04) (See Figure 3.2).

Figure 3.2: Mean time (+/- SEM) taken by participants find the hidden target in Phase 1 and Phase 2.



Distance travelled

The path length data were not normally distributed (Kolmogorov Smirnov P < .001). Outliers were not removed. The assumption of homogeneity of variances was violated (Levene's test of equality of variances P < .001). The assumption of homogeneity of intercorrelations was violated (Box's test of equality of covariance matrices = P < .001).

Phase 1

As a second measure of learning, we examined the distance it took for participants to reach the target. During the first phase, both the Blocking and Control group 2 learned the task and reached the target with reduced distance. The Blocking group reduced their distance from 171.97 vm (+/- 23.11 SEM) on trial 1 to 63.59 vm (+/-

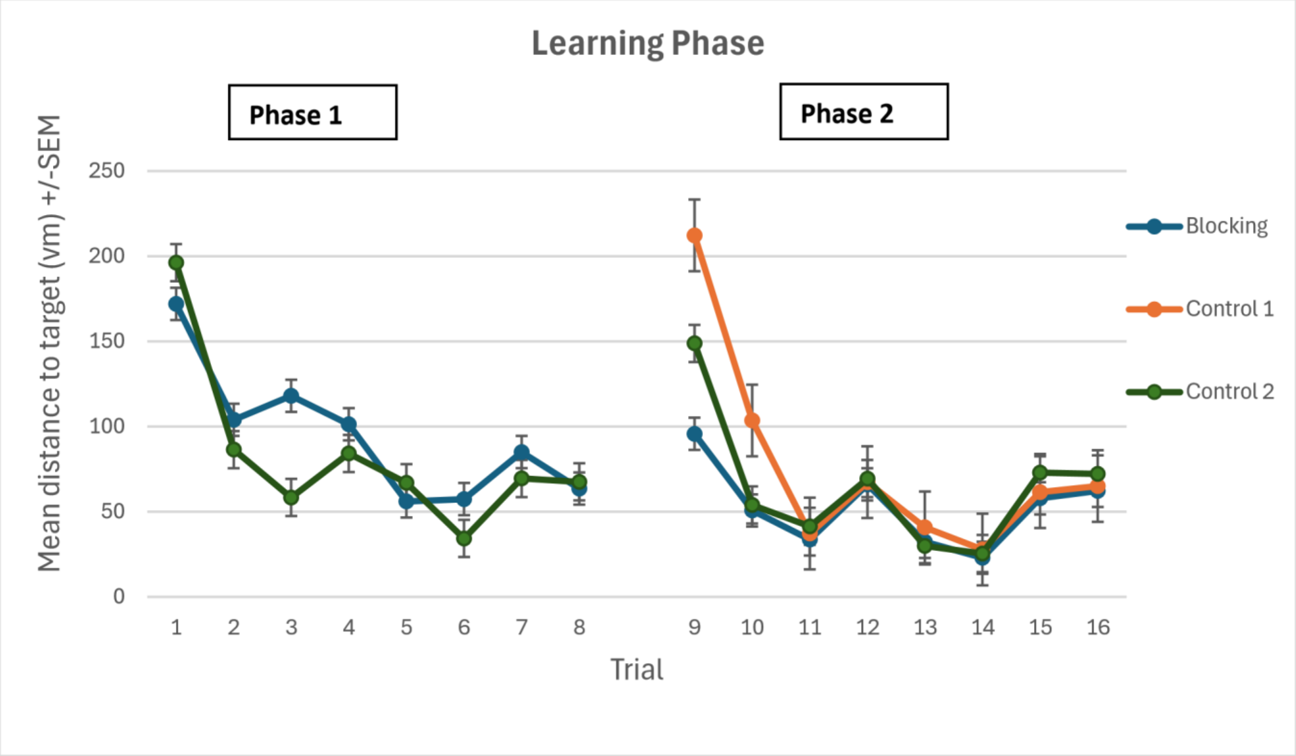
7.92 SEM) on trial 8. Similarly, the control group 2 reduced the distance from 196.21vm (+/- 19.28 SEM) on Trial 1 to 67.52 vm (+/- 5.62 SEM) on trial 8. A 2X8 mixed factorial ANOVA was conducted to analyse path length scores between the Blocking group and Control group 2 during Phase 1 of participant's learning trials (18). There was a significant main effect for trial (F (7,266) = 19.571, p < 0.001, partial eta squared = 0.340 with Bonferroni corrected t-tests revealing that all participants showed a significant reduction in path length scores between trial 1 (mean = 184.09,
SD = 94.76) and trial 8 (mean = 65.56, SD = 30.39). There was no significant trial X group interaction effect noted (F (7, 266) = 1.800, p = 0.087, partial eta squared =.045). There was no statistically significant main effect for group noted (F (1, 38) = 0.716, p = 0.403, partial eta squared =0.018).

Phase 2

As above, a 3X8 mixed factorial ANOVA was conducted to analyse distance travelled to the target between the blocking, control 1 and control 2 groups during Phase 2 of participant's learning trials (9-16). There was a significant main effect for trial (F (7,399) = 54.154, p < 0.001, partial eta squared =0.487) with Bonferroni corrected ttests revealing that all participants showed a significant reduction in path length scores between trials 9 (mean = 152.24, SD = 99.78) and trial 16 (mean = 66.49, SD = 23.21). There was a significant main effect for group (F (2,57) =7.567, P = 0.001, partial eta squared = 0.210). There was a significant trial X group interaction effect noted (F (14,399) = 5.373, p < 0.001, partial eta squared = 0.159). A further One-way ANOVA was conducted to analyse the differences in distance travelled to target between the three groups on trials 9 and 10. There was a statistically significant effect found for trial 9 (F (2, 57) = 8.59, p = 0.001). Post hoc Tukey tests revealed that the Blocking group's path length scores were significantly shorter (mean = 95.73, SD = 81.77) than Control group 1 (mean = 212.22, SD =84.35).

There was a statistically significant effect found for trial 10 (F (2, 57) = 6.15, p = 0.004). *Post hoc* Tukey tests revealed that the Blocking group's path length scores were significantly shorter (mean =50.70, SD = 34.92) than Control group 1 (mean =103.53, SD = 72.00). (See Figure 3.3.)

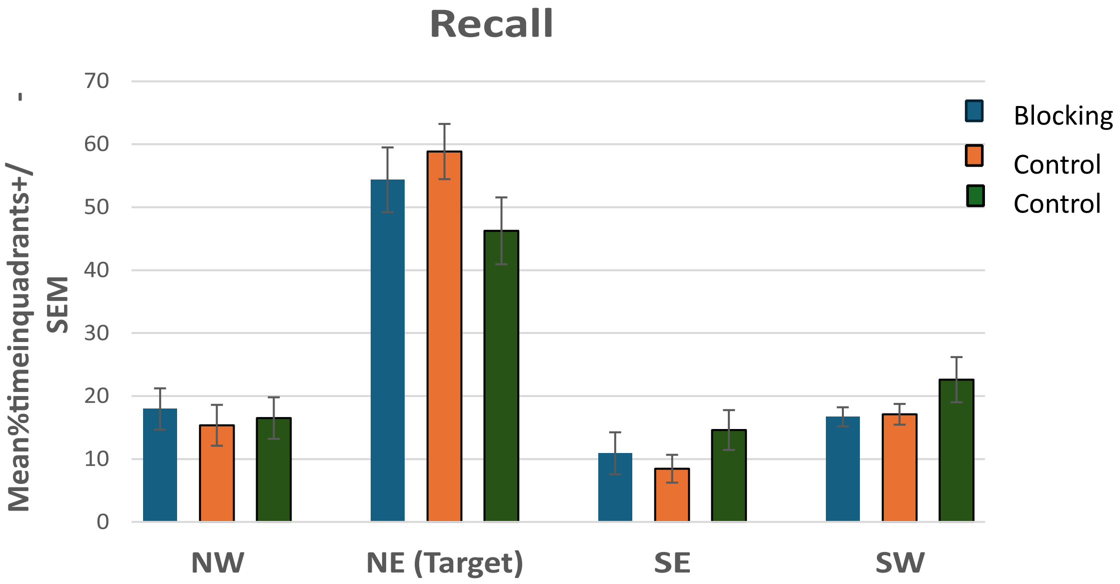
Figure 3.3: Mean path length (+/- SEM) taken by participants to find the hidden target in Phase 1 and Phase 2.



Recall

Following the learning phase, all participants were given a single recall trial where only one cue was available to them (green square cue). A 4X3 mixed factorial ANOVA was conducted to analyse quadrant scores across groups during the retention trial. There was a significant main effect for quadrant (F (3,171) = 65.274, p < 0.001, partial eta squared = 0.534) with significantly more time spent in the NE target quadrant (mean = 53.15%, SD = 22.45) compared to the NW quadrant (mean =16.60% , SD = 14.43, p = 0.854) , SE quadrant (mean =11.32% , SD =13.20, p = 0.339), and SW Quadrant (mean = 18.80%, SD = 11.07, p = 0.171). There was no significant Quadrant X Group interaction effect noted (F (6,171) = 1.258, p = 0.280, partial eta squared = 0.042). There was no significant main effect for group (F (2,57) = 0.748, p = 0.478, partial eta squared = 0.026). All three groups spent a similar amount of time searching for the target in the NE (target) quadrant: Blocking group (54.35%, SD 5.15), Control group 1 (58.85 %, SD 4.38), & Control group 2 (46.25%, SD 5.31). See Figure 3.4).

Figure 3.4: Mean % of time (of 60 seconds) (+/-SEM) spent by groups in each quadrant.



3.4 Discussion

Contrary to what we hypothesised we did not observe a blocking effect using a virtual water maze task with human participants. All groups searched equally in the target quadrant during the recall phase. Our findings are contrary to those of Hamilton and Sutherland (1999) and suggest that the cue learned during phase 1 did not interfere with learning the cue introduced in the second phase. Therefore, our results would support the contention by Hardt et al. (2009) that the novel cue was integrated into a cognitive map. However, there are a number of key differences between our setup and that used by Hamilton & Sutherland which may explain the difference in findings. First, we provided participants with 8 trials in phase 1 and a further 8 in phase 2. In contrast, Hamiliton & Sutherland had 20 trials in phase 1 (5 blocks with 4 trials/block) and 12 trials in phase 2 (3 blocks of 4 trials). Similarly, Buckley et al. (2015) found a blocking effect using 16 stage 1 trials and 12 stage 2 trials. Although it could be argued that participants in the current experiment did not receive enough training to allow interference to occur, we would contend that all participants clearly learned the task in both phases and that the learning curves for our experiment match very closely with that of Hamilton & Sutherland.

A second key difference is the number and location of cues used in the two experiments. Our experiment only had 1 cue in phase 1 and added a second cue in phase 2, whereas Hamilton & Sutherland had 4 cues in phase 1 and added an additional 4 in phase 2. With only a single cue, participants were required to use it and pay attention to it. With 4 cues participants may only have used and learned a subset of cues, an argument put forward by Hardt et al., 2009. Cue feature, particularly the location of cues, seems to play a critical role in determining whether blocking occurs or not. For example, Hardt et al. (2009) found that removal of cues close to the target impaired performance on the probe trial, whereas removal of cues further away had less of an impact, suggesting an overshadowing effect (again see Deery & Commins, 2023, Chapter 2) and that a full cognitive map was not formed as a result. A strength of the current experiment is that we kept the cues equidistant from the goal location, so distance was not an issue. Furthermore, the cues were on the same side as the hidden target, ensuring that they would be used. Although here we had the same number of cues as in Chapter 2, one of the cues in Chapter 2 was located closer to the goal compared to the other. Under such circumstances we found an overshadowing effect (similar to Hardt et al., 2009), whereby the cue closest to the platform overshadowed the cue further away. More than this, participants seemed to ignore the more distant cue completely when in a compound and their performance was a chance level during the recall phase, despite the cues being on the same side of the arena as the goal. Also, when participants had to learn with the single cue further away, they were slower to learn the task (see also Commins et al., 2020) compared to nearer cues.

In the current experiment where distance was ruled out as a factor, participants were able to learn the task equally as well with a single cue or with a compound cue, irrespective of other features (shape, size, colour). We therefore contend that removal of distance as a cue feature, allows cues to be integrated into a cognitive map, but if distance is a feature of the landmark, then rules of associative learning come into play. Therefore, participants can use both associative learning rules and cognitive mapping, but landmark proximity is the determinant of which strategy is used. However, further work needs to be done to help establish this idea. For example, we only used two cues. While keeping distance equivalent, can multiple cues (e.g. 3, 4 or more cues of different sizes, shapes, colours, brightness) be all integrated into a cognitive map as readily, or is there a limit on number? Furthermore, is there a hierarchy of salience characteristics (apart from proximity) or can all cues be integrated readily irrespective of its characteristic? Given that we used cues of different shapes, sizes and brightness our results would suggest there is not a hierarchy, however, it could be argued that the green triangle and green square were not distinctive enough. Furthermore, our cues were on the same side as the target; if the cues were at a further distance (e.g. at opposite side of the arena to the goal – while keeping the cues equidistant to the goal) could these be also integrated into a cognitive map as readily as the nearer cues in the current experiment.

Another finding that emerges from our results suggests that there may be a hierarchy of learning. We found limited extra exploration when a new cue was added during phase 2 – Blocking group. This cue was easily integrated into the cognitive map (as suggested above). There was no significant increase in the time required to find the target on first trial of phase 2 compared to the last trial of phase 1. When two novel cues replaced a single cue there was additional learning (Control Group 2), as represented by a small significant increase on the first trial of phase 2. This increase was not as much as when there was no prior learning at all (Control Group 1). Therefore, familiarity with the task has a benefit. This general pattern was also observed with the Hamilton & Sutherland (1999) study.

Finally, in recent years there has been strong debate over when blocking might occur. For example, cue type (Buckley et al., 2015), cue stability (Buckley et al., 2021), level of instruction (Hardt et al., 2009), strategy used (Dolle et al., 2018) have all an impact of whether blocking occurs in spatial learning or not. Furthermore, there has also been much discussion on the nature of the blocking effect more generally (see Maes et al. 2016; Seraganian, 2023; General Discussion). For example, recently Maes et al. (2016) failed to replicate the blocking effect in 15 experiments. However, there has been much counter-argument to this. Soto (2018) argued that the reason for observed failures to replicate was that many of the experiments used same modality stimuli and were based on outdated models of association (Rescorla & Wagner, 1972; Macintosh, 1975; Pearce & Hall, 1980) - 3 contemporary models of associative learning predict a weak or no blocking effect when stimuli are similar or belonging to the same modality (Wagner, 2003; Kinder & Lachnit, 2003; Soto et al., 2014). This is also a consideration in our experiment where the same stimuli of the modality were employed (visual cues) and may add to a reason for our failure to find a blocking effect. The blocking phenomenon is worthy of continued examination and particular focus should be given to what conditions are required for the observation to occur.

In conclusion, our findings suggest that if proximity is ruled out as a cue feature, then cues irrespective of size, shape or colour are treated equally and are integrated into a cognitive map. Furthermore, we suggest that as proximity is a key feature in location memory this follows the rules of associative learning; near cues compete with other cues, overshadow cues further away (Deery & Commins 2023, Chapter 2) and block the learning of any additional cues (Roberts & Pearce 1999).

Chapter 4

General Discussion

4.1 General Discussion

Overview

This thesis aimed to explore two associative learning phenomena (overshadowing and blocking) that have been extensively studied in the animal literature but has received little attention with respect to human research, particularly in the domain of spatial learning. Landmarks play a critical role in spatial navigation and memory (Chan et al., 2012), with many rodent (Chamizo & Rodrigo, 2006) and human (Albrect & von Stulpnagel, 2021) studies showing that the salience of the landmark can determine how well a particular location is learned and subsequently recalled. Manipulating the position and salience of cues using a virtual navigation and spatial learning task with young adults, allowed us to (1) determine whether the overshadowing and blocking phenomena could be extended to the spatial domain using human participants. (2) The experiments also allowed us to investigate the robustness of these phenomena. For example, although overshadowing and blocking are well established (Kamin, 1968 ;1969b; Hebert et al., 2017; Rodriguez et al., 2011; Chamizo, 2003; Prados, 2011), recent research has raised questions about replicability, universality and the conditions under which the phenomena occur, particularly with respect to blocking (see Maes et al., 2016). (3) The experiments helped to address the current debate regarding two of the most prominent theories of spatial navigation and memory: cognitive mapping theory (O'Keefe & Nadel, 1978) and associative learning theory (Pearce, 2009).

With respect to the last point, cognitive mapping theory argues that navigation operates primarily using what is termed a locale system (O'Keefe & Nadel, 1978). This locale system allows the animal to gather information through exploration of the surrounding environment resulting in the production of a cognitive map. Updating of this map occurs automatically via exploration and allows the animal to use novel short cuts in cases where a route is blocked. In contrast, associative learning theory (Pearce, 2009) suggests that an animal associates particular cues or landmarks with other landmarks and/or the goal within its environment. As a result, navigation is performed by a simple learned cue-goal association. Both these theories make different predictions with respect to overshadowing and blocking. For example, the cognitive map theory suggests that all cues are treated equally and may be incorporated into the map. In contrast, associative learning theory suggests that all cues are not treated equally and are dependent on a cue's salience (brightness, colour, shape, size, proximity); some cues may be learned while others are not, due to cue competition. This would suggest that the associative learning theory would support overshadowing, but the cognitive map theory would not. Likewise, with respect to blocking, cognitive map theory would suggest that new cues would be automatically incorporated into the cognitive map during exploration, whereas the associative learning theory would suggest that any additional new cues would be blocked and not learned.

Overshadowing

Results from Chapter 2 (see also Deery & Commins, 2023) indicate that when cues of equal salience were positioned at different distances to the goal, the nearer cue exerted significantly more control over search behaviour during the recall test than the far cue. In addition to this, it would seem that the far cue was completely ignored – participants searched in a random fashion when presented with this far cue alone. This finding suggests a strong overshadowing effect and is consistent with the associative learning theory (Chamizo et al., 2003; Pearce, 2009). These findings are also in agreement and extend a recent finding by Sansa et al (2019), where the landmarks closest to the goal also exerted more control over searching compared to far cues. In the Sansa study cues were positioned on the opposite side to the goal, where it might be expected that participant’s recall of the platform might be poorer compared to when cues were positioned near the target (see also Commins et al., 2020). The current study positioned both cues on the goal side of the arena to ensure that all participants could pay attention to them; even still, it was found that the nearer cue overshadowed the far one. Research by Herrera et al. (2022) also found an overshadowing of geometry over landmarks, but the effect was observed only when proximal landmarks were used. Overshadowing did not occur when distal landmarks were used. Proximity to a goal, as might be expected, hold a certain degree of importance when it comes to spatial memory. Our results are also consistent with previous rodent studies (Chamizo & Rodrigo, 2004; Chamizo et al., 2006) that have also shown that proximal landmarks exerted more control than distal landmarks (however, see Farina et al., 2015). The results from our experiment showed that the distal cue was completely ignored suggesting that perhaps participants attended and learned only the near cue; this hints at an efficiency strategy suggested by Commins (2018) – it requires less energy to learn 1 rather than 2 cues. It would be interesting to investigate if the cues were equidistant from the goal, would overshadowing occur with other features of the landmarks. For example, would a bigger cue or a brighter cue overshadow a smaller or dimmer cue, holding distance equal? Overall, our findings from the overshadowing chapters lends support to associative theory as the most salient cue overshadowed the lesser salient cue instead of becoming incorporated into a mental map as suggested by cognitive mapping theory.

Blocking

Contrary to what was expected, the second experiment failed to yield a demonstration of blocking in healthy young adult participants. Whilst these results contradicted those of Hamilton and Sutherland (1999), on which the study was based, they also question the universality of the blocking phenomenon. Evidence for blocking in human participants has been previously shown in a number of studies using a circular arena (e.g. Wilson & Alexander, 2008; Pearce et al., 2006), but the blocking effect was not observed when a square enclosure was used (Wilson & Alexander, 2010).

One key difference between the Hamilton and Sutherland study and the current blocking study is that there were fewer cues (4 cues in phase 1 and an additional 4 in phase 2 in Hamilton and Sutherland's study and one cue in phase 1 and a second added in phase 2 in ours) used in the current study and perhaps this was a factor in the failure to observe a blocking effect. Participants could only rely on the cues presented in our study but may have used only a subset of the cues presented in the Hamilton and Sutherland study. The position of cues is also important to consider (see above). Removal of cues near to the target has been shown to impair learning but this is not the case when distal cues are removed (Hardt et al., 2009). In the current study cues were equidistant and the task was learned equally well by participants regardless of cue characteristics or whether cues appeared alone or in a configuration. Results from this study seemed to indicate that when distance is removed as a factor, a cognitive mappingbased learning strategy is employed as opposed to a more associative learning strategy.

Difficulty in replicating the blocking effect in general has been highlighted recently (see Maes et al., 2016). These authors reported 15 failed replications using a variety of experiments. However, one issue with Maes et al's (2016) work, highlighted by Seraganian (2023), is that some of the 15 experiments employed multiple test trials. As such, these experiments failed to replicate Kamin's (1968) original experiments where only a single test trial was employed. Our current experiment, which also used a single test trial, agrees with Maes et al. regarding the difficulty in finding a blocking effect. Another issue identified by Mae's et al's (2016) investigation was the use of poor control conditions in previously published reports. In our experiment we tried to account for such criticisms by using two control conditions, one that had no phase 1 and a second one that had phase 1 using a different cue (therefore the number of learning trials was equivalent to the Blocking group). Overall, our blocking experiment lends support to cognitive mapping theory rather than an associative learning account. The new cue introduced in phase 2 of the experiment appeared to become integrated by participants and did not interfere with the learning of the first cue as would be expected if blocking had been demonstrated.

Support for conflicting theories

The results of our two experiments pose an interesting dilemma. The overshadowing chapter suggests that we use an associative learning mechanism, whereas the blocking chapter suggests we use a cognitive mapping strategy to learn and recall a specific location. How can both be true? The primary difference between the two experiments is the location of the cues. In the overshadowing experiment, one cue was positioned nearer to the goal compared to the other, whereas in the blocking experiment the two cues were kept equidistant from the goal. This suggests that proximity may be the key salient factor at play in support of associative learning theory. When a nearer cue is available, a response-based strategy is employed which is less cognitively taxing than the alternative place-based strategy (Boone et al., 2024). If proximity is removed as a factor, all cues available appear to be treated equally and therefore all are integrated by participants, therefore lending support to cognitive mapping theory. Ultimately, both associative and cognitive mapping strategies can be employed on a given task, but cue proximity appears to determine which of these will be used. Cognitive mapping theory argues that learning occurs via participants' exploration of the environment (O Keefe & Nadel, 1978). Information is gathered during this exploration and integrated into a mental map. As this learning happens via exploration and not prediction (e.g. cue/goal association), it should therefore not be subject to cue competition effects such as blocking. This is reflected in the results of experiment 2. This place-based strategy is reliant on an internal map and is more hippocampal dependent (Morris et al.,1982; O'Keefe & Dostrovsky, 1971).

Overall, when a proximal landmark is available, this appears to elicit an associative strategy of learning but when proximity is removed as a factor, a more explorative cognitive mapping-based strategy of navigation maybe employed. This may simply be because it is easier and therefore less cognitively taxing to associate a nearby cue to an adjacent goal as in experiment 1, hence the use of an associative strategy when proximal cues are present and it is harder to use this strategy when proximity is not a factor, hence the use of a more exploration-based strategy employed in experiment 2 (see also Commins, 2018).

Further investigations

This research can be developed into further experiments designed to test at what point proximity ceases to control behaviour. A replication of experiment 1 could be conducted by maintaining the proximal cue's position near to the goal, but, while it is still near to the goal, it is positioned a further distance away than the cue in experiment 1, ultimately stretching the cues further from the goal. This could be used to determine exactly what point a proximal cue loses its strength when influencing behaviour. Results from experiment 2 could be further explored by maintaining the equidistance of multiple cues (rather than just two) but varying other characteristics slightly such as luminescence / colour/ size to test if these can all be integrated in the same fashion. Alternatively, cues could be stretched further apart whilst maintaining their equidistance. This may determine at what point it becomes difficult for participants to visually incorporate all cues available to them, thereby impacting their ability to integrate into a cognitive map.

Future blocking experiments should also ensure that cues are distinct enough from each other that they can be clearly distinguished between as this may have caused issues with the current study (see Chapter 3 for a discussion). An increase in learning trials in phases 1 and 2 in a similar fashion to Hamilton and Sutherland's blocks of 4 trials may also improve chances of producing a blocking effect. As previously highlighted by Soto (2018) stimuli that are very similar or from the same modality are likely to produce a weaker blocking effect. This has been called into question (Mae's et al., 2018); however future studies using stimuli from different modalities may be worthy of investigation - the influence of cue modality has also been highlighted in rodent studies (e.g. Sanderson et al., 2016).

This research also has the capacity to be extended to an investigation of the neural basis of overshadowing and blocking. There has been limited work on this to date. The NavWell platform in combination with imaging techniques (e.g. EEG, MEG or fMRI) could be used to non-invasively examine what brain areas are active during navigation and whilst these phenomena are occurring (Light et al., 2010). For example, previous work using virtual navigation tasks has been successful at investigating the role of theta oscillations during spatial encoding (Thornberry et al., 2023), indicating that NavWell is a versatile platform that can be used in conjunction with other methods to investigate the neural basis of spatial learning.

There are number of parallels between the phenomena in these experiments and other interference-based observations in the memory literature. Godden and Baddley noted that stronger recall performance when participants were tested in the same environment they learned in (Godden & Baddley, 1975). Contextual cues are important for guiding participants during navigation (Bugmann et al., 2007). It is possible that the configuration change of cues in the overshadowing experiment may have been interpreted as a new context and thus affected participant's recall. This would be worthy of further investigation.

While there are some similarities between the set-up of the RAVLT (Rey, 1958) and a typical blocking paradigm, in order for it to mirror a blocking paradigm one would first have to test participants with one list of words (list A) and then with a combination of list A and list B, then finally test participants with list B. This could certainly form the basis of a procedure for an interesting future experiment.

Gender plays an important role in navigation with differences observed between male and female performance on navigation tasks. Males have been shown to use a hippocampal dependent place strategy to navigate, relying on knowledge of the environment compared to females who rely on a striatum-based response strategy which involves following a previously learned route. These differences in strategy choice can vary depending on age and are worthy of further study as they have a significant impact on performance due to differences in the efficiency of each strategy (Hegarty et al., 2023).

Limitations

Although care was taken to maintain an equal balance of male and female participants, it wasn't always possible to achieve this (23 % male / 72 % female / 4 % not reported in experiment 1, and 38 % male / 62% female in experiment 2). This is a limitation as there are reported differences in navigation strategies between males and females. For example, the strategies used by male participants to explore environments appears to be distinctly different to the those employed by female participants (Astur et al., 1998; Cutmore et al., 2000; Padilla et al., 2017). For example, male participants have been observed travelling longer distances without changing direction and had less frequent returns to previously explored areas giving them a more efficient and successful navigational strategy compared to females (Munion et al., 2019). Furthermore, males tend to favour place-based methods whereas females tend to use response-based strategies (Boone et al., 2018). However, with NavWell, there previously have been no differences in male /female performance reported (Commins et al.,2020). Age also plays a role with older adults favouring response strategies but younger adults showing no particular preference for either (Rodgers et al., 2012; Zhong & Moffat, 2018; Hegarty et al., 2023). It may be worthwhile investigating both overshadowing and blocking in older adult participants in future studies.

Another possible limitation of our experiments is that previous computer gaming experience was not controlled for. It is possible some participants may have been at an advantage due to having a gaming hobby and thus may have performed better on the NavWell task, which is similar to a video game from a first-person perspective. Prior experience of video gaming has been shown to affect performance when using virtual navigation software (Richardson & Collaer 2011, Clemenson & Stark, 2015). It may be advisable to consider excluding participants with extensive gaming experience in future studies to avoid this becoming an issue.

In recent years, VR environments have become an increasingly popular tool for investigating navigational strategies due to their versatility however concerns about their ecological validity have been raised (Van der Ham et al., 2015), that is whether they provide an accurate and comparable representation of real-life navigation. A recent study revealed that when participants were tested in a real-world environment and a replica VR environment, there were significant performance differences regardless of age (Kalantari et al., 2024). VR environments remain a useful tool for experimentation; however, caution should be exercised when interpreting results. As mentioned in the introduction, a mouse and laptop display were used for the experiment which did not have an immersive aspect or involve physical locomotion for the participant. This may have been a limitation as it is not as reflective of real-world navigation as a VR immersive method due to the lack of physical locomotion involved in completing the task.

In addition, although participants did not report experiencing motion sickness using NavWell in these or previous experiments (e.g. Commins et al., 2020; Thornberry et al., 2023), it is often reported in more ‘realistic’ settings (Munafo et al., 2017). Therefore, a balance between using a fully immersive environment with the need to have a more ecologically valid test needs to be found.

Broader implications

This thesis has examined how participants learned and recalled locations in relation to landmarks and why some landmarks exhibit more influence compared to others in an individual’s environment. As this research investigated phenomena related to human navigation, it may be valuable for people with Alzheimer’s Disease or Mild Cognitive Impairment (MCI). Loss of navigational ability has been recognised as being particularly sensitive at detecting early deficits relating to AD (Allison et al., 2016; Tangen et al., 2022). The more knowledge we gather from basic learning phenomena such as overshadowing and blocking during human spatial learning, the better we can apply this knowledge to brain disorders.

In addition, increasing our understanding of why some landmarks appear to have more influence over others may be useful for developing interventions and may assist older adults and/or patients in overcoming difficulties with their day-to-day navigation and orientation. This may be particularly helpful when designing a home environment or indeed in a care setting. What cues/landmarks are important to serve as orientation aids in these locations. As a laboratory tool, the NavWell platform may provide an inexpensive and versatile method of investigation to study general age-related decline of navigation ability and location memory, deficits considered to be early markers of dementia (Fricke et al., 2022).

Concluding remarks

This thesis has demonstrated that overshadowing occurs in healthy young adult participants during human spatial navigation and that the blocking phenomenon did not replicate using a paradigm from an earlier study (Hamilton & Sutherland, 1999). As it stands the thesis presented evidence supporting both the associative learning theory (Pearce, 2009) and the cognitive mapping theory (O' Keefe & Nadel, 1978). It is likely that cue proximity is the pivotal factor at play. We suggest that a near cue overrides all other salient features (brightness, size, shape) and leads participants to simply learn the location of the goal relative to this cue - any other cue irrespective of their salience is simply ignored. We would suggest that this requires a low cognitive effort and limited neural effort. However, if proximity is removed as a feature, then all other cues can be learned and integrated into an overall cognitive map. This, in turn, suggests a greater level of cognitive and neural effort but may lead to greater flexibility. Finally, this research has also extended previous work and demonstrated the usefulness and accessibility of the NavWell tool (Commins et al., 2020) as a method of examining navigation and the role of landmarks with human participants of all ages.

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Appendix A: Self -Report Questionnaire

NavWell Participant ID:

Age __________ Prefer not to say ________

Please circle: Female Male Prefer not to say

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.

Appendix B: Information Sheet

Maynooth University
National University of Ireland Maynooth

Department of Psychology

**Roinn Síceolaíochta
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Information Sheet:

Behavioural and Neural Correlates of Human Spatial Navigation and Memory

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 the Trail Making Task (TMT) for executive functioning, this test will take about 2 minutes and is 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 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, Prof. 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, obody 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.

Appendix C: Informed Consent Form

INFORMED CONSENT FORM

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

This research is being conducted by Róisín Deery, a postgraduate student and D'Andra Andrews, a BSc 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

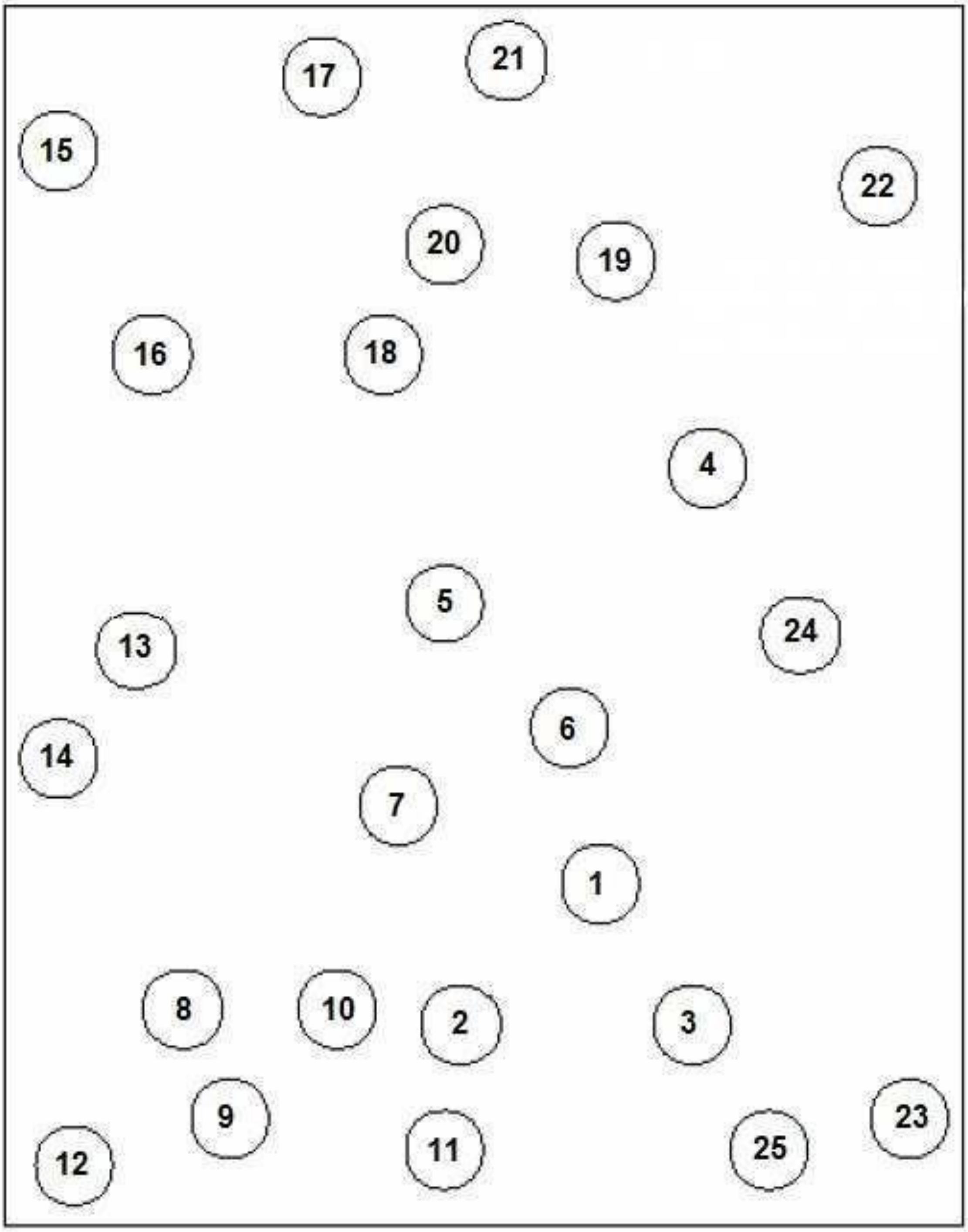
________________________ Researcher

________________________ Date

Appendix D: Trail Making Task

Trail Making Test Part A

Participant No :______________________________ Date: ____________________



Trail Making Test Part B

Participant No :______________________________ Date: ____________________