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Contributions of Motility to Large-scale Search and Navigation

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UNIVERSITY OF PLYMOUTH

Contributions of Motility to Large-scale Search and Navigation

by

Rory Baxter

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in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

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Author's declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award. Work submitted for this research degree at Plymouth University has not formed part of any other degree either at Plymouth University or at another establishment.

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Rory Baxter

Abstract

Navigation and search are fundamental daily activities, however, their ubiquity belies their complexity. These behaviours are reliant upon multiple underlying cognitive processes including our ability to reliably employ viewpoint invariant allocentric and viewpoint dependent egocentric cues. The ability to use these sources of information have been studied extensively in the human spatial cognition literature, largely on desktop PC platforms. Whilst this provides researchers with an immense amount of experimental control, participants remain static, differing fundamentally to the demands of navigation and search in real-world contexts. This thesis presents a series of experiments that interrogate place learning and probabilistic cueing on both desktop PC and immersive virtual reality (VR) platforms. Chapter 2 reports the development of a novel place learning task based on the Blue Velvet Arena task (BVA; Kalová et al., 2005) for both immersive VR and desktop PC platforms. The task included experimental conditions that interrogated the ability to accurately use allocentric or egocentric information in isolation, or both types of information in conjunction. Across a series of experiments, participants appeared to be able to more accurately identify a target location in the immersive VR task, relative to performance on the desktop PC equivalent. The same immersive VR system was employed in Chapter 3 for a replication of Smith et al.'s (2010) probabilistic cueing task, in which participants learned the statistical contingency underpinning a target's spatial distribution. Chapter 3 replicated results reported by Smith et al. (2010) and provide further evidence that allocentric probabilistic cueing may be contingent on supplementary visual information. The experiments reported in this thesis demonstrate the utility of immersive VR as a tool for interrogating human spatial cognition in large-scale environments. Importantly, the cross-platform inconsistencies revealed by the place learning task demonstrate the need to comprehensively test theories of human spatial behaviour across a range of conditions and platforms.

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Chapter 1

General Introduction

Our daily lives are reliant on our understanding of space - it is fundamental to know where we are in the world, where other objects are, and where things are likely to be. For example, when walking to work, we need to identify where we are along the path, where our workplace is, and the direction in which we would need to travel to reach the destination. Similarly, when we search for a bag of frozen peas in the supermarket we need to have an understanding of where the freezer section is located in order to search effectively. Whilst navigation and search are regular features of our everyday lives, this belies their complexity, as they are reliant upon a broad range of component behaviours, and each is reliant upon differing levels of spatial knowledge (Wiener et al., 2009). Indeed, our navigational behaviour is underpinned by knowledge of an environment's layout, as well as knowledge of specific routes between locations taken through an environment. In contrast, search is underpinned by knowledge of previous instances of an object's location within an environment.

These fundamental differences between navigation and search has been addressed through the development of a taxonomy of large scale spatial behaviour (Wiener et al., 2009), that details which behaviours are supported by different types of knowledge. For example, exploration of an environment is fundamentally different from path planning in a familiar environment. Exploration has no specific destination, and is contingent on an absence of survey (map-like) or route knowledge of an environment. In contrast, path planning requires access to survey knowledge of the environment, knowledge of available routes, and a specific destination. Similarly, there are differences within search behaviours, e.g. uninformed vs informed search, with the former lacking survey knowledge of

an environment, whereas the latter is reliant upon it. Scientific interrogation of these behaviours is further complicated by their reliance upon a broad spectrum of underlying cognitive processes. When following a specific path one needs to draw upon perceptual and attentional processes to attend to relevant signs, whereas if one searches for a novel path one needs to rely on the ability to learn and recall the spatial layout of an environment. The complexity and broad spectrum of underlying cognitive processes and behaviours means that across individuals there is enormous scope for difficulties with these spatial behaviours to arise. Difficulties in navigational behaviour have been observed extensively within the literature and are associated with both typical and atypical ageing (Diersch & Wolbers, 2019; Driscoll et al., 2005; Gazova et al., 2013; Kalová et al., 2005; Laczó et al., 2010, 2021; Possin et al., 2016; Wiener et al., 2012, 2013, 2020), autism spectrum condition (ASC; Lind et al., 2013; Ring et al., 2018; Smith, 2015) and hydrocephalus (Buckley & Smith, 2013; Smith & Buckley, 2012). Similarly impairments in search behaviour are associated with Alzheimer's disease (Rösler et al., 2000) and hydrocephalus (Iddon et al., 2004). There are also conditions such as ASC, in which some literature suggests an advantage to visual search behaviour (Hessels et al., 2014; Shiraama et al., 2017), however, recent literature does report some difficulties in large scale search behaviour (Pellicano et al., 2011).

Differences also exist across neurotypical populations. Anecdotally, we can all recall people that are proficient or otherwise at finding their way around the world, or efficiently identifying where objects are located. This is supported extensively by recent literature that shows individual differences in navigational behaviour across a wide range of contexts and tasks (Newcombe, 2018; Wiener et al., 2013). These differences can arise in how we integrate information across different routes in the same environment (Blacker et al., 2017; Nazareth et al., 2018; Weisberg et al., 2014, 2018), how we use landmarks (Padilla et al., 2017), and our ability to reliably compute shortcuts (Furman et al., 2014; Marchette et al., 2011). Furthermore, there is evidence to suggest that these differences may relate to variations in related brain structures. For example London taxi drivers have larger hippocampi (Maguire et al., 2000, 2006), and smaller volume in the right precuneus is associated with poorer performance in a virtual navigation task (Weniger et al., 2011). Similar individual variance is observed in search behaviour, e.g. effective search is modulated by working memory in both adults (Kovesdi & Barton, 2013), and children (Smith et al., 2005). One factor that may underpin these differences in ability across both search and navigation is variation in the ability to accurately interpret and access spatial relationships

within an environment.

1.1 Spatial Reference Frames

A key component of understanding space around us is how we reference objects in our immediate environment, i.e. whether their location is encoded relative to the self, or to other objects in the world around us. These reference points are theorised to form discrete spatial reference frames which are conceptualised as either being allocentric or egocentric in their nature (Burgess, 2006, 2008). Information that is encoded allocentrically is encoded in an absolute space, i.e. it is viewpoint invariant, and independent to the self, as it comprises the spatial relationships between objects in the world around us. In contrast, egocentric spatial information is encoded only to the self and one's perspective. It is dynamic, as egocentric spatial relations shift as we move around the environment. For example, a plate on one's left when sat at a desk, would be on the right should one move to sit on the opposite side of the desk. Allocentric information is considered to be the more cognitively demanding of the two reference frames as it requires the integration of multiple vectors of spatial information, e.g. the direction and distances between multiple objects/locations (Wolbers & Wiener, 2014). Conversely, egocentric information is considered to be computationally simpler, as it only comprises the spatial relationships between external objects and the self. The contrasting nature of these types of information mean that the two types of spatial representation support different kinds of behaviours. For example the rich and flexible information acquired as a part of an allocentric representation of space supports more elaborate and complex behaviours, such as finding novel routes between known locations. Egocentric spatial representations are more likely to be employed in less complex types of behaviour, such as following a route via a series of stimulus-response (S-R) pairs (e.g. turn left at the church then right at the castle), or following a direct vector towards a beacon that leads to a goal location.

How these types of information are represented psychologically has been a prominent topic of research in the spatial cognition literature. One of the most influential theories on this subject is the concept of the cognitive map, first theorised by Tolman (1948) and supported on a neuronal level by O'Keefe & Nadel's (1978) seminal work. Tolman et al. (1946a) conducted a study in which rats were trained to learn a route within a maze that involved several bends in the path to a food reward. At that time, contemporaneous

theories of navigation suggested that rats learned to reach goal locations in experiments through a series of S-R associations, e.g. turn left at the first junction, and right at the second. These S-R associations would comprise egocentric information, as the directional judgements are tied to the rat's directional heading when approaching each junction. Consequently, this information would be of little utility when computing a route that had not been traversed previously. To test what the rats had learned about the space, in a subsequent test phase, the original circuitous route was blocked, but several straight arms were added to the maze, one of which led to the reward location via a direct path. At test, the majority of the rats were able to select the direct path to the goal location, despite not having previously taken that route before. This behaviour is inconsistent with a S-R reinforcement explanation, which led Tolman (1948) to theorise that rodents represented the external world in a mental map that was acquired through exploration of their environment. The cognitive map model was formalised by (O'Keefe & Nadel, 1978), following the discovery of place cells, neurons that fire on the basis of a rodent's location within the environment (O'Keefe & Dostrovsky, 1971; O'Keefe, 1976; O'Keefe & Nadel, 1978). Evidence for homologous place cells in the human medial temporal lobe has been found in humans via single cell neuronal recording during the navigation of a virtual town (Ekstrom et al., 2003). This work provides evidence for a neuronal representation of allocentric space within environments (Burgess, 2006, 2008), and provides a basis for understanding both navigation (Ferguson et al., 2019; Hartley et al., 2003; Marchette et al., 2011; Wiener et al., 2012, 2013; Wolbers & Wiener, 2014) and search (Jiang et al., 2014; Jiang & Won, 2015; Sisk et al., 2021; Smith et al., 2010).

Whilst the cognitive map is considered the basis of allocentric representations of space, egocentric knowledge has been suggested to be reliant upon the viewpoint based recognition of scenes and the integration of self-motion information to support the spatial updating of objects' locations relative to the self (Burgess, 2006; Wang & Spelke, 2002). In an influential study, Simons & Wang (1998) dissociated contributions of viewpoint alignment and self-motion to recognition of a scene across a series of experiments. In this experiment, participants were required to identify which item, from an array presented on a circular table, was moved between training and test phases. At test, the array was viewed from one of two viewpoints, and the table was rotated to either align with each viewpoint, or not, in a fully factorial design. Their results showed advantages to recognition when the participant moved and the array was stationary, or when the viewpoint

remained consistent (i.e. the participant and the array did not move, or both moved in the same direction by the same magnitude). This experiment demonstrated two aspects of egocentric spatial knowledge - the first is a snapshot from a specific viewpoint, which was the most accurate, and the second is an egocentric representation of the array's location relative to the self that is updated when moving between locations. These data have been replicated and extended (Burgess et al., 2004; Simons & Wang, 1998; Wang & Simons, 1999), providing a cornerstone for understanding the basic mechanisms of egocentric spatial knowledge.

The viewpoint-based utility of egocentric information supports the use of strategies based on S-R associations, which, as described previously, comprised the primary explanation of navigational behaviour prior to Tolman's (1948) cognitive map theory. Egocentric information also facilitates the use of distal or proximal cues as beacons, for eliciting an initial heading (Ekstrom & Isham, 2017; Ferguson et al., 2019; Morris, 1981) that leads to a specific destination. For example, one might, when exploring an unfamiliar environment, see a familiar landmark in the distance that can be used as a beacon to take a direct path back to a familiar space. This also underpins S-R forms of navigation, as the decision point would represent a beacon on a path that is then associated with a further egocentric direction (Ekstrom & Isham, 2017).

The use of allocentric and egocentric information is extremely important to both navigation and search. Allocentric information provides us with knowledge of where, relative to other locations in the environment, our destinations are, or where regions in which a target is likely to appear are located. Egocentric information allows us to identify where we currently are, and where our current heading will lead us to. This allows us to learn routes easily through S-R associations, or guide ourselves to regions in which a target rich locations.

1.2 Navigation and Spatial Reference Frames

Across the navigation literature the conceptualisation of spatial reference frames as being either allocentric or egocentric provides a powerful framework for understanding how we acquire and deploy knowledge about the world around us. This framework has provided avenues for interrogating separable allocentric and egocentric contributions across the broad taxonomy of navigational behaviours (Wiener et al., 2009). Its origins lie in the

rodent maze literature, in which rats are trained to learn a specific location within an experimentally controlled environment. An example of this is the Plus Maze, a paradigm originally designed to dissociate allocentric place and egocentric S-R types of spatial learning in rats (Tolman et al., 1946b). In this task, two groups of rats were trained to find food in a '+' shaped maze when starting from one of two opposing ends of the maze. One group was trained using a S-R strategy, so they would be able to find the food by always making a left turn from one of two starting positions, i.e. they associated each junction with an egocentric response to the left. The other group was trained to use an allocentric place strategy, which involved the rats learning that the food was always in a fixed location relative to extra-maze cues i.e. to find the food from one starting position they would need to turn left, and from the other, they would need to turn right. Rats in the place group learned to find the food from both starting positions more quickly than those in the response group. Tolman et al. (1946b) interpreted this as place learning being faster to acquire than response learning, though an alternative interpretation is that the rats' place learning may comprise learning a unique directional response from each of the two starting positions (Blodgett & McCutchan, 1947; Wolbers & Wiener, 2014). The capacity for the Plus Maze paradigm's ability to dissociate response and place strategies has led to several important findings within the literature, such as rats' abilities to flexibly switch between place and response types of navigation (Packard & McGaugh, 1996).

In contrast to the rodent literature, assays of human navigation typically employ a virtual environment (VE), as these provide researchers the opportunity to have participants explore virtual spaces of any size that can be fully experimentally controlled, something that would otherwise be impossible in a real-world space (Huffman & Ekstrom, 2020; Park et al., 2018; Steel et al., 2020). Additionally, experiments that employ VEs are easily compatible with neuroimaging techniques such as functional magnetic resonance imaging (fMRI), allowing the identification of brain regions that are activated during the course of different navigational behaviours (Park et al., 2018; Taube et al., 2013). The use of VEs has facilitated a wide range of research that has examined how allocentric and egocentric knowledge is employed within human navigation in realistic environments, and which brain regions are associated with the use of either type of information.

Common types of behaviours that are employed in assays of allocentric and egocentric contributions to navigation are wayfinding and route following respectively. The former relies on an allocentric representation of space to identify novel shortcuts to reach a

known location, whereas the latter comprises a series of S-R responses at junctions along a route. Hartley et al. (2003) conducted an experiment in which participants completed wayfinding and route following tasks in a naturalistic VE whilst undergoing concurrent fMRI. Their data showed a distinct difference in activation of brain regions during the two tasks, with wayfinding strongly activating the anterior hippocampus, and route following activating the head of the caudate. The data also showed that this differential activation was stronger for individuals who performed better at the wayfinding task, showing individual differences in navigation ability represented on a neuronal level. As the hippocampus is strongly implicated in allocentric spatial representations, its activation in wayfinding tasks provides further evidence, building on the discovery of place cells (O'Keefe & Dostrovsky, 1971; O'Keefe, 1976; O'Keefe & Nadel, 1978), of the integral role of the hippocampus when using allocentric information.

In Hartley et al.'s (2003) study, there was evidence that participants acquired the allocentric representation of space when following routes in the VE. Studies have since focused on the nature of allocentric and egocentric information that is acquired during route following, and how it interacts with the individual differences in navigational behaviour associated with typical and atypical ageing. Wiener et al. (2012, 2013) investigated the allocentric and egocentric route knowledge acquired following the passive learning of a route in younger and older adults. Following an initial route learning phase, Wiener et al. (2012) used a route retracing task to test the knowledge that participants had acquired. This involved participants being shown the route being moved through from the opposite direction to that which they saw initially. As the perspective at each decision point will be different to that encountered during the initial route learning phase, participants would need allocentric knowledge of spatial relations at each decision point. This allocentric representation would then support the mental transformation of the spatial relationships previously observed at decision points and consequently support the selection of the correct directional turn when retracing the route. Previously learned response-based information would therefore be of little utility in this context as the directional association with the landmark would be redundant. Wiener et al.'s (2012) results showed a broad deficit in route retracing for the older adults compared to the younger adults, consistent with attenuated allocentric navigational abilities found during normal ageing.

Wiener et al. (2013) followed this by employing a maze that featured two distinct landmarks at opposite corners of each intersection. This configuration of landmarks allowed

for a more detailed disentangling of allocentric and egocentric knowledge, and the identification of the type of strategy that participants used, when participants approached a junction from an unfamiliar direction. When approaching an intersection from a different direction than that taken when the route was being learned, an allocentric strategy would provide the correct turning, as this would utilise spatial configuration of the two landmarks at the intersection to indicate the correct direction. Response and beacon strategies, however, would elicit different incorrect directions respectively. This is because the incorrect directional response would be associated with the identity of the landmark pair when using a response strategy, and if using the landmark as a beacon, the heading associated with it would also be incorrect. Wiener et al.'s (2013) data showed older adults made more incorrect directional judgements than younger adults when allocentric information was required to solve the test. These studies show navigation tasks that employ VEs can be employed to identify the characteristic individual differences associated with ageing participants and how allocentric and egocentric cues can be disentangled to provide a granular array of participant behaviour.

The use of VEs also provides a platform to have human participants take part in replications of experiments conducted on rats. The Plus Maze paradigm's utility in separating allocentric and egocentric responses within the same environment is one design that has proven influential. The Dual Solution Paradigm (DSP; Marchette et al., 2011) takes the basic premise of the Plus Maze (i.e. dissociating allocentric and egocentric navigation), and adapts it as an assay of allocentric and egocentric preferences in human navigation. In the DSP, participants learn a route through a complex virtual maze before completing a number of tests in the same environment. In each test, they start at a known point along the route, and are tasked with navigating to another part of the route that they would have previously explored. In each test trial, however, there were always two routes to the goal, either the same route that was learned, or a novel route, that was either a shortcut or a longer path than that participants would have taken when route following. Participants could therefore choose to either take the shortcut, suggesting a preference for an allocentric navigational strategy, or the previously learned route, which is indicative of an egocentric navigational strategy. Participants completed the DSP whilst undergoing concurrent fMRI, to identify neural correlates of preferences for using allocentric or egocentric information. As part of the analysis, participants' test behaviours were scored on a solution index, a continuous scale of strategy preference, which correlated

with hippocampal and caudate BOLD activation at test. This corroborates Hartley et al.'s (2003) findings, i.e. participants that preferred to take shortcuts demonstrated greater hippocampal activation, whereas those that preferred to follow the original route demonstrated greater caudate activation. Whilst there were some participants at the extremes of the solution index, many participants employed both types of strategy flexibly, and similarly demonstrated activation of both the caudate and hippocampus at test. Indeed the literature has suggested that allocentric information is more likely to be employed when learning the layout of an environment, and once this has been acquired, individuals then show tendencies to use egocentric spatial information (Iglói et al., 2009). The fMRI data also showed that participants with greater hippocampal activation during learning were more likely to take shortcuts, whereas those that showed greater caudate activation during learning were more likely to follow the original route. This suggests that, whilst participants may be able to employ each type of strategy flexibly, a bias towards certain types of information when encoding a route exists, and predicts the types of strategy used upon retrieval. Furman et al. (2014) followed Marchette et al.'s (2011) study by also employing the DSP alongside fMRI. The results were replicated, however, Furman et al. (2014) also found that the relative activation of the caudate and hippocampus at test was consistent irrespective of the type of strategy being employed. This suggests that there may be a stable bias in terms of navigational strategy that influences how the information acquired when learning a route can be deployed upon retrieval.

This literature shows the utility in examining allocentric and egocentric types of navigational information, as it provides insight into the neuronal correlates of allocentric and egocentric forms of navigation, as well as insight into the specific nature of navigational impairments associated with typical and atypical ageing (see Chapter 1, section 1.2.1). Additionally, the adaptation of the Plus Maze in the DSP shows the utility of translating experimental paradigms designed for rodents into equivalents suitable for examining human navigation. These benefits are also shown when examining place learning, the ability to use allocentric spatial cues within the environment to encode and recall a particular location. This has been primarily examined using the Morris Water Maze, a task designed to interrogate navigational behaviour of rats.

1.2.1 The Morris Water Maze and Virtual Adaptations

The importance of place learning as a component of spatial learning and memory was clear from the early rat maze studies, as it supports the ability to flexibly navigate through complex spaces (Tolman et al., 1946a,b; Tolman, 1948). There are, however, issues with the environments employed in early maze experiments, e.g. the presence of proximal cues inherent to the corridors that are a feature of traditional mazes, such as the Plus Maze (Vorhees & Williams, 2006, 2014). To develop an assay of place learning in rats that addresses this issue, Morris (1981) designed the Morris Water Maze (MWM: Morris, 1981; 1984; Morris et al., 1982). In this task, rats are placed in a circular pool filled with opaque water. Submerged beneath the water is a hidden platform that, once discovered, provides the rat with a welcome escape from swimming. In this environment, place learning can be tested by manipulating the rats' starting positions on each trial, so the only way in which they can acquire the platform's location is through the use of extra-maze cues. Morris (1981) found that rats could acquire the location of the platform within five trials when it was hidden, though asymptotic learning was reached at a slower rate compared to acquisition trials in which the platform was visible.

Morris (1981) subsequently conducted probe trials in which the platform was removed. The rats' ensuing behaviour would indicate what the rat had learned during acquisition trials. If the rat had accurately learned where the platform was located, then they would focus their search in the quadrant of the maze that contained the platform (Morris, 1981). The probe trial results indicated that rats that completed acquisition trials with a hidden platform focused their search in the platform's quadrant, suggesting that they made use of the extra-maze cues, as this was the only information that remained consistent from the acquisition trials. In contrast, rats that completed acquisition trials from the same starting position with a visible platform location did not have a preference for searching in a particular quadrant, indicating that they did not acquire the platform's location using the extra-maze cues.

Subsequent research using the MWM provided detailed insight into the mechanisms that underpin place learning in rats. Morris (1984) demonstrated that the rats were reliant upon the use of extra-maze cues through occluding the cues by draping a curtain around the exterior of the maze. With the extra-maze cues occluded, rats performed at chance levels during probe trials, indicating that they were a vital component of the rats'

strategy to find the platform. To identify whether the extra-maze cues were simply used as egocentric beacon cues for determining initial heading, Morris (1984) occluded the extra-maze environment around the quadrant that contained the platform. This meant that the extra-maze cues would only be of utility if the rats were able to develop an allocentric representation of the platform location, relative to the extra-maze cues' locations. Under these conditions, the rats' performance was only slightly impaired, indicating that the rats were capable of using the spatial configuration of extra-maze landmarks to find the platform. Extra-maze cue manipulation has provided supplementary evidence of rats' abilities to use allocentric information to guide their navigation towards the hidden platform. Fenton et al. (1994) found that when two of four extra-maze cues are removed from view, rodents can continue to use the remaining two extra-maze cues to find the hidden platform. Additionally, Prados & Trobalon (1998) demonstrated that after learning the hidden platform's location using four extra-maze cues, when any two of four were removed, the rats could still navigate to the hidden location. This, combined with evidence from the same study showing an absence of place learning with only one extra-maze cue present, indicate that rats rely on the configuration of extra-maze cues to find the hidden platform.

The MWM has also been informative for identifying the neural substrates of rodent navigational behaviour. Morris et al. (1982) identified that place learning is disrupted by hippocampal lesions, whilst egocentric beacon based cue learning remains spared, indicating both the critical role of the hippocampus to the use of allocentric information, and a dissociation between allocentric and egocentric neural substrates. Additionally, Morris et al. (1990) lesioned the hippocampus and/or subiculum of rats before training them to find the hidden goal in the MWM. Initial training showed impairments to learning the hidden platform's location in the lesioned rats compared to control group, however, after overtraining, all lesioned rat groups were then able to reliably navigate to the hidden platform. Each group of rats then completed a probe trial without the hidden platform. The control group, as expected, focused their search in the hidden platform's quadrant, and after the overtraining, rats with lesions to either the hippocampus or the subiculum also spent a greater than chance amount of time within the target quadrant, indicating that they focused their search in the hidden platform's quadrant. The group with both hippocampal and subiculum lesions, however, performed at near chance levels during the probe, indicating that both the hippocampus and subiculum comprise a part of a

functional network that supports the recall of the target location following initial learning. The simplicity of the MWM design has led to its adoption as the 'gold standard' tool for measuring place learning (Astur et al., 1998). This enhances its translational potential for virtual reality (VR) platforms to interrogate human navigation behaviour and as a consequence, a large proportion of human navigation studies that employ VEs use a virtual Morris Water Maze (vMWM) task (Thornberry et al., 2021). In these tasks participants explore a large scale VE using input from a controller (e.g. a joystick), whilst sat in front of a monitor. The use of VEs allows for the deployment of large scale, experimentally controlled spaces, facilitating the manipulation of environmental cues that would be either impractical or impossible in a real-world environment (Huffman & Ekstrom, 2020; Park et al., 2018; Steel et al., 2020; Taube et al., 2013). A typical vMWM task will involve participants completing acquisition trials with the platform hidden, before finishing with a probe trial, in which the platform is removed. Similar to Morris's (1981) probe trial, those employed in vMWM tasks are designed to isolate the types of information that participants used to learn the platform's location during acquisition trials (Astur et al., 1998). There is, however, little standardisation in the parameters of vMWM design across the literature (Commins et al., 2020; Machado et al., 2019; Thornberry et al., 2021), though there are recent forays into the development and release of software that automates the production of a vMWM task for desktop VR (Machado et al., 2019) and immersive VR platforms (Commins et al., 2020).

Due to the MWM's elegance in measuring place learning ability, it has been widely deployed as an assay of hippocampal functioning across a broad range of populations. Consequently, researchers have used it extensively as a tool to investigate individual differences in place learning across a wide range of populations.

Ageing and the vMWM

Given the integral role of the hippocampus to place learning (Morris, 1984; Morris et al., 1990), the vMWM is a sensitive investigative tool for examining the impact of both typical and atypical ageing on hippocampal function, given its degradation over the lifespan (Cabeza et al., 2002; Geinisman et al., 1995; Raz et al., 2005; Small et al., 2011). An early study examining age effects on vMWM performance was conducted by Moffat & Resnick (2002). Participants, assigned to Young, Middle, or Old groups on the basis of their age,

completed six acquisition trials with the platform hidden, followed by a probe trial. In the acquisition trials, participants in the Old group took significantly longer paths than the other two groups, indicating that the younger participants learned the location of the platform more effectively than the older participants. In the probe trial, the Young group spent a significantly larger proportion of their path in the quadrant that had previously contained the platform, and also crossed the platform's location more often than the other two groups. In contrast, the Old group crossed the platform location on fewer occasions than the other groups in the probe trial. Moffat & Resnick (2002) also administered a novel map drawing task, in which participants were required to indicate the location of the platform on a top down schematic of the vMWM environment. Participants completed three maps that included either the room geometry only, extra-maze landmarks only, or both. Older adults' map drawing was poorer across the three schematics compared to younger adults, though it was poorest when they were required to use the room's geometry to locate the platform. Across all participants, poorer map drawing performance was associated with poorer acquisition of the target location (i.e. longer paths taken in the acquisition trials). This suggests that participants that performed poorly in acquisition trials were less able to reliably employ an allocentric representation of the platform's location relative to the extra-maze featural cues, or the room's geometry. These data provide a rich overview of the impairments in vMWM performance associated with age, i.e. compared to younger adults, older adults' search for the platform is less effective, and explicit knowledge of the platform's location is poorer.

Korthauer et al. (2016) conducted a longitudinal follow up to Moffat & Resnick's (2002) study, using 51 of the same participants, tested on average 8 years later using the same vMWM task. In the follow-up session's acquisition trials, Korthauer et al. (2016) observed no significant change in latencies to find the hidden platform, or acquisition trial path lengths. Similarly, there were no differences between the two experimental sessions in the amount of time or proportion of a path that was spent in the quadrant containing the hidden platform during probe trials. The data from the follow-up experimental session alone, however, revealed age differences in acquisition trial path length (i.e. older participants took longer paths than younger participants), however, there were no age differences for acquisition trial latency, or, in probe trials, dwell duration and path proportion in the hidden platform's quadrant. This study showed no clear within-subject vMWM performance decrement over time, though Korthauer et al. (2016) suggested that this may be due to

a large amount of interindividual variability observed across the two sessions. A more fine grained analysis of individual variance may consequently be more revealing as to the nature of vMWM performance changes over time.

A study conducted by Schoenfeld et al. (2010a) was designed to compare vMWM ageing differences with those observed on a virtual pointing task and the Vandenberg & Kuse (1978) Mental Rotations Task (MRT). Participants first completed a vMWM task that comprised four acquisition before completing the virtual pointing task. In this task, participants followed a route through a VE, and were subsequently required to make directional judgments between landmarks encountered on the route. The virtual pointing task provides a measure of the ability to generate a cognitive map, as it requires knowledge of the spatial relationships between environmental objects (Huffman & Ekstrom, 2019b; Weisberg et al., 2014), and has been shown to be sensitive to age-related decline (Iaria et al., 2009). In contrast, the MRT provides a measure of spatial aptitude that does not include any elements of locomotion, and appears to be more sensitive to sex differences than differences due to age-related factors (Geiser et al., 2008; Linn & Petersen, 1985; Masters & Sanders, 1993; Voyer et al., 1995). Schoenfeld et al. (2010a) found that older adults completed fewer vMWM acquisition trials than younger adults, and were also more inaccurate than younger adults at the pointing task. In contrast, no age based differences were observed in the MRT data. Interestingly, there was an association between performance on the MRT and the vMWM, however, there was no association between pointing task performance and either the vMWM or MRT. These data reflect declines in navigational performance with age, however, these declines may occur differentially for different mechanisms, e.g. the extent to which an individual may struggle with learning the location of an object (i.e. a vMWM acquisition trial) may differ to the extent to which they struggle with developing a cognitive map of an environment (i.e. the pointing task). Schoenfeld et al. (2014) employed the same vMWM task used by Schoenfeld et al. (2010a) to investigate the impact of ageing on reversal learning, the ability to learn a novel platform location, after first learning a different location. Reversal learning has been shown to be dependent upon long-term depression of CA1 cells, which may be adversely effected by ageing (Dong et al., 2013). Younger and older adults were trained on three blocks of four acquisition trials, before completing a probe trial. Subsequent to the probe trial, all groups then completed a final block of acquisition trials to relearn the platform's location. After a 25 minute delay, participants then completed two blocks of reversal learning

trials, in which the platform location was moved to an adjacent quadrant. Similar to Schoenfeld et al.'s (2010a) study, older adults took longer to learn the target's location in the initial acquisition trials, and spent less time in the platform's quadrant in the probe trial compared to younger adults. When completing the reversal learning acquisition trials, older adults also took longer to learn the new location in comparison to younger adults. This experiment replicates previous age-related impairments associated with ageing, and also demonstrated impairments to reversal learning in a vMWM task. The difficulties in acquiring a novel location in a familiar space observed in reversal learning indicates further characteristics of the navigational impairments associated with ageing.

Similar to reversal learning, measuring cumulative proximity to the platform location within a given trial has been shown to be particularly sensitive to age differences in rat MWM tasks, especially compared to 'standard' metrics like path length (Gallagher & Nicolle, 1993). Additionally, unlike path length, cumulative platform proximity can be more easily compared and averaged across trials. Zhong et al. (2017) examined younger and older adults' cumulative proximity to the platform location during a vMWM task. The results showed that higher cumulative proximity scores were obtained by poorer performing adults irrespective of age during acquisition and probe trials, indicating that their search was not focused on the platform's location. Furthermore, better performing older adults' cumulative proximity scores were comparable to younger adults' scores. As there is not a comprehensive decrement across older adults in their cumulative proximity scores, the root of age-related vMWM impairments may lie in fundamentally different approaches between younger and older adults, e.g. in strategy selection or interpretation of task demands.

Whilst typical ageing is associated with impairments to navigational ability, the impairments associated with atypical ageing, e.g. conditions such as Alzheimer's Disease, are much more severe. An indicator of Alzheimer's Disease onset is amnesic Mild Cognitive Impairment (aMCI). The effects of this condition on vMWM performance were studied by Rogers et al. (2017), to identify whether poorer spatial performance associated with Alzheimer's Disease is observed in older adults with aMCI. Rogers et al. (2017) employed a three-stage vMWM that increased in complexity alongside the Montreal Cognitive Assessment (MoCA), a screening tool for mild cognitive dysfunction. Adults with aMCI took longer paths and latencies, and were less successful in acquisition trials compared to a control group of healthy younger adults. MoCA scores for the aMCI group correlated

negatively with trial path length. These data demonstrate the utility of using the vMWM as a complementary tool for the detection of pre-Alzheimer's Disease patients.

Both typical and atypical ageing are characterised by the degradation of brain structure (Fjell & Walhovd, 2010), which means that neuroimaging techniques are of great utility for identifying neurological changes that are associated with ageing. The flexibility of the vMWM means that it can be deployed easily alongside neuroimaging techniques to identify neurological changes associated with vMWM performance. Daugherty et al. (2016) used structural MRI to investigate whether age-related differences had a neuronal basis. This analysis showed that greater subiculum and entorhinal cortex volumes were associated with a faster decrease in path complexity (i.e. more direct paths to the hidden platform) across acquisition trials. Larger cornu ammonis volume was associated with faster decreases in path length, but not complexity. These findings support the idea that place learning is reliant upon separable processes that can be dissociated on the basis of brain structure. This experiment was followed by Daugherty & Raz's (2017) longitudinal study that used the same techniques (i.e. a vMWM task and structural MRI) with a large sample of adults in two sessions, two years apart. Longer path lengths were associated with advanced age, and also smaller cerebellar and caudate volumes. Younger adults took less complex paths in the second session, which contrasts with older adults, whose path complexity scores did not differ significantly between the two sessions. Lower path complexity was also associated with larger parahippocampal volume. Daugherty & Raz (2017) suggested that the dissociation between the behaviours may be representative of each reflecting separable components of navigation. Path length was suggested by Daugherty & Raz (2017) to be an index for perceptual-motor skill, whereas path complexity acts as an index for cognitive mapping. The former is vulnerable to age-related decline (Coats et al., 2013; Seidler, 2006), whereas the latter can improve with repeated testing (Daugherty et al., 2015). Daugherty & Raz's (2017) findings suggest, however, that this improvement is not sufficient to override age-related performance deficits. Overall, the vMWM has proven to be a useful tool for identifying the navigational difficulties that characterise both typical and atypical ageing.

Strategies used in the vMWM

The flexibility of the vMWM paradigm has also led to its adoption as a tool for identifying the underpinnings of effective navigational behaviour. Ferguson et al. (2019) reported that in their vMWM task, participants that preferred to use allocentric cues to find the hidden platform were faster to complete the initial visible platform trials than participants that preferred to use egocentric cues. Additionally, participants that demonstrated a preference for allocentric cue use completed hidden platform trials in less time and took more direct paths than participants that preferred to use egocentric cues. The preference for using either allocentric or egocentric cues were also each associated with reduced error in forced strategy trials for each respective cue. These data indicate that adaptations of the vMWM can be used as an assay of preferences for using certain types of navigational information, similar to the DSP (Furman et al., 2014; Marchette et al., 2011). Whether the measures for preferences developed by Ferguson et al. (2019) translate to navigation in a more naturalistic context is yet to be explored.

Livingstone-Lee et al. (2011) employed eye-tracking to identify fixation patterns associated with the use of allocentric cues or egocentric cues in the vMWM. Participants completed twenty acquisition trials across two environments that were configured to either support allocentric place navigation or egocentric cue navigation, i.e. each environment only had the respective cue type present. The results suggested that all participants were able to adjust their attention to focus on the relevant cue type after a single trial. The same environments were employed by Livingstone-Lee et al. (2014), who assigned two groups of participants randomly to complete acquisition trials in either the allocentric place or egocentric cue VEs. After completing the acquisition trials, participants then completed ten dual-strategy trials in an environment that contained both sets of cues from both acquisition trial VEs. A probe trial followed the dual-strategy trials, in which the egocentric cues were rotated 180 degrees around the edge of the arena, so participants using them as their source of navigational information will identify a different location as the target compared to participants that used allocentric information. All participants that were initially trained in the egocentric cue environment used the egocentric cues in the probe trial, i.e. they focused their search in the region predicted by the egocentric cues. In contrast, only two thirds of participants that were initially trained in the allocentric place environment used the allocentric cues to locate the target during the probe, whereas

the other third used the egocentric cues during the probe trial. This is likely due to some participants in the allocentric place group not attending to the egocentric cue positional change in the probe trial. A verbal probe of participants suggested that those that used egocentric cues after being trained in the allocentric environment were not aware of the egocentric cues' change of location. In contrast participants that did use the allocentric cues during the probe did notice that the egocentric cues had rotated. This experiment suggests that a participant's bias towards using a certain type of navigational information is influenced more by early environmental exposure to specific types of cues.

1.2.2 Real-world Analogues of the Morris Water Maze

Whilst the vast majority of literature employing the MWM paradigm for humans has used experimental platforms that involve participants completing the experiment whilst either lying down in a MRI scanner, or seated in front of a monitor that displays the VE, some researchers have developed real-world interpretations of the MWM task (Bohbot et al., 1998; Gazova et al., 2013; Hort et al., 2007; Kalová et al., 2005; Laczó et al., 2009, 2010, 2015, 2017; Nedelska et al., 2012; Newman & Kaszniak, 2000; Paízková et al., 2016). These real-world equivalents permit a participant to explore the experimental environment physically, and access the full suite of idiothetic self-motion cues that a rodent would have access to when completing the MWM (Taube et al., 2013; see Chapter 1, section 1.4) Bohbot et al. (1998) presented an early iteration of a real world MWM equivalent called the Invisible Sensor Task. In this task, participants were required to explore a room that contained a hidden sensor that, when stepped on, would emit a sound. Participants were recruited to either a control group, or patient groups with lesions in either hemisphere of the hippocampus or parahippocampal cortex. Participants completed one acquisition trial from a starting point by one of two doors in the experimental room. After finding the target, participants were then taken out of the room and led back in from the other door to start a second acquisition trial. After a delay of thirty minutes, participants were led back into the room to the original trial's starting point and asked to walk to the sensor's location to activate it. Between the first two trials, there were no differences between the groups' latencies to find the sensor. In the final post-delay trial, participants with damage to the right hippocampal cortex demonstrated significant impairments in finding the sensor's location. This task demonstrates the impact of damage to the right parahippocampal cortex to recall from place learning even over very few trials.

Newman & Kaszniak (2000) presented a novel real-world task based on the MWM paradigm, in which groups of young or old participants learned the location of a pole in a controlled large scale environment. This environment was created in a laboratory that featured six distinct landmarks close to the walls. Participants initially completed three learning trials that were split into two stages (see Figure 1.1). In the first stage, participants entered the environment and walked to the location of a pole that was standing in the environment, before exiting the experimental space. In the second stage, participants re-entered the space and replaced the pole in its original location, using the landmark cues and/or the egocentric direction/distance from their starting position. Subsequent probe trials were conducted in which some of the cues were removed, to identify whether participants had learned the target location on the basis of the spatial configuration of the landmarks. Finally, participants completed 'rotation' trials, in which the cues were rotated around the environment relative to the original learning trials. In these, egocentric directional and distance information was rendered unreliable, providing a reasonably 'pure' measure of allocentric learning. Newman & Kaszniak's (2000) results showed that older adults placed the target with greater target object placement error across all three trial types compared to the group of younger adults. Both groups performed best when they could use both allocentric and egocentric information in the learning trials, though performance did not differ between probe and rotation trials. These data complement the vMWM literature, showing impairments to spatial learning in older adults.

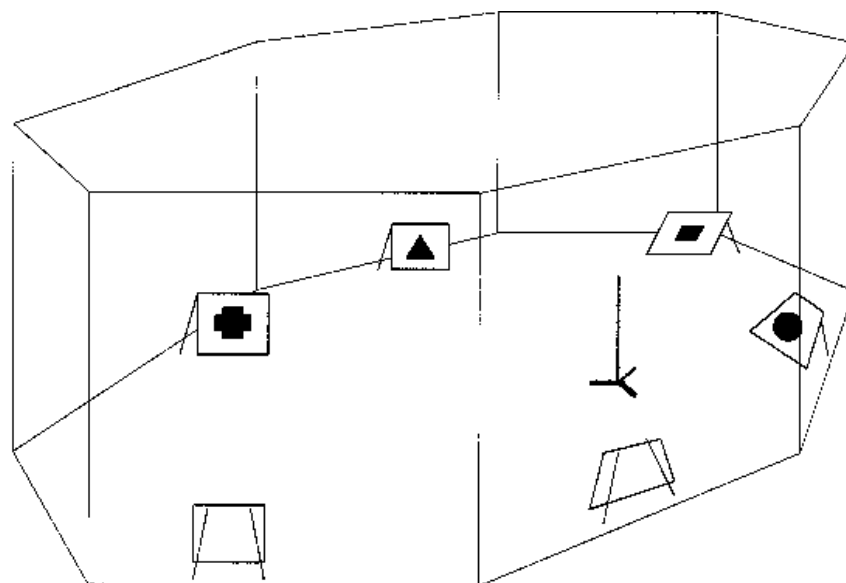


Figure 1.1: A depiction of the environment employed by Newman & Kaszniak (2000). This diagram shows the landmarks that could be used by participants to reorient and identify the target location, as well as a representation of the target object (the vertical pole).

Kalová et al. (2005) presented a similar real-world task called the 'Blue Velvet Arena' (BVA), that has been used extensively to examine the effects of typical and atypical ageing on the use of allocentric and egocentric information (Gazova et al., 2013; Hort et al., 2007; Kalová et al., 2005; Laczó et al., 2009, 2010, 2015, 2017; Nedelska et al., 2012; Paížková et al., 2016). In this task, participants learned the location of a pole across three conditions in a circular environment that contained two landmark cues marked on the environment boundary (see Figure 1.2 for a diagram showing the three trial types). In the first condition (Control), participants could use both allocentric and egocentric information to learn the target location, as it was fixed in relation to the two landmarks, and the trial starting position. In the second condition (Egocentric), the landmarks were removed, so participants could only place the target accurately using the direction and distance from their starting position. In the final condition (Allocentric), the landmarks were presented to participants again, though their starting position changed on each trial, so the target location could only be found relative to the landmarks. Participants initially learned the target location by entering the arena and placing a beacon at its location. Participants then received feedback in the form of a marker on the ground indicating the correct target location. Participants' placement error, i.e. the distance between their placement and the target location was recorded as the principal measure.

The task's ability to dissociate Allocentric and Egocentric sources of information provides rich insight into the nature of impairments associated with typical and atypical ageing. For example, the BVA has shown that a Control sample of younger adults differ little in their rates of placement error across the three conditions (Gazova et al., 2013). Older adults also perform at comparable levels in both the Control and Egocentric conditions, however, their performance in the Allocentric condition is worse, indicating difficulties when using the allocentric cues (Gazova et al., 2013; Hort et al., 2007; Kalová et al., 2005; Laczó et al., 2009, 2010). Individuals with aMCI or Alzheimer's Disease have demonstrated clear difficulties when completing the BVA task (Gazova et al., 2013; Hort et al., 2007; Kalová et al., 2005; Laczó et al., 2009, 2010, 2017; Nedelska et al., 2012; Paížková et al., 2018). Hort et al. (2007) reported that performance was comparable in the Egocentric and Allocentric conditions between individuals with aMCI or Alzheimer's Disease, and was significantly worse than healthy younger and older adults. Nedelska et al. (2012) found that the extent of Allocentric condition error correlated with right hippocampal volume in individuals with aMCI or Alzheimer's Disease, however, this was not the case for

error rates in the Control or Egocentric conditions. This indicates that the comprehensive navigational deficits associated with Alzheimer's Disease and aMCI may have different neural substrates. Overall, the BVA experiments have shown that there is great utility in employing tasks that assess the ability to use allocentric and egocentric navigational information, and are conducted in a real-world environment in which participants are required to explore a space physically and with full motility.

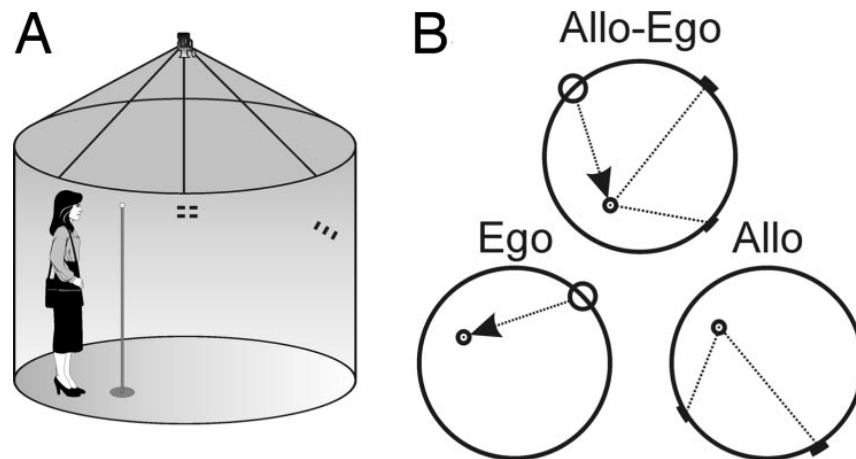


Figure 1.2: Design of the BVA reproduced from Hort et al. (2007). Image A shows a scale diagram of the BVA testing environment. Image B shows the layout of the three trial types. The Allo-Ego (Control) condition shows the spatial relationships between the starting position (large circle), landmarks (short lines on the edge of the arena), and the target location (smaller circle). In the Egocentric trials, the landmarks are removed, and in the Allocentric trials, the starting position varies on each trial, but the target remains in a fixed location relative to the two landmarks.

1.3 Search and Spatial Reference Frames

Place learning is reliant on the ability to learn the location of a singular location (i.e. the hidden platform) relative to environmental cues, and is a fundamental behaviour that we employ with regularity. There are, however, many instances in which we need to learn where objects are likely to appear within a region of space, often in multiple locations within a single environment. Indeed, everyday life routinely entails search for a variety of objects in our environment, be it an unplanned hunt for car keys in the home, or a more leisurely pursuit of groceries in a supermarket. Across the great majority of these contexts, search will be not be a novel experience, but instead informed by prior knowledge about the spatial distributions of our quarries. For example, should we be looking for a pack of frozen peas in a supermarket, we would be best placed to begin our search in the freezer section, rather than hunting around in the fresh fruit and vegetables

aisle. This type of learning in search behaviour is commonly observed in both human and non-human animal foraging (Maya et al., 2019), since natural resources tend to be distributed probabilistically through space (i.e. some regions are more likely to yield resources than others). Therefore, in order to search efficiently, one needs to attend to regions in which the target is likely to appear, and prioritise exploratory activities to those higher probability regions.

Exploitation of probabilistic cues in human search behaviour has been formally described in the anthropological literature, and the patch choice model (Charnov, 1976; Kelly, 2013) explains predictions in subsistence foraging activities on the basis of previous search experience and the perceived likelihood of future successes. However, formal empirical examination of the psychological processes supporting search decisions of this type have primarily taken a much more spartan tack by employing the visual search paradigm. In the canonical version of a visual search task, participants are required to report the presence or the absence of a visually-defined target object that is located amongst an array of distractor items, on a 2D monitor screen. Experiments examining the role of learning in search have shown that participants are indeed sensitive to the spatial statistics of an array, and can bias their search to cued regions of space. In the case of contextual cueing, a particular configuration of an array might be repeated over the course of the experiment, with each repetition further associating the target with a specific location (Brady & Chun, 2007; Chun & Jiang, 1998, 2003). Search behaviour reveals that participants become more efficient at locating the target object within these contexts, compared to trials in which the target is not located in the cued region of space (i.e. uncued trials), although they report no explicit awareness of the repeated search arrays or any associated search strategy. Similar manipulations reveal that participants can also learn where a target is likely to appear on the basis of a statistical contingency (Druker & Anderson, 2010; Geng & Behrmann, 2002, 2005). This probabilistic cueing effect is observed when a participant is presented with a series of randomised arrays, in which the target object is located more often in a certain region of space (e.g. a hemifield, or a quadrant) than another. Over time, participants begin to bias their search towards the cued region, becoming more efficient at locating the target when it appears in the cued region of space and, concomitantly, slower at locating targets in the uncued region. Once again, participants in such experiments do not report any explicit awareness of the contingency, or an associated search strategy, when asked subsequent probe questions, which has led theorists to propose a low-level collicular basis

to the effect (Geng & Behrmann, 2002). The explicitness of participants' awareness may, however, due to the awareness probes lacking sufficient statistical power to provide a reliable measure. Vadillo et al. (2020) suggested that the larger quantity of cued search trials, compared to the typically one-off awareness probes, may result in the latter being a significantly less reliable of participants' awareness of the probabilistic manipulation.

Although visual search is considered a controlled context within which scientists can understand domain-general properties of search (e.g. inhibition of return as a 'foraging facilitator': Klein & MacInnes, 1999), the paradigms described above present qualitatively different demands to those experienced in our everyday search of larger environments (Gilchrist et al., 2001; Smith et al., 2008). Since participants in a visual search task are commonly sat in front of a 2D screen, the search array is typically viewed from only one perspective, and usually in the vertical plane. In contrast, search of a large scale environment requires physical movement around the space, perhaps because the target cannot be directly perceived from the present viewing position, or because it requires physical apprehension. This means that we are likely to view the search environment from multiple perspectives and may, therefore, be required to integrate these egocentric (viewer-centred) representations of search space with a more stable and enduring allocentric (array-centred) reference frame. Moreover, previous studies have shown that having participants move around a stable search array can attenuate an individual's ability to learn about statistical contingencies in search tasks (Chua & Chun, 2003; Jiang & Swallow, 2013; Jiang et al., 2013; Jiang & Won, 2015). Indeed, when these two types of search have been directly compared, results show that the nature of the task demands, (i.e. either visual or physical apprehension of the target), elicit differing sets of results (Smith et al., 2008).

Experimental studies of large-scale search are not overly abundant, but they include foraging tasks that focus on the acquisition of resources in both real-world environments (Rosetti et al., 2016; Maya et al., 2019), and in immersive VEs (De Lillo & James, 2012; De Lillo et al., 2014), as well as tasks that have examined the cognitive processes that underpin large scale search. Similarly, these latter studies have also been conducted in both naturalistic real-world environments (Foulsham et al., 2014) and immersive VR (Ruddle & Lessels, 2006, 2009). Furthermore, explicit examinations of whether visual search phenomena transfer to large scale search have been conducted, specifically looking at contextual cueing (Li et al., 2016, 2018) and probabilistic cueing (Smith et al., 2010; Jiang

et al., 2014; Sisk et al., 2021).

As foraging behaviour is reliant on sensitivity to probabilistic cues, examination of statistical learning in large scale environments has primarily focused on how the spatial distribution of target items affects the organisation of search behaviour, and whether different spatial reference frames have a role to play in the representation of this information. In Smith et al. (2010), a series of experiments was conducted to explore, first, whether the probability cueing effects observed in a visual search task by Geng & Behrmann (2002) extend to large-scale search and, second, how cueing relates to certain parameters of the search context. In a novel laboratory, within which lights and switches were embedded into the floor, participants were asked to search an array by activating the switch at each illuminated location (green) until they revealed the target that changed colour (to red) upon activation. The target was always present in the array, and appeared in one hemifield of the array on 80% of trials (the same contingency applied by Geng & Behrmann [2002]). Their data revealed that participants only showed reliable probabilistic cueing effects when they could employ both allocentric and egocentric spatial reference frames in conjunction, and when the arrangement of the search array was stable across the experimental session (cf. in standard visual search tasks in which a new search array is generated on each trial). Under manipulations that isolated the probability cue to allocentric or egocentric spatial reference frames, they observed no probabilistic cueing effects. These data therefore suggest that probability cueing in large-scale search requires a stable environment that allows the searcher to integrate statistical information across both egocentric (viewer-centred) and allocentric (array-centred) reference frames.

Interestingly, the findings of Smith et al. (2010) contrast with more real-world data presented by Jiang et al. (2014). In their experiments, they tasked participants with finding a coin on the floor of an outside environment, within a large rectangular space. The rectangular area was split into quarters, with the coin appearing in one quadrant more often than the others. Across three experiments, Jiang et al. (2014) employed experimental manipulations that allowed the coin's location to be learned using a combination of allocentric and egocentric spatial reference frames, or using allocentric or egocentric information alone. Jiang et al. (2014) observed strong probability cueing effects in each of their three experiments i.e. when participants could only learn the target's likely location using allocentric or egocentric information alone, or when both types of information could be used in conjunction. These data, demonstrate a contrasting pattern of results

to those observed by Smith et al. (2010), though they may be explained by procedural differences. First, Jiang et al. (2014) study took place in an outside environment; an open space rich with visual cues. This contrasts with the laboratory environment Smith et al. (2010) employed, in which incidental environmental cues were purposefully limited by draping a dark curtain around a circular arena (making conditions closer to a simple visual search task). Ruddle & Lessels (2006, 2009) demonstrate that efficient search is facilitated by the richness of an environment, which might explain the discrepancy in results. Additionally, the demands of each task differed: Smith et al. (2010) paradigm required participants to physically move throughout the array in order to enact their search (akin to a serial self-terminating visual search task), whereas Jiang et al. (2014) task only required participants to indicate that they had identified the location of the target object (i.e. they were not required to physically explore the environment, though the authors state that participants often began the experiment by doing so, before adopting a stationary strategy). The paradigm employed by Jiang et al. (2014) is, therefore, perhaps more similar to a visual search task in terms of its demands, in that participants were not required to move around the space, thus potentially limiting the number of perspectives from which the target could be found. In turn, this may have reduced the processing demands associated with the requirement to learn about the target's statistical distribution, as participants that remained static would not be required to update their position in space.

This argument is supported by the findings of Sisk et al. (2021), who conducted a visual search task in a large-scale immersive VE. Participants were tasked with finding a target letter 'T' amongst an array of distractor letters ('L') in a large square room, while remaining restricted to standing in a central location. The target was probabilistically cued egocentrically, i.e. it was more likely to appear in a region of space that was relative to the participant's initial facing at the start of a trial. Sisk et al.'s (2021) findings showed that participants were only cued when the rich region of space was in front of their starting position. This contrasts with the findings of Jiang et al. (2014), and is most likely due to the absence of the rich visual scene that was present in Jiang et al.'s (2014) study. The rich visual scene will have provided participants with cues for reorientation, whereas the spartan visual scene in Sisk et al.'s (2021) experiment will likely have caused participants to become disorientated, and unable to track their heading over the course of a trial, relative to their original facing at the trial's start.

As a whole, these data present an equivocal picture as to the conditions under which probabilistic cueing can be observed. While Smith et al.'s (2010) and Jiang et al.'s (2014) studies suggest that probabilistic cueing is reliant upon stable environmental cues in the environment, the nature of these cues remains uncertain. Smith et al.'s (2010) findings suggest simply presenting a search array as two distinguishable regions is sufficient to facilitate probabilistic cueing in an allocentric reference frame, however, there remain questions as to how salient the distinguishing characteristics need be in order for participants to learn the distribution of the target object.

1.4 Using Virtual Environments

The widespread use of VEs to examine navigation and large-scale search has provided great insight into the mechanisms that underpin our daily behaviour. They provide a huge amount of experimental control, and permit manipulations that would otherwise be impossible in a real-world environment. Additionally, they interface easily with neuroimaging techniques such as fMRI (Hartley et al., 2003; Marchette et al., 2011, 2014; Weisberg et al., 2019) or MEG (Cornwell et al., 2010; De Araújo et al., 2002) as well as neuromodulation techniques such as transcranial magnetic stimulation (Julian et al., 2016) or transcranial electrical stimulation (Brunyé et al., 2014, 2018; Brunyé, 2018). There is, however, a disconnect between much of this research and our real-world experience of navigation and search. This is primarily due to the nature of translational movement through these VEs, as participants will be using a joystick or a keyboard and be seated in front of a monitor or lying in a MRI scanner (Park et al., 2018; Taube et al., 2013). This differs fundamentally to the way in which we physically explore spaces around us in the real-world. When we do this, we receive a great amount of idiothetic information that informs our ability to update our location in space (Park et al., 2018; Taube et al., 2013; Witmer & Kline, 1998). The inability to access motor, proprioceptive, and vestibular information has been shown to be of importance to both rodents (Stackman et al., 2002; Yoder et al., 2011) and humans (Hejtmanek et al., 2020; Steel et al., 2020; Taube et al., 2013), and the inability to access this information can result in impaired navigational behaviour even in virtual navigation tasks (Brandt et al., 2005). There are also differences in neural activity between desktop and ambulatory forms of navigation. This has been shown using mobile EEG techniques, with greater alpha activity in parietal regions observed in

ambulatory exploration of a VE compared to exploration of a desktop VE (Kober et al., 2012). Additionally, differences in theta oscillation activity, recorded by intra-hippocampal EEG, were observed between real-world navigation tasks and versions conducted on a desktop PC (Bohbot et al., 2017; M. Aghajani et al., 2017). This corresponds to neural activity also observed in freely moving rodents (Aghajani et al., 2015; Ravassard et al., 2013).

These limitations can be addressed by employing tasks that are conducted in real-world environments and require natural locomotion from participants. As previously described, this has been used to great effect to examine place learning (Bohbot et al., 1998; Gazova et al., 2013; Hort et al., 2007; Kalová et al., 2005; Laczó et al., 2009, 2010, 2015, 2017; Nedelska et al., 2012; Newman & Kaszniak, 2000; Paížková et al., 2018) and search (Jiang et al., 2013; Pellicano et al., 2011; Smith et al., 2005, 2008, 2010) in the laboratory, and in real world environments (Foulsham et al., 2014; Howard et al., 2014; Jiang et al., 2014; Schinazi et al., 2013). Whilst they are effective assays of large-scale spatial behaviour, these tasks lack some of the control that is provided by using a VE (e.g. the extra-arena environmental cues visible in Jiang et al.'s [2014] study). This can be remediated through the use of immersive VR systems as tools for examining these behaviours (Diersch & Wolbers, 2019; Park et al., 2018) as participants view the VE on a head mounted display (HMD) that tracks their head and body movements while they then freely move around a fully immersive VE.

Whilst the use of fully immersive VR systems brings a number of benefits, there do remain some limitations. First and foremost is that the size of a VE is fundamentally restricted by the physical space in which the VR equipment is set up (Zhao et al., 2020). Second, some HMDs are tethered to a desktop PC using a wire, which may provide both practical and theoretical issues. Practically, having a trailing cable following participants that cannot see their feet may be problematic as the cable can wind itself around participants' legs, causing a tripping hazard. This can be addressed by attaching the cable to the ceiling, however this may provide participants with a spatial cue that anchors them to the real world space. Omnidirectional treadmills may offer a solution to the first issue, as they permit full 360° movement, across unlimited distances and can be integrated fully with immersive VR equipment (Hejtmanek et al., 2020; Huffman & Ekstrom, 2019a; Ruddle et al., 2011a; Schöberl et al., 2020). There is, however, a debate as to how naturalistic movement is when using an omnidirectional treadmill. There are many models available, however, their effectiveness in permitting full and realistic movement can depend upon

the type of model employed (Park et al., 2018). Additionally, upon first use participants may be forced into awkward positions when using them (Steel et al., 2020), though this may be remediated by training participants before an experiment (Huffman & Ekstrom, 2020; Schöberl et al., 2020). The second issue with VR systems can also be addressed, by the increasing commercial accessibility of wireless VR solutions. Whilst these may be restricted to certain sizes of VEs, they completely eradicate any concerns about trailing cables presenting issues for participants' safety, and any confounding spatial information that they may provide. Fully wireless VR systems have been used successfully thus far (Liang et al., 2018; McAvan et al., 2021; Newman & McNamara, 2021), indicating they may be an ideal tool for investigating naturalistic navigation and search.

Immersive VR systems used in the navigation and search literature can be broadly split into two groups: ambulatory VR systems, and non-ambulatory VR systems. Ambulatory VR systems allow participants full motility within a VE, with unconstrained physical movement and full access to idiothetic and proprioceptive information. Non-ambulatory VR systems comprise an HMD and a movement technique that does not involve physical translation in space, e.g. head rotation, thus reducing access to idiothetic information.

Whilst non-ambulatory VR systems may not capture navigation or search behaviour as completely as ambulatory VR, they remain a useful tool for examining navigation and search behaviours. De Lillo & James (2012) and De Lillo et al. (2014) employed non-ambulatory VR to examine large scale search in adults, comparing the ability to search efficiently across structured or unstructured arrays, in large or smaller environments. Results showed that participants were able to search in an efficient and systematic manner across the two types of array, and within the two different scales of environment. These data show an ability to search effectively across the different combinations of search arrays that is comparable to primate species (Smith & De Lillo, 2022), which demonstrates the ecological validity of non-ambulatory VR systems in this context.

A large proportion of the non-ambulatory VR literature is devoted to directly comparing performance between tasks developed for immersive VR and desktop PC platforms (Commins et al., 2020; Ruddle et al., 1999; Srivastava et al., 2019; Zhao et al., 2020). Commins et al. (2020) found no performance differences between a non-ambulatory immersive VR version of their NAVWELL place learning task and a desktop PC version. Similarly, Zhao et al. (2020) found no differences between a non-ambulatory immersive VR version of the

SILCTON task (Weisberg et al., 2014, 2018, 2019) and a desktop PC version of the same task. In both versions of the SILCTON task in this study, participants translated through the VE by teleporting along a route. This potentially provides a model for facilitating the exploration of a large environment, whilst maintaining a degree of external validity, given the comparable performance at the previously validated desktop PC SILCTON task. These studies suggest increasing immersion during a navigation task may not provide any tangible benefits to place learning or the ability to generate a cognitive map of an environment.

Ruddle et al. (1999) compared navigation across a desktop PC platform, and an immersive VR platform, in which participants explored the virtual space using buttons on a control box. The task required participants to recall routes between different rooms across two distinct VEs. Participants were faster to navigate across the two VEs in the HMD condition, however, there was no difference in path length across the two platforms. This was interpreted as the use of the HMD being more natural (e.g. rotational movements were mapped to head movements), and navigation was consequently less effortful than in the desktop task (e.g. participants did not need to hold a button down to rotate their view). This was supported by the greater rotational head movements observed in the HMD condition, and by the HMD head rotational movements being smaller in magnitude compared to those in the desktop version of the task. Ruddle et al. (1999) suggested that on the desktop version of the task, participants may develop a 'tunnel vision' and may not be fully exposed to the VE as they perform fewer rotational scans of the environment while moving. It is interesting to note, however, that the measures suggest that participants made no clear directional errors on the desktop task. This suggests that desktop participants in this study were no more error-prone during navigation, which is comparable to the findings from Commins et al. (2020) and Zhao et al. (2020), as participants in all three studies did not demonstrate any richer representation of space when using a non-ambulatory VR system, compared to those that completed the same task on a desktop PC.

Findings from Commins et al. (2020), Ruddle et al. (1999), and Zhao et al. (2020) contrast with those of Srivastava et al. (2019), who compared the acquisition of spatial knowledge in a virtual city between non-ambulatory VR and desktop PC versions of the same task. Participants explored a virtual city on one of the two platforms, and their performance was measured by a map drawing task. Srivastava et al. (2019) suggested that in their non-ambulatory VR condition, participants experienced 'cybersickness', which led to

the poorer performance in this condition. Indeed, the disconnect betweenvection, the sensation of movement of the body in space produced purely by visual input, and the proprioceptive information that the body would be receiving while moving through space in a non-ambulatory VR system may be a large issue (Kim et al., 2018a,b). This issue is significantly remediated by ambulatory VR systems, as participants' movement within the VE maps onto their movement in the real-world (Diersch & Wolbers, 2019).

Li et al. (2016, 2018) employed an ambulatory VR that incorporated eye-tracking hardware to explore memory contributions to search within a large-scale VE. Li et al. (2016) compared search within a fully immersive VE comprising two rooms with visual search on 2D snapshots of the same environment. Participants' attention during search was guided by their contextual memory for the environment, though this was stronger in the immersive VR version of the task than in the 2D visual search task, evidenced by participants selecting the correct room more often in the immersive VR version of the task compared to the 2D search task. Li et al. (2018) also examined the role of contextual memory in immersive VR. Target locations were manipulated, and results showed that participants' global representations of the VE facilitate search strategies that involve efficient allocation of attention, reducing energy costs during search. These studies suggest that search is enriched by access to supplementary spatial information from idiothetic cues, which indicates the need to explore search behaviour in the context of more naturalistic immersive 3D environments.

Ambulatory VR systems have also been a useful tool for examining fully motile navigation, with experiments examining how we use allocentric or egocentric information (McAvan et al., 2021; Merhav & Wolbers, 2019; Negen et al., 2019), or how landmarks contribute to place learning (Foo et al., 2005; Zhou & Mou, 2019). Negen et al. (2020) investigated the ability to use allocentric priors to learn where a target object was likely to appear. In an immersive VR environment, participants were required to identify where target objects were located. The target location followed different distributions defined in allocentric coordinates, such that participants would be able to use allocentric cues to guide their locational judgements. Participants were, however, unable to use the allocentric cues to direct their locational judgements, indicating fundamental difficulties in employing allocentric spatial priors, emulating Smith et al.'s (2010)'s probabilistic cueing task findings. Foo et al. (2005) conducted an ambulatory VR experiment that examined the role of

landmarks in shortcut generation, after participants learned routes between different markers within a VE. Participants completed the task within one of three environments, one devoid of landmarks, one with reliable landmarks, and another with unreliable landmarks (that changed their location on each trial). Participants in the reliable landmark environment could accurately generate the correct shortcut between locations, whereas participants in the other two environments were less accurate. Participants were able to recall a route in the spartan VE, however, they were unable to generate the shortcut accurately in this space. It was suggested that human navigation is heavily reliant upon landmark cues in the environment, however, when they are rendered unreliable, humans can then rely on a survey representation to support navigation behaviour.

Zhou & Mou (2019) developed an immersive VR version of the task used by Doeller et al. (2008); Doeller & Burgess (2008), to identify whether cue competition exists between boundary or local landmark cues in ambulatory VR. Participants learned the location of an object relative to either intra-maze local cues or extra-maze boundary cues. The reliability of either type of cue was manipulated to identify if the unreliable presence of either type of cue blocked learning relative to the reliable cue. Zhou & Mou (2019) replicated findings from Doeller et al. (2008); Doeller & Burgess (2008), indicating that the presence of boundary cues can block learning based on local cues, however, this relationship was not reciprocal, i.e. unreliable local cue presence did not block boundary cue learning. Zhou & Mou (2019) also found that participants were more accurate in identifying a target location when using local cues in isolation, compared to using boundary cues in isolation. These data suggest that local cues are of utility when relying on common reference points to form an accurate representation of inter-location spatial relations. In contrast, boundary information is of greatest utility when orienting oneself in space.

McAvan et al. (2021) and Merhav & Wolbers (2019) investigated the spatial memory deficits associated with ageing by using ambulatory VR navigation tasks. McAvan et al. (2021) developed an immersive vMWM that comprised blocks of acquisition trials and subsequent probe trials. Each trial type required participants to make an explicit judgement as to where they thought the target was located. Participants were recruited to either a group of healthy older adults or a control group of younger adults. Older adults were less accurate than younger adults when identifying the location in both acquisition and probe trials, however, neither group demonstrated impaired performance when starting a trial from a novel location within the VE. Additionally, both groups of participants were biased

towards employing strategies that involved using a distal landmark as an egocentric beacon cue. These findings largely mirror those observed in the desktop vMWM literature, with older adults demonstrating less precise spatial memory, however, the use of similar strategies contrasts with Zhong et al.'s (2017) findings, in which older adults employ less effective strategies than younger adults. It may be that the presence of idiothetic information biases participants to use certain strategies over others when completing a task in ambulatory VR.

Merhav & Wolbers (2019) tested older and younger adults' ability to learn locations in immersive VR using either allocentric or egocentric information in isolation, or in conjunction, using a similar paradigm to the BVA (Kalová et al., 2005). Participants initially walked to a target object to learn its location in an immersive VE that either contained landmarks (allocentric and combined conditions), or did not contain landmarks (egocentric condition). Participants then returned to either their original starting position (egocentric and combined conditions), or to a novel location (allocentric condition) to complete the encoding phase. In a second experimental session on the following day, participants underwent the same encoding for half of the objects, and for the other half, completed the encoding phase with the objects in novel locations. During a subsequent test phase, participants were then required to navigate to the target object's location using the available cues. Older adults' recall of the locations was poorer than younger adults' recall across all three conditions. Across both groups, spatial memory was most accurate in the combined condition, and least accurate in the egocentric condition. Older adults also struggled more with the relocated targets, and the extent of their relocation error was correlated positively with the proximity to the original location. This demonstrates poorer spatial memory across the use of both allocentric and egocentric cues in isolation or in conjunction, as well as the interference of previous locations impairing the ability to adapt to reliably identify novel locations.

Ambulatory VR systems have also been employed to examine the underpinnings of spatial representations. Navigational theories present three potential models of how spatial knowledge is represented psychologically (Peer et al., 2021; Warren et al., 2017). The first is a Euclidean or topological map, in which locations are stored in a common coordinate system. The second is graph-based model where locations are nodes that are linked by known paths, but the paths are not associated with metric information. Third is the labelled graph model, in which locations are represented by nodes, however, the routes

between the nodes are associated with path lengths and angles between locations. Warren et al. (2017) conducted a study in which they examined whether participants could learn the layout of an immersive VE environment that incorporated wormholes. The use of wormholes rendered the environment non-Euclidean, as the distances that participant walked would not reflect the actual distances between objects in the environment. Participants' judgements were impacted upon by the presence of the wormholes, as their directional judgements between objects were biased by the wormhole routes (i.e. participants did not account for their truncation of space). This was taken as support for the labelled graph hypothesis due to participants insensitivity to the Euclidean structure of the VE. Murry & Glennerster (2021) also explored participants' ability to generate novel shortcuts in an immersive VE that included one, three or no wormholes. Participants that were trained in the environment with no wormholes generated shortcuts, whereas those trained in the environments that contained wormholes employed response-based strategies, i.e. they recapitulated familiar routes instead of generating novel shortcuts. This was interpreted as evidence of a graph-like representation of space, again based on participants' inability to reliably identify the non-Euclidean nature of the VE. Peer et al. (2021) argued, however, that as participants were not explicitly made aware of the VEs' impossible natures, participants may have relied on a heuristic based around the VEs being structured within the constraints of Euclidean space.

Comparisons between ambulatory VR systems and non-ambulatory VR systems have been conducted using both navigation and search paradigms. Ruddle & Lessels (2006, 2009) compared search across desktop and ambulatory and non-ambulatory immersive VR platforms. Participants' search was most efficient, measured by revisits to previously searched columns and the number of missed or neglected items, when they could employ idiothetic cues, i.e. in the ambulatory VR condition. This is likely due to the additional idiothetic information ensured participants could maintain a more accurate understanding of where they had previously explored in the environment, and consequently a richer spatial representation of the environment.

In the navigation domain, Ruddle et al. (2011b) compared route learning and route retracing in ambulatory immersive VR with non-ambulatory VR, in a complex VE. The results showed that the use of ambulatory immersive VR significantly reduced the number of errors made during navigation. In a similar experiment, Ruddle et al. (2011a) compared route learning and retracing across large and small VEs that were traversed either by

moving forwards and backwards with a joystick while using full body rotations, using a treadmill for linear motion, but rotating with a joystick, or completing all movements with a joystick. In a smaller environment, participants' performance was most accurate when walking freely, which indicates that the idiothetic cue accrual from physical movement is sufficient to generate a richer representation of an environment than physically rotating and moving using a joystick, or using a joystick for all movement. In a larger environment, participants either explored the VE while walking freely on an omnidirectional treadmill, walked in a linear direction on a treadmill while rotating their view using a joystick, moved using a joystick but rotated physically, or used a joystick for all movement. In this experiment, both conditions that involved physically walking through space showed more reliable performance when taking novel shortcuts through the environment. These experiments show the role of idiothetic information in the development of an accurate representation of an environment. It is likely that the physical act of moving through space recruits systems that may not be engaged when exploring a VE on a desktop PC. It is important to note that the differences in control fidelity may explain some of the behavioural differences as well (see Ruddle et al., 1999).

Chrastil & Warren (2013, 2014, 2015) conducted a series of studies in an immersive VR hedge maze to identify the contributions of self-motion to the spatial representation of an environment. In an experiment conducted by Chrastil & Warren (2013), participants learned the locations of objects when either walking, being pushed in a wheelchair, or watching a video of the environment on a PC monitor. Participants were better at generating a novel shortcut after learning the environment's layout by walking, when compared to the participants that explored it in a wheelchair or viewed the environment on a monitor. These findings were replicated by Chrastil & Warren (2014) who found that participants were similarly able to find novel shortcuts between a novel starting location and a known target location. Chrastil et al. (2015) examined contributions of decision making during spatial learning, as well as locomotion methods. The experiment compared participants that walked or navigated through the space seated in front of a monitor, that then either were guided along the space, or made their own navigational decisions. At test, participants that made their own navigational decisions recalled the walked routes more accurately than those that were guided along the routes. Additionally, participants that walked through the environment were able to compute more efficient novel shortcuts than those that were seated in front of a monitor. This suggests that navigational decision

making informs route knowledge acquisition, whereas motile locomotion informs the ability to reliably employ topological graph-like information to generate novel shortcuts in an environment. These studies present implications for theories that focus on the acquisition of metric survey information, i.e. that ambulation is a key component of the acquisition of this knowledge. This then suggests that experiments in which participants do not physically explore an environment may not fully capture the behaviour completely. Hejtmanek et al. (2020) compared navigation in a real-world environment with navigation in a virtual version of the same environment deployed on a desktop PC or within ambulatory VR with an omnidirectional treadmill. Participants learned the layout of the environment on one of the three platforms by walking between six target locations within the building. This was followed by a series of pointing trials, in which participants made directional judgements from two novel locations, in which they pointed towards each of the six target locations. After completing these two blocks of trials either in the real-world building, or within a VE, participants then transferred from the real-world to one of the two VR platforms, or from both VR platforms to the real-world. Participants then completed the same trial blocks within the new context. The results showed that learning did transfer from both the desktop and ambulatory VR platforms to the real-world environment, with a numerical advantage in transfer from the ambulatory VR system compared to the desktop platform. In the pre-transfer trials, participants that completed them in the real-world environment demonstrated greater spatial knowledge than the groups that completed them in either VE platform. These data suggest that omnidirectional treadmill based ambulatory VR may be slightly superior to desktop-based navigation for developing an awareness of an environment's spatial structure. Both platforms are, however inferior to navigation in the real-world, as all measures taken in the real-world demonstrated superior spatial awareness relative to the two virtual platforms.

1.5 Conclusion and Thesis Structure

Overall, the pattern of results from studies that employ immersive VR systems suggests that they are a tool of great utility for examining both navigation and search. There are, however, differences in the types of VR systems used, as ambulatory VR systems support the ability to accrue idiothetic information when exploring a space, which provides a richer understanding of its layout when compared to non-ambulatory VR systems. It is important

to note, however, that even within the range of ambulatory VR systems, those that use omnidirectional treadmills may not capture the same naturalistic behaviour as those that permit free ambulation without constraints. The extent to which VR systems supply idiothetic information has been conceptualised as either operating along a continuum (Huffman & Ekstrom, 2020), or being binary, i.e. there is either no idiothetic input or full idiothetic input associated with motility (Steel et al., 2020). Huffman & Ekstrom's (2020) model suggests that navigation on a desktop interface provides no idiothetic cues to support navigation. Increasing the level of immersion is then expected to increase access to a richer representation of space, however, the behavioural repercussions of this remain unclear. Continuing to explore behaviour across desktop and immersive VR platforms will provide further empirical evidence to support a comprehensive understanding of the relationship between idiothetic information and navigation and search behaviour.

To address these questions, this thesis will present work exploring navigation and search primarily using an immersive VR system, so participants will be fully motile and have access to idiothetic self-motion information. Chapter 2 details the development of a place learning task based on the BVA (Kalová et al., 2005). This task was developed for both immersive VR and desktop PC platforms, and performance on each is directly compared to identify cross-platform differences associated with motility. Chapter 3 presents an immersive VR replication of experiments initially reported by Smith et al. (2010). These experiments are designed to identify whether participants can learn where a target is likely to appear on the basis of allocentric and egocentric cues in conjunction (Experiment 7) or on the basis of allocentric cues alone (Experiment 8).

Chapter 2

Place Learning in Immersive and Desktop Virtual Environments

The importance of allocentric and egocentric information is well documented within the navigation literature (Burgess, 2006, 2008). However, as detailed in Chapter 1, the vast majority of behavioural assays of navigation are conducted on desktop PC VR platforms (Schöberl et al., 2020). Consequently many of the findings reported in the literature are based on experiments in which participants remain static, seated in front of a desktop PC or lying down in an MRI scanner. This means that participants would not have had access to the full suite of idiothetic information that they would otherwise have been able to access when exploring an environment with full motility (Huffman & Ekstrom, 2020; Schöberl et al., 2020; Steel et al., 2020; Taube et al., 2013). Consequently, the sensory input during navigation of static human participants will differ from the types of information that freely moving rodents in the MWM would experience. It is therefore important to address this and examine whether the addition of motility has an effect on the ability to employ allocentric and egocentric information while fully motile (Huffman & Ekstrom, 2020; Park et al., 2018; Schöberl et al., 2020; Steel et al., 2020). One way in which this can be achieved is through the use of ambulatory immersive VR systems.

Chapter 1 described the MWM in depth, a task considered the 'gold standard' task for measuring spatial learning as it provides a framework for isolating the ability to use allocentric cues to locate a hidden platform (Astur et al., 1998). Virtual adaptations of the MWM for desktop PC platforms have been used to great effect to examine the ability to employ allocentric or egocentric information in an experimentally controlled VE (Ferguson et al., 2019; Livingstone-Lee et al., 2011, 2014). Additionally, the translational potential

of the MWM has also led to several adaptations for humans that have been conducted in real-world environments (Bohbot et al., 1998; Gazova et al., 2013; Hort et al., 2007; Kalová et al., 2005; Laczó et al., 2009, 2010, 2015, 2017; Nedelska et al., 2012; Newman & Kaszniak, 2000; Paížková et al., 2016). This includes the BVA (Kalová et al., 2005: see 1.2.2), a task specifically designed to dissociate contributions from allocentric and egocentric information, and which is sensitive to individual differences associated with both typical and atypical ageing. The BVA has been deployed as a measure to identify impairments to spatial memory in older adults (Gazova et al., 2013; Paížková et al., 2016) and individuals with aMCI or Alzheimer's Disease (Gazova et al., 2013; Hort et al., 2007; Kalová et al., 2005; Laczó et al., 2009, 2010; Nedelska et al., 2012).

The design of the BVA requires participants to learn and recall a single location across three conditions, using either allocentric or egocentric information in isolation, or together in conjunction. Whilst previous studies have demonstrated sensitivity of this paradigm for detecting differences associated with ageing (Gazova et al., 2013), it may be insensitive to individual differences in the use of allocentric and egocentric information in healthy younger adults. This is apparent when comparing the pattern of results of the BVA from Gazova et al.'s (2013) younger adult control group with data from Merhav & Wolbers's (2019) ambulatory immersive VR experimental task that similarly dissociated allocentric and egocentric information. In Gazova et al.'s (2013) study a control group of healthy younger adults did not significantly differ in performance across any of the three BVA conditions. In contrast, Merhav & Wolbers (2019) reported that a control group of healthy younger adults did demonstrate behavioural differences when using allocentric or egocentric information in isolation. Young adult participants in Merhav & Wolbers's (2019) study were most accurate when using both allocentric and egocentric information in conjunction, and least accurate when using egocentric information in isolation. A possible reason for this discrepancy is that in the BVA, targets were presented in locations that were consistent across different conditions, meaning that learning may have transferred. In contrast, Merhav & Wolbers (2019) required participants to learn a different location for each experimental condition – i.e. participants were only able to learn the location of the target using the reliable cues available in a given trial. This prevents learning transferring across conditions, meaning that performance in each condition was not supported by prior learning.

The BVA and the task employed by Merhav & Wolbers (2019; see Chapter 1, section

1.4) both present a framework for an experimental task that dissociates the ability to use allocentric and egocentric information to learn the location of a target object. The experiments reported in this chapter chart the development of a task that can be deployed on either desktop PC or ambulatory immersive VR platforms. At present, there have been no direct comparisons between the ability to reliably employ allocentric or egocentric information across different experimental platforms that manipulate the requirement for full physical exploration. This is likely due to the practicality of obtaining such an insight, since the operational requirements of a large-scale equivalent of most variants would be somewhat preclusive. However, the advent of wireless immersive head-mounted VR (see 1.4) affords the ideal opportunity to specify tasks and environments that can be viewed and explored across multiple platforms (Park et al., 2018), allowing for a systematic and controlled comparison between modes of exploration and interaction.

The procedure of the experimental task reported in this chapter is based on the BVA, but also incorporates features from other place learning tasks deployed on both desktop (Doeller et al., 2008; Doeller & Burgess, 2008) and immersive VR (McAven et al., 2021; Zhou & Mou, 2019) platforms. It comprised three stages: Training, Test, and Feedback. During the Training stage, participants were required to navigate towards a pole standing within a virtual arena, and then to pick it up. Upon apprehending the target, participants completed the Test stage, where they were transported to the starting position at the edge of the arena and required to replace the pole at the location that it had previously occupied. This explicit measure of learning has been used in several tasks based on the MWM design (Antonova et al., 2009, 2011; Ferguson et al., 2019; McAven et al., 2021; Merhav & Wolbers, 2019; Negen et al., 2020) as well as assays of real-world place learning (Newman & Kaszniak, 2000), including the BVA (Kalová et al., 2005). Following their replacement of the target object, participants could then compare their placement with the correct location during the Feedback phase to hone their accuracy in subsequent trials.

Similar to the BVA (Kalová et al., 2005), each version of the task reported in this chapter contained the same three conditions: Allocentric (i.e. the target was specified in relation to landmarks, irrespective of starting position), Egocentric (i.e. the target was specified in relation to the navigator's viewpoint at the starting position, irrespective of landmark locations), and Control (i.e. the target was specified in relation to both landmarks and the starting position viewpoint). Each condition featured a unique location to limit the transfer of learning between each condition. This allows a clear comparison between the

ability to use the reliable information present in each condition to learn and recall the target location. In order to ensure parity across Allocentric and Egocentric experimental conditions, landmarks were added to the Egocentric condition. The reason for this is that in the Allocentric condition, participants must inhibit the egocentric relationship between the starting position and the target location. With unreliable landmarks present during Egocentric trials, participants must then similarly inhibit the allocentric spatial relationship between the landmarks and the target location. Whereas this manipulation was not a part of the BVA (Kalová et al., 2005), it would more closely equate the task demands between the Allocentric and Egocentric conditions.

An additional disorientation procedure was included in the immersive VR version of the task - this occurred between the Training and Test stages of a trial, in order to control for the potential confounding contribution of idiothetic cues (e.g. path integration) when participants returned to the starting position at the edge of the arena. Disorientation is a methodological tool used in both rat (Dudchenko et al., 1997) and human maze tasks (McAvan et al., 2021) to act as a control of heading between trials. This was omitted from the desktop PC version of the task due to the ability to instantaneously manipulate the participant's viewpoint to a controlled starting position without the additional accrual of path information.

Experiment 1 presents findings from a prototypical version of the place learning task. A battery of individual differences measures was also deployed in this experiment to identify whether factors that have previously been shown to be associated with different aspects of navigational ability, such as mental rotation (Driscoll et al., 2005; Schoenfeld et al., 2010a), are associated with performance in the novel place learning task. Experiment 2 revised the design of the place learning task, and directly compared versions built for both immersive VR and desktop PC platforms. This comparison allows the interrogation of the role of motility in the use of allocentric and egocentric cue use. To further examine the role of landmarks, and their reliability when using egocentric information, Experiments 3, 4, and 5 each examined the role of unreliable landmarks during Egocentric trials across online desktop PC and immersive VR platforms. Finally, Experiment 6 recruited adults across multiple age groups to identify whether the desktop PC version of this place learning task captures the age-related decline widely associated with increased age (Korthauer et al., 2016; McAvan et al., 2021; Merhav & Wolbers, 2019; Moffat & Resnick, 2002; Schoenfeld et al., 2010a, 2014; Zhong et al., 2017).

2.1 Experiment 1

The purpose of this experiment is to investigate the use of allocentric and egocentric cues in isolation and in conjunction whilst participants are motile. The vMWM has been used previously as a platform for comparing allocentric and egocentric cue use, however, much of this literature has employed tasks designed for desktop PC platforms in which participants are not motile (Ferguson et al., 2019; Livingstone-Lee et al., 2011, 2014). There have been recent investigations into how allocentric cues are used in tasks designed for immersive VR platforms (McAvan et al., 2021; Merhav & Wolbers, 2019; Negen et al., 2020), however few tasks have also included a measure of egocentric cue use (Merhav & Wolbers, 2019). This experiment was designed to identify whether the immersive VR place learning can dissociate between accuracy in replacing the target object when using either allocentric and egocentric cues in isolation, or in conjunction. Participants learned three locations of a wooden pole in a circular arena across three conditions (Control, Allocentric cues only, and Egocentric cues only). Participants learned the location of a target object in an initial Training stage that required them to navigate towards the target object and pick it up, similar to experimental tasks reported in previous literature (Doeller et al., 2008; Doeller & Burgess, 2008; McAvan et al., 2021; Zhou & Mou, 2019). In a subsequent Test stage, participants were required to replace the target in its original location relative to cues that were reliable in the given condition (i.e. the landmarks and starting position, or either type of cue alone). After placing the target, participants received feedback, allowing them to compare their placement to the correct location. Between the Training and Test stages, participants were disoriented to attenuate the influence of any representation of the real-world space that might conflict with their representation of the VE (Foo et al., 2005). This was achieved by having participants walk a figure of eight, and starting each trial from a different physical location within the laboratory.

Alongside the place learning task, participants also completed the Vandenberg & Kuse (1978) MRT and the Kozhevnikov & Hegarty (2001) perspective taking tasks, as well as Santa Barbara Sense of Direction Scale (SBSOD; Hegarty et al., 2002), a self report measure of navigational aptitude. The MRT has previously been associated with vMWM performance (Driscoll et al., 2005; Schoenfeld et al., 2010a) and the perspective taking task has been associated with navigational aptitude (Fields & Shelton, 2006; Hegarty et al., 2006; Kozhevnikov et al., 2006). Recapitulating these associations in this experiment would be

an indicator that the place learning task draws upon similar cognitive underpinnings.

Recent discussion about the computational difficulty associated with the use of allocentric information (Ferguson et al., 2019; Negen et al., 2020; Wolbers & Wiener, 2014) indicates that placement error may be expected to be greatest in the Allocentric condition, and lowest in the Control condition. This does, however, contrast with findings from Merhav & Wolbers (2019) as in their experiment, in which participants were fully motile, greatest placement error was observed in their Egocentric condition. This may suggest that motile navigation may support the acquisition of an accurate allocentric representation of space. To address this equivocality, analyses for experiments reported in this chapter employed Bayesian techniques to quantify evidence for the null hypothesis (Dienes, 2014; Kruschke, 2010; Rouder et al., 2009), should mean scores in certain conditions be similar.

2.1.1 Methodology

Design

The design of this experiment was based on the BVA task (Gazova et al., 2013; Hort et al., 2007; Kalová et al., 2005; Laczó et al., 2009, 2010, 2015, 2017) and employed a within subjects manipulation with a single factor of condition (three levels: Control, Allocentric, Egocentric). During the task, participants learned the location of a target object (a wooden pole) in the Training stage by apprehending it. After collecting the pole, participants then replaced it in its original location during the Test stage. Participants subsequently received feedback within the trial arena, after they completed the Test stage. In the Control condition (see Figure 2.1A), both allocentric cues (i.e. landmarks) and egocentric cues (i.e. the distance and direction from the starting position) were reliable indicators of the target's location - i.e. they remained constant in their spatial relationship with the target location across Training and Test stages. In the Allocentric condition (see Figure 2.1B), only the allocentric cues were reliable indicators of the target location - i.e. the target location maintained a fixed spatial relationship with the landmarks across Training and Test stages, though the starting position varied between them. Finally, in the Egocentric condition (see Figure 2.1C), only the egocentric cues were reliable indicators of the target location - i.e. the target location maintained a fixed spatial relationship with the starting position across Training and Test stages, but the landmarks varied in their position across Training and Test stages, relative to the target location. Participants always completed

the Control condition first, and then the subsequent order of Allocentric and Egocentric conditions was counterbalanced across participants, e.g. half of the participants completed the Allocentric condition second and the Egocentric condition third, whereas the other half completed the Egocentric condition second and Allocentric condition third.

To ensure that performance in any one condition was representative of only that condition's configuration of allocentric or egocentric cues, and to attenuate any influence from previous conditions, novel target locations were employed for each condition.

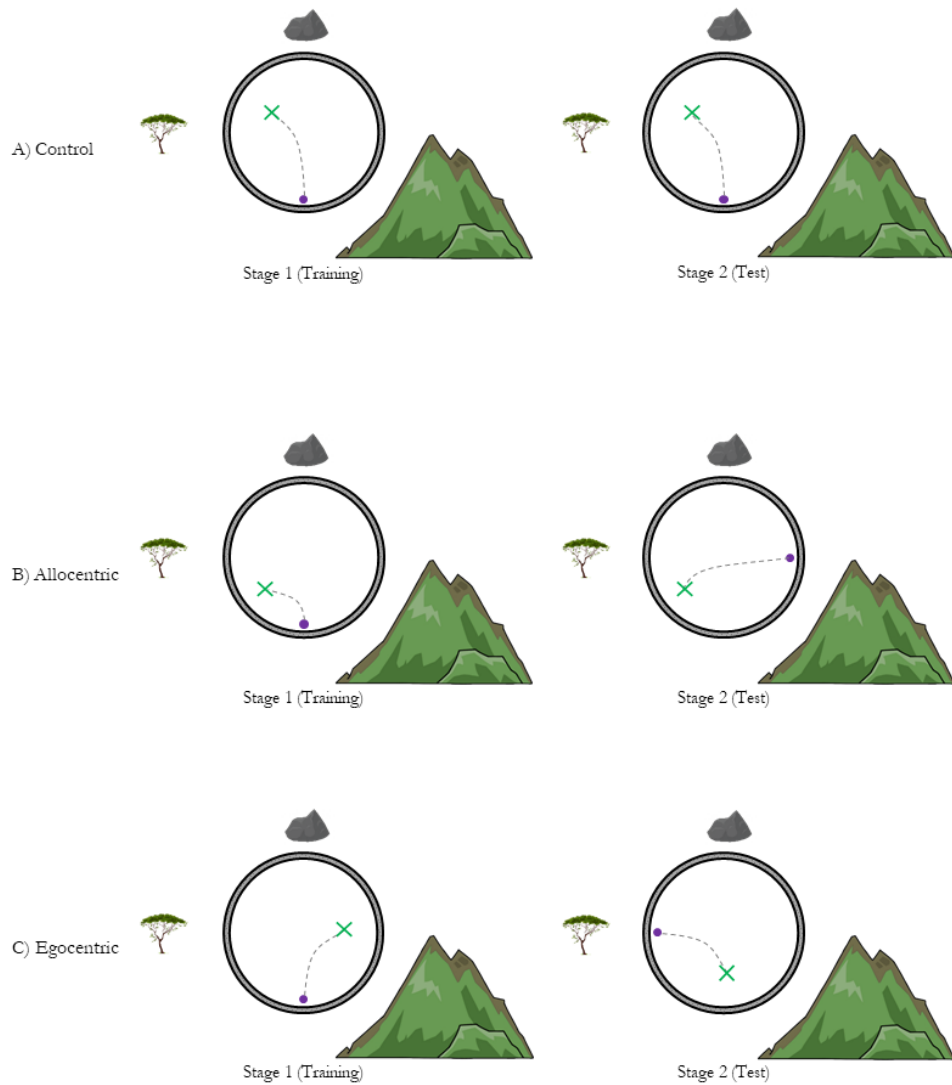


Figure 2.1: This figure shows diagrams of the three conditions. Diagram A shows the relationships between the target location and the starting position and landmarks across Training and Test stages in the control condition. Diagram B shows the relationships between the target location and the starting position and landmarks across training and test stages in the Allocentric condition. In this condition, the target location remains in the same place between Training and Test stages, relative to the landmarks. Diagram C shows the relationships between the target location and the starting position and landmarks across Training and Test stages in the Egocentric condition. In this condition, the target location moves around the environment, but maintains a consistent spatial relationship with the starting position.

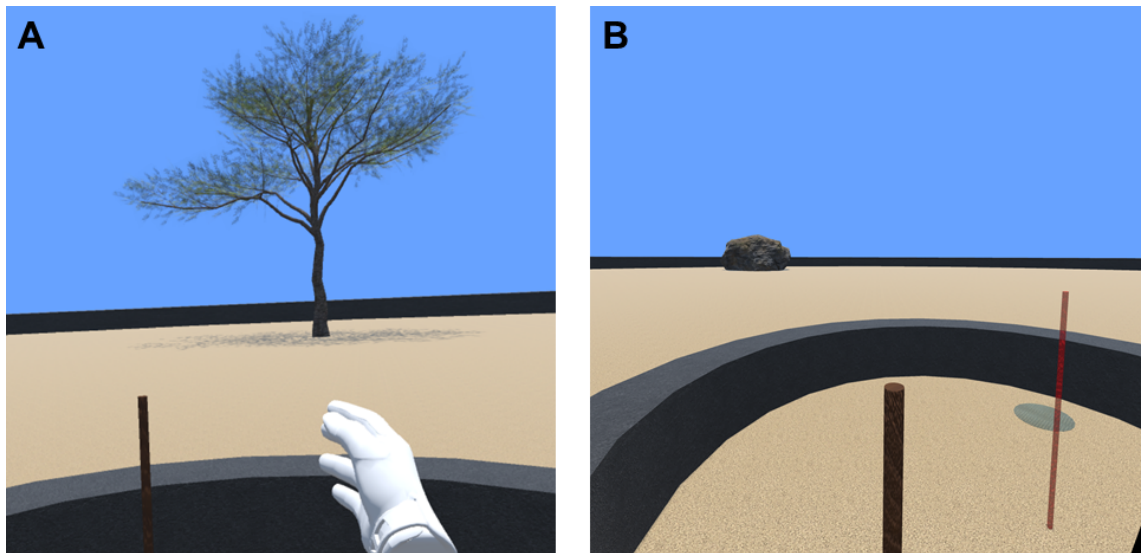


Figure 2.2: These images show screenshots from the Training (A) and Feedback (B) stages. In the Training stage, participants were required to walk to the wooden pole, and learn its location relative to the cues that were reliable for that trial. In the Feedback stage, participants could compare the target's correct location to their placement, as well as the locations of that Test stage trial's starting position and extra-maze landmarks.

Participants

Healthy adult participants were recruited from the University of Plymouth School of Psychology participation pool ($N = 24$, females = 12, males = 12), and were given payment in return for participation. The age of participants ranged from 19 to 60 years ($M = 32$, $SD = 14.4$). No participants reported any effects of cybersickness during this experiment. As this is the first experiment using this novel place learning task, the number of participants recruited for this experiment was informed by Gazova et al.'s BVA experiment.

Apparatus and Materials

This experiment took place in the University of Plymouth's large-scale immersive VR laboratory. This facility features a large (5.4 m x 6.5 m) clear workspace, dedicated to large-scale motile experimental paradigms. The VE was displayed to participants via an HTC Vive Pro VR HMD with an HTC Vive Wireless Adaptor. Participants interacted with the environment using a single HTC Vive Pro controller and their body positions were tracked using a Vive tracker, which was mounted on a belt and worn around the participant's

midriff. A researcher was present in the room throughout each experimental session, and could observe the participant's current view in the HMD through a concurrent display on the desktop PC that was running the experimental task. The HMD was equipped with integrated headphones, through which auditory stimuli could be played to attenuate noise external to the experimental task. The task and VEs were built using Unity Professional Software (Version 2019.2.12; Unity, 2019), and run through the Unity Professional editor, using the SteamVR plugin (Valve Software, 2019). The VE for the experimental trials comprised a circular arena with a diameter of 4.5 Unity metres (U_m). The arena was located on a large sand textured plain with a length and width of 250 U_m . At the centre of this plain, there was a one U_m high circular stone textured wall, with an inner diameter of 4.5 U_m that comprised the environmental boundary for each trial. On the outside of this wall there was an additional circular wall with an inner diameter of 25 U_m that formed a boundary, occluding the participant's view of the plain's edges and the base of the mountain landmark. In the VE there were also three photorealistic landmarks that were obtained from the Unity Asset Store. These comprised a large mountain, a rock, and a tree. The mountain was situated 200 U_m from the centre of the arena, on one of the corners of the plain, so it did not occupy the entirety of the participant's field of view. The rock and the tree were each positioned 15 U_m from the centre of the VE (see Figure 2.3), between the two walls.

During each trial participants could see a 3D model of a single white gloved hand (either left or right, depending on their stated handedness) that was obtained from the Unity SteamVR package (Valve Software, 2019). This hand was positioned in place of the default HTC Vive controller model within the VE, mapping onto a participant's hand movements, and it was used to interact with the target object. The target object, a wood-textured pole that was 1.6 (U_m) in height, was affixed to the hand when it was picked up by participants at the end of the first stage of a trial, to give participants a visual representation as to where the target would be placed during the test stage of a trial.

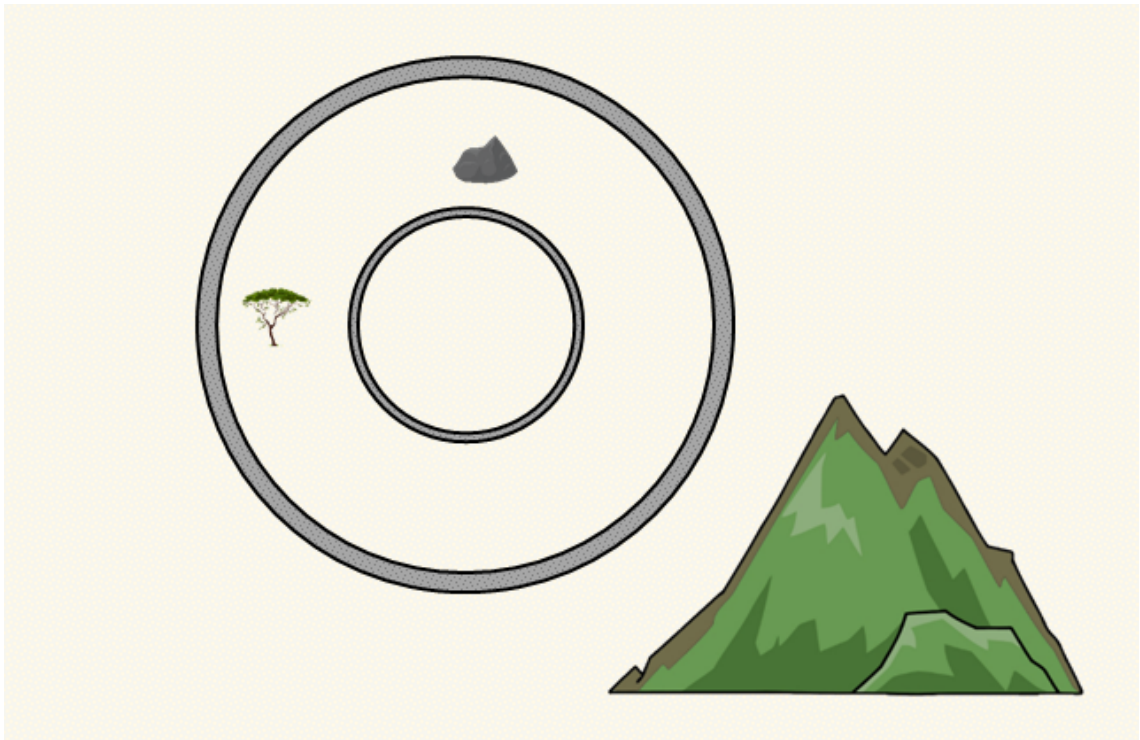


Figure 2.3: This diagram shows a top-down representation of the VE employed in Experiment 1. The mountain located on the outside of the larger arena wall to occlude its base. The tree and rock were both located between the two arena walls.

Procedure

Participants were initially fitted with the VR equipment before they were provided with a demonstration of the SteamVR Chaperone system, a safety feature designed to prevent participants from walking into real-world physical obstacles whilst exploring an immersive VE. It comprised four walls constructed from a green wireframe grid that delineate the boundaries of the experimental space, and only appears when a piece of the VR equipment is moved close to the physical walls of the laboratory. This system was sufficient to prevent participants from coming into contact with the laboratory walls, whilst allowing them to move freely and confidently around the space.

At the start of each stage of the experiment, participants were placed in an empty grey environment that included a starting position marker (a grey disc located on the floor) that was located 2^Um from the centre of the VE. Participants were required to stand on it and face centrally before each trial stage could start - once at this location and heading, participants could press the trigger on the controller to initiate a trial. Between Training

and Test stages, participants were disorientated within the VE. This was achieved by having participants walk into a series of columns that took them in a figure eight path. When participants walked into the final column, the starting position marker for the next trial stage appeared on the floor. See Figure 2.4 for more information.

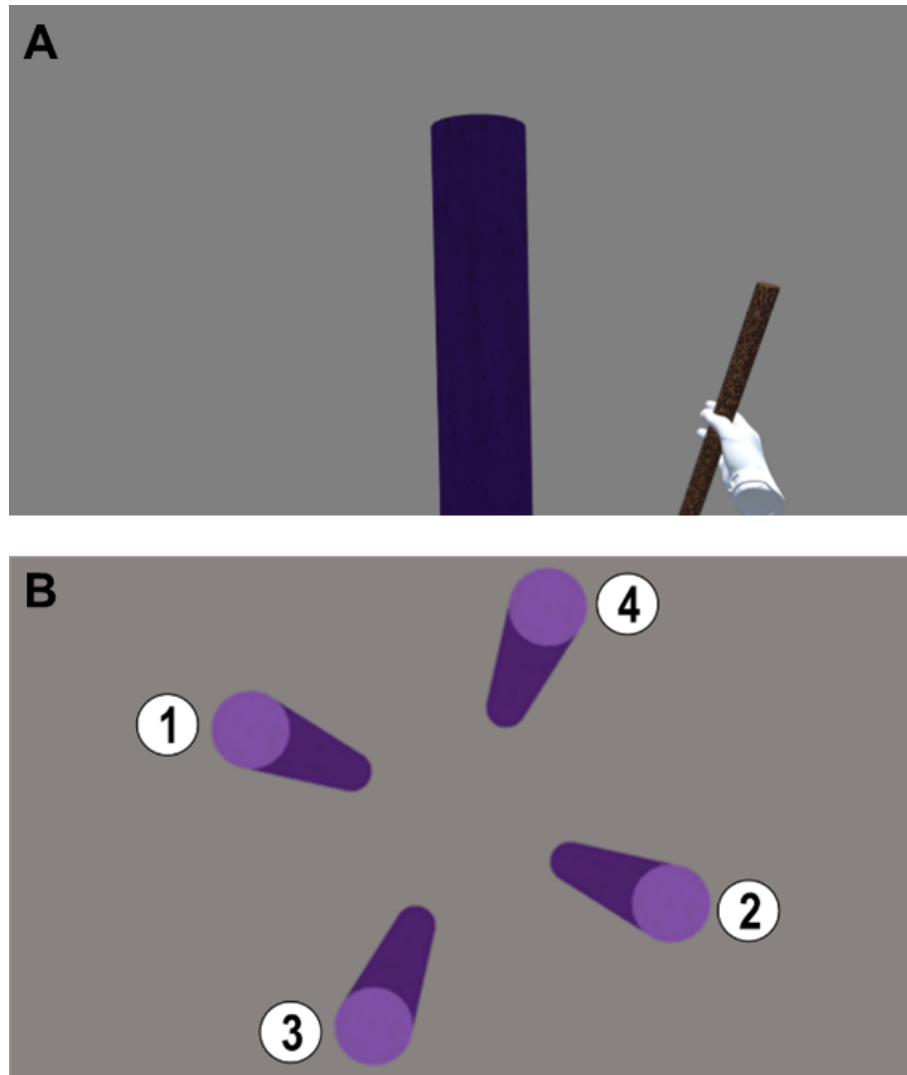


Figure 2.4: These images show a screenshot of the disorientation procedure (A) and a top down schematic of the path walked by participants when being disorientated (B). A purple column appeared in the environment and participants were required to walk into it. When the tracker, worn around participants' waists, collided with the column, it disappeared, and another column appeared in the environment. The path comprised walking into columns 1, 2, 3, 4, in order, before finally returning to column 1.

Each experimental trial comprised three stages: an initial Training stage in which participants learned the target location; a Test stage, in which participants attempted to identify the target location using the available cues; and a final Feedback stage, in which

participants could compare their estimation of the target location with the correct location, alongside other cues (i.e. the landmarks, and a marker indicating their starting position). In the Training stage, participants started close to the edge of the arena boundary, facing centrally. They were required to learn the location of the target object (a vertically-oriented pole) relative to the reliable cues in the given condition by navigating to the pole and then apprehending it (i.e. they picked it up, using an interaction button; see Figure 2.2A for a screenshot of the Training stage). In the subsequent Test stages, participants were returned to a point around the edge of the arena boundary, once again facing centrally. They then used the information available to them to navigate to the location from which they had remembered apprehending the pole, and used the interaction button to place the target at this location. Upon placing the target object, participants then received feedback. This comprised a translucent red version of the target object appearing at the correct location within the VE. Participants could also see the wooden pole where they placed it, as well as the starting position marker for that trial (see Figure 2.2B for a screenshot of the feedback). This information was presented to participants for eight seconds before the environment disappeared, and participants were returned to the starting empty grey environment with a marker indicating the next trial's starting position.

Participants completed 24 trials across the three conditions (eight trials per condition), similar to the BVA task (Kalová et al., 2005). To familiarise participants with the task, they completed four practice trials in a novel environment not used in the experimental trials. Practice trials followed the procedure for the Control condition i.e. participants could learn the target location using either allocentric or egocentric information. For experimental conditions in which the starting position or landmark array were rendered unreliable (respectively, the Allocentric and Egocentric conditions), these cues were randomly rotated around the centre of the arena to one of eight positions, along axes separated by 45 degrees. Their position was also prevented from repeating across consecutive Training and Test stages. Across all conditions, within each platform, the global configuration of the environment (i.e. the relationship between extra-maze landmark cues, and the boundary wall) remained consistent.

At the start of each block of trials, instructions were read aloud to participants from a script. During the initial set of practice trials, the following instructions were provided:

In this experiment, each trial comprised two stages in which you will learn the location of a target

object (a wooden pole). In the first stage, you will learn its location using the available visual information and your start position. Once you have learned the target's location, you will walk towards the target, place the controller model around it, then press the trigger button to pick it up. This will move you onto the next stage of the trial.

After participants completed the Training stage, they then received the following instructions:

In the second stage of each trial you will replace the target in its original location, using the available visual information and its relationship to your starting position. Walk to where you think the target's original location is, then press the trigger button on the controller to place it.

After completing the first Test stage, participants the following instructions, describing the feedback:

After each trial you will receive feedback. You will see two poles appear in the circular arena. The brown pole is located where you placed the target. The translucent red pole is located in the correct location. You will also see a metal circle on the floor. This represents the location that you started the trial from. The target's location will remain consistent within each part of the experiment, so you can use the feedback to become more accurate.

When the practice trials had been completed, the task closed, and participants were placed in a default SteamVR environment that comprised an empty space, visible through the HMD. Participants were then given the opportunity to to ask any questions and take a short break from the HMD by taking it off. After any concerns had been addressed, and the headset had been replaced, participants then completed the first set of experimental trials (i.e. the Control condition) and received the following instructions, based on those reported by Laczó et al. (2009):

You will now complete the experimental trials. In the first part of the experiment, you will be able to learn the location of the target using the available visual information and its relationship to your starting position.

Before participants began the Allocentric condition, they received the following instructions:

In this part of the experiment, you will only be able to learn the location of the target using the available visual information. Ignore its relationship to your starting position.

Before participants began the Egocentric condition, they received the following instruc-

tions:

In this part of the experiment, you will only be able to learn the location of the target using its position relative to your starting position. Ignore all other visual information.

After the immersive VR task had been completed, participants then completed the SBSOD (Hegarty et al., 2002), followed by the perspective taking task (Kozhevnikov & Hegarty, 2001) and the MRT (Vandenberg & Kuse, 1978). The MRT was administered on a desktop PC in the lab over two halves, with participants completing the each group of 12 trials within a three minute time limit. Between each set of trials, participants had the option of a break of up to three minutes.

2.1.2 Analysis

All analyses reported in this chapter were conducted in R (R Core Team, 2020) using the *afex* (Singmann et al., 2016) and *BayesFactor* (Morey & Rouder, 2018) packages. The principal dependent variable was placement error, i.e. the Euclidean distance, in U_m , between where the participant placed the target and where the target should have been placed, based on the reliable cues. Placement error was calculated using the same technique as Newman & Kaszniak (2000) by using Pythagoras' theorem. The duration of the Test stage was also recorded as a supplementary dependent variable. This comprised the latency between participants initiating the Test stage and making their locational judgement. Placement error and latencies were both analysed using a one way repeated measures ANOVA with a single factor of condition (Control, Allocentric, Egocentric). Planned comparisons were conducted between each level of the condition factor, with p-values adjusted using a Bonferroni correction. Finally, placement error, MRT accuracy, Perspective Taking angular error, and the SBSOD were entered into a correlation matrix to identify associations between each of the variables. The SBSOD was coded with higher scores indicating greater navigational proficiency, and lower scores indicating lower proficiency.

Bayes Factors (BF10) were calculated for all ANOVAs, post hoc tests, and correlations to quantify the strength of evidence for the alternative or null hypotheses (Dienes, 2014; Kruschke, 2010; Rouder et al., 2009). The Bayes Factors were interpreted using Jeffreys' (1961) guidelines: a BF10 less than 1 indicates evidence in support of H0 as opposed to H1, whereas BF10 greater than 1 indicates evidence in support of H1 as opposed to H0.

A BF_{10} greater than 3 or lower than 0.33 is considered noteworthy, whereas BF_{10} values between 0.33 and 3 are considered to be only anecdotal evidence (Lee & Wagenmakers, 2014). The higher or lower the value of the BF_{10} , the more compelling the evidence is in favour of the relevant hypothesis, e.g. a BF_{10} of 0.08 is considered strong evidence in favour of H_0 , whereas a BF_{10} of 0.18 would be considered moderate evidence in favour of H_0 .

2.1.3 Results

Placement responses for every trial, are illustrated in Figure 2.5, and descriptive statistics for placement error and latencies are presented in Figures 2.6 and 2.8 respectively. Trial by trial error rates are presented in Figure 2.7.

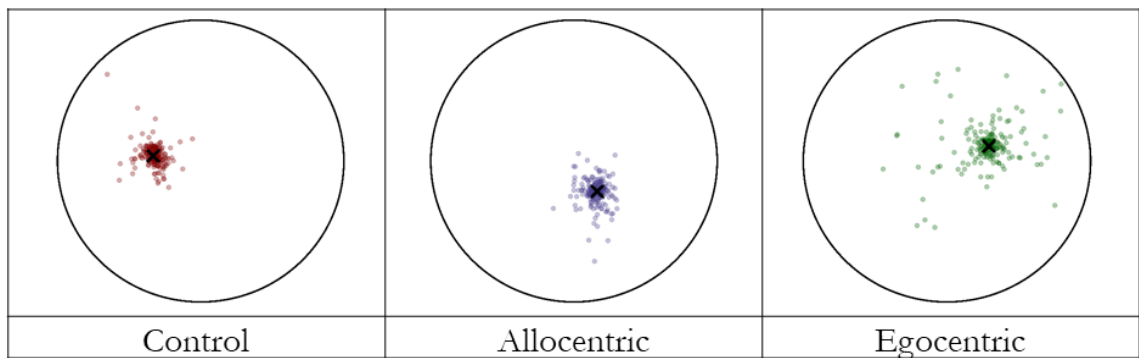


Figure 2.5: This plot shows each participant's placement within each condition. The correct location of the target in each condition is indicated by the black 'X'.

The three way repeated measures ANOVA conducted on the placement data showed inconclusive evidence of a main effect of trial type, $F_{(2, 46)} = 2.81, p = .07, \eta^2 = .086, BF_{10} = 1.68$. The planned comparisons between trial types showed that placement error was significantly lower in the Control condition compared to the Egocentric condition, $t_{(23)} = 2.23, p = .036, BF_{10} = 1.71$. There was no difference between placement error in the Control condition and the Allocentric condition, $t_{(23)} = 0.58, p = .57, BF_{10} = 0.25$. There was inconclusive evidence for a difference in placement error between the Allocentric and Egocentric conditions, $t_{(23)} = 1.8, p = .08, BF_{10} = 0.94$.

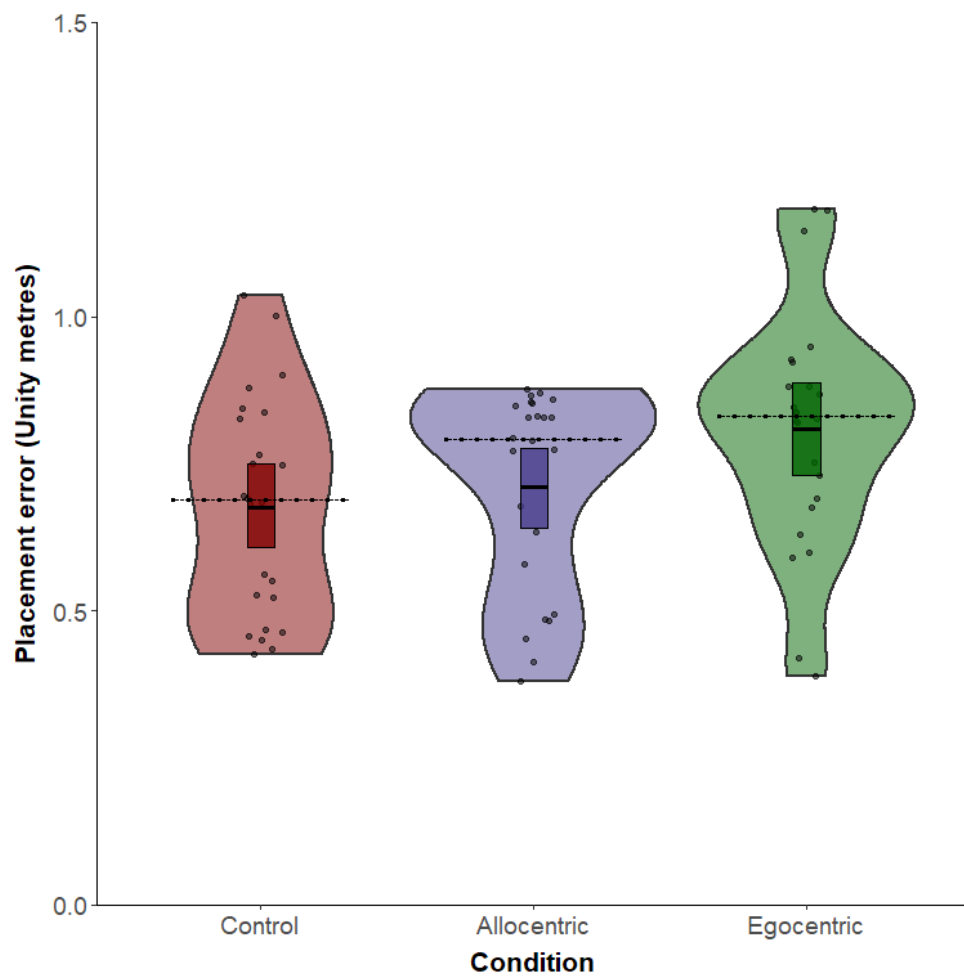


Figure 2.6: Descriptive statistics for placement error in Experiment 1. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

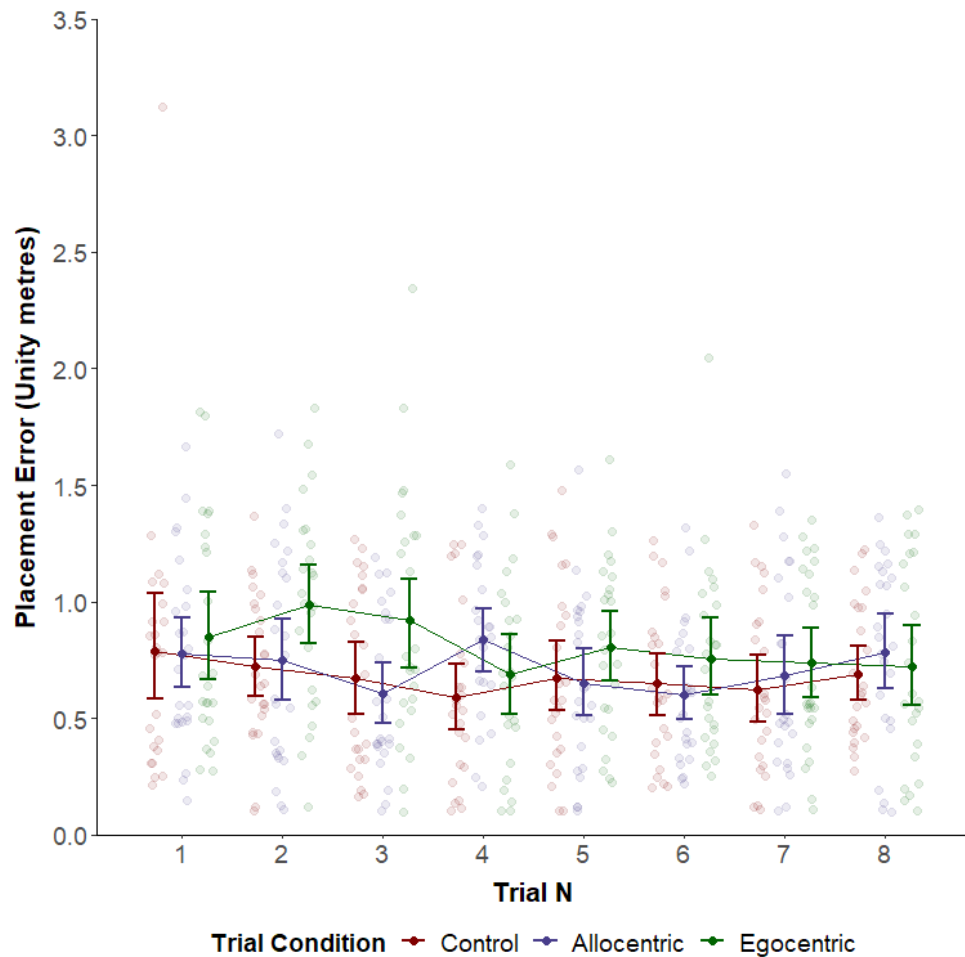


Figure 2.7: This plot shows the placement error for each trial in each condition. The error bars represent standard error are presented either side of the mean score for each trial within each condition. Each jittered point on the plot represents a participant's score for that trial.

The three way repeated measures ANOVA conducted on the latency data showed a main effect of trial type, $F_{(2, 46)} = 14.65, p < .001, \eta^2 = .173, BF10 = 1760$. The planned comparisons between trial types showed that mean latencies in the Control condition were longer than those in the Egocentric condition, $t_{(23)} = 2.46, p = .022, BF10 = 2.53$, and lower than those in the Allocentric condition, $t_{(23)} = 3.08, p = .005, BF10 = 8.36$. In the Egocentric condition, mean latencies were shorter than those in the Allocentric condition, $t_{(23)} = 5.2, p < .001, BF10 = 795$.

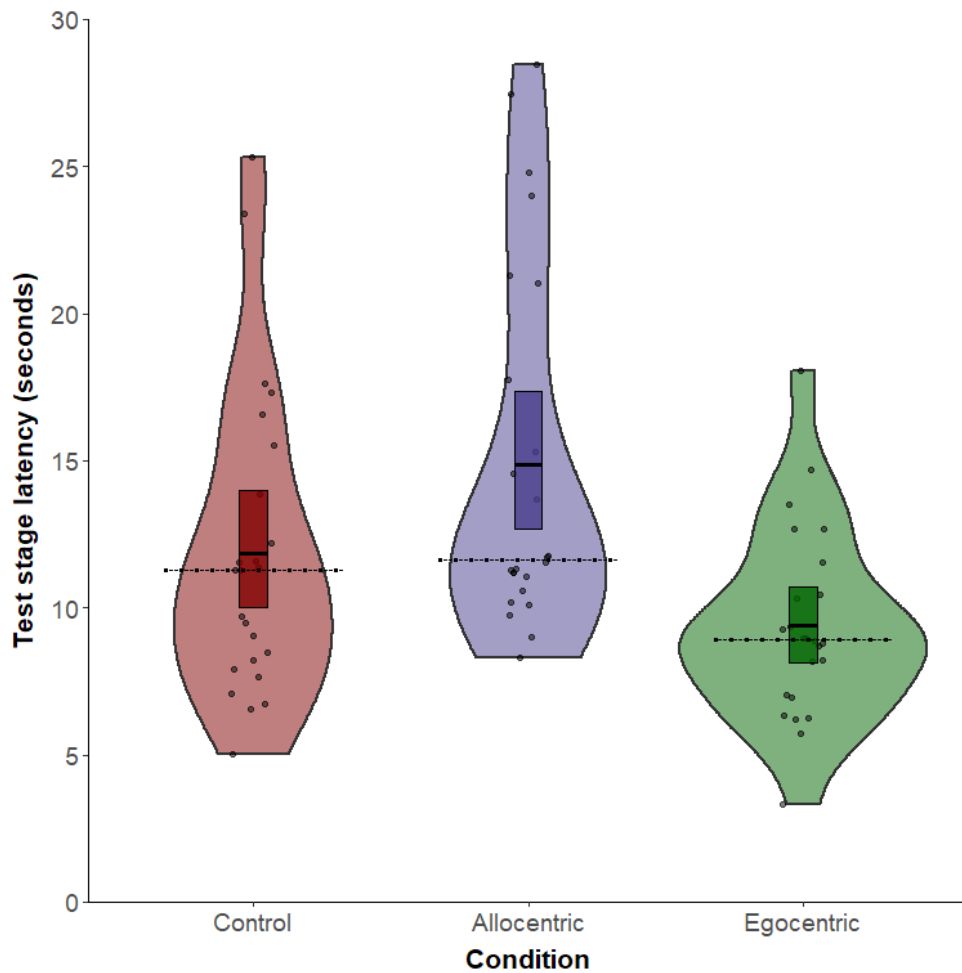


Figure 2.8: Descriptive statistics for Test stage latencies in Experiment 1. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

The correlation matrix is visualised in a correlogram that is presented in Figure 2.9. Within the place learning task, there was a significant negative correlation between placement error between the Control and Allocentric conditions, $R^2 = -0.44$ $p = .031$, $BF10 = 2.94$. There were small correlations between placement error in the Egocentric condition and both the Control condition, $R^2 = -0.13$ $p = .55$, $BF10 = 0.51$, and Allocentric condition, $R^2 = 0.07$ $p = .76$, $BF10 = 0.46$. There was a significant negative correlation between MRT accuracy and Perspective Taking error, $R^2 = -0.69$, $p < .001$, $BF10 = 133$, indicating that greater accuracy on the MRT was associated with reduced angular error on the Perspective Taking tasks. Interestingly the largest correlation between the MRT and place learning task conditions was a negative correlation observed in the Allocentric condition, $R^2 = -0.24$, $p = .26$, $BF10$

= 0.75, however, this correlation is not significant and the Bayes Factor indicates the weight of evidence to support the correlation is anecdotal. There was a significant positive correlation between place learning task placement error in the Egocentric condition and Perspective Taking angular error, $R^2 = 0.54$ $p = .006$, $BF10 = 8.8$. There was also a large but non-significant negative correlation between Allocentric placement error and Perspective Taking angular error, $R^2 = 0.38$ $p = .064$, $BF10 = 1.78$. In contrast there was a large and non-significant negative correlation between Perspective Taking error and placement error in the Control condition, $R^2 = -0.28$ $p = .19$, $BF10 = 0.88$. SBSOD scores did not correlate with placement error in the place learning task Control condition, $R^2 = -0.05$, $p = .8$, $BF10 = 0.45$, Allocentric condition, $R^2 = 0.11$, $p = .61$, $BF10 = 0.49$, or Egocentric condition, $R^2 = 0.17$, $p = .43$, $BF10 = 0.57$.

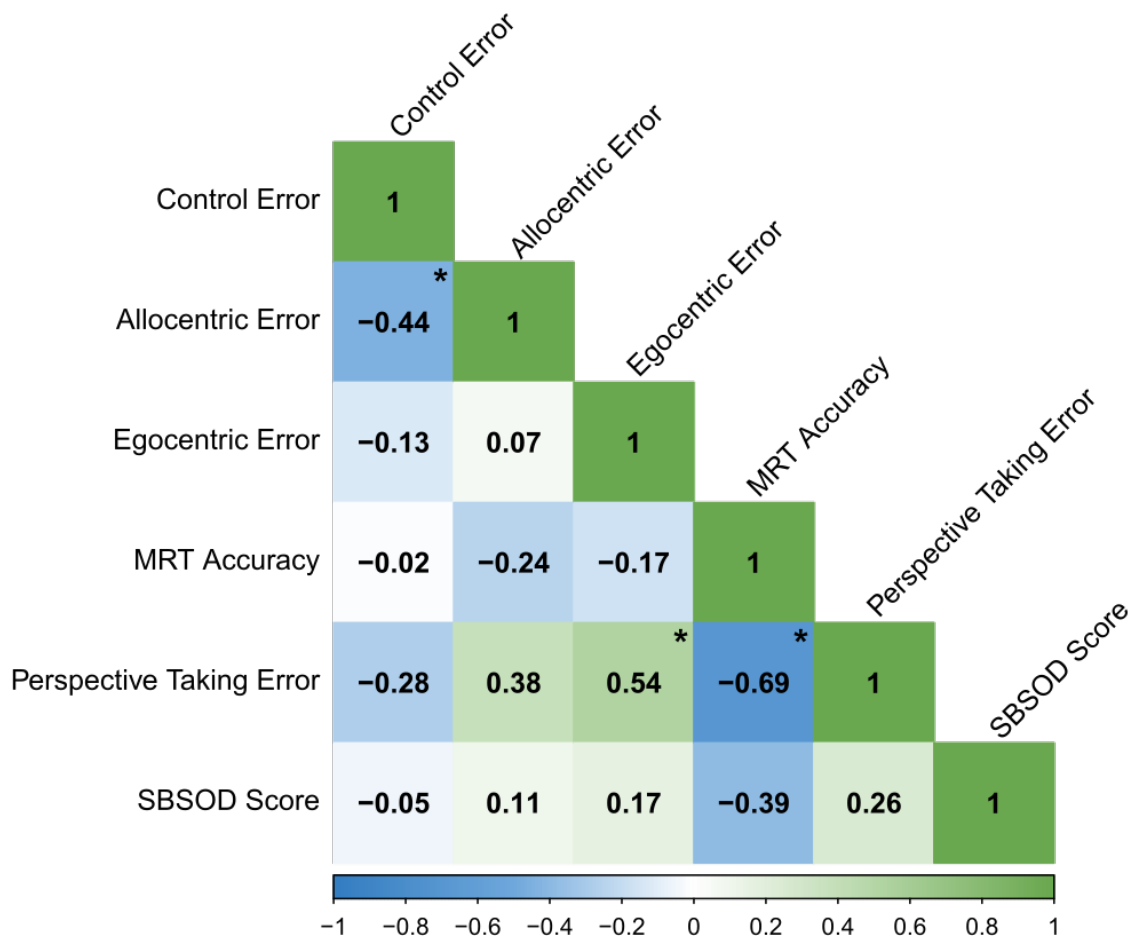


Figure 2.9: This plot visualises the correlation matrix produced in Experiment 1 using a correlogram. The colour scale along the bottom indicates the strength of the correlation. Pearson's R values are reported within the correlogram at the boxes in which the variables intersect. Significant correlations ($p < .05$) are indicated by asterisks.

2.1.4 Discussion

In this experiment, participants completed an immersive VR place learning task based on the BVA (Kalová et al., 2005). The task was designed to measure the ability to learn and recall a location using either allocentric or egocentric information, or both types of information in conjunction. Placement data showed only one clear difference between conditions, with placement error being greater in the Egocentric condition than in the Control condition. There was no difference between placement error in the Control and Allocentric conditions, and there was inconclusive evidence for a difference between the Allocentric condition and Egocentric condition. Additionally, there were differences in latencies to complete the Test stage, with latencies being lowest in the Egocentric condition and greatest in the Allocentric condition.

The placement data recorded in this experiment contrast with those observed in a recent study that dissociated allocentric and egocentric contributions to spatial memory (Merhav & Wolbers, 2019). There was no clear advantage to the Control condition in this experiment, which is surprising, as Merhav & Wolbers (2019) and found placement error, when integrating both allocentric and egocentric information, to be more accurate than when using allocentric or egocentric information in isolation. One reason for this might be that the feedback may have influenced the behaviour of participants. Whilst the feedback was in a similar format to that reported by researchers using the BVA task (Kalová et al., 2005), there is evidence to suggest that navigational information presented from a first-person perspective may be of less utility for generating an allocentric representation of space than information presented from a top-down perspective (Cuevas et al., 2001; Henriksen & Midtbø, 2015; Meng, 2005). This may present an explanation for the negative correlation between placement error in the Control and Allocentric conditions as it may reflect differences in how well participants can accurately use landmarks when starting the Test stage from a new perspective, relative to the trial's Training stage. Participants that may have been able to reliably use the landmarks in the Control condition may have then struggled when they had to ignore the target location's egocentric relationship to their Test stage starting position in the Allocentric condition. Additionally, the first-person perspective in the Feedback stage may have led participants to use viewpoint-based strategies in both the Control and Allocentric conditions (Kolarik et al., 2016). In this task, this would involve moving and rotating both the target and one's view until it aligned with

a memorised snapshot of the VE from the previous Test or Feedback stage (Török et al., 2014). This strategy would be more difficult in the Allocentric condition due to the time limit in the Feedback stage, as there would be a more limited window for participants to generate their visual snapshot. This would potentially explain why some participants that were successful in the Control condition struggled in the Allocentric condition. Presenting feedback from a top-down perspective may then increase the sensitivity of the task through ensuring demands across the Control and Allocentric conditions are more clearly differentiated.

The difference in latencies may reflect behavioural differences in each condition, however, unlike time based measures from the MWM or vMWM, this information is agnostic to the ability to accurately identify the target's location. In this experiment, the latency measure only describes how long it took the participant to make their judgement of the target location, which is independent from the placement error measure that indicates the accuracy of a participant's response. The latency measure does present differences between the three conditions that may reflect the behaviours required in each. For example, latencies were shortest in the Egocentric condition and longest in the Allocentric condition. These data may then reflect the requirement for reorientation in the Allocentric condition before a participant can identify the target location. This is not required in the Egocentric condition as the only reliable cues are the direction and distance from Test stage starting position so participants can walk straight to the target location at the start of the Test stage, reducing the amount of time taken. Whilst these data are informative, without further detailed behavioural data, one cannot make a firm conclusion from these analyses.

Behaviour may have been influenced by the lack of standardisation across the landmarks. Previous place learning experiments have demonstrated how proximal and distal cues are encoded differently (Padilla et al., 2017; Zhou & Mou, 2019), as well as differences between encoding of local and boundary cues (Doeller et al., 2008; Doeller & Burgess, 2008; Ferguson et al., 2019; Livingstone-Lee et al., 2011, 2014; Zhou & Mou, 2019). Proximal cues have been implicated in supporting the precision of a spatial representation (Padilla et al., 2017; Zhou & Mou, 2019), whereas distal and boundary cues have been shown to support reorientation behaviours, and may be coded in an obligatory manner (Doeller et al., 2008). In this experiment, the three landmarks were not all equal in their distance to the arena and each differed in size. As a result, each of the three landmarks may have differed in their utility to participants. For example, the size of the mountain means that it

would occupy much of the visual field when visible. This may have influenced responses from participants including in the Egocentric condition, as the dominant presence of the landmarks (i.e. that they occupy much of the visual field) may have competed with the reliable egocentric information and led to increased placement error across participants.

The only significant correlation between the task battery and the place learning task was a positive correlation between perspective taking error and Egocentric condition placement error. There were, however, interesting correlations that did not reach the threshold for significance, and were only supported by anecdotal Bayes Factors. For example, MRT accuracy was negatively correlated with all three conditions, indicating that those that performed better on the MRT were more accurate with their placements, and reflecting findings observed with the vMWM (Driscoll et al., 2005; Schoenfeld et al., 2010a). Placement error in the Allocentric condition correlated with perspective taking error, similar to results from the Egocentric condition, suggesting that success at these conditions is associated with stronger perspective taking ability. There was an interesting contrast with the Control condition, however, as there was a negative correlation between Control condition placement error and the perspective taking performance. Another finding of note from the correlations is the absence of any correlation between the SBSOD and placement error in the three conditions. This suggests that the SBSOD may lack sufficient sensitivity to load onto performance across the three conditions, or that the experimental task does not capture navigational aptitude as an overall construct.

Overall, Experiment 1 does not show a pattern of results that is entirely consistent with those reported in other experiments (e.g. Gazova et al., 2013; Merhav & Wolbers, 2019). While the high placement error in the Egocentric condition is similar to the results reported by Merhav & Wolbers (2019), it was surprising that the placement error did not differ between the Control and Allocentric conditions. Consequently, the task in its current design may not be sufficiently sensitive to distinguish between the performance in the Allocentric and Control conditions.

2.2 Experiment 2

This experiment comprised a direct comparison between a refined version of the immersive VR versions place learning task described in Experiment 1 and a version designed for a desktop PC platform. This comparison probed whether spatial memory on desktop PC

assays of navigation are underpinned by the same mechanisms as fully-motile equivalents, addressing an important and current theoretical discussion in the literature (Huffman & Ekstrom, 2020; Steel et al., 2020; Taube et al., 2013).

To address some potential limitations with Experiment 1's place learning task, changes were made to the experimental task for both platforms. First, feedback was presented as a top down schematic of the environment. This change means that participants viewed the entire environment from a single perspective, so participants could clearly identify the spatial relationships between the landmarks and the correct location across all three conditions. Similarly, the relationship between the correct location and the starting position can also be more clearly appreciated, attenuating the need for mental translation of that spatial relationship from the participant's first person perspective during the feedback stage. Second, the landmarks were standardised, such that they were all a consistent distance from the centre of the VE, and all looked similar (i.e. they were all rocks of a different shape and colour). This would ensure that no specific landmark dominates the field of view in the VE. To attenuate learning transfer across desktop PC and immersive task platforms, the landmarks were made distinct on the two versions of the task, by presenting them in different colours and shape. This was to reinforce to participants that the environments and their respective target locations were distinct.

If desktop measures of place learning are underpinned by the same mechanisms as fully-motile equivalents (Hartley et al., 2003; Huffman & Ekstrom, 2019a, 2020; Steel et al., 2020; Taube et al., 2013) then one would expect to observe similar performance across the two platforms, with equivalent rates of placement error in both the desktop PC and immersive VR versions of the task. In contrast, if idiothetic information supports more efficient and accurate navigational behaviour than a stationary version of the same task (Ruddle et al., 2011a,b) then one should see more accurate placement behaviour in the immersive VR version of the task. Whilst the literature does suggest that performance may be better on the immersive VR platform, there remains some equivocality about the contributions of idiothetic information to successful navigational behaviour (Hejtmanek et al., 2020).

Finally, the changes made to the design of Experiment 1's place learning task should have made it more sensitive to differences across conditions, as the spatial relationships between the cues in each condition should have been more readily apprehended from a top-down schematic of the environment. As a consequence, both allocentric and egocentric spatial

learning and memory should have been of greater utility, meaning that placement error was expected to be lowest in the Control condition, where both types of information are reliable.

2.2.1 Methodology

Design

The experimental design was within subjects with two factors: platform type (two levels: desktop PC, immersive VR) and condition (three levels: Control, Allocentric, Egocentric). In a single experimental session, participants completed the two versions of the place learning task on both immersive VR and desktop PC platforms. The order in which the tasks were completed was counterbalanced, with half of the participants completing the desktop PC task first, and the other half completing the immersive VR task first. Each version of the task followed the same design as the task employed in Experiment 1, i.e. participants learned the location of a wooden pole in a Training stage, before replacing it in the test stage. Participants completed the same 24 trials, split evenly across the three conditions, and learned a novel target location in each condition (see Figure 2.10). The Control condition was always completed first, before participants then completed either the allocentric or egocentric condition in an order counterbalanced across participants – e.g. half of the participants completed the allocentric trials second and the egocentric trials third during the desktop PC task - this group of participants were then again split into halves that then completed either the Allocentric condition second and Egocentric condition third, or Egocentric condition second and Allocentric condition third in the immersive VR task.

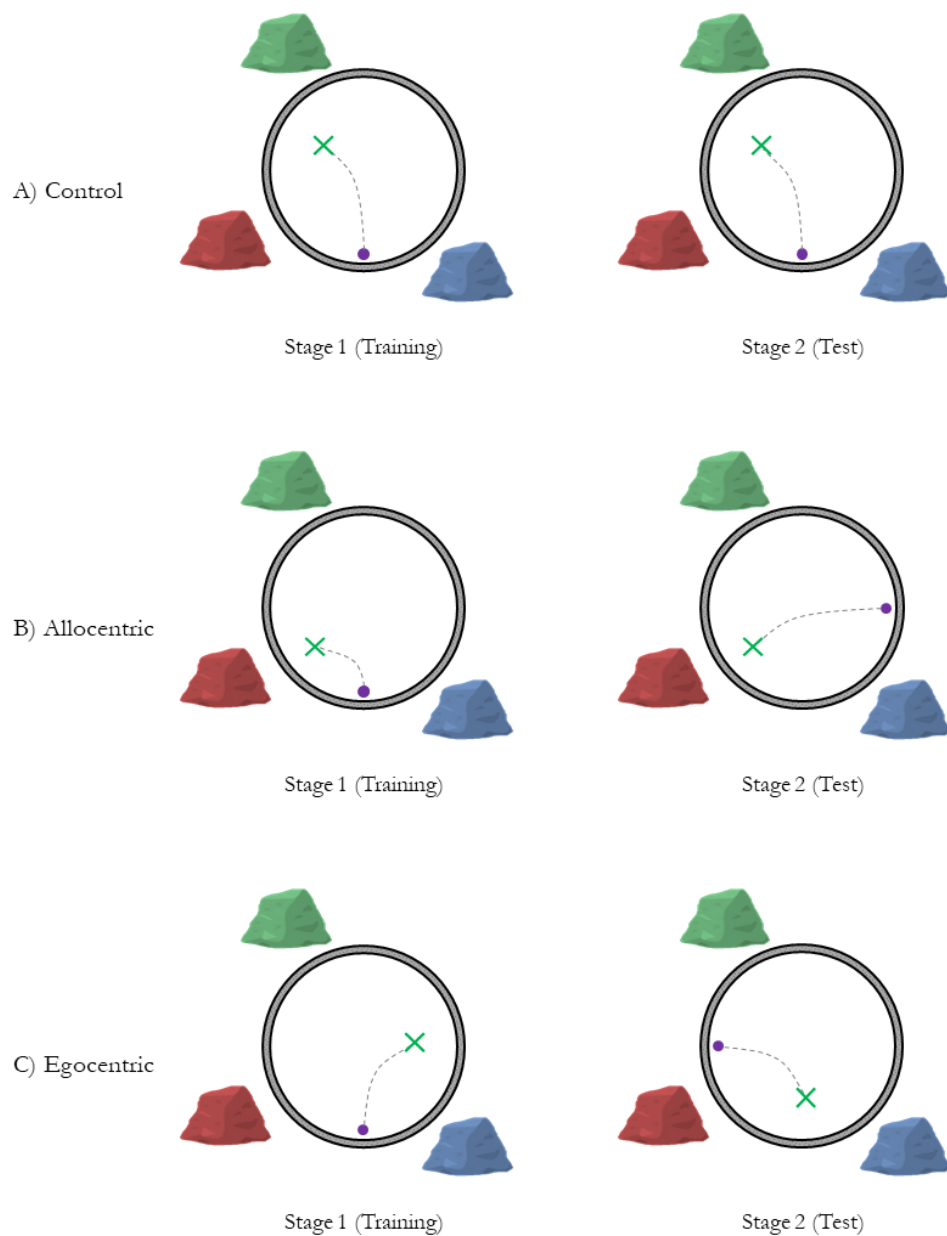


Figure 2.10: This diagram shows the conditions used in both the desktop and immersive VR versions of the task used in Experiment 2. The diagram shows the same information as Figure 2.1, but is adapted to include the landmarks introduced in Experiment 2.

Participants

Healthy adult participants were recruited from the University of Plymouth ($N = 43$: 31 female, 12 male), and were provided with course credit in return for participation. Their ages ranged between 18 and 45 years ($M = 21.5$, $SD = 46$), and each participant was physically able to traverse the laboratory space unaided. No participants demonstrated or reported any side effects (e.g. simulator sickness) from interacting with the immersive VR

system. A sample size of 43 participants is sufficient to detect medium effect sizes.

Apparatus and Materials

As in Experiment 1, the experiment took place in the University of Plymouth's large-scale immersive VR laboratory, and the same wireless immersive VR system was used for the immersive VR version of the task. The environments were similar to Experiment 1's environments, however, there was no outer wall. The only boundary was the circular wall demarcating the bounds of the freely navigable space within the VE. The diameter of the inner wall was the same as Experiment 1 for the immersive VR version of the task (4.5 m), however, the inner diameter of the arena was larger in the desktop PC version of the task (25 m), to account for the reduced precision of the controls in the desktop PC task. On the outside of the arena, in each version of the task, there were three rocks that functioned as landmarks. These rocks differed in colour and shape for each of the two versions of the task, to ensure that participants were aware that the environment in each platform's task was distinct. In the desktop PC version of the task, the rocks were red, green, and blue, and each was 20 m in width, and ranged from 6.5 m to 8 m in height. In the immersive VR version of the task, the rocks were purple, green, and brown, and each was 1.5 m in width, and ranged from 1 m to 1.8 m in height. The target object in both versions of the task was the same wooden pole employed in Experiment 1. Additionally, the same white gloved hand used in Experiment 1 was visible in both task versions, as a proxy for the participant's hand.

Participants completed the desktop PC version of the task on the same high-end PC that ran the immersive VR version, and it was displayed on a 21 inch monitor located 45 cm from the participant. Participants explored the environment with an Xbox controller, using the left analogue joystick to move, and using the green A button to interact with the target object (i.e. to pick it up or to place it). The perspective was 1 m high, and the camera had a 60° field of view.

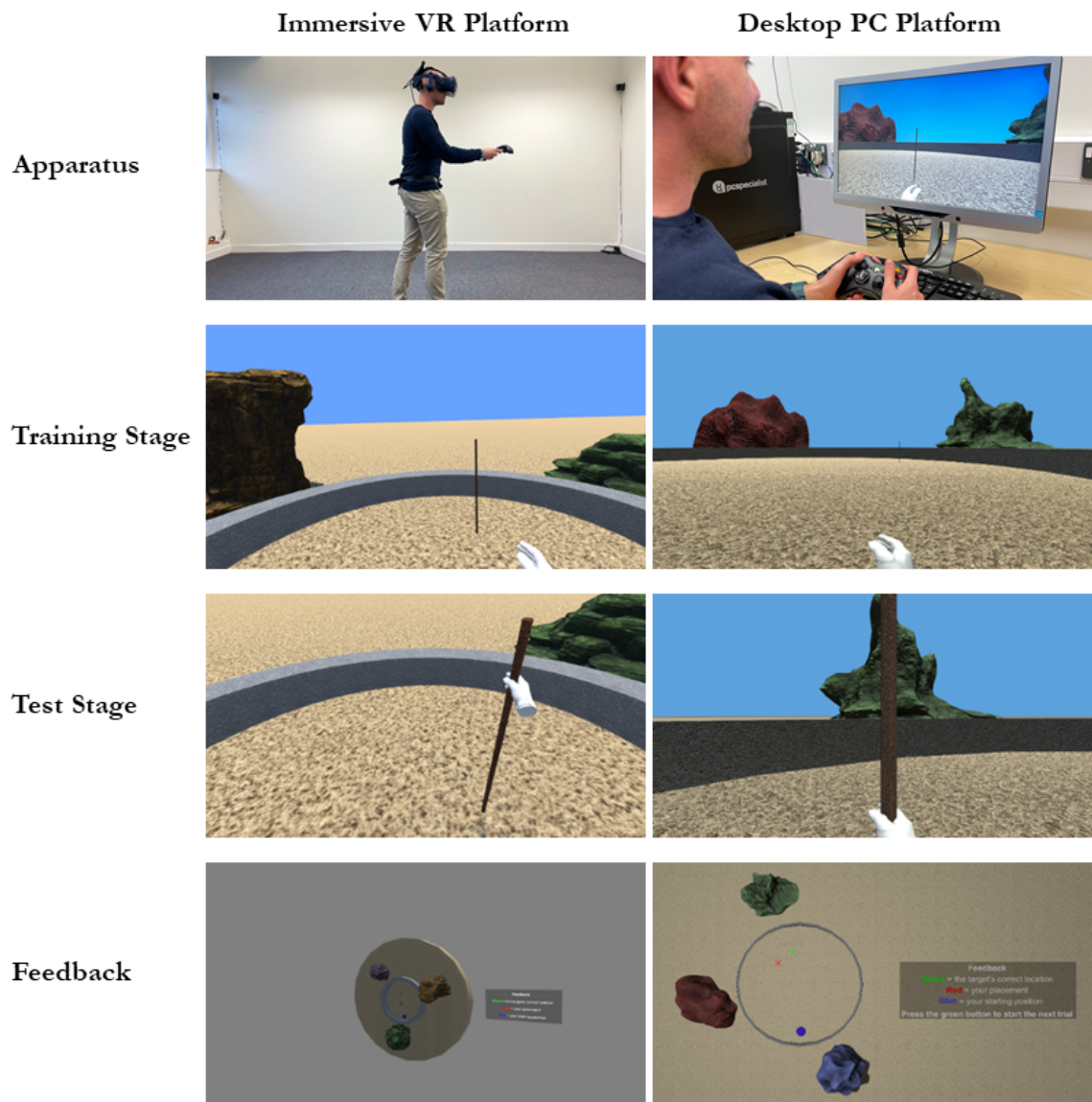


Figure 2.11: This diagram shows images depicting immersive and desktop versions of the experimental task and the apparatus used for each. The images of the VEs illustrate respective Training stages (showing the viewpoint from the starting position, prior to participants navigating to the target), Test stages (where they are relocated and then required to replace the target), and Feedback stages (where the accuracy of their response is depicted on a top-down map of the arena).

Procedure

In this experiment, participants completed both desktop and immersive VR versions of the experimental task. The procedure for each task followed the same method used in Experiment 1, i.e. participants complete an initial Training stage in which they learn the

target location and pick the target up, then replace the target in a subsequent Test stage, using the reliable cues for the current condition. After the Test stage participants received feedback, which in this experiment, for both versions of the task, comprised a top-down schematic of the environment, including the landmarks and the boundary wall. Illustrated within this schematic was the correct location of the target, their estimate of the location (i.e. where they had placed the pole), and their starting position around the perimeter of the wall (see Figure 2.11).

The main difference between the two platforms were that in the desktop PC version of the task, participants were automatically moved back to the starting position at the end of each trial stage, whereas in the immersive VR version of the task, participants had to walk to the starting position marker after each trial stage. Participants did not complete a disorientation procedure in the desktop PC version of the task, as there would be no requirement to extinguish any representation of the real-world laboratory space, acquired when walking between starting positions.

Before completing any experimental trials, participants completed practice trials on both platforms to ensure they were familiarised with the controls for each task. As in Experiment 1, practice trials were completed in novel environments that were distinct to those employed in the experimental trials.

In the desktop PC version of the task, instructions were presented to participants as black text on a grey screen. During the initial set of practice trials that participants completed, the following instructions were given to participants:

In this experiment, each trial comprised two stages in which you will learn the location of a target object (a wooden pole). In the first stage, you will learn its location using the available visual information and your start position. You move the display around the environment using the left stick on the controller. Once you have learned the target's location, you will then move the display so the hand is touching the target, and then press the green button to pick it up. This will move you onto the next stage of the trial.

After participants completed the Training stage, they then received the following instructions:

In the second stage of each trial you will replace the target in its original location, using the available visual information and its relationship to your starting position. You will move the display using the left stick on the controller, and when you want to place the target in the original location, you

will press the green button on the controller.

After completing the first Test stage, participants the following instructions, describing the feedback:

After each trial you will receive feedback. You will see two signs in the circular arena. The red X is where you placed the target. The green X is where it should have been placed. You will also see a blue circle. This represents the location that you started the trial from. The target's location will remain consistent within each part of the experiment, so you can use the feedback to become more accurate.

Before participants completed the first set of experimental trials (i.e. the control condition), they received the following instructions:

You will now complete the experimental trials. In the first part of the experiment, you will be able to learn the location of the target using the available visual information and its relationship to your starting position.

Before participants began the allocentric condition, they received the following instructions:

In this part of the experiment, you will only be able to learn the location of the target using the available visual information. Ignore its relationship to your starting position.

Before participants began the egocentric condition, they received the following instructions:

In this part of the experiment, you will only be able to learn the location of the target using its position relative to your starting position. Ignore all other visual information.

Instructions for the immersive VR version of the task were the largely same as those used in Experiment 1, and were similarly read from a script to ensure consistency. The only change to the instructions were those read to the participant during the first Feedback stage, which were modified to reflect the changes made to the feedback for this experiment, and were the same as those presented to participants on screen in the desktop PC version of the task.

2.2.2 Analysis

The principal dependent variable for this experiment was again placement error, however, for this experiment, the measure was scaled to allow a direct comparison across the two platforms. Scaled placement error was calculated by dividing the placement error for each trial by the inner diameter of the boundary wall on each respective platform. Both scaled placement error and latencies were analysed using a two (platform: immersive VR, desktop PC) x three (trial type: Control, Allocentric, Egocentric) repeated measures ANOVA. Both repeated measures variables analysed using the ANOVAs were corrected for sphericity by the afex package for R (Singmann et al., 2016) using a Greenhouse Geisser correction. Planned comparisons were conducted between each level of the condition factor for each platform, and between each platform for each condition. P-values calculated for these comparisons were adjusted using a Bonferroni correction. Finally, to identify whether performance was similar across platforms on an individual level, correlations were conducted between the two platforms for each condition.

2.2.3 Results

Placement responses for every trial and participant, are illustrated in Figure 2.12, and descriptive statistics for the scaled placement error and latencies are presented in Figures 2.13 and 2.15 respectively. Mean values of scaled placement error values for each trial in each condition are presented in Figure 2.14.

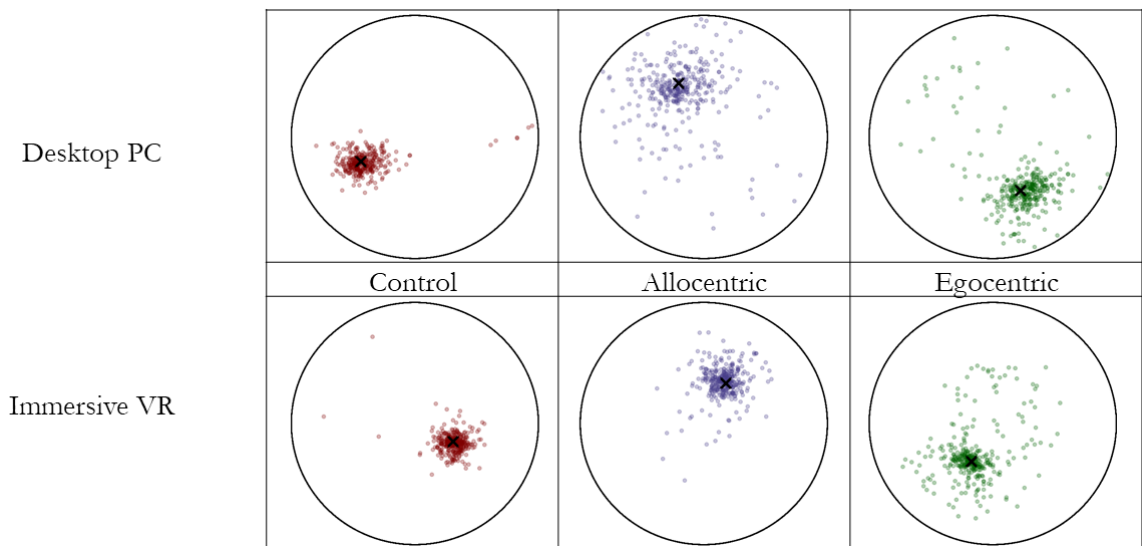


Figure 2.12: This plot shows each participant's placement within each condition for each task. The correct location of the target in each condition is indicated by the black 'X'.

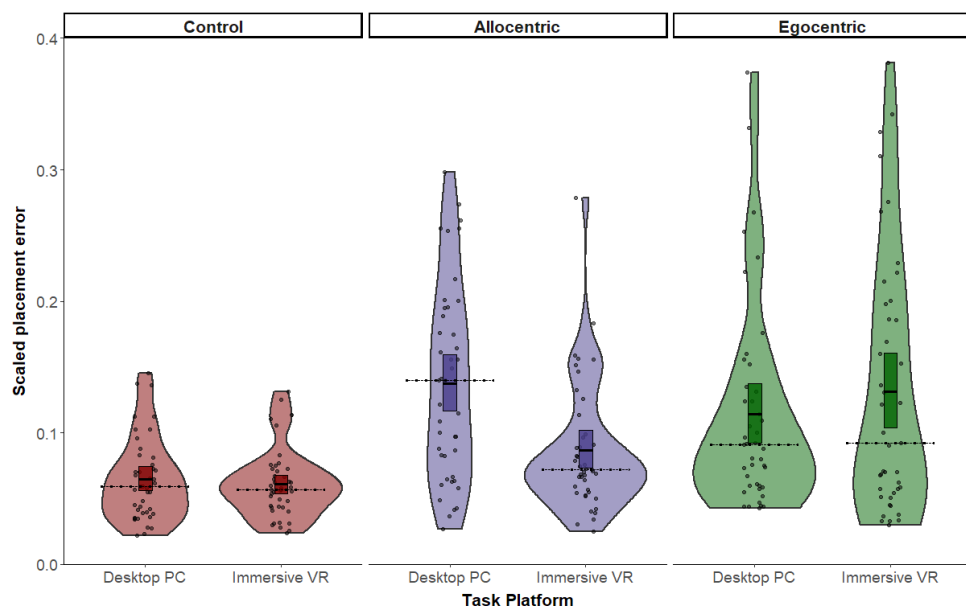


Figure 2.13: Descriptive statistics for scaled placement error for both task versions employed in Experiment 2. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

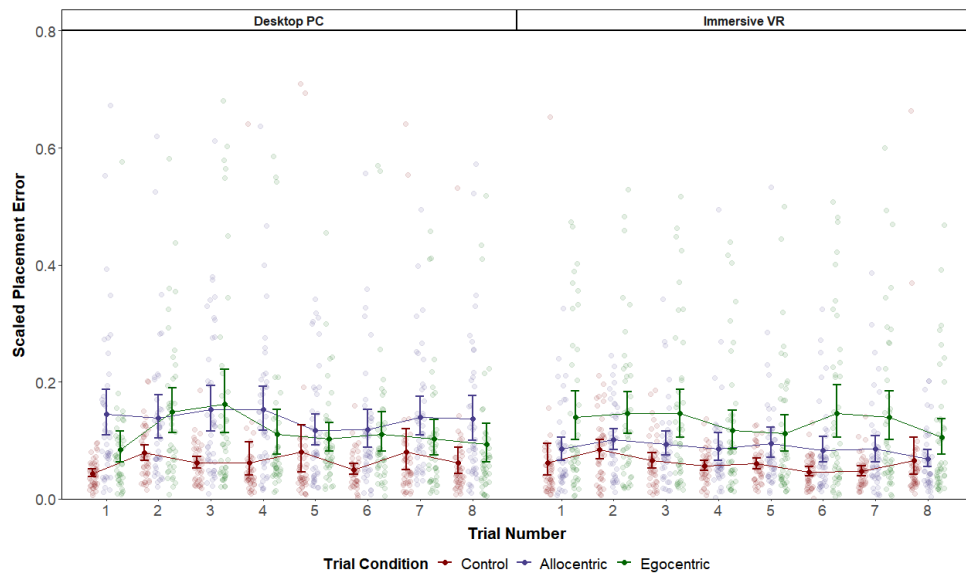


Figure 2.14: This plot shows the placement error for each trial in each condition for both tasks. The error bars represent standard error are presented either side of the mean score for each trial within each condition. Each jittered point on the plot represents a participant's score for that trial.

For the 2x3 repeated measures ANOVA conducted on the mean scaled placement error data, there was a main effect of trial type, $F_{(1.69, 70.77)} = 22.26, p < .001, \eta_p^2 = .346, BF10 = 8.2 \times 10^{07}$, and an interaction effect, $F_{(1.52, 63.99)} = 8.91, p < .001, \eta_p^2 = .175, BF10 = 52$. There was, however, no effect of task platform, $F_{(1, 42)} = 3.4, p = .072, \eta_p^2 = .075, BF10 = 0.4$.

The planned comparisons showed that on the desktop PC platform, placement error was lower in the Control condition than in the Allocentric condition, $t_{(42)} = 6.73, p < .001, BF10 = 3.9 \times 10^5$, and the Egocentric condition, $t_{(42)} = 4.03, p = .002, BF10 = 113$. There was no difference between the desktop Allocentric and Egocentric conditions (though the Bayes Factor was inconclusive), $t_{(42)} = 1.58, p = 1, BF10 = 0.52$.

On the immersive VR platform, placement error was lower in the Control condition than in the Egocentric condition, $t_{(42)} = 4.85, p < .001, BF10 = 1204$, and there evidence to suggest that placement error was lower in the Control condition than in the Allocentric condition, $t_{(42)} = 3.26, p = .02, BF10 = 15$. Additionally, placement error was lower in the Allocentric condition than the Egocentric condition, $t_{(42)} = 3.13, p = .03, BF10 = 11$.

There was Bayes Factor evidence to suggest that participants' scaled placement error did not differ between the desktop PC and immersive VR Control conditions, $t_{(42)} = 0.63, p = 1, BF10 = 0.2$, and the two platforms' Egocentric conditions, $t_{(42)} = 1.13, p = 1, BF10 =$

0.3. This contrasted with data from the two platforms' Allocentric condition, as scaled placement error was lower in the immersive VR Allocentric condition than in the desktop PC Allocentric condition, $t_{(42)} = 4.22, p = .001, BF10 = 193$.

The 2x3 repeated measures ANOVA conducted on the latency data showed evidence of a main effect of condition, $F_{(1.44, 60.34)} = 13.49, p < .001, \eta_p^2 = .243, BF10 = 613$, and platform, $F_{(1, 42)} = 5.13, p = .029, \eta_p^2 = .11, BF10 = 613$. There was also an interaction effect, $F_{(1.82, 76.32)} = 14.8, p < .001, \eta_p^2 = .261, BF10 = 5.8$.

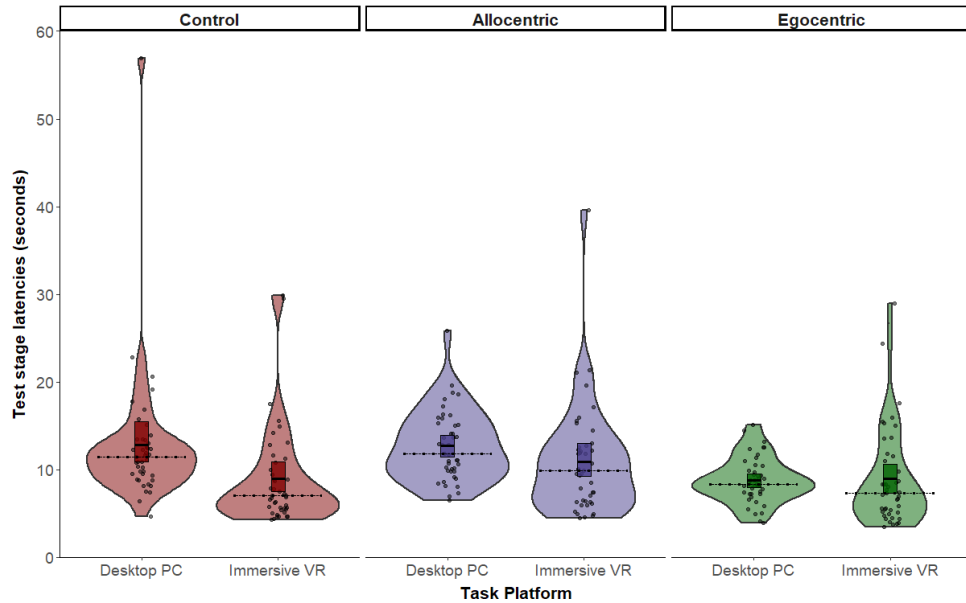


Figure 2.15: Descriptive statistics for Test stage latencies in both versions of the task employed in Experiment 2. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

Planned comparisons for the latency data showed that on the desktop PC platform, latencies were lower in the Egocentric condition than in the Control condition, $t_{(42)} = 4, p = .002, BF10 = 104$, and the Allocentric condition, $t_{(42)} = 8.14, p < .001, BF10 = 2.97 \times 10^7$. There was no difference between latencies in the desktop PC Control and Allocentric conditions, $t_{(42)} = 0.13, p = 1, BF10 = 0.166$.

On the immersive VR platform, latencies were faster in the Control condition than in the Allocentric condition, $t_{(42)} = 3.89, p = .003, BF10 = 76$, and lower in the Egocentric condition than the Allocentric condition, $t_{(42)} = 4.02, p = .002, BF10 = 110$. There was no difference

between latencies in the immersive VR Control and Egocentric conditions, $t_{(42)} = 0.07, p = 1, BF10 = 0.165$.

There was Bayes Factor evidence to suggest that participants' latency did not differ between the desktop PC and immersive VR Control conditions, $t_{(42)} = 0.63, p = 1, BF10 = 0.2$. Similarly, there was Bayes Factor evidence to also suggest that participants' est stage latency did not differ between the desktop PC and immersive VR Egocentric conditions, $t_{(42)} = 1.13, p = 1, BF10 = 0.3$. In contrast, latency was greater in the desktop PC Allocentric condition than in the immersive VR Allocentric condition, $t_{(42)} = 4.22, p = .001, BF10 = 193$.

The placement error correlation analyses revealed weak Bayesian Evidence of an absence of a correlation between placement error on each platform in the Control condition, $R^2 = 0.11, p = .48, BF10 = 0.43$. In contrast, there was evidence of a correlation between placement error on each platform in the Egocentric condition $R^2 = 0.39, p = .01, BF10 = 6.16$. In the Allocentric condition, there was inconclusive evidence for the presence of a correlation between placement error on each platform, $R^2 = 0.24, p = .12, BF10 = 0.98$. For a visualisation of these data, see Figure 2.16.

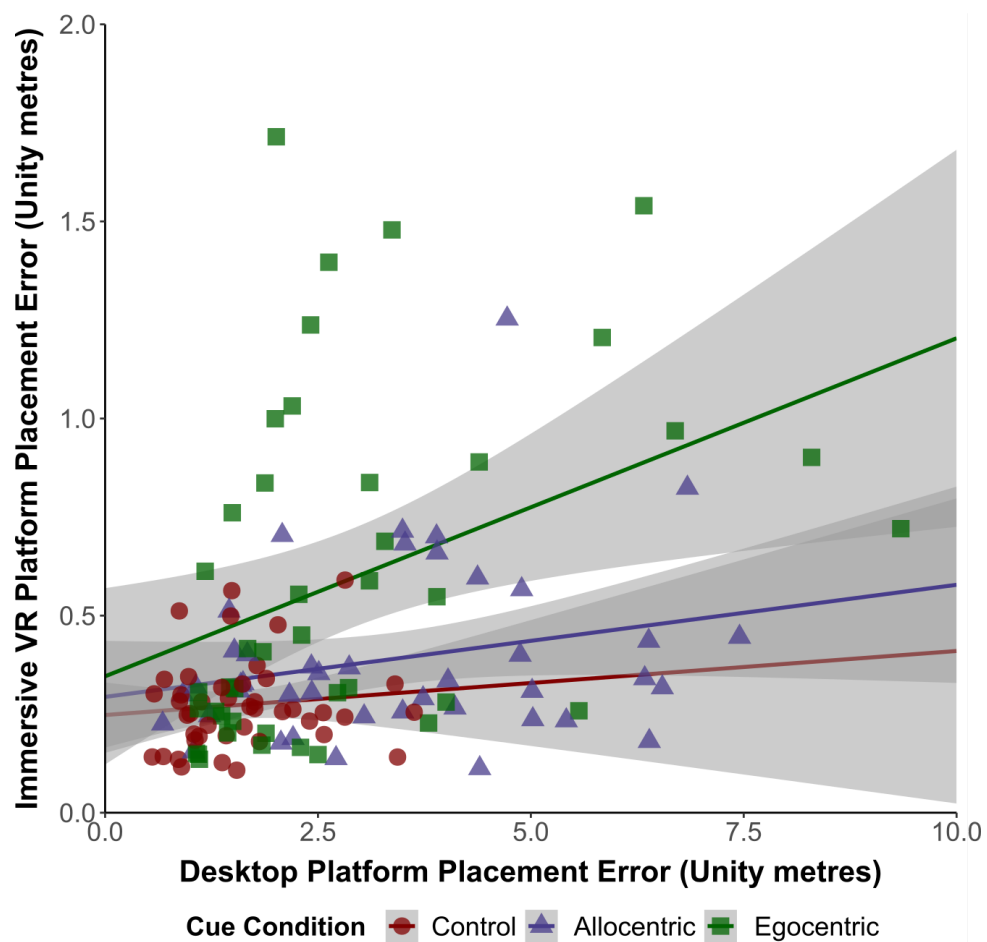


Figure 2.16: This plot presents correlations between placement error in each condition, across the two platforms. Regression lines for each correlation are displayed on the plot with 95% confidence intervals drawn either side in grey.

2.2.4 Discussion

To examine the contribution of idiothetic information to spatial learning and memory, participants completed two versions of the same task across immersive VR and desktop PC platforms. In both versions, participants replaced the target most accurately in the Control condition, when they could use both allocentric and egocentric cues in conjunction. Additionally, performance was equivalent between platforms, relative to size of their respective VE. In contrast, the dissociation of allocentric and egocentric cues revealed that participants were more accurate at estimating the target location in the immersive VR Allocentric condition than the desktop PC Allocentric condition - this contrasts with the Egocentric condition, in which no difference was observed across the two platforms. Trials in the Allocentric condition were performed more accurately than those in the Egocentric

condition in the immersive VR task, whereas there was no reliable difference between the two conditions in the desktop PC task. Furthermore, whilst performance across platforms was positively correlated for the Egocentric conditions, there was no positive correlation between platforms for the Allocentric and Control conditions. Together, these findings show that the use of spatial cues to learn and recall target locations was not consistent across platforms. In particular, performance based on allocentric cues alone, considered the hallmark of place learning, was superior when idiothetic cues were available.

These observations are not commensurate with much contemporary theory. Assays of human place learning are underpinned by the assumption that that desktop (or MRI scanner-based) tasks recruit the same navigational mechanisms as a fully-motile equivalents, and the retrieval of spatial information is considered to be modality independent (Huffman & Ekstrom, 2019a; Wolbers et al., 2011). The advantage seen for allocentric trials within the immersive task, in relation to egocentric trials, also contrasts with previous research highlighting computational difficulties associated with allocentric navigational information use (desktop: Ferguson et al., 2019; immersive: Negen et al., 2020). However, Merhav & Wolbers (2019) found that recall of a location using allocentric cues was more accurate than egocentric cues in immersive VR, in a space of a similar size to that used in this experiment. The differences across the Allocentric conditions may reflect the impact of an environment's size, as previous research has emphasised that navigational cues may be employed differently across scales (Learmonth et al., 2008; Montello, 1993; Padilla et al., 2017; Wolbers & Wiener, 2014). Virtual assays of human place learning are typically conducted in large-scale desktop environments and may, therefore, not capture the same behaviour in smaller scales. Indeed, across physically navigable VEs, advantages have been observed for the use of allocentric information compared to egocentric information (Merhav & Wolbers, 2019), and for motile navigation compared to desktop navigation (Ruddle et al., 2011a,b). These results indicate that Huffman & Ekstrom's (2020) model may not fully capture how idiothetic cues contribute to the use of allocentric information during navigation.

Similar to Experiment 1, results from the immersive VR task also contrast with the findings of Gazova et al. (2013), who reported similar accuracy across control, allocentric and egocentric conditions for a control group of healthy young adults. It is, however, important to note two important differences between the two tasks' designs the task reported here featured novel target locations for each condition, and this experiment's egocentric

condition included the presence of unreliable landmarks. This was to identify how participants learned and recalled spatial information in each condition individually, and to equate their demands - i.e. in the Allocentric condition, one is required to suppress the influence of egocentric cues, and so an appropriate equivalent for the Egocentric condition was to suppress the influence of landmarks. However, previous research has shown that unreliable landmarks can disrupt the use of path-based spatial representations (Zhao & Warren, 2015a,b), and that boundary information can interfere with the use of egocentric cue based navigation (Doeller et al., 2008). Whilst this may account for some difficulties in using the egocentric cues in this experiment, it is important to note that (Merhav & Wolbers, 2019) reported that navigation was less accurate in an equivalent immersive VR Egocentric condition, compared to equivalent Control and Allocentric conditions.

These data could be interpreted as a demonstration that the inclusion of idiothetic cues facilitates the formation of an accurate cognitive map of the test environment (Steel et al., 2020). However, if this were the case then one should expect a similar improvement in the immersive VR task's Control condition. This was not apparent, and so these data present an equivocal account as to the role of idiothetic cues in the development of a map-like representation of space. It may be that participants are more likely to use beacon-like strategies in an immersive VR context, as reported by McAvan et al. (2021) in an immersive VR place learning task. This strategy involves using a single extra-maze landmark as a heading guide. The more frequent use of beacon strategies contrasts with experiments examining strategy use on versions of the vMWM designed for desktop PC platforms, in which young adults employ a mixture of beacon or place cue strategies, i.e. employing more than one landmark to locate the hidden platform Schoenfeld et al. (2010a, 2017). These findings suggest that immersive VR contexts may fundamentally change a preference for employing the available cues in a VE, though this can only be specified when interrogating path data.

2.3 Experiment 3

The onset of the COVID-19 pandemic necessitated the transition to remote data collection. This experiment comprised the development of a prototypical version of the desktop-based place learning task that can be deployed via a web browser for remote data collection. Whilst this meant a fundamental rethink of the experiments planned for this thesis, it

presents opportunities for rapid, lower cost data collection (Nosek et al., 2002), and access to wider and more diverse pools of participants Huber & Gajos (2020).

Collecting data online requires a number of considerations that would otherwise not be apparent with laboratory based testing (Sauter et al., 2020). These relate to data quality, presentation of the experimental tasks, and the extent to which to data collected online generalises those collected in the laboratory (Segen et al., 2021). Generally, these issues can be addressed through thorough piloting experimental tasks due to be deployed online across a variety of hardware (Kraut et al., 2004; Sauter et al., 2020), and by including clear instructions (Reinecke & Gajos, 2015). Whilst there is evidence to suggest that there may be greater variability in data collected online (Hilbig, 2016; Huber & Gajos, 2020), there have been a number of successful online replications of experiments conducted in a laboratory (Armitage & Eerola, 2020; Bartneck et al., 2015; Dandurand et al., 2008; de Leeuw & Motz, 2016; Gould et al., 2015; Saunders et al., 2013; Segen et al., 2021).

Following on from lines of enquiry in Experiments 1 and 2, the presence of unreliable landmarks was manipulated within the Egocentric condition, to identify if participants can more accurately locate the target location when they are absent compared to when they are present. To achieve this, participants were assigned to two groups. One group of participants, Landmark Present, completed the version of the desktop task that was employed in Experiment 2, and encountered unreliable landmarks in the Egocentric condition. The other group, Landmark Absent, completed Control and Allocentric trials in an identical format to those encountered by the Landmark Present group, however, they completed the Egocentric condition with no landmarks present in the environment. Previous research using immersive VR platforms has indicated that the presence of unreliable landmarks can disrupt the use of path-based spatial representations (Zhao & Warren, 2015a,b), which form the basis for the Egocentric representations employed in this experiment. Similarly, Doeller et al. (2008) reported that boundary information can interfere with the use of egocentric cue based navigation in a navigation task completed on a desktop PC interface. If the presence of unreliable landmarks disrupted the use of egocentric information, then placement error in the Landmarks Present group would have been greater than placement error in the Landmark Absent group during Egocentric condition trials.

In this experiment, paths and viewpoint rotations were also recorded as additional dependent variables. These measures provided a more detailed insight as they quantify

behaviours related to the strategies that participants employed (Kallai et al., 2005; Schoenfeld et al., 2017). For example, the most effective strategy in the Egocentric condition would be to take a direct vector to the presumed starting position. This behaviour can then be compared between the two Egocentric groups, to identify the impact of the presence of unreliable landmarks, as they may induce maladaptive reorienting behaviours, which would be represented by less efficient paths when they are present. Additionally, one can predict that the Egocentric condition would include more efficient paths and viewer viewpoint rotations than the Allocentric condition. The reason for this is that a core behaviour in the Allocentric condition is reorientation. This would involve less efficient paths to the presumed target location and more viewpoint rotations as participants would be required to explore the environment to apprehend the current configuration of the landmarks.

The data recorded from the Landmarks Present group was expected to replicate the pattern of results observed in the Experiment 2's desktop PC task, with placement error being lowest in the Control condition, and no difference in placement error between the Allocentric and Egocentric conditions. The Landmarks Absent group was expected to show a similar pattern of results, with placement error being lowest in the Control condition and greatest in the Allocentric condition, however their placement error in the Egocentric condition was expected to be lower than that observed in the Landmarks Present group. Additionally, in the Egocentric condition, participants in the Landmarks Absent group were expected to take more direct routes during the Test stage, and make fewer viewpoint rotations than the Landmarks Present group. This would indicate maladaptive pathing behaviour from the Landmarks Present group when replacing the target in the Test stage.

2.3.1 Methodology

Design

This experiment comprised a 3x2 mixed design with a within subject factor of condition (three levels: Control, Allocentric, Egocentric) and a between subjects factor of landmark presence during the Egocentric condition trials (two levels: Landmarks Present, Landmarks Absent). In a single experimental session, participants completed the desktop PC version of the place learning task via a web browser based interface. The design of this experiment is presented visually in Figure 2.17. The task was otherwise identical to the

desktop PC version of the task developed for Experiment 2. The order of Allocentric and Egocentric conditions was counterbalanced as closely as possible.









Condition	Training Stage	Test Stage
Control trials		
Allocentric trials		
Egocentric trials (Landmarks Present Group)		
Egocentric trials (Landmarks Absent Group)		

Figure 2.17: This diagram shows the design of this experiment. The Control and Allocentric conditions are the same as in Experiments 1 and 2. The Egocentric condition differed based on which group each participant was assigned to. Participants in the Landmarks Present group saw unreliable landmarks during the Egocentric condition, whereas the participants in the Landmarks Absent group completed Egocentric trials with no visible landmarks present.

Participants

Adult participants were recruited for this experiment from either the University of Plymouth School of Psychology undergraduate participant pool in exchange for course credit ($N = 168$), or volunteered to participate via social media ($N = 104$). Due to attrition, 65 participants from the voluntary group did not complete the experiment leaving a final sample of 207 adults (female = 149, male = 58). Participants were randomly assigned to

Landmarks Present ($N = 95$) or Landmarks Absent ($N = 112$) groups. This number of participants is sufficient to detect medium effect sizes.

Apparatus and Materials

This experiment comprised a version of the desktop place learning task used in Experiment 2 that was exported from Unity as a WebGL application. The task was uploaded and hosted on the University of Plymouth JATOS server (Lange et al., 2015), and data was written to the JATOS server at the end of each trial. The only difference between the two tasks was the controls. In this experiment's version of the task, instead of using an Xbox controller, participants moved around the environment using the arrow keys on their keyboard, and interacted with the task using the space bar.

Procedure

At the start of the experiment, participants were presented with the following instructions:

During this experiment:

Please make sure that you are in a quiet room, free from distraction.

Please turn off your phone so that it does not distract you.

If you wear glasses or contact lenses when using a computer, please put them on now.

Finally, if you have not already done so, please click on the blue button in the bottom right hand corner of the browser window to make the task full screen.

After reading these instructions, participants then completed the 4 practice trials and 24 experimental trials. The instructions for these trials were identical to those used in the desktop task in Experiment 2, but with references to the controller changed to reference the keyboard controls. Additionally, in this experiment, paths were tracked across all experimental trials. The coordinates and y-axis rotation value of the participant's viewpoint within the Unity build were logged every 500 milliseconds during both training and test stages.

2.3.2 Analysis

As with preceding experiments the principal dependent variable was the placement error. Indices of path efficiency and viewpoint rotations were computed using the path data collected in this experiment. The path efficiency index comprised the Euclidean distance between the start and end of a participant's path divided by the cumulative distance travelled during the trial. Higher values would represent more direct paths whereas lower values would reflect more circuitous paths. The viewpoint rotation index was calculated by dividing the trial's cumulative total of angular rotational movements by its duration. Higher values from this measure are indicative of a larger number of viewpoint rotations within a trial, whereas lower values indicate fewer viewpoint rotations within a trial.

Placement error, latencies, the path efficiency index, and the viewpoint rotation index were all analysed using 2x3 mixed ANOVAs with a repeated measures factor of trial type (three levels: Control, Allocentric, Egocentric) and a between subjects factor of landmark presence during the Egocentric condition (two levels : Landmarks Present, Landmarks Absent). As in Experiment 2, the afex package for R (Singmann et al., 2016) corrected these measures for sphericity using the Greenhouse Geisser correction. Planned comparisons were conducted between each level of the condition factor for each platform, and between each group for each condition. P-values calculated for these comparisons were adjusted using a Bonferroni correction.

As a number of participants in this experiment did not complete the place learning task (see section 2.3.1), their data was excluded from the final analysis. Additionally, participants that took breaks of longer than a minute between trials, or between trial stages (e.g. between the Training and Test stages) were excluded from the final analyses.

2.3.3 Results

Placement responses, for every trial, are illustrated in Figure 2.18, and descriptive statistics for placement error, latencies, and the path efficiency and viewpoint rotation indices are presented in Figures 2.19, 2.21, 2.22, and 2.23 respectively. Trial by trial error rates are presented in Figure 2.20.

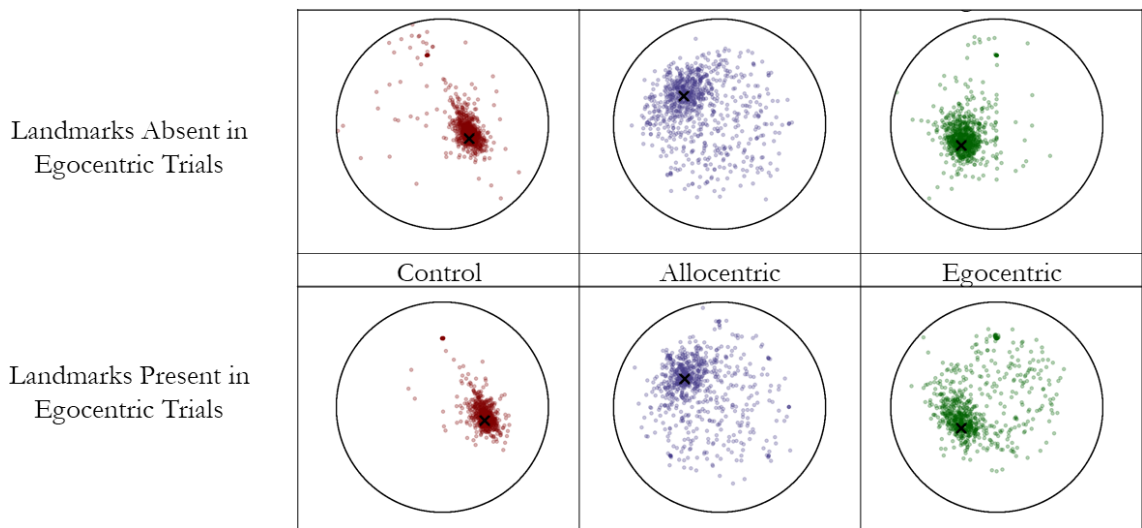


Figure 2.18: This plot shows each participant's placement within each condition. The correct location of the target in each condition is indicated by the black 'X'.

The placement error ANOVA revealed a main effect of trial type, $F_{(1.92, 394.34)} = 124.45$, $p < .001$, $\eta_p^2 = .38$, $BF10 = 1.22 \times 10^{35}$, and an interaction effect, $F_{(1.92, 394.34)} = 32.11$, $p < .001$, $\eta_p^2 = .135$, $BF10 = 6.07 \times 10^{10}$. There was also a main effect of landmark presence during Egocentric trials that indicated placement error was greater in the Landmarks Present group, $F_{(1, 205)} = 4.41$, $p = .037$, $\eta_p^2 = .02$, $BF10 = 2.14$, though the Bayes Factor suggests this evidence is inconclusive.

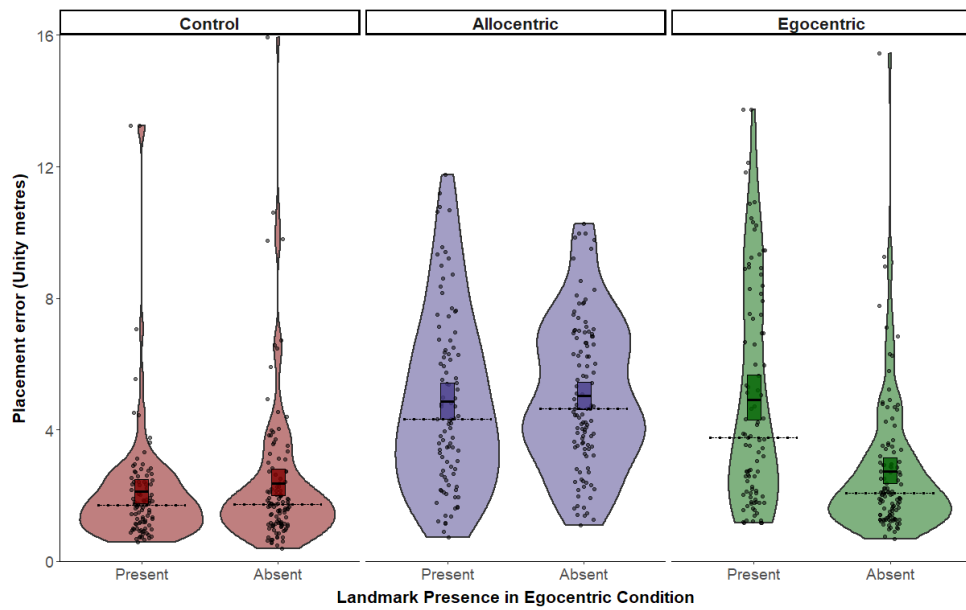


Figure 2.19: Placement error descriptive statistics for each group in Experiment 3. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

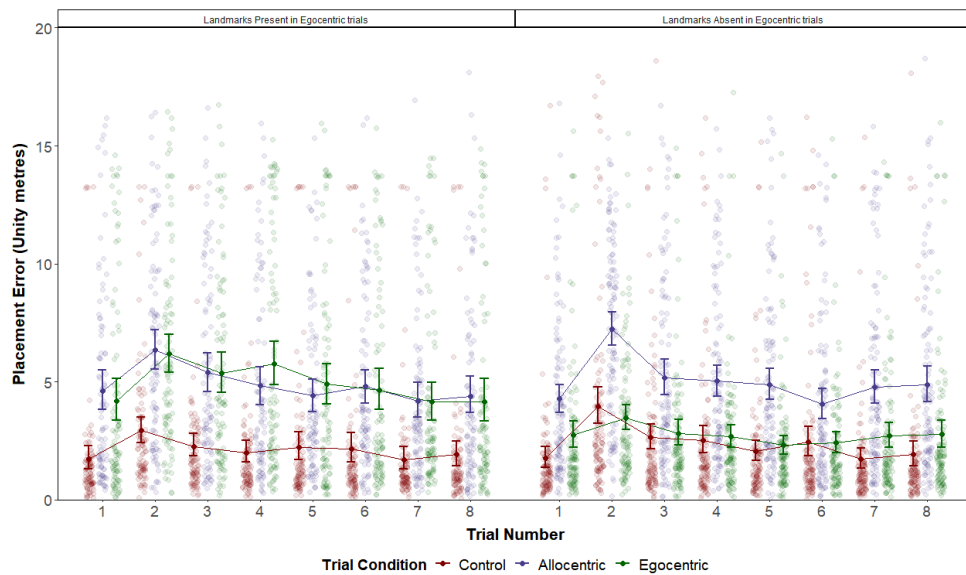


Figure 2.20: This plot shows the placement error for each trial in each condition. The error bars represent standard error are presented either side of the mean score for each trial within each condition. Each jittered point on the plot represents a participant's score for that trial.

Planned comparisons showed that in the Landmarks Present group, placement error was

lower in the Control condition than in the Allocentric condition, $t_{(94)} = 11.17, p < .001, BF10 = 8.7 \times 10^{15}$, and the Egocentric condition, $t_{(94)} = 9.37, p < .001, BF10 = 1.74 \times 10^{12}$. There was no difference between the desktop Allocentric and Egocentric conditions, $t_{(94)} = 0.13, p = 1, BF10 = 0.12$.

In the Landmarks Absent group, placement error was lower in the Control condition than in the Allocentric condition, $t_{(111)} = 12.16, p < .001, BF10 = 1.13 \times 10^{19}$, and placement error was lower in the Egocentric condition than in the Allocentric condition, $t_{(111)} = 11.59, p < .001, BF10 = 6.14 \times 10^{17}$. There was no significant difference between placement error in the Control and Egocentric conditions, $t_{(111)} = 2.24, p = .25, BF10 = 1.14$.

There was no difference in placement error between the Landmark Present and Landmark Absent group in the Control condition, $t_{(204.85)} = 0.88, p = 1, BF10 = 0.216$ and in the Allocentric condition, $t_{(183.54)} = 0.48, p = 1, BF10 = 0.17$. Placement error was lower for the Landmark Absent group than the Landmark Present group in the Egocentric condition, $t_{(152.3)} = 5.49, p < .001, BF10 = 2.6 \times 10^5$.

The latency ANOVA showed a main effect of trial type, $F_{(1.61, 329.09)} = 72.99, p < .001, \eta_p^2 = .263, BF10 = 2.24 \times 10^{35}$, and an interaction effect, $F_{(1.61, 329.09)} = 4.32, p = .021, \eta_p^2 = .021, BF10 = 1.82$. There was no main effect of landmark presence during Egocentric trials, $F_{(1, 205)} = 0.5, p = .482, \eta_p^2 = .002, BF10 = 0.195$.

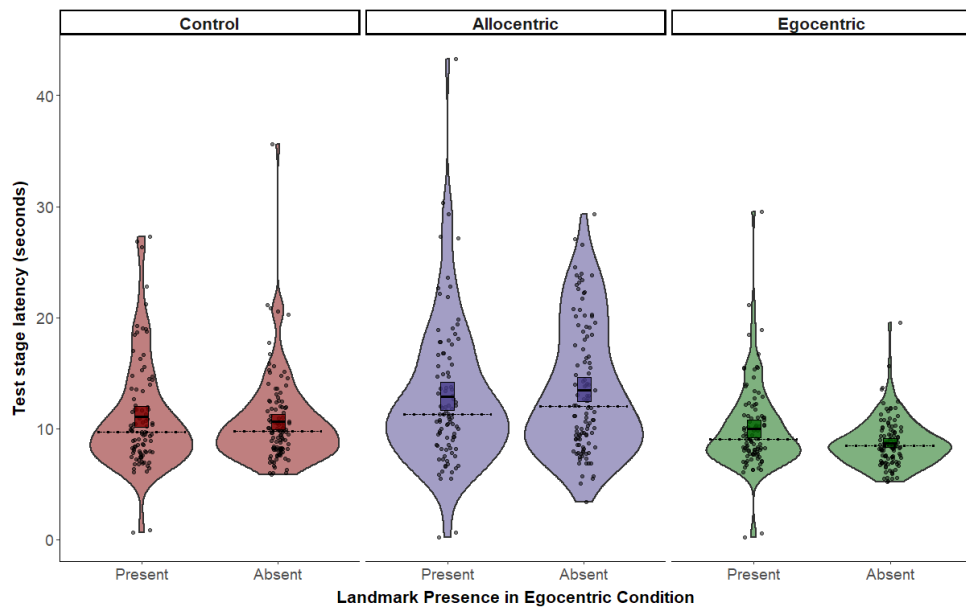


Figure 2.21: Test stage latency descriptive statistics for each group in Experiment 3. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

The planned comparisons on the latency data indicated that in the Landmarks Present group, latencies were lower in the Control condition than in the Allocentric condition, $t_{(94)} = 3.33, p = .011, BF10 = 18.84$. Latencies were lower in the Egocentric condition than both the Control condition, $t_{(94)} = 3.53, p = .006, BF10 = 33.51$, and Allocentric condition, $t_{(94)} = 5.23, p < .001, BF10 = 13584$.

In the Landmarks Absent group, latencies were lower in the Control condition than in the Allocentric condition, $t_{(111)} = 6.26, p < .001, BF10 = 1.4 \times 10^6$. Similar to the Landmark Present group, latencies were lower for the Landmark Absent group in the Egocentric condition compared to both the Control condition, $t_{(111)} = 5.7, p < .001, BF10 = 113986$, and the Allocentric condition, $t_{(111)} = 10.3, p < .001, BF10 = 7.599 \times 10^{14}$.

There was no difference in latencies between the Landmark Present and Landmark Absent group in the Control condition, $t_{(181.02)} = .67, p = 1, BF10 = 0.19$ and in the Allocentric condition, $t_{(189.64)} = 0.66, p = 1, BF10 = 0.187$. Latencies were lower for the Landmark Absent group than the Landmark Present group in the Egocentric condition, $t_{(142.13)} = 2.9, p = .04, BF10 = 10.6$.

The path efficiency index ANOVA indicated that there was a main effect of trial type, $F_{(1.50, 323.36)} = 363.68, p < .001, \eta_p^2 = .63, BF10 = 1.17 \times 10^{100}$, and an interaction effect, $F_{(1.50, 323.36)} = 8.59, p < .001, \eta_p^2 = .038, BF10 = 104$. There was a significant main effect of landmark presence during Egocentric trials, suggesting that paths taken by the Landmarks Present group were less efficient than those taken by the Landmarks Absent group, $F_{(1, 215)} = 3.92, p = .049, \eta_p^2 = .018, BF10 = 0.26$, however, the Bayes Factor suggests that the evidence indicates there is no difference between the groups.

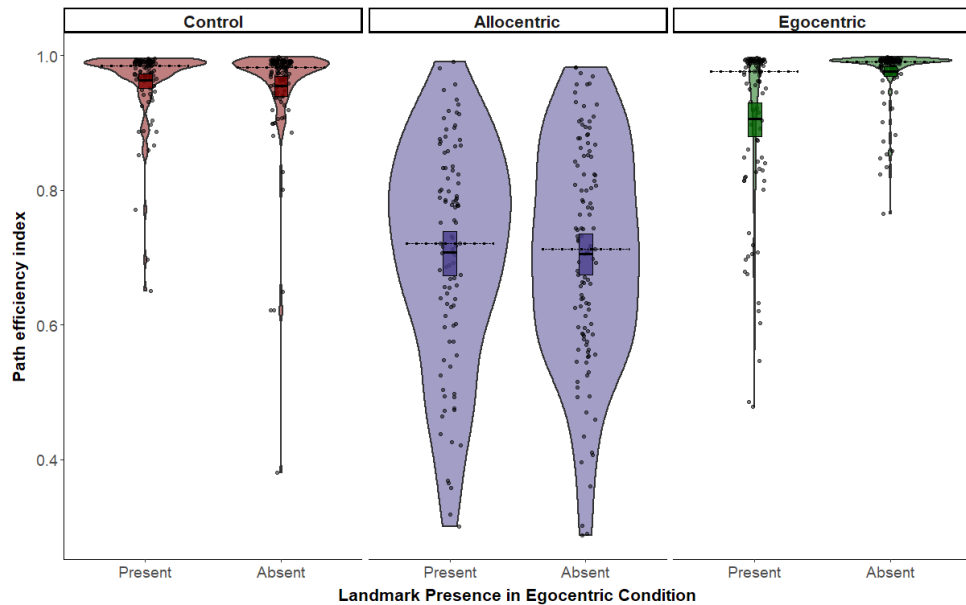


Figure 2.22: Path efficiency descriptive statistics for each group in Experiment 3. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

The planned comparisons conducted on the path efficiency index data showed that in the Landmarks Present group, participants' paths were more efficient in the Control condition than in both the Allocentric condition, $t_{(98)} = 2.22, p < .001, BF10 = 1.61 \times 10^{24}$, and the Egocentric condition, $t_{(98)} = 4.27, p < .001, BF10 = 384$. Path efficiency was greater in the Egocentric condition than in the Allocentric condition, $t_{(98)} = 10.7, p < .001, BF10 = 1.31 \times 10^{15}$.

In the Landmarks Absent group, participants' paths were more efficient in the Control condition than in the Allocentric condition, $t_{(117)} = 15.53, p < .001, BF10 = 9.77 \times 10^{38}$. Path efficiency was greater in the Egocentric condition than in both the Control condition, $t_{(117)}$

= 3.7, $p < .001$, $BF10 = 50$, and Allocentric condition, $t_{(117)} = 17.5$, $p < .001$, $BF10 = 1.35 \times 10^{31}$.

There was no difference in path efficiency between the Landmark Present and Landmark Absent group in the Control condition, $t_{(206.64)} = 0.57$, $p = 1$, $BF10 = 0.2$, and in the Allocentric condition, $t_{(208.7)} = 0.13$, $p = 1$, $BF10 = 0.15$. Path efficiency was greater for the Landmark Absent group than the Landmark Present group in the Egocentric condition, $t_{(5.3)} = 5.75$, $p < .001$, $BF10 = 2.98 \times 10^6$.

The ANOVA conducted on the viewpoint rotation index revealed a main effect of trial type, $F_{(1.65, 354.50)} = 446.88$, $p < .001$, $\eta_p^2 = .675$, $BF10 = 2.14 \times 10^{116}$, and an interaction effect, $F_{1.65, 354.50} = 18.66$, $p < .001$, $\eta_p^2 = .08$, $BF10 = 1.76 \times 10^7$. There was no between groups effect of landmark presence during Egocentric trials according to Bayes Factor evidence, $F_{(1, 215)} = 5.43$, $p = .021$, $\eta_p^2 = .025$, $BF10 = 0.29$.

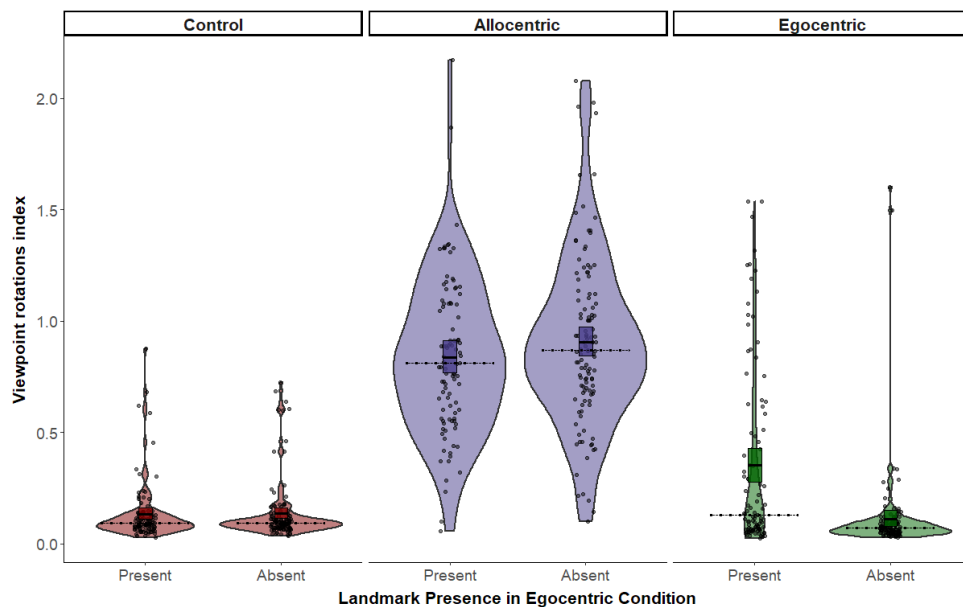


Figure 2.23: Viewpoint rotation descriptive statistics for each group in Experiment 3. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

The viewpoint rotation index planned comparisons showed that in the Landmarks Present group, participants made more view rotations in the Allocentric condition than in both the Control condition, $t_{(98)} = 19.87$, $p < .001$, $BF10 = 6.83 \times 10^{32}$, and the Egocentric condition, $t_{(98)} = 9.33$, $p < .001$, $BF10 = 1.95 \times 10^{12}$. Participants in the Landmarks Present group made

more viewpoint rotations in the Egocentric condition than in the Control condition, $t_{(98)} = 5.04, p = 1, BF10 = 6887$.

In the Landmarks Absent group, participants also made more view rotations in the Allocentric condition than in both the Control condition, $t_{(117)} = 20.56, p < .001, BF10 = 1.92 \times 10^{37}$, and the Egocentric condition, $t_{(117)} = 20.39, p < .001, BF10 = 8.89 \times 10^{36}$. Participants in the Landmarks Absent group made a similar number of viewpoint rotations in the Egocentric condition compared to the Control condition, $t_{(117)} = 1.75, p < .001, BF10 = 0.44$.

There was no difference in the number of viewpoint rotations between the Landmark Present and Landmark Absent group in both the Control condition, $t_{(208.67)} = 0.15, p = 1, BF10 = 0.16$, and the Allocentric condition, $t_{(213.19)} = 2.73, p = 1, BF10 = 0.38$. Participants in the Landmarks Present group made more viewpoint rotations than participants in the Landmarks Absent group during the Egocentric condition trials, $t_{(135.17)} = 5.33, p = 0.039, BF10 = 203594$.

2.3.4 Discussion

In this experiment participants completed an online version of the desktop PC place learning task using a browser based interface. Participants were assigned to one of two groups that completed Egocentric condition trials with or without unreliable landmarks present. There was no difference between groups' placement error in the Control and Allocentric conditions, with placement error being greater in the Allocentric condition than in the Control condition, replicating findings from Experiment 2's desktop PC version of the place learning task. In the Egocentric condition, however, placement error in the Landmark Present group was greater than placement error in the Landmark Absent group, indicating that the presence of unreliable landmarks disrupts the ability to reliably learn and recall a location using egocentric information in isolation. The presence of unreliable landmarks in Egocentric condition trials also influenced path efficiency and the number of viewpoint changes within a trial. Participants in the Landmarks Present group took less direct paths to their eventual placement location and made more viewpoint rotations during Egocentric condition trials than participants in the Landmarks Absent group. The path efficiency and viewpoint rotation indices also differed across the conditions within each group. Participants took more direct paths to their placement location and made fewer viewpoint rotations than they did in the Allocentric condition. These additional

measures provide a more detailed insight into behaviour, specifying the characteristics of their navigation within each condition.

The path data supplements placement error and latency as an additional metric that provides insight into behaviour across all three conditions and begins to present explanations for the differences across conditions in placement error. In the Control condition both groups took efficient paths, and made relatively few viewpoint rotations, compared to the Allocentric condition. This suggests that participants used the landmarks present in their immediate point of view to support their target placements in the Test stage. As the landmarks were consistent in their locations across Training and Test stages, this would be a reliable strategy and is indicative of a beacon-cue strategy, as the immediately visible landmarks were sufficient to direct the responses of most participants. The path data in the Control condition contrasted with the data collected from the Allocentric condition. In the Allocentric condition, participants made the greatest number of viewpoint rotations, and largely took inefficient paths, relative to the Control and Egocentric conditions. This is likely indicative of participants observing the difference in landmarks locations between Training and Test stages, and reorienting to the landmarks' new Test stage position. This reorientation would by its nature decrease how direct a participant's path would be, and would also require the participant to scan around the environment to identify where the landmarks are located during the Test stage.

Interestingly, there is a clear difference between the two groups in the Egocentric condition for the path efficiency and viewpoint rotation measures. Participants in the Landmarks Present group took less direct paths to where they thought the target was located, and rotated their viewpoint more during the Egocentric Test stage, compared to the Landmarks Absent group. These behaviours may indicate that participants were reorienting to the unreliable landmarks, and as a result, would then face difficulties in recapitulating the path between the starting position and the target in the Training stage. The use of these metrics to clearly specify what participants in each group were doing during Egocentric trials provides a richer insight into behaviour than exploring placement error and latencies alone.

Interestingly, the distributions of both the path efficiency measure and viewpoint rotation index are extremely wide for all three conditions. This indicates great variability across participants in both behaviours, and may reflect individual participants employing dif-

ferent strategies, a phenomenon that has been extensively reported in the rodent MWM and human vMWM literature (Garthe et al., 2009; Graziano et al., 2003; Kallai et al., 2005; Schoenfeld et al., 2010b, 2017; Vouros et al., 2018; Wolfer et al., 1998; Wolfer & Lipp, 2000; Wolfer et al., 2001). Whilst the task demands in the canonical vMWM are sufficiently different from this place learning task that some strategies would be ineffectual (e.g. enfilading through a region of space until one encounters the hidden platform) there are some strategies that would transfer across tasks. One strategy reported by Kallai et al. (2005) is *Visual Scan*, which involves reorienting to the landmarks' configuration from a static position at the start of a trial and then taking a direct vector to the hidden platform. This may be reflected in this experiment by the participants that tended to take more direct paths during the Allocentric trials. Alternatively, participants may instead employ a *Thigmotaxis* strategy (Kallai et al., 2005), in which they move around the inner edge of the arena till they reach the proximity of the goal location before then taking a direct vector to it, from a point on the arena edge. This would be captured by participants taking extremely indirect paths and making a greater number of viewpoint rotations. A more detailed analysis of the path data would be beneficial and provide greater specificity when characterising behaviour.

The results from this experiment show that the presence of unreliable landmarks during the Egocentric condition has a deleterious effect on placement error, supporting findings from both immersive VR (Zhao & Warren, 2015a,b) and desktop PC task platforms (Doeller et al., 2008). The path and viewpoint rotation data suggest that participants take more inefficient paths and look around the environment more when unreliable landmarks are present, compared to when they are absent. This behaviour may reflect maladaptive reorienting to unreliable landmarks. Whilst reorientation is essential to success during the Allocentric condition, it is much less useful in the Egocentric condition as the spatial relationship between the landmarks and the target location is inconsistent. This may provide an explanation as to why the two groups differ in placement error in the Egocentric condition, as participants in the Landmarks Present group may then be reorienting at the start of each trial. In contrast, participants in the Landmarks Absent group would not encounter landmarks in the Egocentric condition and would consequently have no need to look around the environment, and would only need to focus on taking a direct route to where they thought the target was located. These data suggest that the presence of unreliable landmarks in Experiment 1 and 2 may be the reason for the greater placement

error in each experiment's respective Egocentric conditions. It is, however, important to note that in Merhav & Wolbers's (2019) experiment participants completed an equivalent Egocentric condition without the presence of reliable landmarks, and the data indicated that participants made greater locational errors in this condition relative to equivalent Control and Allocentric conditions. It will therefore be important to identify the impact of landmarks when using Egocentric information with an immersive VR version of this task. This experiment also shows clear benefits for collecting data online using experimental tasks designed to operate within web browser interfaces. Whilst there was greater attrition amongst participants that received no direct reward for participation, the entire sample still replicated the findings from Experiment 2's desktop task in the Control and Allocentric conditions, indicating that online data collection can be used to successfully replicate data collected in the laboratory (Armitage & Eerola, 2020; Bartneck et al., 2015; Dandurand et al., 2008; de Leeuw & Motz, 2016; Gould et al., 2015; Saunders et al., 2013; Segen et al., 2021), even with participants that completed the experiment for no direct compensation (Huber & Gajos, 2020; Reinecke & Gajos, 2015). This suggests that desktop tasks that explore navigational behaviour could benefit from online data collection techniques for rapid and low cost acquisition of data.

In sum, this experiment has demonstrated a clear negative impact of unreliable landmarks on performance during Egocentric condition trials in a desktop PC version of the place learning task. Whilst this needs to be replicated on an immersive VR platform, it does begin to explain the pattern of data observed in Experiment 2's desktop PC task. Furthermore, the detail provided by performance measures that incorporate elements of Test stage paths, begins to specify more clearly why placement error differs between conditions, and between the groups in the Egocentric condition. This experiment also serves as evidence for the benefits of collecting data online with tasks that measure large scale spatial abilities in 3D spaces. This will facilitate the rapid and low cost acquisition of data for future experiments.

2.4 Experiment 4

Experiment 3 demonstrated the impact that the presence of unreliable landmarks has on the ability to accurately employ egocentric information in isolation on a desktop platform. Experiment 4 is designed to replicate Experiment 3, to ensure that findings from the online

version of the place learning task can be recapitulated.

In the recent past, the reliability of results reported in the Psychological sciences has been raised as an important issue (Pashler & Wagenmakers, 2012). It is therefore important to ensure that results can be replicated to ensure that theoretical inferences are drawn from robust evidence. This is important particularly when collecting data online due to concerns regarding its generalisability (Segen et al., 2021) and the innate lack of environmental control associated with online data collection (Kraut et al., 2004; Sauter et al., 2020). Experiment 4 employed the Prolific (Palan & Schitter, 2018) participant system to recruit participants to complete the online version of the desktop PC place learning task reported in Experiment 3. Participants in this experiment all received monetary compensation for their time, unlike participants in Experiment 3 (who received either no recompense, or course credit). Previous experiments have highlighted that uncompensated participants (e.g. a proportion of the sample from Experiment 3) may not perform any differently from those that do receive compensation (Huber & Gajos, 2020; Reinecke & Gajos, 2015), however, this may explain the high level of attrition in Experiment 3. This experiment will then provide further investigation as to the reliability of different samples recruited for online experiments.

2.4.1 Methodology

Design

This experiment used the same 2 factor mixed design employed in Experiment 3, with a within subject factor of condition (three levels: Control, Allocentric, Egocentric) and a between subjects factor of landmark presence during the Egocentric condition trials (two levels: Landmarks Present, Landmarks Absent). As in previous experiments, the order of Allocentric and Egocentric conditions was counterbalanced across participants.

Participants

Adult participants were recruited from Prolific's participant pool in return for monetary recompense ($N = 71$, male = 41, female = 28). The ages of participants ranged from 18 to 45 ($M = 26.6$, $SD = 6.3$). Participants were randomly assigned to Landmarks Present ($N = 35$) or Landmarks Absent ($N = 36$) groups. This number of participants is sufficient to

detect large effect sizes.

Materials

The experimental task employed in this experiment was identical to that used in Experiment 3, except it was hosted as a custom experiment build on the Gorilla online platform (Anwyl-Irvine et al., 2020). Participants were advised to only run the experiment in Google Chrome, Mozilla Firefox, or Safari web browsers, as the experiment had not been tested in other web browsers. Additionally, to ensure a stable frame rate for the experiment, participants were advised to only complete the experiment if they were using a computer that was no older than four years.

Procedure

The procedure for this experiment, including the instruction text, was identical to that used in Experiment 3, except that participants were recruited for the experiment through the Prolific participation system (Palan & Schitter, 2018).

2.4.2 Analysis

This experiment employed the same analyses as Experiment 3 for the same dependent variables, e.g. a 2x3 mixed ANOVA with a repeated measures factor of trial type (three levels: Control, Allocentric, Egocentric) and a between subjects factor of landmark presence during the Egocentric condition (two levels : Landmarks Present, Landmarks Absent). Planned comparisons were similarly conducted between each level of the condition factor for each platform, and between each group for each condition. P-values calculated for these comparisons were adjusted using a Bonferroni correction.

2.4.3 Results

Placement responses, for every trial, are illustrated in Figure 2.24, and descriptive statistics for placement error, latencies, and the path efficiency and viewpoint rotation indices are presented in Figures 2.25, 2.27, 2.28, and 2.24 respectively. Trial by trial error rates are presented in Figure 2.26.

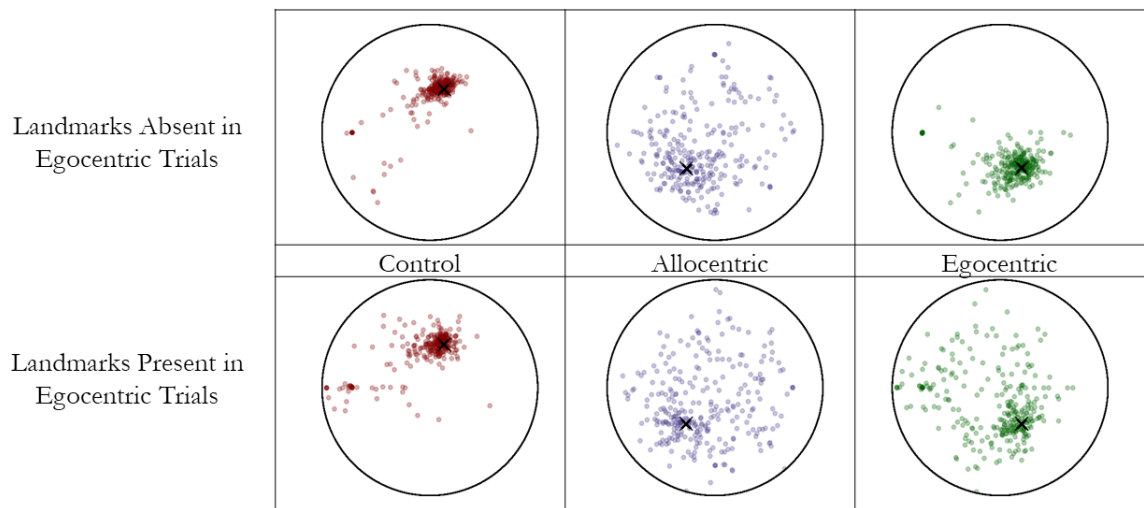


Figure 2.24: This plot shows each participant's placement within each condition. The correct location of the target in each condition is indicated by the black 'X'.

The placement error ANOVA revealed a main effect of trial type, $F_{(1.95, 134.71)} = 48.18, p < .001, \eta_p^2 = .41, BF10 = 2.66 \times 10^{12}$, a main effect of landmark presence during Egocentric trials, $F_{(1, 69)} = 6.95, p = .01, \eta_p^2 = .091, BF10 = 4.42$, and an interaction effect, $F_{(1.95, 134.71)} = 8.75, p < .001, \eta_p^2 = .112, BF10 = 90.3$.

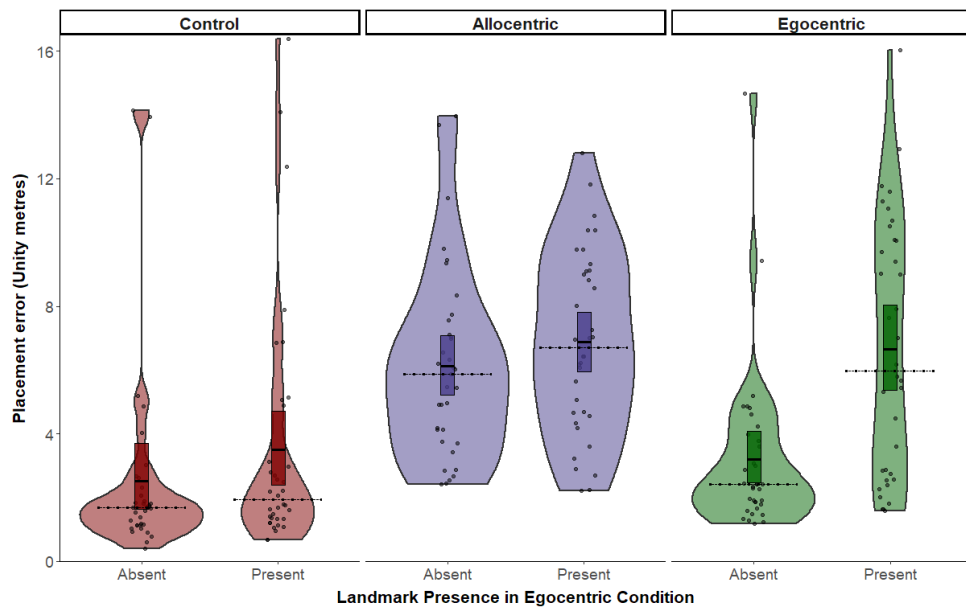


Figure 2.25: Placement error descriptive statistics for each group in Experiment 4. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

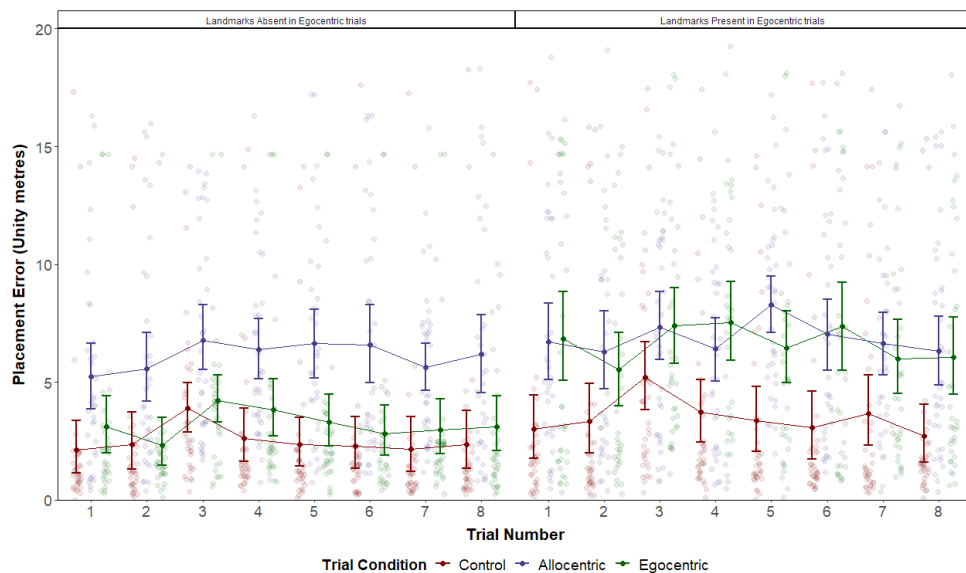


Figure 2.26: This plot shows the placement error for each trial in each condition for the two groups. The error bars represent standard error are presented either side of the mean score for each trial within each condition. Each jittered point on the plot represents a participant's score for that trial.

The planned comparisons for placement error revealed that in the Landmarks Present

group, placement error was lower in the Control condition than in the Allocentric condition, $t_{(35)} = 6.08, p < .001, BF10 = 27587$, and the Egocentric condition, $t_{(35)} = 5.21, p < .001, BF10 = 2351$. There was no difference between the desktop Allocentric and Egocentric conditions, $t_{(35)} = 0.37, p = 1, BF10 = 0.19$.

In the Landmarks Absent group, placement error was lower in the Control condition than in the Allocentric condition, $t_{(34)} = 8.6, p < .001, BF10 = 2.42 \times 10^7$. There was no conclusive evidence of a difference between placement error in the Control and Egocentric conditions, $t_{(34)} = 2.45, p = .176, BF10 = 2.43$. Placement error was lower in the Egocentric condition than in the Allocentric condition, $t_{(34)} = 6.82, p < .001, BF10 = 191230$.

There was no evidence to support differences in placement error between the Landmark Present and Landmark Absent group in the Control condition, $t_{(66.84)} = 1.21, p = 1, BF10 = 0.45$ and in the Allocentric condition, $t_{(68.56)} = 1.09, p = 1, BF10 = 0.41$. Placement error was lower for the Landmark Absent group than the Landmark Present group in the Egocentric condition, $t_{(60.2)} = 4.31, p < .001, BF10 = 362$.

The latency ANOVA showed a significant main effect of trial type, albeit with inconclusive Bayes Factor support, $F_{(1.81, 124.7)} = 4.71, p = .013, \eta_p^2 = .064, BF10 = 2.1$, and a significant interaction effect, $F_{(1.81, 124.7)} = 4.94, p = .011, \eta_p^2 = .067, BF10 = 5.15$. There was no main effect of landmark presence during Egocentric trials, $F_{(1, 69)} = 0.52, p = .474, \eta_p^2 = .007, BF10 = 0.37$.

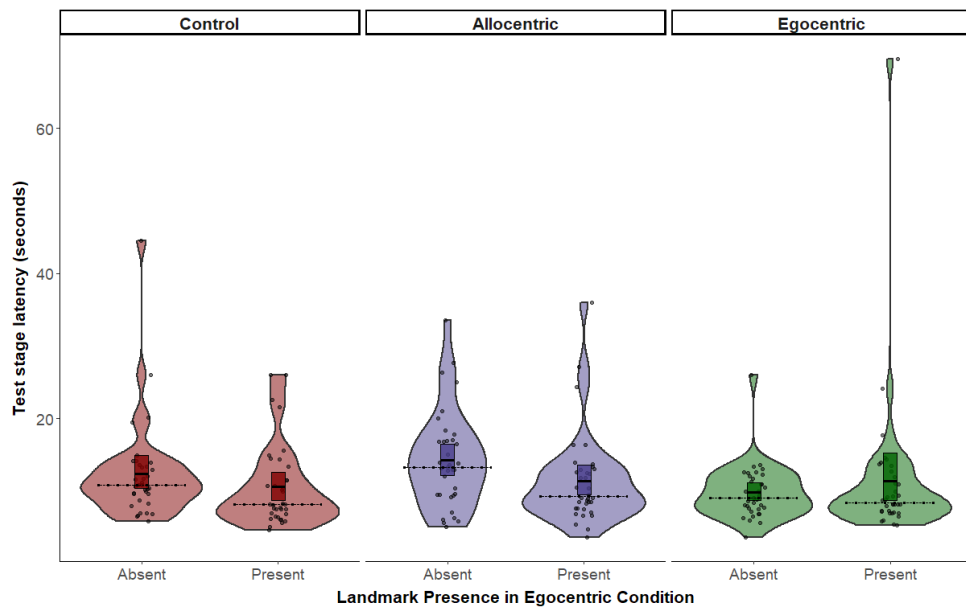


Figure 2.27: Test stage latency descriptive statistics for each group in Experiment 4. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

The latency planned comparisons indicated that there was no significant difference between latencies in the Control and Allocentric conditions, $t_{(35)} = 1.73, p = .83, BF10 = 0.69$. Latencies did not differ between the Egocentric condition and both the Control condition, $t_{(35)} = 0.64, p = 1, BF10 = 0.22$, and the Allocentric condition, $t_{(35)} = 0.02, p = 1, BF10 = 0.18$. In the Landmarks Absent group, there was no significant difference between latencies were lower in the Control and Allocentric conditions, $t_{(34)} = 1.53, p = 1, BF10 = 0.52$, or the Control and Egocentric conditions, $t_{(34)} = 2.34, p = 0.23, BF10 = 1.97$. In contrast to the Landmarks Present group, latencies in the Landmarks Absent group were lower in the Egocentric condition than in the Allocentric condition, $t_{(34)} = 5.23, p < .001, BF10 = 2353$.

There were no conclusive differences in latencies between the Landmark Present and Landmark Absent group in the Control condition, $t_{(65.54)} = 1.2, p = 1, BF10 = 0.45$ and in the Allocentric condition, $t_{(68.68)} = 1.86, p = 0.61, BF10 = 1.06$. There was no difference in latencies between the two groups in the Egocentric condition, $t_{(43.9)} = 0.85, p = 1, BF10 = 0.33$.

The ANOVA conducted on the path efficiency index indicated that there was a main effect

of trial type, $F_{(1.74, 116.46)} = 67.53, p < .001, \eta_p^2 = .502, BF10 = 2.33 \times 10^{17}$, and an interaction effect, $F_{(1.74, 116.46)} = 11.17, p < .001, \eta_p^2 = .143, BF10 = 909$. There was no between subjects effect of landmark presence during Egocentric trials, $F_{(1, 67)} = 0.77, p = .011, \eta_p^2 = .011, BF10 = 0.23$.

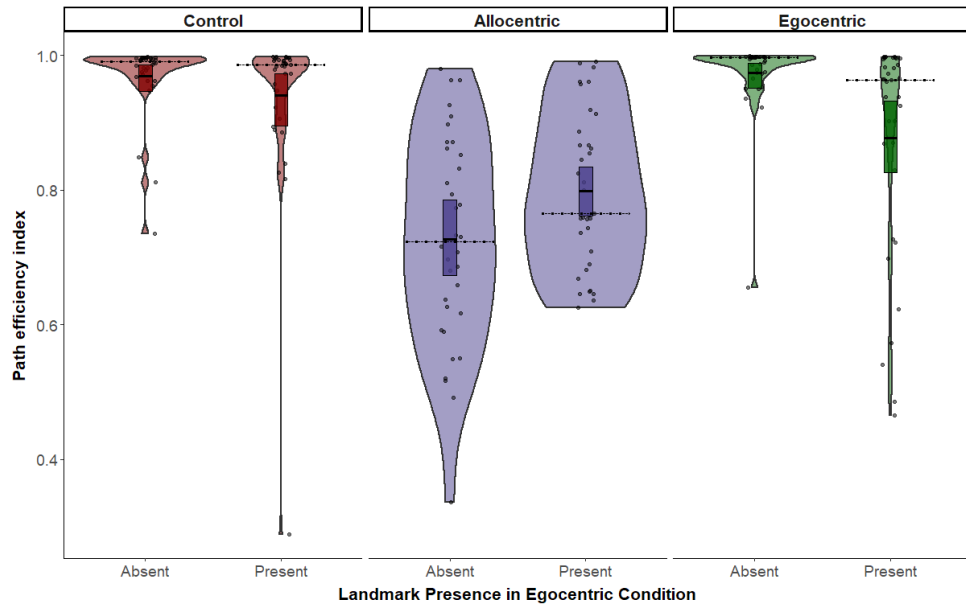


Figure 2.28: Path efficiency descriptive statistics for each group in Experiment 4. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

The planned comparisons conducted on the path efficiency index data revealed that in the Landmarks Present group, participants' paths were more efficient in the Control condition than in the Allocentric condition, $t_{(34)} = 5.76, p < .001, BF10 = 10218$. There was inconclusive evidence to support a difference between path efficiency in the Control and Egocentric conditions for the Landmarks Present group, $t_{(34)} = 2.48, p = 0.164, BF10 = 2.57$. Path efficiency was greater in the Egocentric condition than in the Allocentric condition, $t_{(34)} = 2.72, p = .001, BF10 = 4.17$.

In the Landmarks Absent group, participants' paths were more efficient in the Control condition than in the Allocentric condition, $t_{(33)} = 8.42, p < .001, BF10 = 1.13 \times 10^7$. Path efficiency did not differ between the Egocentric condition and the Control condition, $t_{(33)} = 0.503, p = 1, BF10 = 0.21$. Paths in the Egocentric condition were more efficient than those in the Allocentric condition, $t_{(33)} = 9.11, p < .001, BF10 = 6.52 \times 10^7$.

There was no clear evidence of differences in path efficiency between the Landmark Present and Landmark Absent group in the Control condition, $t_{(47.94)} = 1.2$, $p = 1$, $BF10 = 0.49$, or in the Allocentric condition, $t_{(60.54)} = 2.13$, $p = 1$, $BF10 = 1.71$. Path efficiency was greater for the Landmark Absent group than the Landmark Present group in the Egocentric condition, $t_{(43.22)} = 3.29$, $p = .018$, $BF10 = 18.75$.

The viewpoint rotation index ANOVA showed that there was a main effect of trial type, $F_{(1.72, 115.25)} = 69.68$, $p < .001$, $\eta_p^2 = .51$, $BF10 = 6.85 \times 10^{15}$. There was a significant main effect of group, $F_{(1, 67)} = 8.46$, $p = .005$, $\eta_p^2 = .112$, $BF10 = 0.92$, though the Bayes Factor for the group effect suggests the evidence is inconclusive. There was also inconclusive evidence of an interaction between the two independent variables, $F_{(1.72, 115.25)} = 2.97$, $p = .063$, $\eta_p^2 = .0342$, $BF10 = 0.68$.

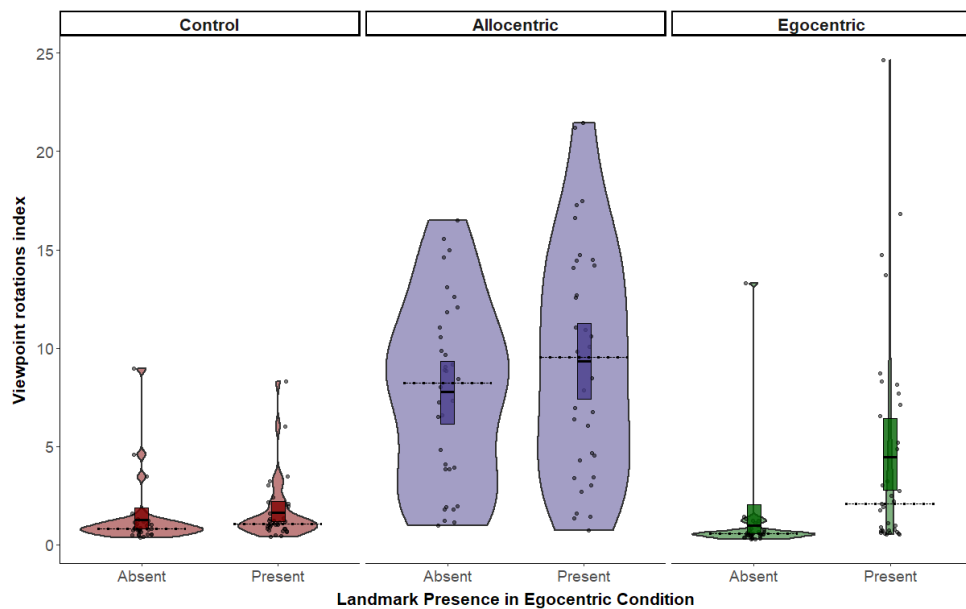


Figure 2.29: Viewpoint rotation descriptive statistics for each group in Experiment 4. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

Planned comparisons conducted on the viewpoint rotation data indicated that in the Landmarks Present group, participants made more view rotations in the Allocentric condition than in both the Control condition, $t_{(34)} = 7.36$, $p < .001$, $BF10 = 855305$, and the Egocentric condition, $t_{(34)} = 3.97$, $p < .001$, $BF10 = 79.8$. Participants in the Landmarks Present group also made more viewpoint rotations in the Egocentric condition compared

to the Control condition, $t_{(34)} = 2.99$, $p = 0.046$, $BF10 = 7.67$.

In the Landmarks Absent group, participants also made more view rotations in the Allocentric condition than in both the Control condition, $t_{(33)} = 8.41$, $p < .001$, $BF10 = 1.12 \times 10^7$, and the Egocentric condition, $t_{(33)} = 8.39$, $p < .001$, $BF10 = 1.06 \times 10^7$. There was no difference in viewpoint rotations between the Control and Egocentric conditions for participants in the Landmarks Absent group, $t_{(33)} = 0.75$, $p = 1$, $BF10 = 0.24$.

There was no significant difference in the number of viewpoint rotations between the Landmark Present and Landmark Absent group in the Control condition, $t_{(66.97)} = 0.98$, $p = 1$, $BF10 = 0.37$, and in the Allocentric condition, $t_{(64.4)} = 1.25$, $p = 1$, $BF10 = 0.48$. There was, however, evidence to suggest that the Landmark Present group made a greater number of viewpoint rotations than the Landmark Present group in the Egocentric condition, $t_{(44.46)} = 3.41$, $p = .013$, $BF10 = 25.73$.

2.4.4 Discussion

Experiment 4 replicated the design of Experiment 3 by using the same online version of the desktop place learning task with participants assigned to groups that completed the Egocentric condition with or without landmarks. The results indicated that Experiment 4 successfully replicated Experiment 3 as there was a clear differences in behaviour between the Landmarks Present and Landmarks Absent groups in the Egocentric condition, measured by placement error, path efficiency, and the number of viewpoint rotations. These measures indicated that placement accuracy was worse, their paths less efficient, and they made more viewpoint rotations when unreliable landmarks were present in the Egocentric condition.

Experiments 3 and 4 indicate that placement accuracy is reliably disrupted by the presence of unreliable cues. In both experiments, participants were static, as the tasks were completed on a desktop PC interface. It is therefore important to identify whether motility attenuates the effect of the unreliable landmark disruption in the Egocentric condition, as the egocentric cues are primarily based on path integration processes, and as a consequence may benefit from the input of idiothetic self-motion information.

2.5 Experiment 5

Experiment 5 translates the design of Experiments 3 and 4 to the immersive VR system employed in Experiments 1 and 2. This experiment will further detail the extent to which the presence of unreliable landmarks disrupts performance in the Egocentric condition, and how this interacts with internal-self motion cues accrued by motile participants. As in Experiments 3 and 4, the study design was mixed, featuring the same between subjects manipulation of unreliable landmark presence in the Egocentric condition. This should address the impact of unreliable landmarks during the acquisition and recall of egocentric spatial information when participants are fully motile. Similar to Experiments 3 and 4, if the presence of unreliable landmarks disrupted placement accuracy in the Egocentric condition, then placement error should be lower in the Landmarks Absent group than the Landmarks Present group for Egocentric trials.

Experiment 5 also presented a replication of the immersive VR Allocentric and Egocentric conditions previously used in Experiment 2. Results from the immersive VR place learning task employed in Experiment 2 indicated that placement error was superior in the Allocentric condition compared to the Egocentric condition. Whilst this is consistent with results reported by Merhav & Wolbers (2019), compelling evidence from other navigation experiments suggests that participants may struggle more when using Allocentric information in isolation compared to the use of Egocentric information in isolation (Ferguson et al., 2019; Negen et al., 2020; Wolbers & Wiener, 2014). Replicating Experiment 2's pattern of results in the immersive VR task's Allocentric condition will provide further evidence to suggest that recall of a target location using allocentric information may be more reliable when participants have access to self-motion cues.

2.5.1 Methodology

Design

The design of this experiment matched the design employed in Experiments 3 and 4, i.e. it was mixed, with a within subject factor of condition (three levels: Control, Allocentric, Egocentric) and a between subjects factor of landmark presence during egocentric trials (two levels: Landmarks Present, Landmarks Absent).

Participants

Healthy adult participants were recruited from the University of Plymouth ($N = 48$: 34 female, 14 male), and were provided with course credit in return for participation. Their ages ranged between 18 and 36 years ($M = 21$, $SD = 2.6$), and each participant was physically able to traverse the laboratory space unaided. No participants demonstrated or reported any side effects (e.g. simulator sickness) from interacting with the immersive VR system. Participants were randomly assigned to Landmarks Present ($N = 24$) or Landmarks Absent ($N = 24$) groups. This number of participants is sufficient to detect small effect sizes.

Apparatus and Materials

The apparatus and materials used in this experiment were almost identical to those used for the immersive VR task in Experiment 2. The only difference was that two versions of the experimental task were designed, one in which unreliable landmarks were present in the Egocentric condition, and a version in which landmarks were not visible during the Egocentric condition. The experimental task recorded path data at increments of 500ms within every trial.

Procedure

The group to which participants were assigned dictated the version of the immersive VR place learning task that they completed during the experiment, i.e. those in the Landmarks Present group completed Egocentric trials with the unreliable landmarks visible, and those in the Landmarks Absent group completed Egocentric trials with the unreliable landmarks removed. This experimental task's procedural details (including the provided instructions) were otherwise identical to those employed in the immersive VR version of the task in Experiment 2.

2.5.2 Analysis

Analyses for this experiment were identical to those employed in Experiment 4. The only differences were in the objects that were tracked for path data. Viewpoint rotation was recorded from the headset to capture a participant's rotational head movements. The X

and Z path coordinates were recorded from the tracker that participants wore around their belt.

2.5.3 Results

Placement responses, for every trial, are illustrated in Figure 2.30, and descriptive statistics for placement error, latencies, and the path efficiency and viewpoint rotation indices are presented in Figures 2.31, 2.33, 2.34, and 2.30 respectively. Trial by trial error rates are presented in Figure 2.32.

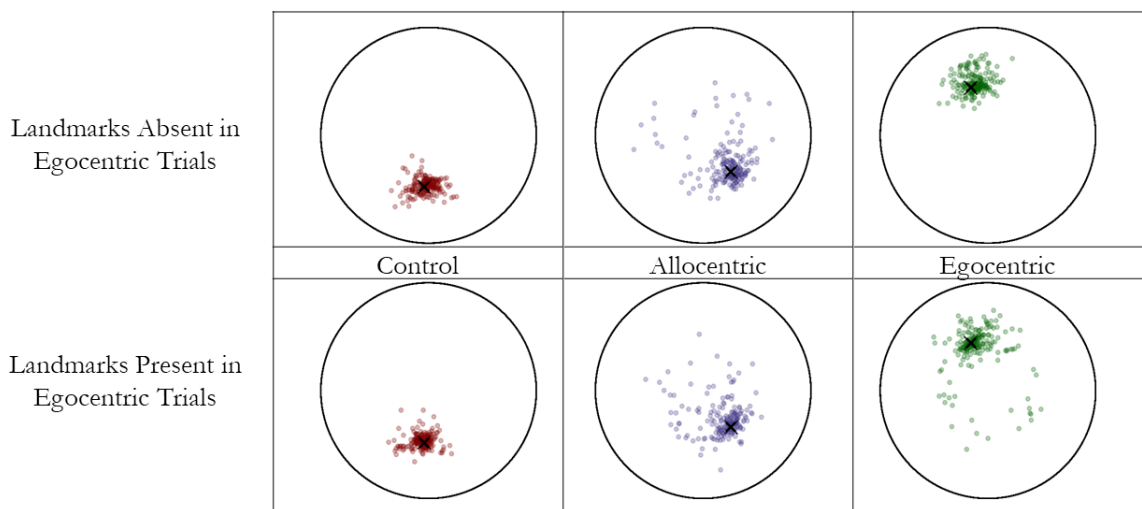


Figure 2.30: This plot shows each participant's placement within each condition for the two groups. The correct location of the target in each condition is indicated by the black 'X'.

A mixed ANOVA conducted on placement data revealed a main effect of trial type, $F_{(1,20, 55.10)} = 12.81, p < .001, \eta_p^2 = .22, BF10 = 3843$. There was no between subjects main effect of landmark presence during Egocentric trials, $F_{(1, 46)} = 0.41, p = .527, \eta_p^2 = .009, BF10 = 0.26$, and no interaction, $F_{(1,20, 55.10)} = 1.01, p = .333, \eta_p^2 = .022, BF10 = 0.26$.

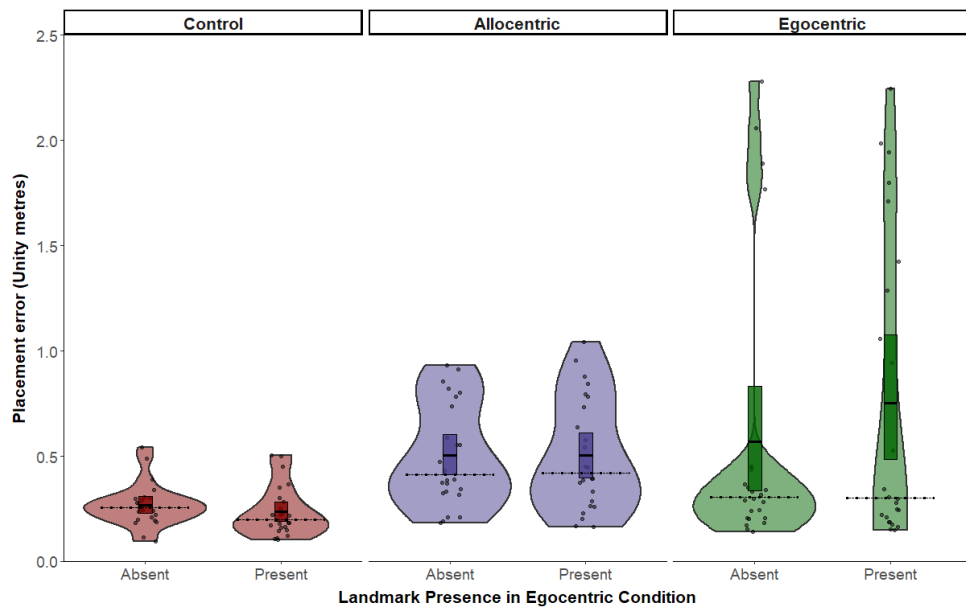


Figure 2.31: Placement error descriptive statistics for each group in Experiment 5. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

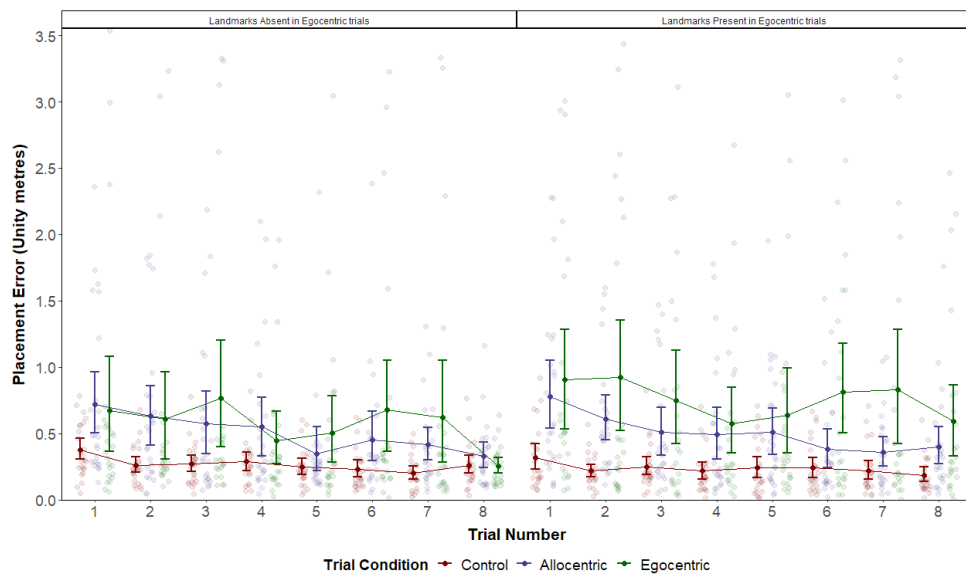


Figure 2.32: This plot shows the placement error for each trial in each condition for both groups. The error bars represent standard error are presented either side of the mean score for each trial within each condition. Each jittered point on the plot represents a participant's score for that trial.

The planned comparisons indicated that in the Landmarks Present group placement error

was lower in the Control condition than in the Allocentric condition, $t_{(23)} = 5.57, p < .001, BF10 = 1926$, and the Egocentric condition, $t_{(23)} = 3.77, p = .009, BF10 = 34.8$. There was no significant difference between the Allocentric and Egocentric conditions, $t_{(23)} = 1.66, p = .993, BF10 = 0.71$.

In the Landmarks Absent group, placement error was lower in the Control condition than in the Allocentric condition, $t_{(23)} = 4.66, p < .001, BF10 = 249$. There was no conclusive evidence of a difference between placement error in the Control and Egocentric conditions, $t_{(23)} = 2.29, p = .283, BF10 = 1.88$. There was no difference in placement error between the Egocentric and Allocentric conditions for the Landmarks Absent group, $t_{(23)} = 0.51, p = 1, BF10 = 0.24$.

There was no evidence to support differences in placement error between the Landmark Present and Landmark Absent group in the Control condition, $t_{(44.77)} = 0.96, p = 1, BF10 = 0.42$, and in the Allocentric condition, $t_{(45.64)} = 0.03, p = 1, BF10 = 0.29$. There was also no evidence to suggest there was a difference in placement error between the Landmark Absent and Landmark Present groups in the Egocentric condition, $t_{(45.66)} = 0.92, p = 1, BF10 = 0.41$.

The mixed ANOVA conducted on latency indicated that there was a significant main effect of trial type, $F_{(1.26, 57.92)} = 61.53, p < .001, \eta_p^2 = .572, BF10 = 6.38 \times 10^{14}$. There was, however, no evidence for differences between groups, $F_{(1, 46)} = 0.19, p = .662, \eta_p^2 = .004, BF10 = 0.28$, nor of an interaction effect, and a significant interaction effect, $F_{(1.26, 57.92)} = 1.01, p = .337, \eta_p^2 = .022, BF10 = 0.25$.

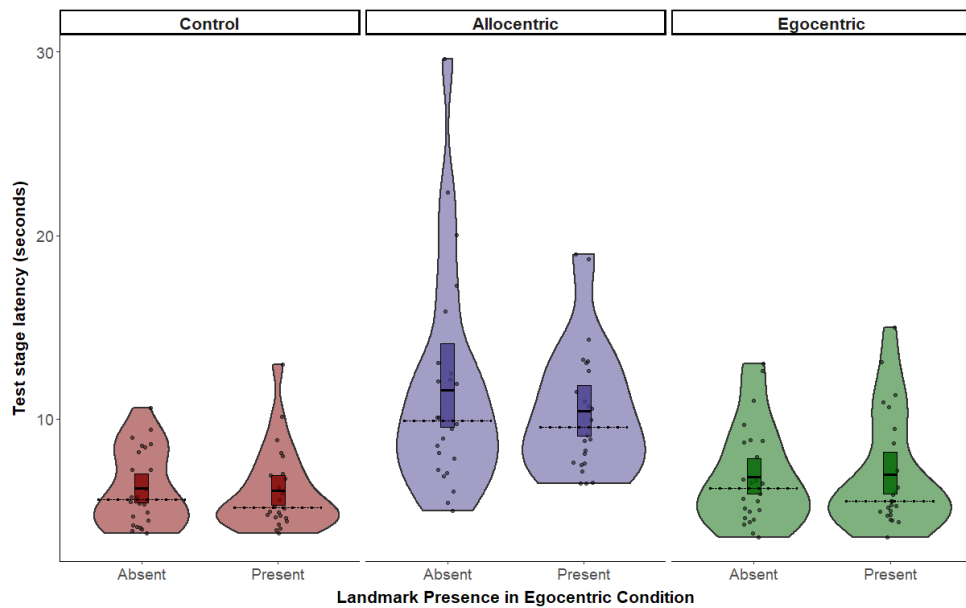


Figure 2.33: Test stage latency descriptive statistics for each group in Experiment 5. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

latencies planned comparisons in the Landmarks Present group revealed that latencies were greater in the Allocentric condition than in both the Control condition, $t_{(23)} = 6.2, p < .001, BF10 = 7428$, and Egocentric condition, $t_{(23)} = 6.7, p < .001, BF10 = 21749$. There was inconclusive evidence of a difference in latencies between the Control and Egocentric condition, $t_{(23)} = 2.03, p = 0.489, BF10 = 1.22$.

In the Landmarks Absent group, latencies were shorter in the Control condition than in both the Allocentric condition, $t_{(23)} = 5.7, p < .001, BF10 = 2261$, and the Egocentric condition, $t_{(23)} = 2.9, p = .067, BF10 = 6.23$. latencies were greater in the Allocentric condition compared to the Egocentric condition, $t_{(23)} = 5.5, p < .001, BF10 = 1455$.

There were no differences in latencies between the Landmark Present and Landmark Absent group in the Control condition, $t_{(45.75)} = 0.21, p = 1, BF10 = 0.29$ and in the Egocentric condition, $t_{(45.05)} = 0.17, p = 1, BF10 = 0.29$. There was no conclusive difference in latencies between the two groups in the Allocentric condition, $t_{(37.6)} = 0.81, p = 1, BF10 = 0.38$.

The ANOVA conducted on the path efficiency index indicated that there was a main effect of trial type, $F_{(1.83, 84.04)} = 167.88, p < .001, \eta_p^2 = .785, BF10 = 1.44 \times 10^{30}$. There was, however,

no between groups effect of landmark presence in Egocentric trials, $F_{(1, 46)} = 0.05$, $p = .827$, $\eta_p^2 = .001$, $BF10 = 0.23$, and no significant interaction effect, $F_{(1.83, 84.04)} = 1.34$, $p = .267$, $\eta_p^2 = .028$, $BF10 = 0.36$.

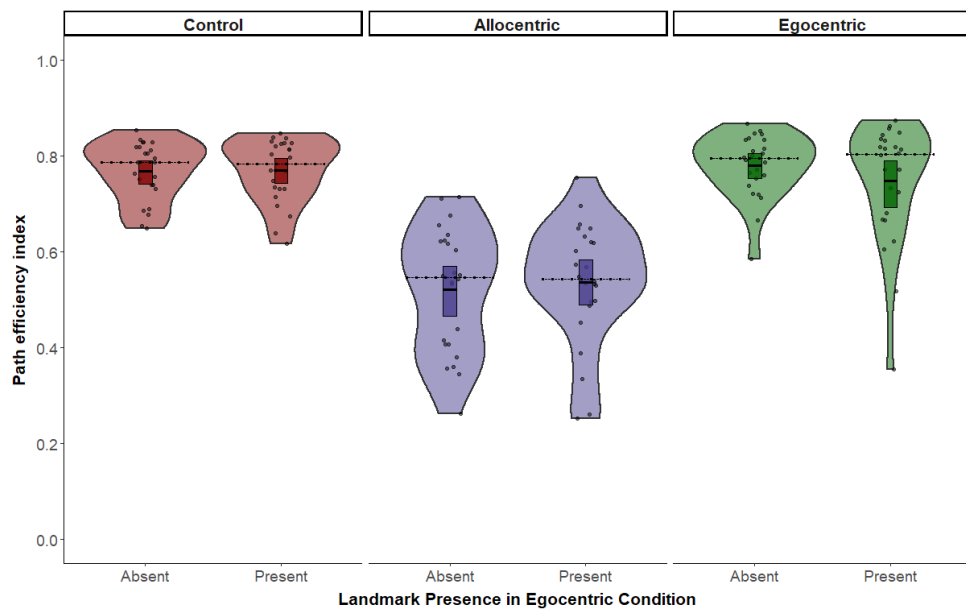


Figure 2.34: Path efficiency descriptive statistics for each group in Experiment 5. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

The planned comparisons on the path efficiency data showed that in the Landmarks Present group, participants' paths were less efficient in the Allocentric condition compared to both the Control condition, $t_{(23)} = 5.59$, $p < .001$, $BF10 = 5.59 \times 10^6$, and the Egocentric condition, $t_{(23)} = 10.16$, $p < .001$, $BF10 = 1.91 \times 10^7$. Paths in the Egocentric condition were no more efficient than those in the Control condition, $t_{(23)} = 0.93$, $p = 1$, $BF10 = 0.32$.

In the Landmarks Absent group, participants' paths were similarly less efficient in the Allocentric condition compared to both the Control condition, $t_{(23)} = 10.7$, $p < .001$, $BF10 = 4.84 \times 10^7$, and the Egocentric condition, $t_{(23)} = 12.07$, $p < .001$, $BF10 = 4.44 \times 10^8$. There was no significant evidence to suggest that paths in the Egocentric condition were more efficient than those in the Control condition, $t_{(23)} = 1.2$, $p = 1$, $BF10 = 0.41$.

There were no differences in path efficiency between the Landmark Present and Landmark Absent group in the Control condition, $t_{(45.74)} = 0.07$, $p = 1$, $BF10 = 0.29$, and no significant

differences in both the Allocentric condition, $t_{(45.99)} = 0.42$, $p = 1$, $BF10 = 0.31$, and the Egocentric condition, $t_{(34.85)} = 1.11$, $p = 1$, $BF10 = 0.48$.

The ANOVA conducted on the viewpoint rotation index indicated that there was a main effect of trial type, $F_{(1.98, 91.27)} = 83.87$, $p < .001$, $\eta_p^2 = .646$, $BF10 = 8.94 \times 10^{19}$. There was no between subjects effect of landmark presence in Egocentric trials, $F_{(1, 46)} = 1.56$, $p = .216$, $\eta_p^2 = .033$, $BF10 = 0.33$, and no clear evidence of an interaction between the two independent variables, $F_{(1.98, 91.27)} = 1.92$, $p = .152$, $\eta_p^2 = .04$, $BF10 = 0.51$.

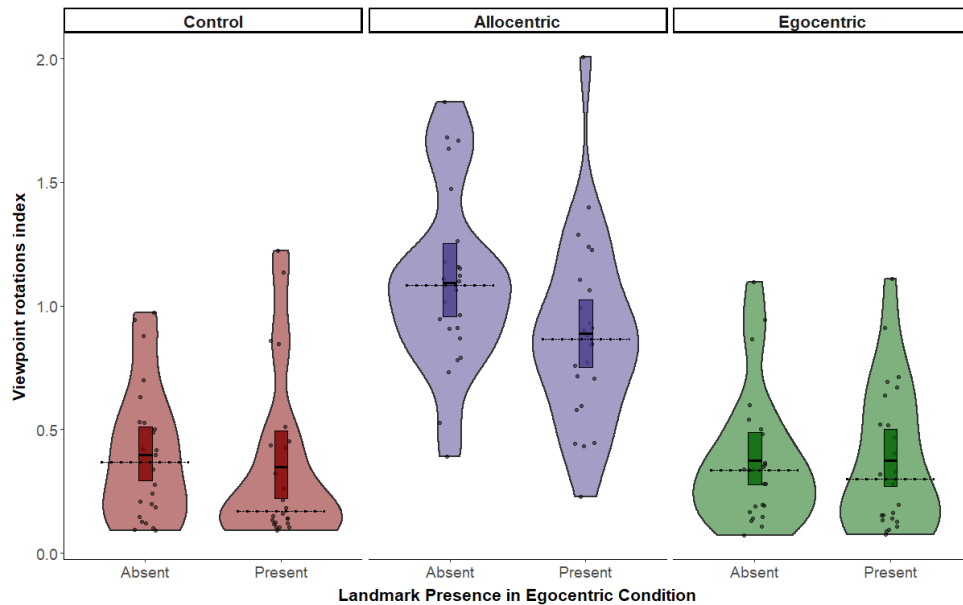


Figure 2.35: Head turn descriptive statistics for each group in Experiment 5. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

The planned comparisons between viewpoint rotation data revealed that in the Landmarks Present group, participants made more view rotations in the Allocentric condition than in both the Control condition, $t_{(23)} = 7.56$, $p < .001$, $BF10 = 134645$, and the Egocentric condition, $t_{(23)} = 6.26$, $p < .001$, $BF10 = 8669$. There were no difference between the number of head rotations in the Control and Egocentric conditions for the Landmarks Present group, $t_{(23)} = 0.35$, $p = 1$, $BF10 = 0.23$.

In the Landmarks Absent group, participants also made more view rotations in the Allocentric condition than in both the Control condition, $t_{(23)} = 8.17$, $p < .001$, $BF10 =$

465287, and the Egocentric condition, $t_{(23)} = 9.15, p < .001, BF10 = 3.07 \times 10^6$. There was no difference between the number of head turns in the Landmarks Absent group between the Control condition and the Egocentric condition, $t_{(23)} = 0.32, p = 1, BF10 = 0.23$.

There was no difference between the number of head rotations between the Landmark Present and Landmark Absent group in the Control condition, $t_{(44.11)} = 0.55, p = 1, BF10 = 0.33$, and inconclusive evidence of a difference between the groups' number of head rotations in the Allocentric condition, $t_{(45.88)} = 1.93, p = 0.54, BF10 = 1.27$. Bayes Factor evidence indicated that there was no difference in the number of head rotations between the Landmark Absent group and the Landmark Present group in the Egocentric condition, $t_{(45.78)} = 0.01, p = 1, BF10 = 0.29$.

2.5.4 Discussion

Experiment 5 was designed to replicate Experiments 3 and 4 on an immersive VR platform. The results indicated that there were no clear differences between the Landmarks Present and Landmarks Absent groups in the Egocentric condition across placement error, latencies, path efficiency, and head turns measures. This suggests that the idiothetic information accrued through motile exploration of a space is sufficient to override interference from the presence of unreliable landmark cues.

A cross-experiment comparison would indicate whether the group results reported in this experiment differ to those reported in Experiment 4. There would be some difficulties in this, however, as the comparison would need to control for differences across the two platforms (see Experiment 2 Discussion, section 2.2.4). Additionally, this analysis will involve two between subjects factors (i.e. Experiment Number and Landmark Presence in Egocentric Trials), which may require a greater number of participants to be appropriately powered. A thorough comparison could be conducted using an appropriate experimental design that could focus exclusively on the Egocentric condition and require participants to complete Egocentric trials with and without landmarks present, in a counterbalanced order. This would be a more practical design for analysis purposes, as fewer participants would be required, and interindividual variability would be reduced.

In lieu of a cross-experiment comparison, a firm conclusion as to whether there are differences in placement error in Experiments 4 and 5 cannot be made. The results do, however, show that in Experiment 4 there was extreme evidence for a difference in

placement error between the Landmarks Present and Landmarks Absent groups in the Egocentric condition (Jeffreys, 1961). In contrast, in Experiment 5, the analysis revealed that mean placement error did not differ between the two groups in the Egocentric condition. This inconsistency may then indicate that the two tasks do not quite capture the same behaviour. Furthermore, this discrepancy implies that other desktop PC assays of human navigation may be missing core components of navigational behaviour (Steel et al., 2020; Taube et al., 2013). Recent research has suggested that human navigation is underpinned by visual information (Hejtmanek et al., 2020; Huffman & Ekstrom, 2019a). This is not consistent with the differing patterns of results observed in Experiment 4 and Experiment 5. When navigation was primarily conducted in a visual modality, i.e. in Experiment 4, participants were less accurate when using egocentric information to identify the target location in the presence of unreliable landmarks. This indicates that unreliable visual information disrupts the ability to reliably use egocentric information to find the target location. This disruption was not observed in Experiment 5, suggesting that access to internal self-motion cues during motile navigation may attenuate the influence of unreliable visual information. The results from both experiments, when taken together, indicate that despite the importance of visual information to navigation, the extent to which individuals depend on it differs based on the navigational modality (Steel et al., 2020). This has important theoretical implications for theories of navigation that are based on results from desktop PC assays of navigational behaviour, as they would be based on data that has not been validated against naturalistic, fully motile navigation.

Whilst the results of Experiment 5 did not replicate the findings from Experiments 3 and 4 in the Egocentric condition, the pattern of results from the Landmarks Present group was similar to those reported in Experiment 2's immersive VR task in all three conditions. These results are also consistent with those reported by Merhav & Wolbers (2019), suggesting that when participants are fully motile, participants can navigate most accurately when integrating allocentric and egocentric information in conjunction. Additionally, the results of the immersive VR tasks reported in Experiments 2 and 5, as well as those reported by Merhav & Wolbers (2019), suggest that participants are more accurate at identifying a location in space when using allocentric information in isolation than egocentric information. Furthermore, this advantage is apparent irrespective of the presence of unreliable landmarks during assays of egocentric information use.

Whilst the key manipulation in Experiments 3, 4, and 5 was the between groups manip-

ulation of landmark presence during the Egocentric condition trials, it is interesting to note that the efficiency of paths were broadly similar across the two platforms in both the Control and Allocentric conditions. Participants in both Experiment 4 and 5 took indirect paths during Allocentric condition trials and made the greatest number of viewpoint rotations or head turns. This suggests that participants may employ similar strategies irrespective of the task platform. While Experiment 2 suggests that the precision of spatial representations may differ in the Allocentric condition across platforms, Experiments 4 and 5 suggest that navigational strategies may remain consistent across platforms.

Similar to Experiment 2, Experiments 4 and 5 indicate that there are differences in navigation related to access to motility. Experiment 5 demonstrated that the presence of unreliable landmarks does not influence the use of egocentric self-motion information when identifying a target location. Whilst this is a clear difference across the two platforms, it is important to note that the scale of the two environments did differ on each platform. Huffman & Ekstrom (2019a) presented a model of idiothetic cue utility in human navigation that suggests that idiothetic information may be of greater utility in smaller scale environments. This would present an explanation for the differences across the experiments, however, this may then suggest that navigation may not be primarily reliant on a modality independent visual input (Hejtmanek et al., 2020; Huffman & Ekstrom, 2019a; Steel et al., 2020).

2.6 Experiment 6

The data reported in this chapter indicate that the versions of the place learning task for the desktop PC and immersive VR platforms each produce differing patterns of results. In contrast, within each platform, results have been replicated and are seemingly robust. This experiment was designed to further validate the desktop PC version of the task by examining how age effects performance across the three task conditions (Commins et al., 2020).

Chapter 1 reviewed the vMWM literature that describes the age-related decline associated with place learning in humans (Korthauer et al., 2016; McAvan et al., 2021; Merhav & Wolbers, 2019; Moffat & Resnick, 2002; Schoenfeld et al., 2010a, 2014; Zhong et al., 2017), as well as the real-world MWM analogue, the BVA, which also demonstrates difficulties associated with age Gazova et al. (2013); Kalová et al. (2005); Laczó et al. (2009). This

literature indicates that age-related decline impacts individuals' abilities to use allocentric information (Gazova et al., 2013; Iaria et al., 2009; Merhav & Wolbers, 2019; Moffat & Resnick, 2002), and that older adults are more likely to employ compensatory egocentric mechanisms for navigation than use allocentric navigational strategies (Rodgers et al., 2012). As this task was based on the design of the BVA, this experiment was expected to show that placement error in the Allocentric condition increases with age. Placement error was also expected to increase with age in the Control and Egocentric conditions, however, the extent of this increase was expected to be not as severe as the decline associated with the use of Allocentric information. A model for the expected results is reported by Gazova et al. (2013), who used the BVA to compare groups of healthy younger and older adults. Gazova et al. (2013) observed the expected decline in older adults' Allocentric condition accuracy, and a much less steep decline in older adults' Egocentric condition accuracy. Gazova et al. (2013) did not, however, employ a Middle aged group in their experiment, though studies employing a vMWM task have looked at age across the life span and found a linear decline in place learning ability across Young, Middle, and Old age groups (Driscoll et al., 2005).

The version of the place learning task used in this experiment will be the Landmarks Absent version used in Experiment 4. The reason for this, is that it may comprise a purer measure of egocentric cue use, as participants were not required to inhibit attentional focus to unreliable landmark stimuli. Additionally, this version of the task more closely mimics the demands of the tasks employed by both Gazova et al. (2013) and Merhav & Wolbers (2019), as in these experiments, there were no landmarks present in their respective Egocentric conditions. Furthermore, Biss et al. (2013) and Lustig & Jantz (2015) report a greater susceptibility to interference from task irrelevant stimuli in older adults. This may mean that the presence of unreliable yet familiar landmarks has a more detrimental effect on older adults than younger adults, masking either group's respective ability to use egocentric information to identify the target location.

2.6.1 Methodology

Design

This experiment comprised a 3x3 mixed design with a within subject factor of condition (three levels: Control, Allocentric, Egocentric) and a between subjects factor of age group

(three levels: Young, Middle, Old). In a single experimental session, participants completed the desktop PC version of the place learning task via a web browser based interface. The task was otherwise identical to the desktop PC version of the task developed for Experiment 2. The order of allocentric and egocentric conditions was counterbalanced as closely as possible in this experiment.

Participants

Adult participants were recruited for this experiment from the Prolific participant pool in return for monetary compensation. Participants were assigned to one of three groups based on their age, Young (ages from 18 to 39), Middle (ages 40-59), and old (60 or older), following previous research exploring the effects of age on place learning (Driscoll et al., 2005). A total of 151 participants were recruited for this experiment. In the Young group, 53 participants were recruited (26 female, 27 male, $M = 27.2$, $SD = 4.9$, range from 20 to 39). In the Middle group, 52 participants were recruited (26 female, 26 male, $M = 47.9$, $SD = 4.9$, range from 40 to 59). Finally, in the Old group, 46 participants were recruited (24 female, 22 male, $M = 65.4$, $SD = 4.7$, range from 60 to 77). This number of participants is sufficient to detect medium effect sizes.

Apparatus and Materials

This experiment deployed the Landmarks Absent version of the desktop place learning task used in Experiment 4 that was hosted on Gorilla. In this experiment, all participants completed the Egocentric condition without landmarks present following Gazova et al. (2013) and Merhav & Wolbers (2019).

Procedure

This experiment followed the same procedure for Experiment 4, except all participants completed the version of the experiment in which no landmarks were visible in the Egocentric condition.

2.6.2 Analysis

The analyses in this experiment followed those conducted in Experiments 3, 4, and 5. The only difference is that instead of employing a between subjects manipulation of landmarks presence during Egocentric condition trials, there was a between subjects factor of age group with three levels (Young, Middle, Old). Placement error, latencies, path efficiency, and viewpoint rotations were then subjected to a mixed 3x3 ANOVA. Planned comparisons were also similar to those used in previous experiments, as the variables were compared for each condition within each group, and within each condition across each group.

The principle DVs (placement error, test stage latency, test stage path efficiency, and test stage viewpoint rotations) for all three age groups were collapsed and entered into correlation matrices for each of the three conditions. This will identify relationships between each of these variables, providing insight into behavioural differences across the three conditions.

2.6.3 Results

Placement responses, for every trial, are illustrated in Figure 2.30, and descriptive statistics for placement error, latencies, and the path efficiency and viewpoint rotation indices are presented in Figures 2.31, 2.33, 2.34, and 2.30 respectively. Trial by trial error rates are presented in Figure 2.32.

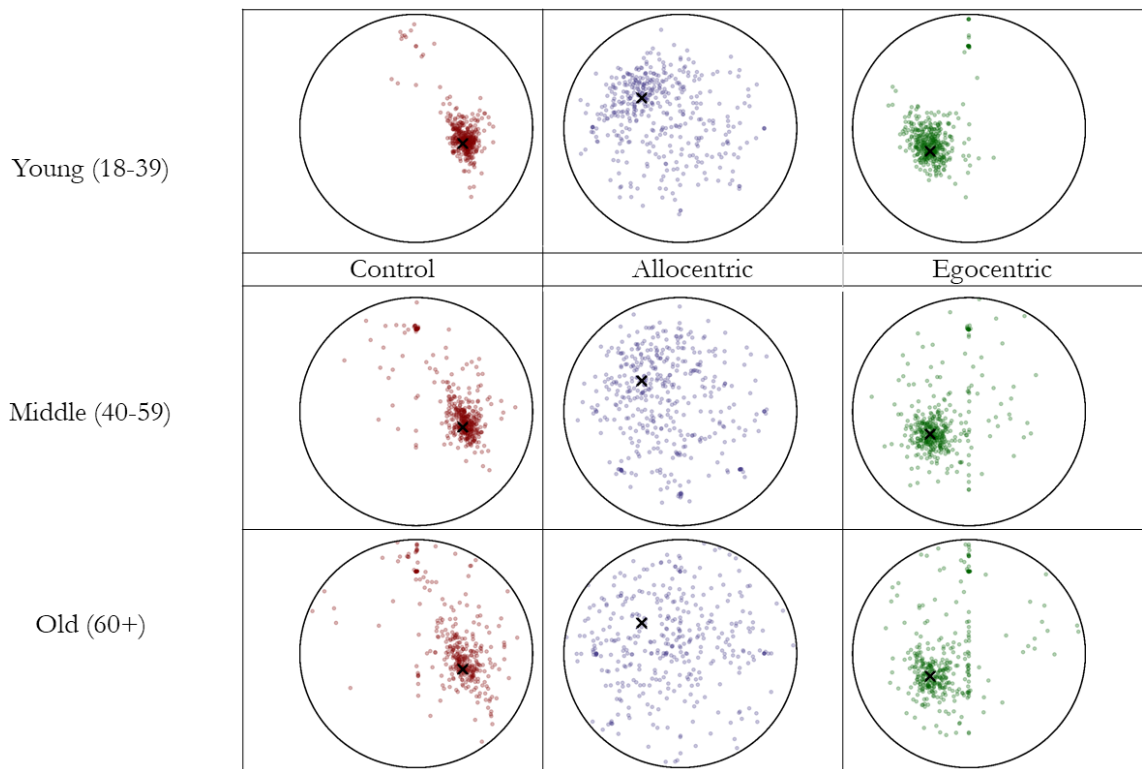


Figure 2.36: This plot shows each participant's placement within each condition across all three groups in Experiment 6. The correct location of the target in each condition is indicated by the black 'X'.

The placement error ANOVA revealed a main effect of trial type, $F_{(1.56, 231.61)} = 159.2, p < .001, \eta_p^2 = .52, BF10 = 4.74 \times 10^{44}$, and between subjects main effect of age group, $F_{(2, 148)} = 12.9, p < .001, \eta_p^2 = .15, BF10 = 2449$. There was no interaction effect, $F_{(3.13, 231.61)} = 0.69, p = .566, \eta_p^2 = .009, BF10 = 0.031$.

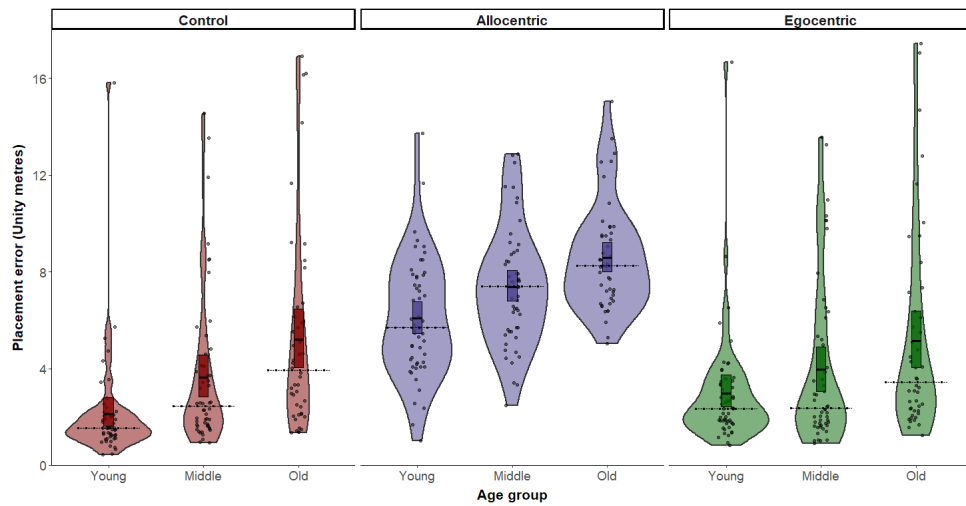


Figure 2.37: Placement error descriptive statistics for each group in Experiment 6. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

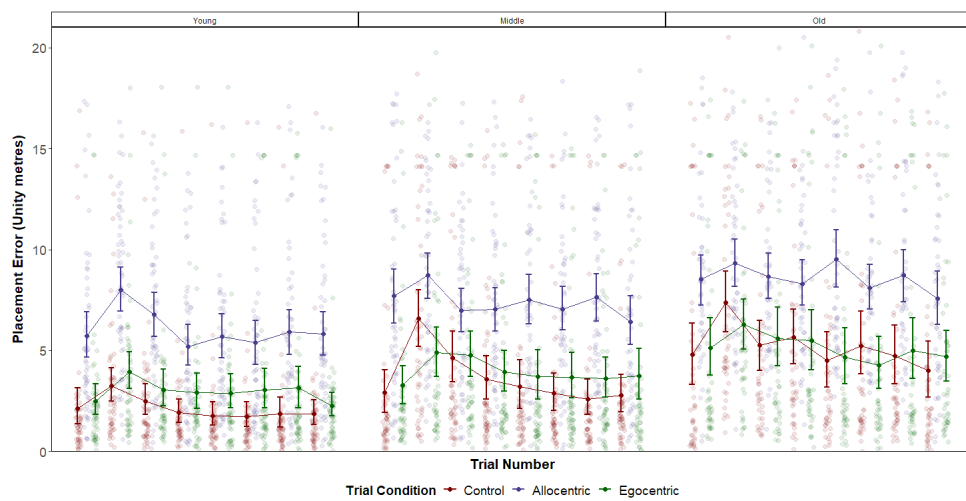


Figure 2.38: This plot shows the placement error for each trial in each condition across the three groups. The error bars represent standard error are presented either side of the mean score for each trial within each condition. Each jittered point on the plot represents a participant's score for that trial.

The planned comparisons for this experiment showed that in the Young group, placement error was lower in the Control condition than in the Allocentric condition, $t_{(52)} = 12.5$, $p < .001$, $BF10 = 2.11 \times 10^{14}$, and the Egocentric condition, $t_{(52)} = 4.2$, $p < .001$, $BF10 = 233$. Placement error was lower in the Egocentric condition than in the Allocentric condition,

$t_{(52)} = 9.1, p < .001, BF10 = 3.03 \times 10^9$.

In the Middle age group, placement error was greater in the Allocentric condition than in the Control condition, $t_{(51)} = 9.5, p < .001, BF10 = 1.05 \times 10^{10}$, and the Egocentric condition, $t_{(51)} = 7.9, p < .001, BF10 = 4.67 \times 10^7$. Placement error did not differ between the Control condition and the Egocentric condition, $t_{(51)} = 1.2, p = 1, BF10 = 0.3$. In the Old group, placement error was greater in the Allocentric condition than in the Control condition, $t_{(45)} = 5.9, p < .001, BF10 = 34166$, and the Egocentric condition, $t_{(45)} = 5.9, p < .001, BF10 = 32399$. Placement error did not differ between the Control condition and the Egocentric condition, $t_{(45)} = 0.15, p = 1, BF10 = 0.16$.

Between the Young and Middle age groups, Bayes Factor evidence indicated that placement error in the Young group was lower in the Control condition, $t_{(91.3)} = 2.85, p = .097, BF10 = 7.34$, and the Allocentric condition, $t_{(102.97)} = 2.74, p = 0.131, BF10 = 5.5$. There was no conclusive evidence for a difference between the two groups' Egocentric condition placement error, $t_{(92.5)} = 1.71, p = 1, BF10 = 0.77$.

Between the Young and Old age groups, Bayes Factor evidence indicated that placement error in the Young group was lower in the Control condition, $t_{(67.05)} = 4.54, p < .001, BF10 = 2142$, the Allocentric condition, $t_{(96.82)} = 5.36, p < .001, BF10 = 20401$, and the Egocentric condition placement error, $t_{(70.35)} = 3.13, p = .045, BF10 = 19.7$.

Between the Middle and Old age groups, there was no conclusive evidence for differences in the Control condition, $t_{(84.18)} = 2.1, p = .73, BF10 = 1.51$, and the Egocentric condition, $t_{(86.88)} = 1.56, p = 1, BF10 = 0.64$. Bayes Factor evidence indicated that placement error in the Middle age was lower in the Allocentric condition than the Old age group's, $t_{(95.94)} = 2.56, p = .217, BF10 = 3.57$.

The mixed design 3x3 ANOVA conducted on latencies showed a main effect of trial type, $F_{(1.91, 282.28)} = 50.03, p < .001, \eta_p^2 = .253, BF10 = 8.58 \times 10^{15}$, and between subjects main effect of age group, $F_{(2, 148)} = 13.13, p < .001, \eta_p^2 = .15, BF10 = 3388$. There was no interaction effect, $F_{(3.81, 282.28)} = 2.1, p = .086, \eta_p^2 = .027, BF10 = 0.28$.

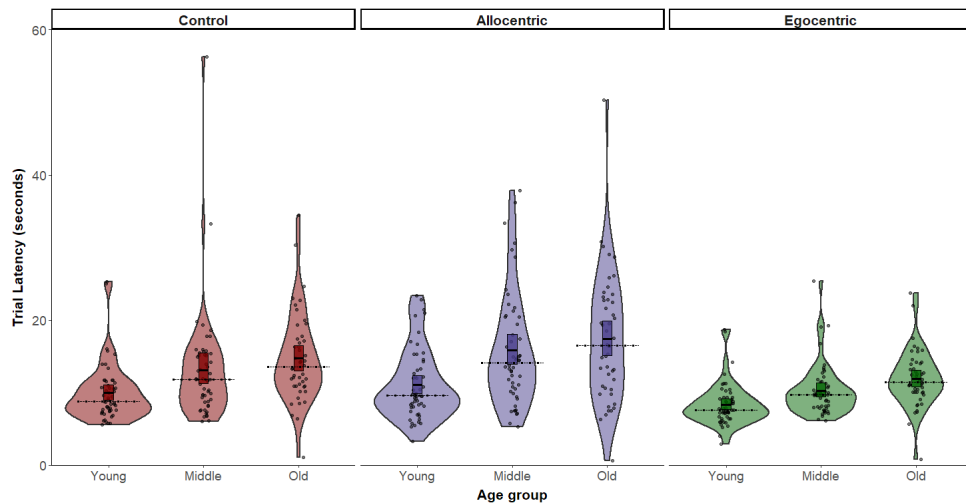


Figure 2.39: Test stage latency descriptive statistics for each group in Experiment 6. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

Test stage planned comparisons indicated that in the Young group, latencies were lower in the Egocentric condition than in the Control condition, $t_{(52)} = 4.72, p < .001, BF10 = 1089$, and the Allocentric condition, $t_{(52)} = 5.11, p < .001, BF10 = 3795$. There was no conclusive evidence for a difference in latencies between the Control and Allocentric conditions, $t_{(52)} = 1.92, p = 1, BF10 = 0.82$.

In the Middle age group, latencies were lower in the Control condition than in the Allocentric condition, $t_{(51)} = 3.27, p = .034, BF10 = 15.8$. Egocentric latencies were lower compared to both the Control condition, $t_{(51)} = 2.9, p = .1, BF10 = 6.15$, and the Allocentric condition, $t_{(51)} = 5.92, p < .001, BF10 = 54338$.

In the Old group, Bayes Factor evidence indicated that latencies were lower in the Control condition than in the Allocentric condition, $t_{(45)} = 2.59, p = .233, BF10 = 1089$. Latencies were lower in the Egocentric condition than those in the Control condition, $t_{(45)} = 4.2, p = .002, BF10 = 194$, and the Allocentric condition, $t_{(45)} = 5.39, p < .001, BF10 = 7027$.

Between the Young and Middle age groups, Bayes Factor evidence indicated that latencies in the Young group were shorter in the Control condition, $t_{(76.1)} = 2.6, p = .214, BF10 = 3.93$, and in the Egocentric condition, $t_{(98.49)} = 3.06, p = .052, BF10 = 12.2$. Latencies in the Young group were shorter in the Allocentric condition than those in the Middle age group, $t_{(84.35)}$

= 3.72, $p = .006$, $BF10 = 82.9$.

Between the Young and Old age groups, latencies in the Young group were lower in the Control condition, $t_{(75.44)} = 4.48$, $p < .001$, $BF10 = 1457$, the Allocentric condition, $t_{(67.39)} = 5.11$, $p < .001$, $BF10 = 959$, and the Egocentric condition, $t_{(82.03)} = , p < .001$, $BF10 = 13594$.

Between the Middle and Old age groups, there was no conclusive evidence for differences in latencies in the Control condition, $t_{(94.9)} = 1.17$, $p = .73$, $BF10 = 0.38$, and the Egocentric condition, $t_{(91.41)} = 2.18$, $p = 1$, $BF10 = 1.75$. There was no difference between the Middle and Old age groups' latencies, $t_{(90.8)} = 0.93$, $p = 1$, $BF10 = 0.32$.

The path efficiency ANOVA showed a main effect of trial type, $F_{(1.38, 203.5)} = 143.4$, $p < .001$, $\eta_p^2 = .494$, $BF10 = 2.35 \times 10^{42}$, and a significant interaction effect, though the Bayes Factor was inconclusive, $F_{(2.77, 203.50)} = 3.01$, $p = .035$, $\eta_p^2 = .039$, $BF10 = 1.31$. The Bayes Factor indicated there was no effect of age group, $F_{(2, 147)} = 1.83$, $p = .164$, $\eta_p^2 = .024$, $BF10 = 0.142$.

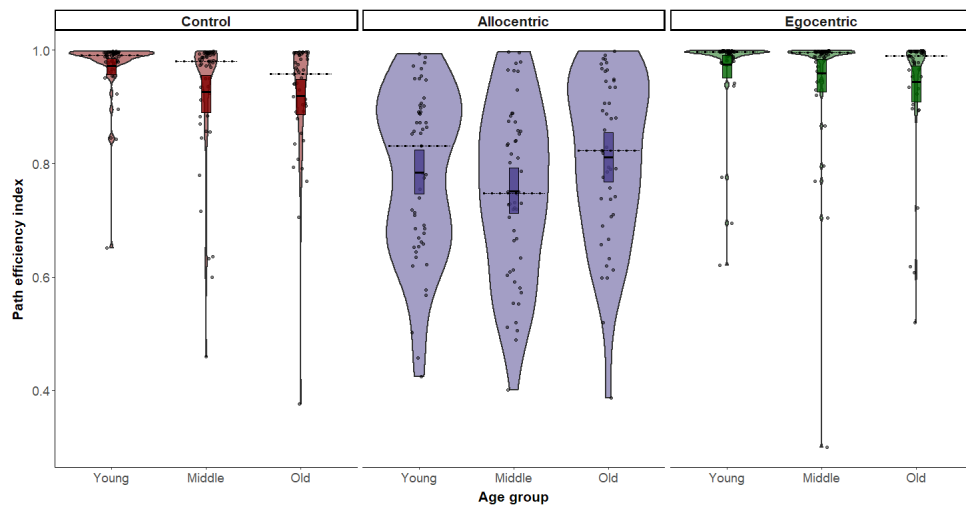


Figure 2.40: Path efficiency descriptive statistics for each group in Experiment 6. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

The planned comparisons for the Young group showed that the path efficiency index was lower in the Allocentric condition than in the Control condition, $t_{(52)} = 9.71$, $p < .001$, $BF10 = 2.83 \times 10^{10}$, and the Egocentric condition, $t_{(52)} = 9.62$, $p < .001$, $BF10 = 2.03 \times 10^{10}$. There was no difference in path efficiency between the Control and Egocentric conditions, $t_{(52)} = 0.26$, $p = 1$, $BF10 = 0.154$.

Similar to the results for the Young group, in the Middle age group, path efficiency index was lower in the Allocentric condition than in the Control condition, $t_{(51)} = 7.1, p < .001, BF10 = 3.18 \times 10^6$, and the Egocentric condition, $t_{(51)} = 8.57, p < .001, BF10 = 4.99 \times 10^8$. There was no conclusive evidence of a difference in path efficiency between the Control and Egocentric conditions, $t_{(51)} = 2.39, p = 0.367, BF10 = 2.02$.

In the Old group, path efficiency data followed the same pattern of results as the Middle age group. Older path efficiency index was lower in the Allocentric condition than in the Control condition, $t_{(44)} = 4.26, p = .002, BF10 = 222$, and the Egocentric condition, $t_{(44)} = 5.59, p < .001, BF10 = 12573$. There was no conclusive evidence of a difference in path efficiency between the Control and Egocentric conditions, $t_{(44)} = 2.22, p = 0.575, BF10 = 1.47$.

Between the Young and Middle age groups, Bayes Factor evidence indicated that the Young group's paths were more efficient in the Control condition, $t_{(72.39)} = 2.58, p = .217, BF10 = 3.92$. There were no evidence of a difference between the two groups' path efficiency in the Allocentric, $t_{(102.64)} = 1.12, p = 1, BF10 = 0.36$, and no difference between the Egocentric conditions, $t_{(86.84)} = 0.84, p = 1, BF10 = 0.29$.

Between the Young and Old age groups, the Bayes Factor evidence to indicated that the Young group's paths were more efficient in the Control condition, $t_{(62.72)} = 2.97, p = .076, BF10 = 14.1$. There was no difference in path efficiency between the two groups in the Allocentric condition, $t_{(93.28)} = 0.903, p = 1, BF10 = 0.31$, and no evidence of a difference in the Egocentric condition, $t_{(73.2)} = 1.64, p = 1, BF10 = 0.75$.

Between the Middle and Old age groups, there was no difference in path efficiency in the Control condition, $t_{(94.43)} = 0.32, p = 1, BF10 = 0.23$, and the Egocentric condition, $t_{(93.22)} = 0.71, p = 1, BF10 = 0.27$. There was also no conclusive evidence of a difference between the two groups' path efficiency in the Allocentric condition, $t_{(93.84)} = 1.96, p = 0.956, BF10 = 1.14$.

The viewpoint rotation index ANOVA showed a main effect of trial type, $F_{(1.17, 172.53)} = 210.29, p < .001, \eta_p^2 = .589, BF10 = 2.86 \times 10^{49}$, and an interaction effect, $F_{(2.35, 172.53)} = 20.16, p < .001, \eta_p^2 = .215, BF10 = 7.59 \times 10^{11}$. The Bayes Factor indicated that evidence for a between groups effect was inconclusive even though the p-value was significant, $F_{(2, 147)} = 4.33, p = .015, \eta_p^2 = .056, BF10 = 0.8$,

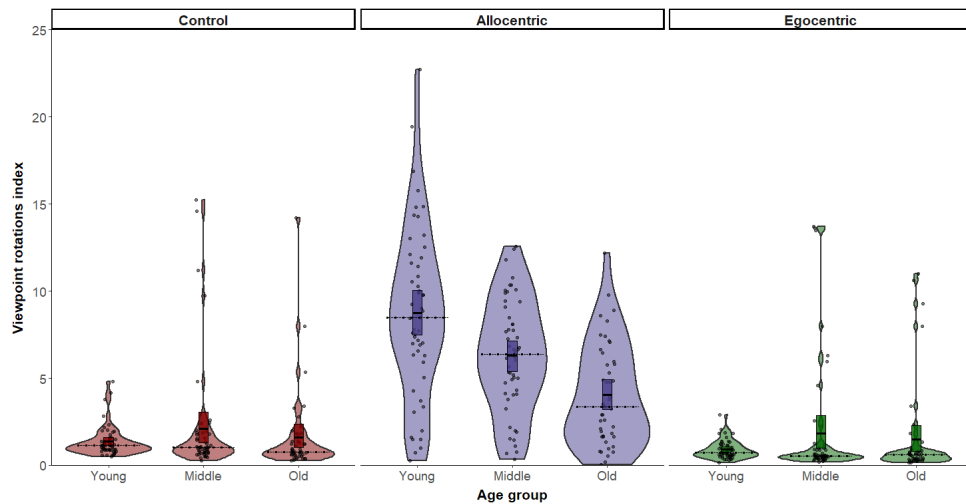


Figure 2.41: Viewpoint rotation descriptive statistics for each group in Experiment 6. The cross bars show the mean score at the centre, and 95% confidence intervals at the extremes. The dotted lines represent median scores. Points represent individual mean scaled placement errors per condition, and the distribution of mean scaled placement errors is shown along the flanks of the violin plots.

The planned comparisons for the Young group revealed that they made more viewpoint rotations in the Allocentric condition than in the Control condition, $t_{(52)} = 11.16, p < .001, BF10 = 3.23 \times 10^{12}$. Participants also made fewer viewpoint rotations in the Egocentric condition than in the Control condition, $t_{(52)} = 3.67, p = .01, BF10 = 46$, and the Allocentric condition, $t_{(52)} = 12.26, p < .001, BF10 = 1.02 \times 10^{14}$.

In the Middle age group, participants made more viewpoint rotations in the Allocentric condition than in the Control condition, $t_{(51)} = 7.98, p < .001, BF10 = 6.66 \times 10^7$, and the Egocentric condition, $t_{(51)} = 8.19, p < .001, BF10 = 1.36 \times 10^8$. There was inconclusive Bayes Factor evidence to determine whether there was a difference between viewpoint rotations in the Egocentric condition and Control condition in the Middle age group, $t_{(51)} = 1.67, p = 1 < .001, BF10 = 0.55$.

In the Old group, participants made a greater number of viewpoint rotations in the Allocentric condition compared to the Control condition, $t_{(44)} = 5.97, p < .001, BF10 = 42906$, and the Egocentric condition, $t_{(44)} = 5.68, p < .001, BF10 = 16744$. In the Old group there was no difference in the number of viewpoint rotations between the Egocentric and Control conditions, $t_{(44)} = 0.51, p = 1, BF10 = 0.18$.

Between the Young and Middle age groups, the Young group made more viewpoint

rotations in the Allocentric condition, $t_{(90.66)} = 3.05, p < .001, BF10 = 11.4$. There was inconclusive evidence of differences between the two groups in the Control condition, $t_{(58.21)} = 1.59, p = 1, BF10 = 0.65$, and in the Egocentric condition, $t_{(53.46)} = 1.95, p = 1, BF10 = 1.15$.

Between the Young and Old age groups, the Young group made more viewpoint rotations in the Allocentric condition, $t_{(87.18)} = 5.88, p < .001, BF10 = 76594$. There was no difference between the two groups in the Control condition, $t_{(54.04)} = 5.88, p = 1, BF10 = 0.27$, and inconclusive evidence to support a difference in the groups' Egocentric conditions, $t_{(46.85)} = 1.4, p = 1, BF10 = 0.59$.

Between the Middle and Old age groups, there was no difference in the number of viewpoint rotations in the Control condition, $t_{(92.6)} = 0.86, p = 1, BF10 = 0.29$, or in the Egocentric condition, $t_{(94.53)} = 0.56, p = 1, BF10 = 0.25$. Participants in the Middle age group made a greater number of viewpoint rotations in the Allocentric condition than participants in the Old age group, $t_{(94.78)} = 3.58, p = .01, BF10 = 47.2$.

The correlation matrices for each of the conditions are visualised in correlograms presented in Figure 2.42. In the Control condition, there was a significant positive correlation between placement error and the number of viewpoint rotations, $R^2 = .48, p < .001, BF10 = 2.42 \times 10^7$. There were also negative correlations between path efficiency and placement error, $R^2 = -.69, p < .001, BF10 = 1.82 \times 10^{19}$, Test stage latencies, $R^2 = -.41, p < .001, BF10 = 1.1 \times 10^5$, and viewpoint rotations, $R^2 = -.38, p < .001, BF10 = 1.67 \times 10^4$. There were no significant correlations between Test stage latency and both placement error, $R^2 = .03, p = .697, BF10 = 0.203$, and the number of viewpoint rotations, $R^2 = -.14, p = 0.092, BF10 = 0.74$.

In the Allocentric condition, there was a significant positive correlation between placement error and the path efficiency, $R^2 = .25, p = .002, BF10 = 18.7$. There were negative correlations between path efficiency and Test stage latencies, $R^2 = -.51, p < .001, BF10 = 4.81 \times 10^8$, and between viewpoint rotations and placement error, $R^2 = -.44, p < .001, BF10 = 1.03 \times 10^6$, Test stage latencies, $R^2 = -.21, p = 0.01, BF10 = 4.86$, and viewpoint rotations, $R^2 = -.23, p = .005, BF10 = 8.32$. There was no significant correlation between Test stage latency and both placement error, $R^2 = -.06, p = .45, BF10 = 0.25$.

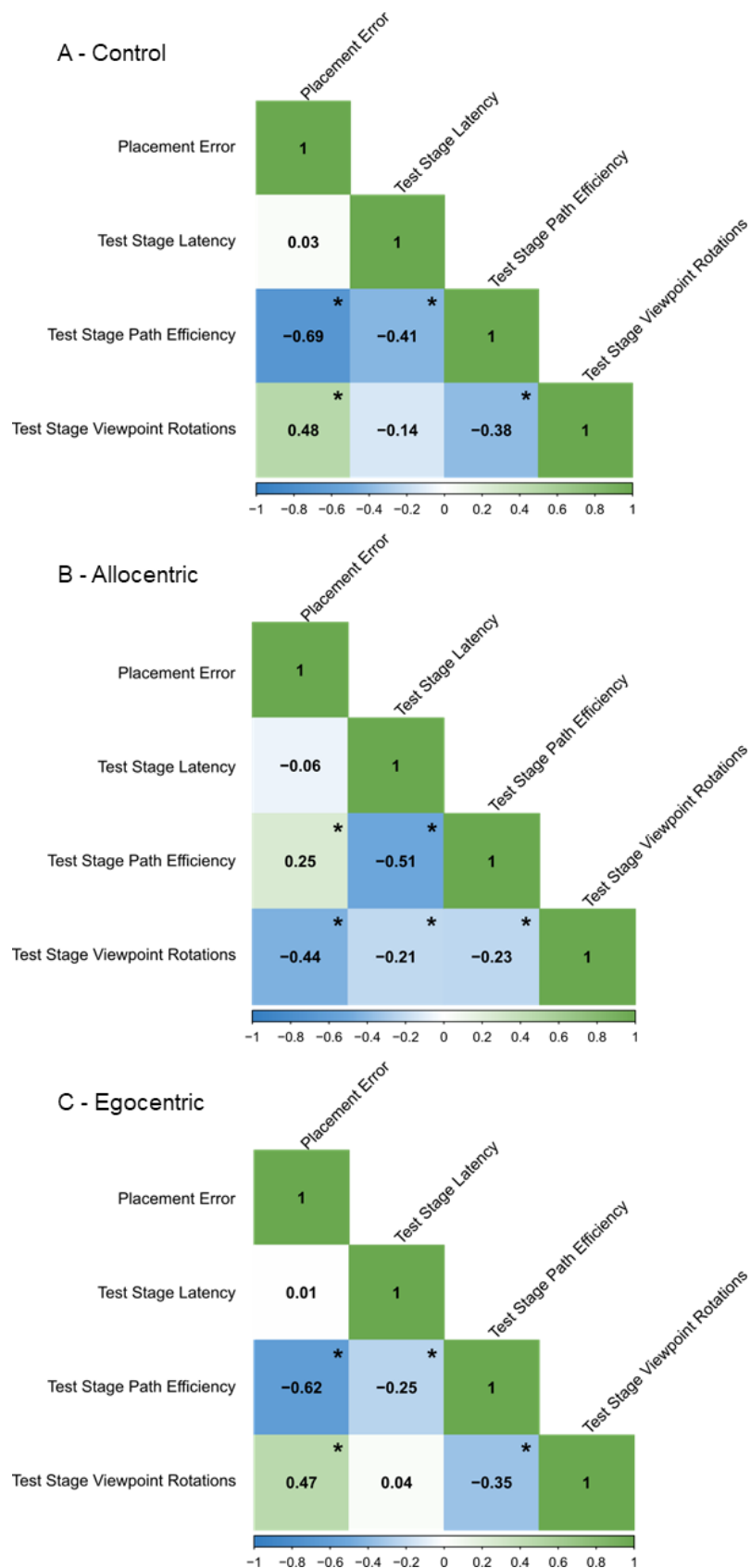


Figure 2.42: This presents correlograms for each trial condition in Experiment 6, collapsed across the three groups. The colour scale along the bottom indicates the strength of the correlation. Pearson's R values are reported within the correlogram at the boxes in which the variables intersect. Significant correlations ($p < .05$) are indicated by asterisks.

In the Egocentric condition, there was a significant positive correlation between placement error and the number of viewpoint rotations, $R^2 = .47$ $p < .001$, $BF10 = 8.36 \times 10^6$. There were also negative correlations between path efficiency and placement error, $R^2 = -.62$ $p < .001$, $BF10 = 1.08 \times 10^{14}$, Test stage latencies, $R^2 = -.25$ $p = .002$, $BF10 = 16.49$, and viewpoint rotations, $R^2 = -.35$ $p < .001$, $BF10 = 1998$. There were no significant correlations between Test stage latency and both placement error, $R^2 = .01$ $p = .91$, $BF10 = 0.19$, and the number of viewpoint rotations, $R^2 = .04$ $p = 0.66$, $BF10 = 0.21$.

2.6.4 Discussion

In this experiment, participants, recruited to either Young, Middle, or Old age groups, completed the Landmarks Absent version of the place learning task. The results replicated the widely reported age-related decline in the ability to accurately employ allocentric information, as there was strong evidence to suggest that placement error increased across each age group in the Allocentric condition. This relationship was less clear for placement error in the Egocentric condition, which provides further evidence for a less severe age-related decline in the processing of egocentric information, compared to the decline associated with the use of allocentric spatial cues.

The results from the Allocentric condition replicate the widely reported age-related decline observed in the processing of allocentric information, as placement error increased across the age groups (Gazova et al., 2013; Korthauer et al., 2016; McAvan et al., 2021; Merhav & Wolbers, 2019; Moffat & Resnick, 2002; Newman & Kaszniak, 2000; Schoenfeld et al., 2010a, 2014; Zhong et al., 2017). This indicates that the place learning task reported here has construct validity in its ability to quantify this difference and suggests that the task has utility as a measure of aptitude in using either allocentric or egocentric information in isolation. Results from the viewpoint rotation analysis indicate that participants in the younger groups made a greater number of view rotations than participants in the older groups. This may explain why participants in the older age groups demonstrated poorer placement accuracy in the Allocentric condition, as they may not reorient fully in the VE before they make their placement in the Test stage. This would constrain the ability to generate an accurate allocentric representation of space as less information would be processed, and consequently led to greater placement error in these trials.

As this task was conducted on a desktop PC platform, participants are unable to access

idiothetic self-motion information while navigating, unlike the immersive VR version. Experiments have shown that the age-related decline effect has been observed on both immersive VR (McAvan et al., 2021; Merhav & Wolbers, 2019) and desktop PC platforms (Korthauer et al., 2016; Moffat & Resnick, 2002; Schoenfeld et al., 2010a, 2014; Zhong et al., 2017), and has also been reported in real-world MWM equivalents (Gazova et al., 2013; Newman & Kaszniak, 2000), so it would be interesting to examine whether the immersive VR version of the place learning task would similarly capture the age-related decline in the use of allocentric information. The expectation would be that the results would be similar to those reported by McAvan et al. (2021) and Merhav & Wolbers (2019), with clear differences in the Allocentric condition associated with advanced age, and less severe differences observed between age groups in the Egocentric condition.

This experiment employed the Landmarks Absent version of the Egocentric condition as it may reflect a purer assay of the ability to use egocentric information accurately (Merhav & Wolbers, 2019), and as a consequence, may be less susceptible to age-related navigational decline. Whilst this experiment replicated the less strong decline in egocentric navigational ability relative to the decline in allocentric cue use Rodgers et al. (2012), it would be interesting to identify how much disruption the unreliable landmarks would cause for older adults in the Egocentric condition. The amount of disruption may be greater in older adults than younger adults, as previous research has shown that increased age is associated with reduced cognitive control. This includes a greater susceptibility to interference from task irrelevant stimuli (Biss et al., 2013; Lustig & Jantz, 2015), which may mean that the presence of unreliable landmarks in the Egocentric condition could exhibit a greater negative impact on older adults' placement error than any landmark-related disruption observed in younger adults during Experiments 3 and 4.

The correlations between the behavioural measures presented some interesting relationships that indicate differences in participant behaviour across conditions. In both the Control and Egocentric conditions, the correlational analyses revealed that participants that took more efficient paths were more accurate at identifying the target location. Similarly in these two conditions, when participants made more viewpoint rotations, they were less accurate at finding the target location. These similarities may indicate that participants employ similar behaviours to complete the task in the Control and Egocentric conditions. This behaviour can be interpreted as being reliant on replicating the Training stage direction and distance in the Test stage, as accurate participants appear to rotate

their viewpoint only a little, and take direct paths to where they think the goal location is. The reliable landmarks in the Control condition provide a beacon that improves the accuracy of this behaviour, whereas their absence in the Egocentric condition means that participants are reliant on internal cues to hone their accuracy.

The relationships between variables in the Control and Egocentric condition contrast with those observed in the Allocentric condition. In the Allocentric condition, a greater number of viewpoint rotations was associated with greater accuracy, and more efficient paths were associated with lower accuracy. This suggests that participants were more successful when they looked around the arena, and took more circuitous paths to where they thought the target location was. This would likely reflect participants reorienting and navigating to the location of the landmarks during the Test stage, due to their role as the only reliable cues in the Allocentric condition. This would be expected, and alongside the correlational data from the Control and Egocentric conditions does suggest that the desktop PC version of the task is measuring the behaviours expected for success at this place learning task.

This experiment compared the performance of Young, Middle, and Old age groups using the desktop PC version of the place learning task to identify whether the task is sensitive enough to measure age-related decline. The results indicated that the task successfully replicated previous findings, showing clear decrements to the processing of allocentric spatial information in older adults, and less severe decrements to the ability to reliably use egocentric spatial information. This suggests that the task represents a robust tool for measuring these different aspects of navigational behaviour (Commins et al., 2020), and should be used to explore further individual differences in the future, e.g. sex differences, and differences between clinical populations.

2.7 General Discussion

This chapter reports six experiments that describe the development and refinement of a place learning task designed to dissociate both allocentric and egocentric contributions to navigation. Versions of the task were developed for immersive VR systems that permit full physical exploration of a space, and desktop PC interfaces, in which participants would remain static, sat in front of a computer, in an attempt to identify whether the nature of the task platform is related to differences in behaviour.

Experiment 1 comprised an initial attempt to design the immersive VR version of the task. Placement error was greatest in the Egocentric condition, similar to findings reported by Merhav & Wolbers (2019), though there were no differences in placement error between the Control and Allocentric conditions. The battery of associated cognitive tasks revealed some interesting correlations, for example, strong performance on the MRT was associated with strong performance during Allocentric trials. Whilst this finding replicates literature that examined mental rotation alongside desktop PC place learning (Driscoll et al., 2005; Schoenfeld et al., 2010a), the data indicated that performance did not significantly differ between the Control and Allocentric conditions. This contrasts with findings reported by Merhav & Wolbers (2019) and may mean that this initial design of the task was not sufficiently sensitive to record differences in placement error between the Control and Allocentric conditions.

The format in which participants received trial feedback was modified for Experiment 2, in attempt to make the task more sensitive between differences in the Control and Allocentric conditions. This was successful, as both desktop PC and immersive VR versions of the place learning task showed that placement error was more accurate in the Control condition than in the Allocentric condition. Experiment 2 also directly compared performance between the two versions of the task designed for each platform. This comparison showed no differences in scaled placement error in either the Control or Egocentric condition, however, there was a large difference in scaled placement error in the Allocentric condition, across the two platforms. This cross-platform inconsistency presents an important theoretical implication as assays of allocentric navigation on desktop platforms may not match those conducted with fully motile participants. Importantly, data from the Allocentric condition contrasts greatly with models of human navigation that suggest that idiothetic self-motion cues primarily support behaviour reliant upon egocentric cues (Huffman & Ekstrom, 2020).

Experiment 3 was designed in response to the onset of the COVID-19 pandemic, and involved the deployment of the desktop PC version of the place learning task to a format suitable for completion within a web-browser. This experiment also explored the role of unreliable landmarks during Egocentric condition trials, as their presence may disrupt the ability to reliably learn the Egocentric spatial information (Doeller et al., 2008; Zhao & Warren, 2015a,b). The between subjects manipulation of landmark presence had an effect on placement error, as participants in the Landmarks Absent group replaced the

target more accurately than those in the Landmarks Present group during Egocentric trials. This experiment also recorded path data, including the number of viewpoint rotations. These data indicated that during the Egocentric condition, participants in the Landmarks Present group took less efficient paths and made more viewpoint rotations than participants in the Landmarks Absent group. This behaviour may reflect reorientation to the unreliable landmarks, which would explain the decrement in Egocentric trial placement error observed for this group.

Experiments 4 and 5 were designed to respectively replicate Experiment 3 and extend the design to the immersive VR version of the place learning task. Experiment 4 replicated the results of Experiment 3 fully, suggesting that the desktop PC version of the task is reliable, and that participants can more reliably acquire and employ Egocentric information when unreliable landmark cues are not present. The results from Experiment 5, however, demonstrated a different set of results. In Experiment 5's Egocentric condition there were no clear differences between the two groups in measures of placement error, path efficiency, and the number of head turns. This finding was unexpected, as influential theories of navigation are based on assuming equivalence between desktop PC and fully motile forms of navigation (Hartley et al., 2003; Taube et al., 2013). The findings from Experiments 4 and 5 indicate that unreliable visual information wields less disruptive influence on the use of egocentric information when participants are motile, compared to when navigation is primarily conducted via a visual modality.

The desktop PC version of the task was validated in Experiment 6, through a comparison of performance across the lifespan. The placement error measure indicated that the well documented age-related decline was observed in the Allocentric condition, and that a broad general age-related decrement was observed in comparisons between Young and Old groups in the Control and Egocentric conditions. These data suggest that the task is sensitive to individual differences across participants, suggesting that the task could be used in the future as a tool for characterising differences in allocentric or egocentric spatial behaviour that are associated with clinical conditions, as the vMWM has been used previously with conditions such as Alcohol Use Disorder (Ceccanti et al., 2018), Fetal Alcohol Syndrome (Hamilton et al., 2003), Schizophrenia (Folley et al., 2010), Transcranial Global Amnesia (Bartsch et al., 2010), and Traumatic Brain Injury (Skelton et al., 2000; 2006). A further advantage of the task reported here is that the inclusion of an Egocentric condition provides a supplementary diagnostic component of egocentric spatial precision

that is lacking in the vMWM.

The correlation analyses in Experiment 6 demonstrate interesting relationships between the behavioural measures. They suggest that in the Control and Egocentric conditions, successful navigation to the target location during the Test stage is reliant on both taking efficient paths, and making fewer viewpoint rotations. This likely reflects participants attempting to replicate the path taken to the target in the Training stage during the Test stage. In contrast, in the Allocentric condition, accurate performance is associated with a greater number of viewpoint rotations and more circuitous paths, which may reflect reorientation behaviours. These analyses present a richer understanding of participants' behaviour during this task, and may demonstrate that success in each condition is contingent on behaviours associated with the condition's reliable cues.

The key theoretical implication from the experiments reported in this chapter is that there are clear performance differences between desktop and immersive VR adaptations of the same task. Much of the navigation literature is based on the assumption of equivalence between motile exploitation and that conducted when a participant is static, e.g. that navigation is reliant upon an amodal representation formed by the visual system (Huffman & Ekstrom, 2019a; Wolbers et al., 2011). This theory is not commensurate with the results reported in this chapter, as results from the immersive VR version of the place learning task suggest motility does inform the precision in identifying a target location using either Allocentric or Egocentric information. This implication of these findings is that navigational theories should be empirically challenged using assays of behaviour that incorporate motility.

Whilst these findings may imply challenges for established navigational theory, it is important to recognise caveats to the results reported in this chapter. The nature of the task designed in this chapter's experiments may be susceptible to cross-platform differences in the fidelity of control and movements within the VE. For example, on the immersive VR platform, one has much greater granular control over the location of the target during the Test stage, as it is attached to the controller and consequently has as many degrees of freedom in movement as the participant's arm. In contrast, on the desktop PC platform, the extent of a participant's control over the location of the target object is limited to a single linear axis dictating forwards and backwards movement, and the translational rotation of the viewpoint. This facilitates a greater precision in the use of landmarks, and may

increase their utility in the immersive VR version of the task, as one can more accurately align the target object with fixed reference points in the environment. This is potentially reflected in literature that reports strategy differences across desktop PC and immersive VR place learning tasks, for example, McAvan et al. (2021) reported that groups of both younger and older adults employed beacon strategies focusing on a single landmark to find a target location in an immersive VR task. This contrasts with data reported from vMWM tasks conducted using desktop PCs, in which younger and older adults favoured qualitatively different strategies, with older adults employing less efficient navigation behaviours (Schoenfeld et al., 2010b). These cross-platform behavioural differences may explain the placement error differences across platforms (e.g. in the Allocentric condition) reported in this chapter.

A further caveat is the differences between the scales of environments employed in the two versions of the task. Extant literature has reported that different types of navigational cues may be offer more or less utility across scales (Learmonth et al., 2008; Montello, 1993; Padilla et al., 2017; Wolbers & Wiener, 2014), and that larger scale vMWM environments can exert a negative impact upon the difficulty with which participants find the hidden platform (Commins et al., 2020). There may then be scale-related differences between the two tasks that affect the patterns of results reported in Experiments 2, 4, and 5. Indeed, Huffman & Ekstrom (2020) presented a model that hypothesised that proprioceptive information may be of greater utility in smaller scale environments. This may provide an explanation as to the lack of cross-platform equivalence in Experiment 2's Allocentric condition, however, Huffman & Ekstrom's (2020) would also predict placement error advantages in the immersive VR task, in both the Control and Egocentric conditions. As Experiment 2's data only showed a cross-platform difference in the Allocentric condition, the relationship between scale and motility associated with the task platform should be more thoroughly interrogated experimentally.

2.8 Conclusion

The experiments reported in this chapter demonstrate clear differences in the patterns of results between motile navigation using an immersive VR system, and static navigation conducted on a desktop PC platform. Whilst the observed results are consistent with data reported from each of the two platforms (Ferguson et al., 2019; Livingstone-Lee et al., 2014;

Merhav & Wolbers, 2019), the cross-platform differences indicate that a more detailed interrogation of behaviour is required to refine the emerging picture. This is particularly important as these data highlight the need to ensure that theories of navigational behaviour are also adequately tested in immersive VR contexts, as opposed to solely on desktop PC platforms. The use of immersive VR systems provides an opportunity for participants to naturalistically navigate through an experimentally controlled environment, and also permits manipulations that would otherwise be impossible within a real-world context (e.g. employing 'wormholes' to test theories of spatial representation: Murry & Glennerster, 2021; Warren et al., 2017). The increased use of these methodological approaches are necessary for interrogating theories of navigation that are currently based on desktop assays of human behaviour in conjunction with immersive assays of rodent behaviour. There are challenges in equating platforms, e.g. environmental scale and the fidelity of control, but it remains essential that these theories are tested as comprehensively as possible to obtain a veridical understanding of navigational behaviour.

Chapter 3

Probabilistic Cueing in Immersive VR

Sensitivity to the spatial distribution of search targets requires a robust representation of space to ensure that one remains oriented and focuses effort in target-rich regions. As described in Chapter 1, assays of this behaviour are largely found in the visual search literature in which participants, whilst static, look for a target on a fixed 2D array. This is fundamentally different to real-world search, in which one explores space physically, and needs to develop and maintain an updated representation of the immediate environment, to ensure search remains efficient (Gilchrist et al., 2001).

This chapter reports the development of a large-scale search task that examines probabilistic cueing. Its design is based on the task employed by Smith et al. (2010), and involves participants searching for a target amongst an array of distractors in a large scale circular environment. Smith et al. (2010) report a series of experiments that each interrogate the parameters under which probabilistic cueing can be observed in this context. In sum, a probabilistic cueing effect was only observed when participants could successfully integrate both allocentric and egocentric cues in conjunction. These findings contrast with those reported by Jiang et al. (2014), who observed probabilistic cueing effects when participants could use only allocentric or egocentric cues in isolation. Jiang et al.'s (2014) findings can be reconciled with those reported by Smith et al. (2010) as the environment employed by Jiang et al. (2014) comprised a rich visual scene, which contrasts greatly with the controlled laboratory based environments employed by Smith et al. (2010).

The use of immersive VR can address these differences by presenting participants with a physically explorable 3D space that is a controlled environment. Immersive VR has been employed previously in studies examining search behaviour and foraging in large scale

environments (De Lillo & James, 2012; De Lillo et al., 2014; Li et al., 2016, 2018; Ruddle & Lessels, 2006, 2009), though it has not previously been used to examine probabilistic cueing. In Experiments 6 and 7, the same wireless immersive VR system used in Experiments 1, 2, and 5 from Chapter 2 was employed. The use of an immersive VE allows total control over an experimental environment, to an extent that is impossible in tasks conducted in the real world, so the visual information available to participants is limited to that visible within the VE. For example, in the experiments reported here, the environment was hidden between trials, ensuring that participants only had access to cues in the environment during trials. This is simpler and more controlled than blindfolding a participant, and maintains a level of experimental control that has perhaps been lacking in previous assays of large-scale cueing behaviour.

The two experiments reported in this chapter each employed a large-scale search task that was based on the design of Smith et al. (2010) and were conducted in immersive VR. This would present a validation of the immersive VR, as the platform has been underutilised in the search literature. It is therefore important to identify whether findings from tasks conducted in real-world contexts generalise to those that employ immersive VR systems. The experiments were designed to assess whether findings from Smith et al.'s (2010) study could be replicated in an immersive VR context. In particular, Experiments 2 and 3 from that study were recapitulated, since the former (Experiment 2) established a probabilistic cueing effect in large scale search, whereas the latter (Experiment 3) found that the effect was not observed when the cue was specified in an allocentric reference frame only. Since Jiang et al. (2014) found that cueing was observed when it was specified in allocentric coordinates, the present investigation allowed us to examine whether these contrasting effects were due to the information present within the search environment. Ensuring effects reported in previous research are replicated provides an opportunity to address a perceivable weakness in the field of Psychology as a whole, i.e. whether previously published experimental findings are robust and can actually be replicated (Pashler & Wagenmakers, 2012). This is particularly pertinent in contexts where contrasting findings are reported across experiments.

As with the Experimental analyses reported in Chapter 2, adoption of Bayesian analytical techniques will allow the quantification of evidence for null results, which, if replicating Smith et al.'s (2010) null findings, will provide a quantification of evidence for an absence of a difference between experimental conditions (Dienes, 2014), e.g. if participants fail to

acquire the statistical distribution of the target in space.

3.1 Experiment 7

This experiment was designed to investigate whether the conditions in which the basic large-scale probability cueing effect reported by Smith et al. (2010; Experiment 2), transfer to an immersive VR context. Participants searched for a target column within a fixed search array i.e. the locations to be searched remained stable across trials, rather than being arranged differently on each trial (as is usually the case in a standard visual search paradigm). The target appeared in one half of the array on 80% of trials (cued) and in the other half on the remaining 20% of trials (uncued). As the starting position was in the same location for the duration of the experiment, the cued side was specified in both allocentric (array-centred) and egocentric (from the perspective of the participant, at the beginning of each trial) reference frames. The cued region could therefore be identified in relation to the layout of the array (allocentric response), or on the basis of an initial directional response at the start of each trial (egocentric response).

Experiment 7 was also designed to incorporate additional measures of individual difference in order to ascertain whether participant performance in other visuospatial domains might predict sensitivity to probability cues (i.e. the likelihood that a spatial cue is learnt). Deployment of supplementary measures of spatial cognition have been previously employed to specify the possible cognitive foundations of individual variance in search behaviour Smith et al. (2005). Alongside the search task, participants also completed the Vandenberg & Kuse (1978) Mental Rotation task (MRT; adapted by Peters et al., 1995) and the Kozhevnikov & Hegarty (2001) Perspective Taking task. The MRT is a measure of mental object rotation, in which participants are presented with a series of geometric shapes, rotated along their axes, and are required to identify which of the shapes are the same. The Perspective Taking task is a measure of the ability to shift one's imagined perspective to another location. Participants are presented with a top down array of objects, and required to imagine themselves at the location of one whilst facing another their task is then to indicate the egocentric direction of a third object, from their imagined point of view. Both tasks were administered as they have previously been found to predict large scale spatial abilities such as navigation (Kozhevnikov et al., 2006; Schinazi et al., 2013). Furthermore, the nature of allocentric manipulation in Experiment 8, might require

participants to engage in a mental transformation of the space, as the cued region of space would be fixed, but their starting position and heading would change from trial to trial. In addition, participants completed the Santa Barbara Sense of Direction Scale (SBSOD; Hegarty et al., 2002), a self-report measure of navigational ability, to identify if there was a link between large scale search efficiency and more general large scale spatial abilities such as navigation. Participants also completed the amended Edinburgh Handedness Inventory (Oldfield, 1971), as laterality has previously been associated with search efficiency (Smith et al., 2005) although not necessarily in the case of probability cueing Smith et al. (2010).

3.1.1 Methodology

Design

As described previously, the search array was randomly generated and comprised two hemispaces, comprising 8 columns each. Following the contingency employed by Smith et al. (2010) and Geng & Behrmann (2002, 2005), the target column was located in the cued side of the array on 80% of trials, and in the uncued side on the remaining 20% of trials. The identity of the cued and uncued regions were counterbalanced across participants i.e. 50% of participants were cued to one allocentrically-defined region, irrespective of their starting position, and 50% were cued to the other. During the search task, participants were required to search the array for the target column: specifically, the column that changed colour when activated. There was always a target column present in each trial, and its identity was randomised under the constraints that there would be 4 trials in which the target was located in the cued region of space (cued trials) and 1 trial in which the target was located in the uncued region of space (uncued trial) out of every 5 trials. The identity was further constrained, with each column on the cued side being the target once every 8 cued trials. A similar constraint was applied to the uncued trial targets, with each uncued column being a target every 40 trials. This reduced the probability of a column being selected as the target for two consecutive trials, to attenuate potential repetition priming effects (Walthew & Gilchrist, 2006).

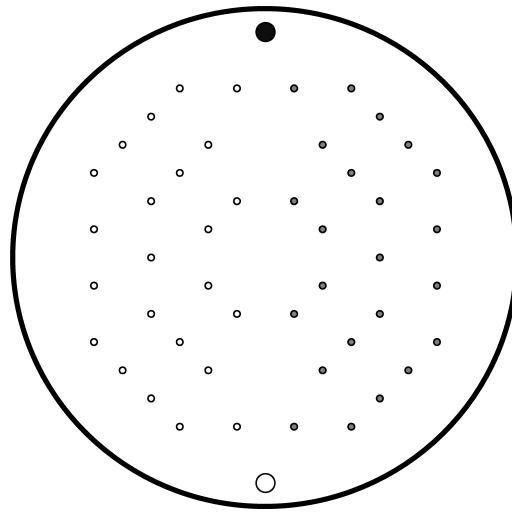


Figure 3.1: A schematic diagram of the virtual environment. The two hemispheres of potential column locations are indicated by the smaller white and grey circles. The two larger white and black circles represent starting positions. In Experiment 7, only the white starting position was used, whereas in Experiment 8, the identity of the starting position for each trial was randomised under constraints.

Participants completed 80 trials, 64 of those being cued and the remaining 16 being uncued. The trials were split into two blocks of 40 trials which, in Experiment 7, were either side of a break of up to 5 minutes. As only one participant elected to take a short break in Experiment 7, the option was removed for Experiment 8.

Participants

Participants were recruited from the University of Plymouth ($N = 24$; 19 female), and were given course credit in return for participation. The age of participants ranged from 18 to 28 years ($M = 20.33$, $SD = 2.32$). Each participant was physically able to explore the immersive VR space, and did not experience any side effects from the use of the HMD (see Experiment 7 Results, section 3.1.3). This number of participants is sufficient to detect large effect sizes.

Apparatus and Materials

This experiment took place in the University of Plymouth's large scale immersive VR laboratory, and used the same immersive VR system described in Chapter 2 (see Chapter 2, section 2.1.1 for further detail). The task and VEs were built using Unity Professional

Software (Version 2019.2.12; Unity, 2019), and run through the Unity Professional editor, using the SteamVR plugin (Valve Software, 2019). The VE for the experimental trials comprised a circular arena with a diameter of 4.5 Um . The textures used in the experiment were photorealistic seamless textures, selected to minimise the presence of additional landmarks cues in the environment. The search array comprised 16 columns, each 1 Um tall with a diameter of 20 Unity centimetres (Ucm). These were textured with a seamless photorealistic texture, coloured within the Unity software to be red (RGB: 158-0-0). The target column, when found by a participant changed colour from red to turquoise (RGB: 43-124-255).

The search array used in the experimental trials was randomly generated for each participant, under specified constraints. Columns were generated in 16 out of 46 possible locations, organised in concentric octagons with the mid-sagittal column of potential locations removed (this was so that no potential locations were positioned directly on the midline of the search space, from the perspective of the starting positions; see Figure 3.1). The array was centred within the circular arena, and its entirety fit within a 3x3m region. The mid-sagittal axis was used to divide the locations into cued and uncued hemispaces. Half of the columns would be placed at randomly selected locations in the cued region and the remaining 8 columns would be placed at randomly selected locations in the uncued region (see figure 2A for an example of an array, and 2B for a participant's in-trial perspective of that same array). This randomised distribution of the columns across each side of the array ensured that each region's layout was distinct for each participant, across both experiments.

Participants' starting position in this experiment was located 2.1 Um from the centre of the space, along the mid-sagittal axis, and was indicated by a green disc with a diameter of 50 Ucm .

Procedure

At the start of the experimental session, participants completed the SBSOD (Hegarty et al., 2002), the amended Edinburgh Handedness Inventory (Oldfield, 1971; Schachter, 2000), and the VR Sickness (Kim et al., 2018a) questionnaires. Participants then completed the Perspective Taking task (Kozhevnikov & Hegarty, 2001) and the MRT (Peters et al., 1995; Vandenberg & Kuse, 1978). The MRT was administered over two halves, with participants

completing the each group of 12 trials within a 3 minute time limit, with a 3 minute break between both halves.

Once the questionnaires and cognitive measures were completed, participants were then equipped with the VR system. Before starting the experimental task they were shown the Steam VR Chaperone system as in the immersive VR experiments conducted in Chapter 2. The system was sufficient to ensure that no participants experienced any contact with the walls of the laboratory, but were also confident to move freely around the search space without fear of unexpected collision.

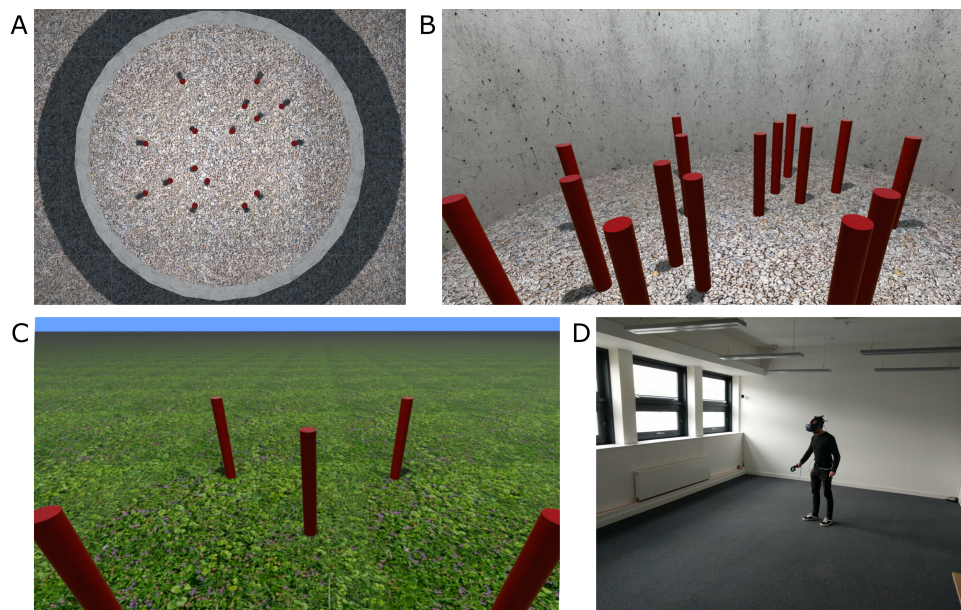


Figure 3.2: Screenshots taken from the experimental task showing: A) a top down view of the experimental environment, B) the experimental trial environment, and C) the practice trial environment. Image D) shows the VR equipment employed in this study, as well as the space in which the experiments were conducted.

Participants initially completed four practice trials, which took place in a simplistic environment comprising a single plane and a search array with 5 columns identical to those used in the experimental trials. These columns were located at the centre of the environment and arranged in the formation that one would see on dice (i.e. four columns forming vertices of a square, with the final column positioned in the centre; see figure 3.2C). In each practice trial, the target column was one of the four corner columns, each designated in a random order.

Starting positions for each trial (both practice and experimental) were initially indicated

with the environment hidden from view i.e. the entire visual scene was black, and the only visible object was the marker for the starting position. Participants were required to stand over this marker and to press the trigger on the controller to initiate the trial. The trial would only initiate when the tracker (worn around each participant's midriff), was positioned over the starting position marker. When correctly stood at this location, participants intuitively faced towards the centre of the arena to begin each trial. Once the trial had been initiated the experimental environment was revealed to participants and the starting position marker was hidden. Participants would be required to inspect the columns in the search array to find the target. An inspection involved placing the controller inside of a column and pressing the trigger. To compensate for the relative difference in tactile feedback, compared to the mechanical activation of individual switches in Smith et al.'s (2010) study, each inspection was accompanied by audio feedback (a buzzer sound) to make participants aware that their action had been registered by the program. When the target column had been inspected, it changed colour and participants received alternative audio feedback (a chime) indicating that the target had been found. The trial environment remained visible with the target column still highlighted in turquoise for 5 seconds, after which the environment, including the search array, was hidden from view (the entire environment faded to black), and the starting position marker for the next trial was then made visible to participants.

At the end of the experiment, and after removing the HMD, participants were asked about their awareness of the probabilistic manipulation. This assessment comprised three probe questions, with the first asking participants if they used a specific strategy to find the target on each trial. If participants did not respond by explicitly stating that they focused their search on the cued regions, they were then asked if they had a sense of where the target was likely to appear on a given trial. If they did not answer this question with an indication that they thought the target was likely to appear in the cued region, they were asked a final question: If I told you that the target was more likely to be in one side, would you be able to guess which one? These measures have been previously used to assess the level of explicit awareness of probabilistic manipulations (Chun & Jiang, 1998; Smith et al., 2010), and provide insight into the extent of a participant's awareness (i.e. a correct answer after the first question demonstrates clearer knowledge of the manipulation than a correct answer to a binary left/right alternate forced choice). After the probe questionnaires had been answered, participants then completed the VR Sickness questionnaire (Kim et al.,

2018a) again.

3.1.2 Analysis

Four main dependent variables were analysed in the two experiments here reported. The first was the latency between the trial beginning and the target being found, recorded to millisecond accuracy. Second was the total number of individual inspections to search locations (i.e. activation of columns) made in a single trial. Third was the length of the search path taken by the participant, in U m. This was computed from the distance between the starting position and the first column inspected, then the distance between all subsequent columns inspected. The final measure was the percentage of trials in which a column in the cued region of space was visited first. Search latency, path length, and the number of searches made were each analysed using a 2 (Probability: cued, uncued) \times 2 (Block: Block 1, Block 2) repeated measures ANOVA. First choice data in each block was analysed using a one sample t-test, compared against a chance level of .5 (i.e. an equal proportion of first visits to each side). First choice data was also compared using a paired samples t-test, to compare the proportion of trials which started with an inspection in the cued region across trial blocks. As awareness of the cued region might not be the only factor that drove which column was first inspected by a participant, t tests were also conducted on the proportion of trials in which the first inspected column was located in the region that included the closest column to the starting position, an indicator of a systematic approach to first inspection choice. As the array layouts were randomised, for some participants, there were two regions in which the closest columns were equally proximal. In these instances, trials that met this condition in both Experiment 7 and 8 were removed from the analyses. Additionally, similar analysis was conducted on the proportion of trials in which the region to the left of the participant's starting location was inspected first, which would be indicative of a left side bias (Sosa et al., 2010). These two supplementary analyses were compared to a chance level of .5.

The measures above, along with those recorded from the SBSOD and Edinburgh Handedness Inventory questionnaires, and the perspective taking task and MRT were analysed using a Pearson's correlation, to identify associations between these variables. As efficient searching in this task involves focusing search in the cued region of space, difference values were calculated for search latency, path length and the number of searches made in

a trial. These values comprised the difference between mean values on cued and uncued trials for each measure, for each participant. A larger value would indicate a participant who was more efficient at learning the probabilistic distribution, as it indicates a focus on the cued region of space. These difference measures, alongside the first choice measures, may provide insight into individual differences in search strategy (i.e. do individuals follow a systematic search pattern, or do they prioritise their search in a particular region of space?). Additionally, the number of revisits to each previously inspected column were recorded for each participant, and entered in to the correlation matrix, as this provides a further measure of search efficiency (i.e. more efficient search involves fewer revisits to previously inspected columns). For the correlation analysis, participants' probe question answers were coded depending on which question, if any, they correctly identified the cued region. If they identified it correctly in the first question, their probe question score was coded as 3, if they identified it in the second question, their score was coded as 2, and if they identified it in the final question, their score was 1. If they did not identify the cued region correctly in the final forced-choice component, their score was coded as 0.

Laterality Quotient, as measured by the Edinburgh Handedness Inventory, was coded such that lower scores indicated left laterality, and higher scores indicated right laterality. The SBSOD was coded in the same way as Experiment 7, with higher scores indicating greater navigational proficiency, and lower scores indicating lower proficiency. For the VR Sickness Questionnaire, lower scores were coded as a lower severity of side effects, and higher scores coded as indicating more severe side effects.

As in the experiments reported in Chapter 2, Analyses were conducted in R (R Core Team, 2020) using the afex (Singmann et al., 2016) and BayesFactor (Morey & Rouder, 2018) packages.

3.1.3 Results

Descriptive statistics for trial latencies, path length, the number of column inspections, and percentage of trials with a first choice in the cued region are visualised in Figure 3.3. For latency to find the target, there was a significant effect of probability, $F_{(1, 23)} = 8.96$, $p = .006$, $\eta_p^2 = .27$, $BF10 = 66.48$. There was a significant effect of probability on measures of both path length, $F_{(1, 23)} = 12.17$, $p = .002$, $\eta_p^2 = .18$, $BF10 = 7340.34$, and the total number of inspections made $F_{(1, 23)} = 11.1$, $p = .003$, $\eta_p^2 = .33$, $BF10 = 35293.47$. This revealed shorter

search paths and fewer inspections for cued trials, compared to uncued trials. In contrast, for path length, there was no significant effect of block, $F_{(1, 23)} = 3.4$, $p = .08$, $\eta_p^2 = .13$, $BF10 = 0.37$, and no significant interaction between the factors $F_{(1, 23)} = 0.02$, $p = .88$, $\eta_p^2 = .001$, $BF10 = 0.28$, with the Bayes Factor suggesting an absence of an interaction. Similarly, for the number of inspections, there was also no significant effect of block $F_{(1, 23)} = 2.47$, $p = .13$, $\eta_p^2 = .1$, $BF10 = 0.34$, and no significant interaction between the factors $F_{(1, 23)} = 0.03$, $p = .87$, $\eta_p^2 = .001$, $BF10 = 0.31$, with the Bayes Factor again suggesting an absence of an interaction.

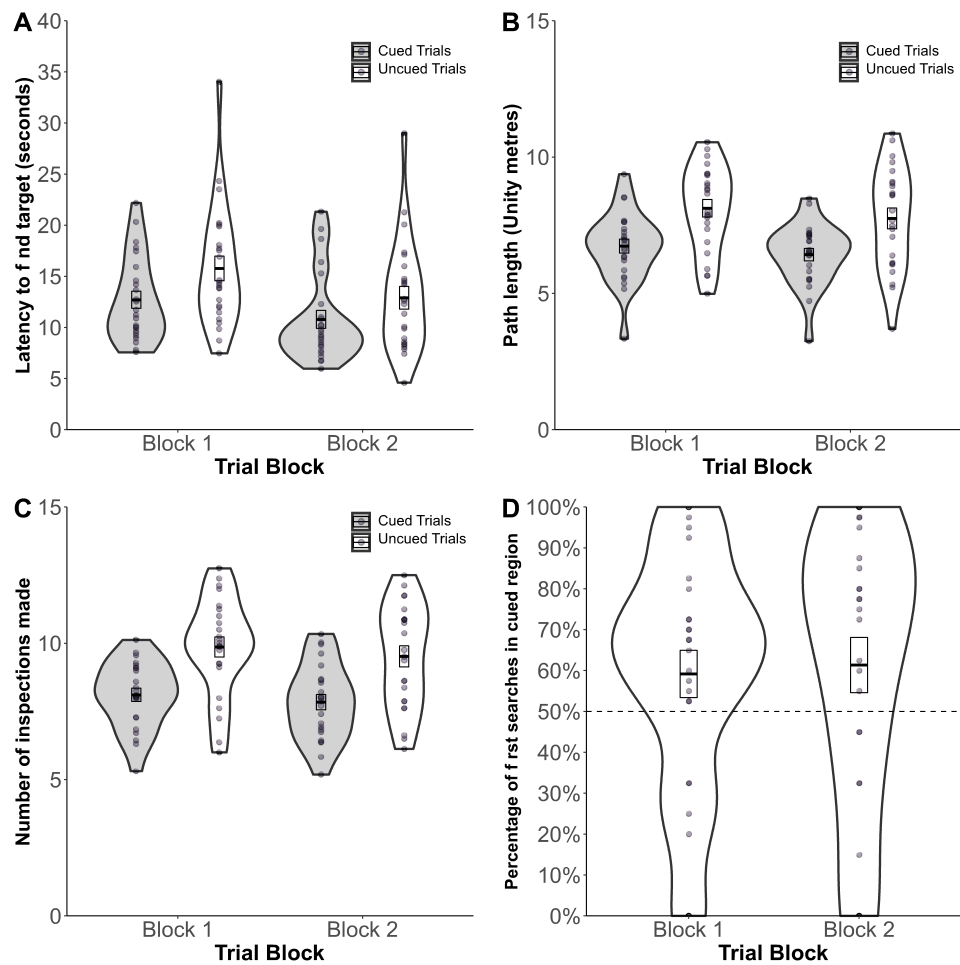


Figure 3.3: Data visualisation for Experiment 7. Each violin plot shows the distribution of the condition along its flank, and mean scores for each participant along its central axis. The crossbars show the mean value per condition, and are bounded by standard error. Plot (a) shows the mean latency to find the target for each trial type in each block. Plot (b) shows the mean path length for each trial type in each block. Plot (c) shows the mean number of column inspections made in each trial type in each block. In plot (d), the chance value of 50% is indicated by the dashed horizontal line.

The percentage of trials that started with an inspection in the cued region of space did not differ to a chance level of .5 in trial Block 1, $t_{(23)} = 1.58, p = .13, BF10 = 0.64$ or in trial Block 2, $t_{(23)} = 1.68, p = .11, BF10 = 0.73$. Furthermore, there was evidence to suggest that there was no difference between the number of trials that began with an inspection of the cued region in trial Block 1 and in trial Block 2, $t_{(23)} = 1.97, p = .34, BF10 = 0.33$. To identify alternative antecedents of participants' first choice of column to inspect, a second t-test was performed that compared the percentage of searches that started with an inspection of a column in the region closest to the starting position (i.e. the side of the array featuring the closest column to the starting position, regardless of the side that it occupied) to chance ($M = 67.2\%$, $SE = 6.4\%$). Five participants were removed from this analysis as there were two columns equally close to the starting position in the randomly generated arrays on each trial). This showed a significant difference to a criterion of .5, $t_{(23)} = 2.7, p = .015, BF10 = 3.79$. Finally, to investigate whether a participant's first choice was driven by a left side bias (Sosa et al., 2010), a final t-test was conducted on the percentage of trials starting with a search in the left side of the array (irrespective of the side of the probability cue). The mean percentage of trials started with an inspection in the left side of the array was 52.3%, with SE of 1.3%. There was no significant difference from a chance value of .5, though there was no evidence of an absence of a difference, $t_{(23)} = 0.36, p = .72, BF10 = 0.23$.

In total, 83.33% of participants correctly identified the cued region in their responses to the awareness probes: 12.5% identified the cued region in the first question (score: 3), 20.833% identified the cued region in the second question (score: 2), and 50% identified the cued region in the third and final question (score: 1). To provide a basic assay of participants' awareness of the manipulation, a binomial test was conducted on the probe question data. For the purposes of this test, participants were coded as being aware of the manipulation if they responded with the correct identity of the cued region in any of the three questions (i.e. they had a score of 1 or above). The results showed that the number of participants that correctly identified the cued region (at any stage of the probe procedure) was significantly greater than chance (i.e. 50% of participants), $p < .001$, and there was decisive evidence to support this, $BF10 = 126.253$.

Difference measures between cued and uncued trials were calculated for trial latency, path length, and the number of inspections in a trial. These, alongside the participant's level of awareness (measured by the probe questions), the percentage of trials in which the cued region was inspected first, and the percentage of trials in which the closest column was

Table 3.1: Correlation matrix with p values for variables in Experiment 7.

	FCCue	FCClo	Revisits	MRT	PTE	SBSOD	LQ	PA	LatDiff	InspDiff	PathDiff
FCCue	1										
FCClo	-0.191	1									
Revisits	-0.09	-0.08	1								
MRT	-0.16	0.15	-0.4	1							
PTE	0.31	0.05	0.24	-0.04	1						
SBSOD	0.15	-0.23	-0.16	-0.1	0.03	1					
LQ	-0.08	-0.47*	-0.02	-0.08	-0.07	-0.51*	1				
PA	-0.11	0.1	-0.39	0.2	-0.03	0.09	-0.13	1			
LatDiff	0.29	-0.14	-0.19	-0.33	-0.26	0.15	-0.19	0.01	1		
InspDiff	0.22	-0.2	-0.28	-0.28	-0.26	0.14	-0.08	0	0.92****	1	
PathDiff	0.22	-0.22	-0.32	-0.2	-0.27	0.15	-0.09	-0.01	0.92****	0.99****	1

FCCue: percentage trials with the first choice in cued region; *FCClo*: percentage trials starting with the first choice of the closest column; *MRT*: mental rotation task accuracy; *PTE*: perspective taking task error; *SBSOD*: Santa Barbara Sense of Direction Scale; *LQ*: amended Edinburgh Handedness Inventory Laterality Quotient; *PA*: probe question level of awareness; *LatDiff*: difference between latency to find the target on cued and uncued trials; *InspDiff*: difference between the number of inspections on cued and uncued trials; *PathDiff*: difference between path length on cued and uncued trials.

*** $p < .0001$, * $p < .05$.

inspected first, were entered into a correlation matrix alongside the SBSOD and Edinburgh Handedness Inventory questionnaires, and the data from the MRT and Perspective Taking Task (see Table 3.1). There were significant correlations between each of the difference measures: trial latency and path length, $R^2 = .92$, $p < .001$, $BF10 = 3.723e+7$; trial latency and number of columns inspected, $R^2 = .92$, $p < .001$, $BF10 = 6.028e+7$; and, path length and the number of columns inspected, $R^2 = .99$, $p < .001$, $BF10 = 2.055e+133$, with each correlation supported by decisive evidence from the Bayes Factor. This suggests that they reliably measured the same aspects of search performance. There was also a significant correlation between the Edinburgh Handedness Laterality Quotient (LQ) and SBSOD scores, $R^2 = .51$, $p = .011$, $BF10 = 5.934$, which suggests there is strong evidence that, in this sample, participants who were more strongly lateralised to the left, self-reported as better navigators. Furthermore, there was also a significant negative correlation, albeit with inconclusive Bayesian support, between LQ and the proportions of trials that started with an inspection in the closest region of the array, $R^2 = -.47$, $p = .044$, $BF10 = 1.872$. This indicates that the more left lateralised a participant was, the more likely they would be to inspect a column in the closest side of the array first.

It is interesting to note that there was no significant correlation between the proportion of trials starting with a search in the cued region and the difference measures for: trial latency, $R^2 = .29$, $p = .16$, $BF10 = 0.632$; searches made, $R^2 = .22$, $p = .31$, $BF10 = 0.411$; and, path length, $R^2 = .22$, $p = .30$, $BF10 = 0.418$. Furthermore, there were also no significant correlations between probe awareness and the difference measures for: trial latency, $R^2 = 0.26$, $p = .23$, $BF10 = 0.5$; searches made, $R^2 = .18$, $p = .39$, $BF10 = 0.358$; and, path length, $R^2 = .18$, $p = .39$, $BF10 = 0.359$. This suggests that the extent of a participant's explicit awareness of the statistical contingency was not necessarily related to their search efficiency, and that sensitivity to the probabilistic cue may not have guided the initial choice of inspection location.

To identify whether participants suffered any negative effects from using the VR equipment, a t-test was conducted on the pre- ($M = 2.85$) and post-experiment ($M = 1.88$) VR Sickness questionnaire scores. This test was found no significant difference between the two measures, $t = 1.54$, $p = .137$, $BF10 = 0.61$, suggesting that sensations of nausea did not differ between pre- and post-experiment measures, though there was only anecdotal evidence from the Bayes Factor to suggest an absence of this difference.

3.1.4 Discussion

The immersive VR search task used in this experiment successfully replicated the probability cueing effect previously been reported in large-scale real-world search (Smith et al., 2010; Experiment 2). Participants were faster to find the target in trials when it was located in the cued side of space and, therefore, slower to activate it when it appeared in the uncued side. This is indicative of a search bias towards the cued (or rich) side of space and was also reflected in other dependent measures i.e. participants also took a shorter path to find the target, and made fewer inspections, when it was in the cued region. Furthermore, many participants (83.33%) correctly identified that the target was more likely to appear in the cued region of space when their awareness of the manipulation was probed.

There were, however, two general findings that were not consistent with those of Smith et al. (2010) in their Experiment 2. First, there was evidence that participants were no more likely to begin their search in the rich region of space than in the sparse region of space. This is likely due to procedural differences as, in the present experiment, there was often no cost to inspecting the closest column due to its potential proximity to the starting location.

Indeed, this interpretation is supported by the observation that participants inspected the side of the array that contained the closest column more often than chance. This contrasts with Smith et al.'s (2010) search array, in which both the cued and uncued region were more distal from the starting position, thus associating greater cost with the first inspection. The second difference was that the present experiment showed evidence for an absence of interaction effects (between trial type and experimental block) for the behavioural measures of search efficiency. This indicates that the cueing effect was likely established early on, and that its strength was maintained across the course of the experiment. This differs from the results from Smith et al.'s (2010) Experiment 2, in which a cueing effect was observed within the first half of the experiment, and was further strengthened across the course of the experiment.

A further procedural difference between this experiment and Smith et al.'s (2010) Experiment 2 is that the test environment was not continuously visible during the course of the experiment, with the array and environmental setting being hidden from view between trials. One might expect this to have impacted upon the probabilistic cueing effect, especially given the narrative of Smith et al.'s (2010) six experiments. However, only slight discrepancies between experimental findings were apparent i.e. the absence of a cueing effect in first-visit behaviour, and the lack of interaction effects between trial type and block. This is perhaps further evidence for the integral role of the array's perceptual stability to probabilistic cueing in large scale space i.e. in the studies reported by Smith et al. (2010), and Jiang et al. (2014), the search tasks were conducted in real physical spaces, where the environment could not be hidden from participants (although Jiang et al. (2014) employed a blindfold when setting-up individual trials). In contrast, the current paradigm allowed for the environment to be extinguished between search trials, which may have increased task difficulty for some participants if they required themselves to be reoriented in the test space at the start of each trial (i.e. as a result of the unstable percept of the array). Finally, the observed probabilistic cueing effect further confirms that it can be robust to movement around a large scale space (see also: Jiang et al., 2014). This contrasts with visual search evidence for a deleterious effect of egocentric movement on some forms of statistical learning (e.g. in the case of contextual cueing: Jiang et al., 2013).

One surprising element of the results is the apparent absence of a relationship between some of the performance measures. The lack of reliable correlation between the awareness probe and behavioural measures of search efficiency is surprising, since one would expect

an explicit awareness of where the target is likely to be in space to drive the focus of a participant's search. This may be a result of the awareness measure not being sufficiently sensitive to pick up on performance over the course of the experiment, or the binary nature of the choice not reflecting the pattern of participant behaviour (Vadillo et al., 2020). Furthermore, if a participant appeared to be searching efficiently, then it would be expected that they would focus their initial search in that region, and yet first inspection choice was not correlated with measures of search efficiency. This further supports the idea that first choice was, instead, seemingly driven by the proximity of locations to the starting position.

It is worth noting that, contrary to predictions, there was no reliable relationship between additional measures of spatial ability (i.e. mental image manipulation, sense of direction) and performance in the large-scale search task. This might perhaps be due to the combination of cues available to participants in this first experiment i.e. the identity of the cued region could be learned using contributions from both allocentric and egocentric spatial reference frames (i.e. it was fixed with respect to both), which has previously been found to produce strong cueing effects Smith et al. (2010). As such, it is predicted that the manipulation of spatial reference frames in Experiment 8 might also reveal stronger evidence for individual differences in performance.

3.2 Experiment 8

Experiment 8 followed the design of Smith et al.'s (2010) Experiment 3, and was conducted to investigate whether the probabilistic cueing effect could be observed when the cue was specified in an allocentric reference frame only and, therefore, decoupled from the participant's starting position. This manipulation was achieved by specifying two starting positions, either side of the centre of the arena. This meant that a change in starting position would be associated with a change in egocentric perspective at the beginning of the trial, but the cued region of space would occupy a fixed allocentrically-defined region within the virtual environment. Whilst there were no distinguishing landmarks within the circular arena, there were a number of cues that could contribute to participants successfully updating their location in the environment and building a statistical association between the target and the environment. First, the two different starting positions consistently occupied the same location in space, meaning that path integration (and similar idiothetic

mechanisms based on movement through space) should contribute to a coherent and consistent sense of beginning each search from one of two particular places. Furthermore, each hemifield of the space contained its own distinct configuration of search locations, providing stable information about the display, and a core cue to distinguish one side from the other.

The same battery of supplementary measures used in Experiment 7 was deployed in Experiment 8. If participants acquire the statistical distribution of the target location, then these measures may provide insight into underlying behaviours that may supplement allocentric statistical learning.

3.2.1 Methodology

Design

This experiment mostly follows the general procedure detailed in Experiment 7. However, in this particular version of the task, participants began each trial from one of two different starting positions. The starting position for each trial was counterbalanced, with 20 trials in each block starting from one end of the midline and 20 trials from the other, with an even split every 10 trials. The order in which the starting positions were selected for each trial was block randomised based on these constraints. Additionally, the target identity and trial type was randomised with counterbalancing constraints. These constraints were devised so that each column would be a target an equal number of times in each trial block. Additionally, the starting position for each trial was counterbalanced so that each starting position would be used in an equal number of trials in each block.

Participants

Participants were recruited from the University of Plymouth (N = 23; 21 female, 2 male), and were given course credit in return for participation. The age of participants ranged from 19 to 34 years (mean = 21.57, SD = 3.58). Each participant was physically able to explore the immersive VR space without experiencing any negative effect from the use of the immersive VR system (see Experiment 8 Results). This number of participants is sufficient to detect large effect sizes.

Materials & Procedure

This experiment employed the same apparatus, materials and procedure as Experiment 7. The only change was the introduction of a second trial starting position that was located on the opposite side of space from the original starting position. The two starting positions were both 2.1^Um either side of the central point of the arena along the midline and were either green or orange. The green starting position indicated the starting position to be used for the subsequent trial, and the orange starting position marker was unused.

3.2.2 Results

Descriptive statistics for trial latencies, path length, the number of column inspections, and percentage of trials with a first choice in the cued region are visualised in Figure 3.4. There was a significant effect of block on search latency in this experiment, $F_{(1, 22)} = 36.2$, $p < .001$, $\eta_p^2 = .62$, $BF10 = 28$, indicating that participants were faster to find the goal in Block 2, compared to Block 1. There was, however, no reliable effect of probability on search latency, $F_{(1, 22)} = 0.09$, $p = .77$, $\eta_p^2 = .004$, $BF10 = 0.23$, with the Bayes Factor suggesting there was no difference between cued and uncued trial latencies. Furthermore, there was an absence of an interaction between the two factors, $F_{(1, 22)} = 0.63$, $p = .44$, $\eta_p^2 = .03$, $BF10 = 0.33$.

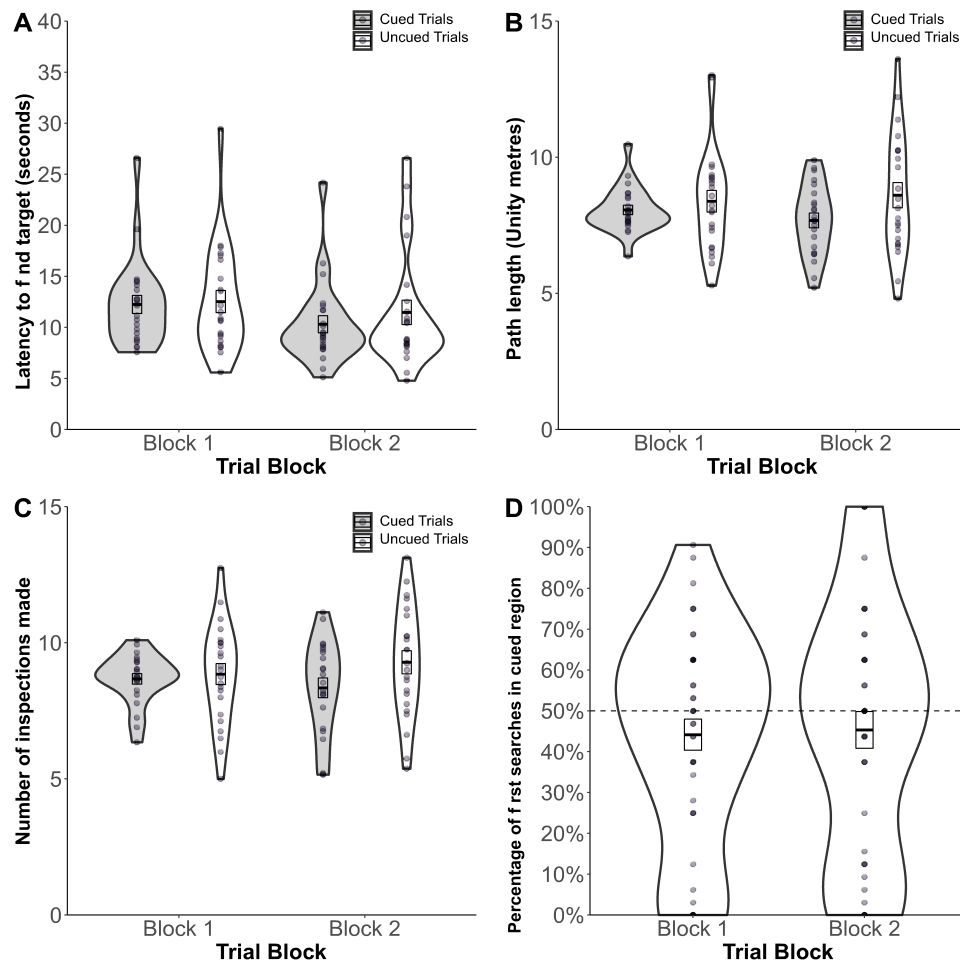


Figure 3.4: Data visualisation for Experiment 8. Each violin plot shows the distribution of the condition along its flank, and mean scores for each participant along its central axis. The crossbars show the mean value per condition, and are bounded by standard error. Plot (a) shows the mean latency to find the target for each trial type in each block. Plot (b) shows the mean path length for each trial type in each block. Plot (c) shows the mean number of column inspections made in each trial type in each block. In plot (d), the chance value of 50% is indicated by the dashed horizontal line.

Analysis of path length revealed no significant effects of either probability, $F_{(1, 22)} = 2.25$, $p = .15$, $\eta_p^2 = .09$, $BF10 = 1.36$ or block, $F_{(1, 22)} = 0.19$, $p = .67$, $\eta_p^2 = .008$, $BF10 = 0.24$, nor was there a significant interaction between factors, $F_{(1, 22)} = 1.1$, $p = .31$, $\eta_p^2 = .05$, $BF10 = 0.42$. A similar pattern of results was observed for the number of inspections made, with no significant effects of either probability, $F_{(1, 22)} = 1.15$, $p = .29$, $\eta_p^2 = .05$, $BF10 = 0.68$ or block, $F_{(1, 22)} = 0.09$, $p = .77$, $\eta_p^2 = .004$, $BF10 = 0.22$, nor was there a significant interaction between factors, $F_{(1, 22)} = 1.17$, $p = .29$, $\eta_p^2 = .05$, $BF10 = 0.9$.

Similarly to Experiment 7, participants were no more likely to initially inspect a column in

the cued region of space than chance in trial Block 1, $t(22) = 0.9$, $p = .381$, $BF10 = 0.32$ or trial Block 2, $t(22) = 0.97$, $p = .35$, $BF10 = 0.33$. Again, as in Experiment 7, participants did not start their search more often in the cued region in trial Block 2 than in trial Block 1, $t(22) = 0.58$, $p = .57$, $BF10 = 0.26$. Furthermore, for the trials that permitted appropriate analysis (half of the data for nine participants were excluded due to one starting position being equally close to both region), participants did inspect the region which contained the closest column more often than a chance value of .5 ($M = 55.2\%$, $SE = 4.51\%$), $t(22) = 3.59$, $p = .002$, $BF10 = 22.98$. Finally, there was decisive evidence to suggest that participants inspected the right side of the array first, relative to their starting position, more often than chance ($M = 18.2\%$, $SE = 0.53\%$), $t(22) = 12.19$, $p < .001$, $BF10 = 3.061 \times 10^7$.

In total, 56.52% of participants correctly identified the cued region at some point in the awareness probe procedure: 17.4% identified the cued region in the first question (score: 3), 13.01% identified the cued region in the second question (score: 2), and 26.09% identified the cued region in the third and final question (score: 1). The binomial test for awareness in Experiment 8 showed that the proportion of participants that correctly identified the cued region of space in one of the probe questions was not significantly greater than chance (i.e. 50% of participants), $p > .05$, and there was substantial evidence to suggest that there was no difference between the number of participants that did or did not identify the cued region, $BF10 = 0.306$.

A similar correlation matrix to that presented in Experiment 7 was generated to identify relationships between variables (see Table 3.2). In this experiment, there was a significant negative correlation, albeit with inconclusive Bayesian support, between the proportion of trial starting with an inspection of a column in the closest region first, and the proportion of trials initiated by inspecting a column in the cued region first, $R^2 = -.45$, $p = .031$, $BF10 = 2.31$. This indicates that participants started each trial inspecting either the cued region or the region that contained the closest column, irrespective of whether this closest region was cued or uncued. Additionally, the percentage of trials in which the cued region was inspected first correlated with the difference measures for trial latency, $R^2 = .46$, $p = .027$, $BF10 = 2.559$, number of columns inspected, $R^2 = .49$, $p = .018$, $BF10 = 3.69$, and path length, $R^2 = .49$, $p = .017$, $BF10 = 3.77$, though there was only anecdotal evidence from the Bayes Factor to support the correlation with the latency difference measure. This indicates that participants who inspected a column in the cued region first were more likely to search efficiently, as well as the inverse, that participants that did not search in the cued region

Table 3.2: Correlation matrix with p values for variables in Experiment 8.

	FCCue	FCClo	Revisits	MRT	PTE	SBSOD	LQ	PA	LatDiff	InspDiff	PathDiff
FCCue	1										
FCClo	-0.45*	1									
Revisits	0.22	-0.48*	1								
MRT	-0.15	0.11	-0.07	1							
PTE	-0.12	0.08	-0.16	-0.63**	1						
SBSOD	-0.04	-0.37	0	-0.31	0.13	1					
LQ	0.06	-0.18	-0.01	-0.16	-0.04	0.11	1				
PA	-0.36	0.37	-0.04	0.01	0.36	-0.29	-0.17	1			
LatDiff	0.46*	-0.02	0.17	-0.15	-0.01	-0.09	0.12	0.16	1		
InspDiff	0.49*	-0.02	0.14	-0.17	-0.06	-0.14	0.19	0.14	0.94****	1	
PathDiff	0.49*	-0.08	0.19	-0.14	-0.1	-0.12	0.28	0.13	0.93****	0.96****	1

FCCue: percentage trials with the first choice in cued region; *FCClo*: percentage trials starting with the first choice of the closest column; *MRT*: mental rotation task accuracy; *PTE*: perspective taking task error; *SBSOD*: Santa Barbara Sense of Direction Scale; *LQ*: amended Edinburgh Handedness Inventory Laterality Quotient; *PA*: probe question level of awareness; *LatDiff*: difference between latency to find the target on cued and uncued trials; *InspDiff*: difference between the number of inspections on cued and uncued trials; *PathDiff*: difference between path length on cued and uncued trials.

$p < .0001$ '****', $p < .01$ '**', $p < .05$ '*'

first were more likely to be inefficient.

There was a significant negative correlation between the number of trials in which the region that contained the closest column was inspected first, and the number of revisits in a trial, $R^2 = -.48$, $p = .019$, $BF10 = 3.42$. This suggests that participants who inspected this closest region first may have searched systematically in a travelling salesman approach, thus reducing the likelihood of having to revisit a column. There was also a significant negative correlation between Perspective Taking task error and MRT accuracy, $R^2 = -.63$, $p = .001$, $BF10 = 33.56$, which contrasts with the lack of such a correlation in Experiment 7. Similarly to Experiment 7 there were significant correlations between the three difference measures, trial latency and path length, $R^2 = .93$, $p < .001$, $BF10 = 5.9 \times 10^7$, trial latency and number of columns inspected, $R^2 = .94$, $p < .001$, $BF10 = 1.11 \times 10^8$, and path length and the number of columns inspected, $R^2 = .96$, $p < .001$, $BF10 = 1.11 \times 10^{10}$, again indicating, with decisive evidence from the Bayes Factor analysis, that all three variables are measuring the same aspects of performance.

Similar to Experiment 7, It is interesting to note that there was no significant correlation between awareness probe responses and the difference measures for: trial latency, R^2

=0.33, $p = .12$, $BF10 = 0.8$; searches made, $R^2 = .39$, $p = .64$, $BF10 = 1.3$; and, path length, $R^2 = .37$, $p = .08$, $BF10 = 1.8$. Additionally, there was no significant correlation between probe awareness and the proportion of trials initiated with an inspection in the cued region, $R^2 = .03$, $p = .9$, $BF10 = 0.26$. This suggests that the extent to which participants were explicitly aware of the statistical contingency was not related to their search efficiency, and that sensitivity to environmental statistics may not have guided their initial choice of inspection.

Similar to the analysis for Experiment 7, a t-test was conducted on the pre- ($M = 3.57$) and post-experiment ($M = 3.91$) VR Sickness questionnaire scores. This test also found no difference between the two scores, $t = 0.54$, $p = .598$, $BF10 = 0.25$, suggesting that participants did not suffer adverse effects from using the VR equipment in this experiment.

3.2.3 Discussion

To investigate whether probability cueing could occur in an allocentric reference frame (i.e. biasing search to a particular region of environmental space, regardless of egocentric viewpoint), participants began each trial from one of two starting positions that were located at either end of the array's mid-sagittal axis. The data showed that, on the whole, there was no reliable probabilistic cueing effect across each of the behavioural measures, with search behaviour not seeming to differ between cued and uncued trials, and participants' first inspection likely being driven by the proximity of the search locations to their starting position. These measures of efficiency are supported by the analysis of the probe questions, which presented additional evidence to suggest that participants did not explicitly learn about the manipulation (57% of participants identified the cued region). It may be, however, that the type of awareness probe employed in this experiment was not sensitive enough Vadillo et al. (2020), which is, as in Experiment 7, indicated by the absence of correlations between the awareness probe questions and measures of search efficiency. A greater understanding of participants' awareness may be elicited through more regular probe trials, following the formats described by Vadillo et al. (2020). These could be introduced in regular trial blocks during the experiment and comprise participants ranking their opinion on how likely the target was to appear in a specific region. This is supported by the awareness probe question not being associated with other measures of search efficiency, in either this experiment, or Experiment 7, indicating that it

may not appropriately capture a participant's awareness of the probabilistic distribution of the target's location.

There may, however, be individual differences in the degree to which participants formed or applied particular search strategies. This is shown by correlation analysis demonstrating that participants who tended to search in the cued region of space first were more efficient at finding the target, with these participants taking shorter paths, inspecting fewer columns on cued trials than on uncued trials, and finding the target faster, though there was only anecdotal evidence to support this last correlation. This is suggestive of a strategy that involved focusing search on the cued region. In contrast, participants that did not show a tendency to inspect a column in the cued region first tended, instead, to preferentially search the closest column, indicated by the negative correlation between these two measures. This is suggestive of an alternative strategy, which involved initiating search with an inspection of the closest column, and systematically inspecting each column in the array using a travelling salesman-type strategy. This would not be an efficient strategy for this task, due to the target's probabilistic distribution. This inefficiency is shown by the absence of a strong correlation between the proportion of trials initiated with an inspection of the closest column and the differences between trial types in latency, path length, and number of inspections. Furthermore, the significant negative correlation between the number of revisits and the number of trials that started with an inspection of the closest column also suggests a systematic approach, since a strict travelling salesman strategy (i.e. inspecting the next closest location) should be more likely to preclude revisits to previously inspected locations.

This potential difference in strategy selection may reflect individual differences in the ability for participants to orient at the start of each trial within the virtual environment. Since the environment was extinguished between trials, it is possible that participants may not have been able to develop a stable allocentric representation of the cued regions' location. If one was disoriented in this environment, then the most effective strategy would be to select the closest column and then systematically inspect the subsequent closest columns. There is, however, evidence that even children can generate an allocentric representation of navigated space when blindfolded (Bostelmann et al., 2020), which would suggest that participants in this experiment should have been able to reliably orient in the test environment, and maintain an enduring representation of their place within it, even when it was hidden from view.

These findings extend and replicate those of Smith et al.'s (2010) Experiment 3, with evidence indicating an absence of a group-level probabilistic cueing effect for a cue specified within an allocentric reference frame. This indicates that Smith et al.'s (2010) findings were not necessarily a product of a specific procedure, and suggests that the immersive VR iteration of the task provides a reliable replication. A core difference between this Experiment and the equivalent reported by Smith et al. (2010) is in the physical costs associated with making an inspection i.e. whereas participants in VR made an inspection by pressing a trigger at waist height, Smith et al.'s apparatus required them to bend down and activate switches that were embedded in the floor. One might predict that such differences would have a large effect on search behaviour (for discussion on search costs and memory see: Gilchrist et al., 2001), and yet the present results suggest that the reduced energy demands did not seem to moderate behaviour in response to a probability cue.

Once again, it is worthy of note that participants' search performance was unrelated to spatial and navigational abilities, as measured by the battery of individual differences tasks. This lack of a clear relationship may reflect the relatively sparse nature of the search environment, with fewer visual cues than are typically available in the large scale spatial tasks that are usually predicted by these measures (see Wolbers & Hegarty, 2010). Further related to this is the relative instability of the environment. In the present paradigm the search environment was extinguished between trials, which contrasts with the real world environments employed by Smith et al. (2010), and Jiang et al. (2014). This may cause initial difficulties for participants attempting to integrate the search environment across trials, when required to switch starting positions. Resolving the impermanence of the trial environment may instead be linked to spatial Working Memory (WM), which has been found to be a predictor of search efficiency in children (Smith et al., 2005).

3.3 General Discussion

In the two experiments reported here, probabilistic cueing in large-scale search was examined using a novel immersive VR methodology. Both experiments replicated research conducted by Smith et al. (2010; Experiments 2 and 3), with the methodology adapted for use in immersive VR. In each experiment reported here, participants were required to search for a hidden target, defined as the column (within an array of identical columns)

that changed colour when it was activated. The location of the target was probabilistically determined, with 80% of targets being located in the cued hemispace and 20% of targets appearing on the uncued hemispace. Sensitivity to this cue was gauged with an array of dependent measures, which indicated whether participants biased their search to the cued region of space and, therefore, were less efficient at locating the target when it was in the uncued region. Experiment 7 followed the design of Smith et al.'s (2010) Experiment 2, and broadly replicated their findings. A probabilistic cueing effect was observed in the behavioural measures, with participants demonstrating greater search efficiency (i.e., faster search time, shorter paths, and fewer inspections) when the target was located in the cued region. In addition, over three probe questions, the majority of participants correctly identified the cued region. There was a discrepancy between the findings of this experiment and its progenitor, however, in first-choice data: whereas Smith et al. (2010) found that participants were significantly more likely to begin their search in the cued region, this was not observed in the present experiment. Instead, first choice appeared to be driven by the proximity of a region to the starting position, as participants inspected a column in the region containing the closest column more often than chance. This likely results from the procedural differences between this experiment and those reported by Smith et al. (2010), as items to be inspected in the present experiment could be located within touching distance of the starting position, whereas in Smith et al. (2010), there was always a buffer zone containing no potential target objects between the starting position and the array. Having established that probability cueing could be observed in a VR replication of a previous real-world paradigm, the second experiment examined whether participants were sensitive to a cue that was restricted to an allocentric reference frame. Because participants in Experiment 7 began each search trial from the same starting position, the cue was defined in both allocentric co-ordinates (i.e., it was more likely to appear in a particular half of the array) and egocentric co-ordinates (i.e., depending on counterbalancing, it was more likely to appear either to the right or to the left of the starting position, when facing the array). The predictive properties of the starting position were, therefore, removed in Experiment 8 (a replication of Smith et al.'s [2010] Experiment 3) by introducing two starting positions at opposite ends of the mid-sagittal axis, which were used equally across the course of the experiment. The cued region remained fixed relative to the environment, although the changes in a participant's perspective meant that it no longer occupied a predictable egocentric region at start. Results from this experiment,

like those from Smith et al.'s (2010) Experiment 3, revealed no probabilistic cueing effect - i.e., there was no evidence that targets in the cued region of space were located any more efficiently than targets in the uncued region. Furthermore, there was evidence to suggest that awareness of the probability manipulation was at chance level, across participants, and there was no evidence that awareness was related to the behavioural measures. Akin to the findings of Experiment 7, first-choice behaviour appeared to be driven by the proximity of the search locations to the starting positions. This suggests that future experiments employing this sort of task should ensure there is sufficient distance between the starting positions and the array to more clearly isolate whether the initial inspection is driven by an awareness of the target's distribution in space.

These data represent the first demonstration of a large-scale probability cueing effect in immersive VR. Not only do they replicate the previous findings of Smith et al. (2010), but they also extend them to a different search context, and provide an important proof-of-concept that behavioural effects observed in veridical environmental space can be reliably observed in a virtual equivalent. Interestingly, however, the data do not assist in the reconciliation of differential findings obtained by Smith et al. (2010) and Jiang et al. (2014), with the latter demonstrating that probabilistic cueing can be observed in an allocentric spatial reference frame. Because the present findings are consistent across different manifestations of the basic Smith et al. (2010) paradigm, these broad differences in observing an allocentric basis to cueing might perhaps be explained by more fundamental procedural differences between the two tasks. Jiang et al.'s (2014) experiment was conducted outdoors on a university campus, where there was a great deal of visual information available to participants. In contrast, the experiments presented here and in Smith et al. (2010) were conducted in controlled laboratory spaces, with the only visual cue to environmental structure being the configuration of a stable search array. The VR environment was perceptually richer than the apparatus used by Smith et al. (2010), and general luminance levels were higher (to approximate daylight), but there was still an absence of extraneous (i.e., extra-array) visual cues to location and orientation, compared with those present in the naturalistic setting used by Jiang et al. (2014). It has previously been demonstrated that more impoverished visual environments can attenuate search efficiency (Ruddle & Lessels, 2006, 2009), and it would therefore make sense that participants in Jiang et al.'s (2014) study were able to develop a stronger allocentric representation of space, given a greater amount of available cues. This interpretation is

supported by the results of Smith et al.'s (2010) Experiment 5, in which the two halves of the search array were differently coloured (i.e., red vs. green). Under those conditions, and with an alternating starting position, an 'allocentric' probability cueing effect was observed, presumably because the combination of allocentric information with an additional featural cue (i.e., a distinguishing colour) assisted sensitivity to search statistics (note that colour alone was not sufficient to cue participants in the same study). This evidence perhaps highlights the importance of salient landmarks when learning about a probabilistic spatial distribution in a fixed region of space.

Aside from the nature of the search environment, and cues available within it, it is also possible that the requirements of the search process itself might contribute to the presence or absence of particular behavioural effects (see Gilchrist et al., 2001; Smith et al., 2008). In the experiments reported here, and in those reported by Smith et al. (2010), participants were required to physically explore the space, and interact with each potential search location to ascertain whether it was the target. This can be considered equivalent to a serial self-terminating (or effortful) search in the visual search domain, but where search itself is not visually guided by item-based characteristics (Duncan & Humphreys, 1989; Treisman & Gelade, 1980). However, in Jiang et al.'s (2014) study, participants were required to only locate the target and identify its colour, and could successfully complete the task from their starting position by visually scanning the environment. Physical exploration of an environment requires continual spatial updating to localise oneself in the context of the experimental environment (e.g., Gallistel, 1990). It is likely that this is more demanding than observing an array from a fixed perspective, and may therefore also contribute to the differences observed in probabilistic cueing across the studies. Indeed, this qualitative difference between the tasks is perhaps akin to the difference between a typical visual search task, in which the search array is commonly observed from a single perspective, and a large-scale search task (as examined by Smith et al., 2008), with each task providing differing patterns of results. It is important to note the difficulty in fully dissociating allocentric and egocentric contributions to spatial learning in large-scale search. In Experiment 7, participants would be able to make use of both egocentric and allocentric spatial information at the trial's start; however, once participants began to explore the space, the egocentric cue would be of limited use, as their viewpoint would move around the environment. This means that what was once to one side of them would not remain so throughout the whole trial. To completely isolate an egocentric cue in

search, the task would more closely resemble a traditional visual search task, with the array visible only from a single perspective. This would ensure that all viewpoint-centred spatial relations would remain the same, but are unachievable within the constraints of this task's design. Furthermore, in Experiment 8, those participants who appeared to search focus their search in the cued region may have been able to guide their initial search on the basis of two separate egocentric response strategies from each of the starting positions, i.e., that the target was more likely to appear on one side of the array relative to one starting position, and on the opposite side from the other starting position.

Alongside the environmental or task-related factors that might modulate the learning of statistical cues in search, potential individual differences that could underlie the presence or absence of a cueing effect were also explored. For example, a related study (Pellicano et al., 2011) found that children with autism were less likely to learn the same probabilistic cue than typically developing children, and that this was associated with the guidance of search behaviour (i.e., children with autism were, comparatively, less optimal and less systematic in their search paths). In the case of typical adults, as examined in the present study, it is generally apparent that some individuals learned about the cue, whereas others did not. As such, the absence of a general cueing effect in Experiment 8 may not necessarily reflect the absence of learning across the entire sample, but a noisier dataset. Identification of the factors that predict learning would, therefore, allow us to disentangle the relative contributions of paradigmatic differences to our understanding of cueing effects. These experiments focused on behavioural measures of small-scale spatial abilities that have previously been found to predict general navigational abilities (i.e., object rotation and viewpoint rotation), as well as self-report assays of sense of direction and handedness (for a more in-depth discussion of these factors, see Hegarty et al., 2006; Wolbers & Hegarty, 2010). The results of our analyses were that none of these measures were associated with search performance in either of the experiments reported here. This is somewhat surprising in the case of Experiment 8, as one might expect that the spatial updating and spatial translation required to identify that the cued side of space was in a fixed region relative to the environment are typically required in wayfinding behaviours. As such, one could therefore conclude that large-scale search, or the modulation of search behaviour on the basis of spatial statistics, are not functions that necessarily rely upon the same cognitive underpinnings as spatial navigation.

In contrast to exploring the individual predictors of cueing, analysis of the relationship

between different indices of search behaviour might provide an alternative insight into inter-individual variability in performance (for a recent example, see Munion et al., 2019). This process revealed significant correlations in Experiment 8, between the proportion of trials that started with an initial inspection in the cued region of space, and the behavioural measures of search efficiency (i.e. search latency, path length, and the difference between the number of columns inspected in the cued and uncued regions). This suggests that there were some participants who did learn about the probabilistic distribution of the target. The observation is further underpinned by the negative correlation between participants who tended to start their search with the closest column rather than the cued region. An interpretation of this negative association is that participants differed in terms of the rigidity, or systematicity, of their search patterns. So, whereas some participants modulated their search in response to the probabilistic cue, becoming more efficient over time, others systematically began their search with the closest target, irrespective of the cue, which negatively affected efficiency.

These individual differences in search strategy could be further explored by examining whether there is a link between measures of search efficiency and spatial WM. A link has already been identified in children, with a greater spatial WM span predicting more efficient search behaviour (Smith et al., 2005). Of further interest would be the dissociation between locational and relational spatial WM (Ackerman & Courtney, 2012; Blacker et al., 2016). Locational spatial WM comprises memory for specific locations presented on a 2D display, whereas relational spatial WM comprises the memory of spatial relationships between two or more objects presented on a 2D display. Relational spatial WM may be of particular interest to examine, as it was found to be a predictor of the ability to integrate the layout of landmarks on two distinct routes into a larger coherent mental representation of space (Blacker et al., 2017). This behaviour involved integrating spatial information across multiple different starting positions, so it may be that this similarity indicates shared underpinning cognitive processes. It is, however, important to note that these potential differences in strategic approach may stem from participants not being able to reliably orient themselves at the start of each trial, and therefore that they may have been unable to distinguish the region in which the target was more likely to appear. A disoriented participant, if searching efficiently, would inspect the closest column to their starting position, and then proceed to inspect the remaining columns in a travelling salesman-like approach (i.e., systematically work through the search array, minimising

the amount of movement between inspections), which may be represented by participants initially inspecting columns in the closest side of the array to the starting position more often than the column in the other side of the array. Furthermore, this disorientation may be shown by the effect of trial block on the trial latency measure in Experiment 8, as this might encapsulate participants' initial disorientation at the start of the experiment leading to longer initial trial latencies as they slowly orient, followed by shorter trial latencies that are facilitated by swifter reorientation at the start of each trial.

As paradigms and techniques are designed to be more valid, sensitive, and replicable laboratory assays of human search behaviour, it is encouraging that the experiments presented here provide support for the use of immersive VR in the experimental study of larger scale search behaviours. By employing immersive VR, participants were fully motility when exploring the VE, which affords some confidence that behaviour would not be affected by any potential artefacts derived from more artificial methods of exploration (Ruddle & Lessels, 2006, 2009). In addition, the use of a wireless HMD removes a cue that could aid a participant's self-localisation (i.e., the HMD's cable). Furthermore, the use of immersive VR addresses some of the aforementioned broader issues that affect experimental studies of large-scale spatial behaviour. For example, the immersive VE offers full control of the perceptual information available to the participant, thus eliminating some of the potential confounds present in previous studies, such as extraneous visual information (Jiang et al., 2014), while still affording specification of an environment that is not as quite as artificial or abstract as an array of lights presented on the floor of a laboratory (Smith et al., 2005, 2008, 2010; Pellicano et al., 2011). This level of control, therefore, facilitates further examination of the static and dynamic environmental cues that guide human search behaviour, in a manner that would not otherwise be possible. The findings presented here reinforce the previous demonstration (Smith et al., 2010) that probabilistic cueing can be reliably observed in large-scale search when participants are able to combine allocentric and egocentric cues, but is not facilitated when egocentric cues have no predictive validity (i.e., the cue is solely specified within an allocentric spatial reference frame). It may be that different approaches to searching for the target (i.e., systematic search vs. focusing on cued regions) underpin allocentric probabilistic cueing in visually impoverished scenes. Further research investigating individual differences in search strategy would, therefore, be a fruitful line of future research, and a more comprehensive battery of measures may be necessary to reveal the cognitive and perceptual underpinnings of variation.

3.4 Conclusion

The examination of search behaviour presents a valuable tool for investigating theories of spatial cognition, as the variable nature of the target's location presents a different set of task demands to learning a single location, as one does during place learning. The experiments reported in this chapter demonstrate that participants were able to learn where a target was likely to be located when their starting position was stable. This was disrupted when the target rich region was defined in allocentric space through participants starting trials from two different locations. These findings indicate conditions under which participants can learn probabilistically where an object is likely to appear, i.e. that it needs to be stable in allocentric coordinates, and that participants need a stable egocentric reference at the start of each trial. These conditions can be further interrogated through the deployment of supplementary landmark information, as in Smith et al.'s (2010) Experiment 5, as well as Jiang et al.'s (2014) experiments. Further interrogation of these parameters will provide valuable insight as to the necessary conditions for probabilistic learning of a target's distribution to occur.

Chapter 4

General Discussion

Chapter 2 reports the development of a place learning task based on design of the BVA (Kalová et al., 2005), and also incorporates elements from other studies exploring place learning (Doeller et al., 2008; McAvan et al., 2021). The task was designed for use with desktop PC platforms as well as with an immersive VR system that permits full motility. The same manipulations employed in the BVA were employed in the place learning task, to measure relative aptitude in using allocentric or egocentric information in isolation, or both types of information in conjunction. In this task, allocentric information comprised the spatial relationship between the target location and an array of extra-arena landmarks, whereas egocentric information comprised the direction and distance vectors between the target location and the participant's starting location. In each trial, participants learned the location of a target object (a wooden pole) by navigating to its location and picking it up in a Training stage. Participants were subsequently placed back into the arena for a Test stage that required them to return to the location from which they apprehended the target object and replace the target, relative to the current trial condition's reliable information. Feedback was then provided to participants to allow them to hone their accuracy in subsequent trials.

Experiment 1 involved the deployment of a prototypical version of the place learning task developed for the immersive VR system, alongside a battery of individual difference measures. This supplementary task battery included the MRT (Vandenberg & Kuse, 1978), Perspective Taking Task (Kozhevnikov & Hegarty, 2001), and the SBSOD (Hegarty et al., 2002), which have each shown associations with navigational ability in previous literature (Driscoll et al., 2005; Fields & Shelton, 2006; Hegarty et al., 2006; Kozhevnikov et al., 2006;

Schoenfeld et al., 2010a). The results from Experiment 1 indicated that participants found the target location with the greatest amount of error in the Egocentric condition, and that target placement accuracy did not differ between the Allocentric and Control conditions. The battery of individual differences measures showed a relationship between Allocentric condition accuracy and the MRT, replicating findings from the place learning literature (Driscoll et al., 2005; Schoenfeld et al., 2010a). The pattern of results in the place learning task partly replicated findings reported by Merhav & Wolbers (2019), i.e. that placement error was greatest in the Egocentric condition. The results did differ with respect to the Control and Allocentric conditions however, as Merhav & Wolbers (2019) reported greater placement error in their Allocentric condition compared to their Control condition. The equivalence between Control and Allocentric placement error in Experiment 1 then suggests that this prototypical version of the place learning task was not sufficiently sensitive to discriminate between performance in Control and Allocentric conditions. To address this, the task underwent revisions to its design and methodology in Experiment 2. In Experiment 2, a redesigned version of the place learning task was developed for both immersive VR and desktop PC platforms. The revisions comprised an adjustment of the trial feedback format, such that it was provided in the form of a top-down schematic of the environment, and the standardisation of the landmarks, to ensure that no single landmark was of greater salience than the others. Experiment 2 employed a within subjects design that involved all participants completing both the immersive VR and desktop PC versions of the task on each platform, which each included all three trial conditions (Control, Allocentric, and Egocentric). The results indicated that on both platforms, placement error was lowest in the Control condition. This indicated that the adjustments made to the design of the place learning task were sufficient to discriminate between placement error in the Control and Allocentric conditions. To facilitate a cross-platform comparison, placement error was scaled on the basis of the inner diameter of the VE employed on each platform. This comparison revealed that participants did not differ in their placement accuracy in both the Control and Egocentric conditions across the two platforms. In the Allocentric condition, however, participants were more accurate in identifying the target location on the immersive VR platform than they were on the desktop PC platform. This cross-platform difference may indicate that participants can more accurately employ allocentric information when they are fully motile. This presents profound theoretical implications for the navigation literature, as much theory assumes equivalence between

freely moving rodents and static human participants that complete navigation tasks on desktop PC platforms, e.g. the cognitive map (Hartley et al., 2003).

The onset of the COVID-19 pandemic presented significant issues for the collection of data within a laboratory, particularly when using immersive VR systems. Consequently, Experiment 3 was designed to translate the desktop PC version of the place learning task for deployment in web-browsers, for remote data collection. This version of the task introduced a between-subjects manipulation to interrogate the role of unreliable landmarks in Egocentric condition trials, in which participants completed the Egocentric trials with unreliable landmarks either present or absent in the VE. Whilst high placement error in the Egocentric condition is expected based on previous literature (Merhav & Wolbers, 2019), it is important to identify whether the presence of landmarks influences participants' placement accuracy given the importance of landmarks to human navigation (Doeller et al., 2008; Zhao & Warren, 2015a,b). The results from this experiment replicated desktop PC performance in Experiment 2 in both the Control and Allocentric conditions. There was, however, a large difference between the two groups in the Egocentric condition, indicating that the presence of unreliable landmarks disrupts the accuracy with which participants can employ egocentric information to identify a target location. Analysis of participants' paths indicated that participants made more viewpoint rotations and took less efficient paths to where they thought the target was located in Egocentric trials when unreliable landmarks were present. This suggests that participants may have been reorienting to the landmarks in the Egocentric condition, a behaviour that is maladaptive due to the unreliable nature of the landmarks cues in the Egocentric condition.

In Experiment 3, a large number of participants were recruited on a voluntary basis and received no recompense for their participation and from this portion of the sample, a large proportion of participants dropped out of the study. To identify whether this impacted the results, Experiment 4 replicated Experiment 3 by recruiting participants from the Prolific participant recruitment platform (Palan & Schitter, 2018), which would ensure that all participants were fully remunerated for their participation. Experiment 4's results replicated the findings from Experiment 3 fully, suggesting that the collection of data online represents a useful tool for rapid acquisition of data from desktop PC navigation tasks.

Experiment 5 translated the experimental design of Experiment 3 and 4 to the immersive

VR version of the place learning task used in Experiment 2. The results indicated that there were no clear differences between the Landmarks Absent and Landmarks Present groups in their Egocentric condition placement accuracy, or in the efficiency of their path and the number of head turns in the Test stage, contrasting with the results from Experiments 3 and 4. This was a surprising set of results as influential navigational theories within the literature assume equivalence between desktop PC and motile forms of navigation (Hartley et al., 2003; Taube et al., 2013). The contrast suggests that unreliable visual information is less disruptive to motile navigators when they are using egocentric information, highlighting the importance of idiothetic-self motion cues to human navigation.

Experiment 6 was designed to validate the desktop PC version of the place learning task by comparing performance between participants of different ages (Commins et al., 2020). Participants were recruited to Young, Middle, and Old age groups, following research examining the impact of ageing on navigation reported by Driscoll et al. (2005). For this experiment, unreliable landmarks were omitted from the Egocentric condition, as literature suggests that familiar but task irrelevant stimuli may exhibit a disruptive influence on older adults, which may confound the requirement to suppress the presence of unreliable landmarks in the Egocentric condition. The placement accuracy data from the Allocentric condition replicated the widely reported decline in the ability to use allocentric information accurately, across the lifespan. Similarly, an expected general decline in placement accuracy was observed in the Control and Egocentric conditions, between the Young and Old age groups. Interestingly, in the Allocentric condition, there was also a decline in the number of viewpoint rotations with increased age, which may present an explanation for the observed age-related decline in the Allocentric condition, i.e. that older adults may scan the environment less, and as a consequence construct a less accurate spatial representation of the environment. The results from Experiment 6 indicate that the desktop PC place learning task may be a reliable and sensitive tool for identifying individual differences in the ability to use both allocentric and egocentric information. Whilst the vMWM has been used for this purpose, the task developed across Chapter 2 presents a supplementary Egocentric measure that is not included in the canonical vMWM task.

Chapter 3 describes two experiments designed to examine probabilistic cueing in immersive VR, and whether it is associated with a range of individual difference measures. Experiment 7 replicated Smith et al.'s (2010) Experiment 2 in an immersive VR context. In

a large-scale immersive VR environment, participants were required to search an array of columns and locate a target column through interacting with each. The target was distributed probabilistically with a statistical contingency, such that it appeared in a rich region of space on 80% of trials, and it appeared in a sparse region of space in the remaining 20% of trials. Alongside this search task, participants completed the MRT (Vandenberg & Kuse, 1978), Perspective Taking Task (Kozhevnikov & Hegarty, 2001), and SBSOD (Hegarty et al., 2002) due to their previous associations with spatial abilities. In the search task, participants demonstrated a probabilistic cueing effect across a range of measures, as their search behaviour was more efficient when the target was in the cued region of space, successfully replicating the findings from Smith et al.'s (2010) Experiment 2. The battery of individual difference measures did not demonstrate any strong associations with search efficiency in this experiment, suggesting that probabilistic cueing, in the context of this experiment, may be independent to these measures.

Experiment 8 replicated Smith et al.'s (2010) Experiment 3, and was designed to identify whether the probabilistic distribution of the target's location could be acquired when it was specified in allocentric coordinates. This was achieved by having participants start trials from one of two starting positions either side of the arena, meaning that the rich and sparse regions would not be specified by a singular egocentric representation from the starting position. Similar to Experiment 7, the same battery of individual measures was employed, as each task has been linked to behaviours that are reliant upon the use of allocentric information. Results from this experiment indicated that participants as a whole failed to acquire the statistical contingency that underpinned the target's location, as participants were no more efficient at finding the target during trials in which it appeared in the rich region of space, as opposed to the sparse region of space, replicating the findings from Smith et al.'s (2010) Experiment 3. Correlational analyses of the probabilistic cueing task measures did, however, indicate that there may be individual differences between participants and whether they focused their search in the rich region of space. Participants that started more trials with a column inspection in the rich region of space were more likely to take less time to find the target, inspect fewer columns before finding the target, and taking a shorter path. There was also a negative correlation between the number of trials that were started with an inspection in the target rich region and the number of trials started with an inspection in the region closest to the starting position. This may be indicative of participants either starting each trial with an inspection of the closest column

or instead focusing on the target rich region of space and starting their search there.

The place learning and probabilistic cueing tasks reported in Chapters 2 and 3 each represent valuable tools for understanding spatial cognition in humans, despite fundamental differences in the demands of each task. The place learning task is designed to interrogate the precision with which one can learn an single location using either allocentric or egocentric information, or both types in conjunction. In contrast, the probabilistic cueing task examines whether participants can learn where an object is likely to appear in space. Despite these differences, both tasks are reliant upon participants developing a spatial representation of the environment to direct either a locational judgement or to the focus of one's search. Interestingly, the accuracy with which participants could employ an allocentric representation of each task's VE seemed to differ across the two paradigms. In the Allocentric condition in the immersive VR place learning task (Experiments 1, 2, and 5) participants were more accurate at identifying the target location compared to the Egocentric trials. In the probabilistic cueing task presented in Experiment 8, however, participants appeared not to focus their search in the target rich region, suggesting that they failed to acquire the probabilistic distribution of the target when it was defined in allocentric coordinates. This may stem from differences in the learning conditions for each experiment. In the place learning task, participants are presented with the target location in the Training stage, and receive feedback to hone their accuracy in each trial, so their learning is reinforced twice in each trial, and participants acquire knowledge of the target location early on in the condition. This contrasts with the essence of a probabilistic cueing paradigm, as participants begin with no knowledge of where the target is likely to appear across the course of the experiment. Reinforcement only occurs later in the experiment and requires participants to track the identity of the columns that had previously been the target. The data from Experiment 8 showed that participants were faster to find the target in the second half of the experiment compared to the first, however, this increase in efficiency was agnostic as to whether the target was located in the rich or sparse regions of the search array. This suggests that participants were not focusing their search on the target rich region of space in Experiment 8. These differences may have been compounded by the utility of the landmark cues in each respective environment. In the place learning task, the landmarks are extremely salient and designed to facilitate an allocentric representation of a single target location relative to their configuration. In contrast, in the probabilistic cueing task, the only reliable landmarks comprised the distribution of columns in the

search array, which are comparatively subtle compared to the landmarks visible in the place learning task. Landmark salience has previously been identified as a source of difficulties in developing an allocentric representation of space (Zhou & Mou, 2019), and this may then be responsible for the differences with which participants can acquire and flexibly employ an allocentric representation of space in the two tasks reported in this thesis.

The experimental work presented here provides extensive evidence for the utility of immersive VR systems as tools for exploring human spatial cognition in large-scale environments. The place learning task presents an adaptation of the BVA that successfully distinguishes between the use of allocentric and egocentric spatial abilities on an immersive VR platform. The task can also be deployed on a desktop PC platform, which captures the widely reported age-related decline in the ability to accurately employ allocentric spatial representations (Gazova et al., 2013; Korthauer et al., 2016; McAvan et al., 2021; Merhav & Wolbers, 2019; Moffat & Resnick, 2002; Newman & Kaszniak, 2000; Schoenfeld et al., 2010a, 2014; van der Ham et al., 2020; Zhong et al., 2017). Whilst this may validate components of the task due to the recapitulation of results reported in the navigational literature (Commins et al., 2020), there are clear differences in the patterns of results across the desktop PC and immersive VR platforms. The probabilistic cueing task successfully replicated findings reported by Smith et al. (2010), finding a cueing effect when the rich region of space was defined in both allocentric and egocentric coordinates, but not when it was only defined in allocentric coordinates. These data contrast with those reported by Jiang et al. (2014), indicating that probabilistic cueing based on regions defined allocentrically requires a rich visual scene. Looking at the work as a whole, there remain a number of avenues for future work that build on the experiments reported in Chapters 2 and 3. These comprise an exploration of individual differences in navigation and search, interrogating the contributions of motility to spatial representations, and identifying how landmarks contribute to both navigation and search behaviour.

4.1 Future Work

4.1.1 Individual Differences

The place learning task described in Chapter 2 was based on the design of the BVA (Kalová et al., 2005), that has been used extensively with both healthy older adults (Gazova et al., 2013), and older adults with amnesic and non-amnesic MCI (Hort et al., 2007; Laczó et al., 2009, 2010, 2015; Paízková et al., 2016, 2018; Sheardova et al., 2013), as well as individuals with Alzheimer's disease (Kalová et al., 2005; Laczó et al., 2009, 2010; Nedelska et al., 2012). Through investigating the difficulties associated with both typical and atypical ageing, the BVA has provided insight into how the use of allocentric and egocentric information is affected. In Experiment 6, the desktop PC version of the place learning task was completed by groups of younger, middle aged, and older adults, and replicated two of the core findings from the BVA. These comprised a marked age-related decline in the ability to use allocentric information reliably across each of the three groups, and a more general decline in the Control and Egocentric conditions between the groups of younger and older adults. Consequently, this experiment demonstrates the utility of the desktop PC place learning task as a tool for identifying individual differences in navigational ability, as it replicates results from tasks conducted in real-world environments with motile participants. A logical next step would be identify whether the same age-related decline is observed in the immersive VR version of the place learning task. There is some concern within the navigational literature regarding the suitability of immersive VR systems for use by older adults due to issues relating to cyber-sickness susceptibility and embodiment (Diersch & Wolbers, 2019; Schöberl et al., 2020), however, there have been multiple reports of older adults completing immersive VR tasks with little trouble (Huygelier et al., 2019; McAvan et al., 2021; Merhav & Wolbers, 2019). Employing immersive VR to explore the effects of ageing would not only present further evidence for decrements in older adults' navigation in a physical space following the BVA (Gazova et al., 2013), but the additional incorporation of a middle-age group would be of utility for identifying whether the extent of decline is a gradual process through the lifespan, or if there is an onset of difficulties at a specific age (Driscoll et al., 2005).

A further advantage for exploring the place learning tasks with different populations would be the ability to identify differences in participants' path data. These data were not

explored in the BVA, and as a result, the immersive VR place learning task will be able to provide additional detail as to the impairments associated with ageing. Experiment 6 identified that in the Allocentric condition, the directness of participants' paths did not change with age, whereas the number of viewpoint rotations did decrease with age. This more granular analytical approach would present a clearer quantification of behavioural differences across populations and would begin to explain decrements observed in placement accuracy. For example, the fewer viewpoint rotations associated with increased age in Experiment 6 would potentially result in a less robust formation of a spatial representation of the landmark configuration due to fewer opportunities to visually apprehend the configuration of the landmarks. These data could also be used for more fine-grained categorisation of participants' strategies, as with data from rodent MWM and human vMWMW tasks (Garthe et al., 2009; Graziano et al., 2003; Kallai et al., 2005; Schoenfeld et al., 2010b, 2017; Vouros et al., 2018; Wolfer et al., 1998; Wolfer & Lipp, 2000; Wolfer et al., 2001). Whilst the MWM and the place learning tasks presented in Chapter 2 differ in their demands, e.g. finding a hidden platform vs identifying a specific location in space, there may be overlap in some behaviours. In the vMWM, participants have been reported as using a Visual Scan strategy (Kallai et al., 2005), in which they first look around their starting location, then, once oriented, take a direct path to the hidden platform. Similar behaviours would be successful in the novel place learning task's Allocentric condition, as participants are required to orient to the configuration of the landmarks before making their judgement of the target's location. Indeed, McAvan et al. (2021) reported that in a place learning task with similar demands, both younger and older participants used a beacon based strategy to direct their judgements of a target location (i.e. by using a single landmark to direct their path). This finding suggested that whilst there were age-related differences in placement accuracy, that there were few strategic differences indicates that the placement accuracy differences related to the precision of an individual's spatial representation instead of inefficient or inappropriate strategic behaviours.

In sum, the place learning task reported in Chapter 2 presents a novel tool for both desktop PC and immersive VR platforms for identifying individual differences in the ability to use allocentric or egocentric information. The vMWM literature presents a range of opportunities in which this task could be used as it has been deployed with differing populations, including Alcohol Use Disorder (Ceccanti et al., 2018), Fetal Alcohol

Syndrome (Hamilton et al., 2003), Schizophrenia (Folley et al., 2010), Transcranial Global Amnesia (Bartsch et al., 2010), and Traumatic Brain Injury (Skelton et al., 2000; 2006). By employing the immersive VR place learning task one can begin to understand whether there are difficulties in these conditions associated with the use or acquisition of idiothetic self-motion cues, as well as providing an assay of egocentric cue use, which is traditionally omitted from vMWM tasks. This would potentially present a more comprehensive profile of differences that characterise a population's navigational behaviour than the vMWM alone would.

Individual differences can also be investigated using the probabilistic cueing task. Experiment 8 demonstrated that there were likely differences as to whether participants learned the statistical contingency underpinning the target's distribution in space. These data suggested that participants were either systematic in their search, starting with the nearest column and then working through the search array in a travelling salesperson-like approach, or they started their search in the cued region of space. The latter group, as they may not have been taking a systematic approach to inspecting columns may then have become disoriented, as the data indicated that participants that started searching in the cued region were more likely to make revisits to previously inspected columns. Further investigation of this phenomenon would be worthwhile, as it may be that participants differ in terms of how systematic their search is, and how quickly they can acquire the probabilistic rule underpinning the target's location. Indeed, Pellicano et al. (2011) employed Smith et al.'s (2010) probabilistic cueing task to identify differences between neurotypical children and children with an autism spectrum condition (ASC). This experiment found that whilst children with ASC did learn to focus their search in the target rich region of space, they took longer to learn the probabilistic distribution of the target, and were less systematic in their search than typical children.

As the probabilistic cueing task employed by Pellicano et al. (2011) was sensitive enough to characterise large-scale search in children with ASC, the task may then represent a useful tool for identifying individual differences in spatial cognition. Consequently, the task could be deployed as a tool for investigating search differences in clinical populations that have been reported as being impaired in search behaviour relative to typical populations, for example individuals with Alzheimer's Disease (Ramzaoui et al., 2018; Tales et al., 2011) or Attention Deficit Disorder (Karatekin & Asarnow, 1998; Luo et al., 2021; Weiler et al., 2002). Using these tools, researchers can gain a more comprehensive understanding of the

different navigational or search profiles of different populations. This will indicate areas that may be susceptible to interventions to ameliorate specific impairments associated with each condition.

4.1.2 The role of landmarks and motility in navigation

The principal reason for the development of the place learning task in Chapter 2 was to create an assay of navigational ability that incorporates motility through the use of an immersive VR system. The addition of motility to a navigator provides access to idiothetic self-motion cues, and as a consequence, access to spatial information that would otherwise not be available when completing a task on a desktop PC platform (Steel et al., 2020; Taube et al., 2013). The results from Chapter 2 indicate that motility appears to support navigation in two ways. First, in Experiment 2, more accurate target placements were made in the Allocentric condition on the immersive VR version of the task than in the desktop PC version. This suggests that participants could integrate self-motion cues to develop a richer allocentric representation of space. Second, Experiments 3 and 4 indicated that the presence of unreliable landmarks disrupts participants' accuracy when using egocentric information in isolation on a desktop PC platform, but in Experiment 5, there was no disruption evident in the immersive VR version of the task. This indicates that access to idiothetic self-motion information reduces the disruption from the presence of unreliable landmarks, when using egocentric cues to navigate.

Both of these cross-platform behavioural differences are not commensurate with influential navigation theories, as they are based on the assumption that static humans navigating on a desktop PC platform are equivalent to freely moving rodents. This is principally based on equivalence observed in neuroimaging studies, with brain regions demonstrating activation in motile rodents showing similar activation in human navigators exploring virtual spaces, for example, in the vMWM (Possin et al., 2016; Schoenfeld et al., 2017; Woolley et al., 2013). This comparison may be fundamentally limited, as it omits the contributions of idiothetic self-motion cues to human navigation (Steel et al., 2020; Taube et al., 2013). Whilst motility has been shown previously to provide navigators with a richer representation of space (Ruddle et al., 2011a,b), it is important to note that there may be some procedural differences that could also explain the cross-platform differences, such as differences in environmental scale and the fidelity of the controls within the VE.

Environmental scale has previously been reported as a potential influence on navigational behaviour, as it may affect the utility of landmark cues. Padilla et al. (2017) investigated how proximal and distal landmarks relate to sex differences within place learning, and found a male advantage for the use of both proximal and distal cues in large-scale environments. In smaller environments, however, there was only a male advantage in distal cue use – females were equally adept at using proximal cues as males. Padilla et al. (2017) suggested that this difference was due to proximal cues being encoded more as distal cues in the larger environment, due to their relative distance to the navigator. A parallel can be drawn between the immersive VR and desktop PC place learning tasks reported in Chapter 2, as the smaller scale immersive VR environment may lead to the landmarks being processed as proximal cues. Proximal cues have been shown to benefit the accuracy of a spatial representation of an environment on immersive VR platforms (Zhou & Mou, 2019), which may explain the immersive VR advantage in the Allocentric condition in Experiment 2.

The differences in scale could be addressed by conducting the immersive VR place learning task on an omnidirectional treadmill. This affords researchers the opportunity to have participants explore virtual spaces with motility, whilst being unconstrained by the physical space in which the experiment is being conducted (Huffman & Ekstrom, 2019a; Schöberl et al., 2020). It is important to note, however, that exploration on an omnidirectional treadmill may be relatively artificial compared to free and untethered ambulation (Steel et al., 2020), and may not come easily to participants. To counter this difficulty, researchers using omnidirectional treadmills often train participants first to ensure they are comfortable when exploring an immersive VE on an omnidirectional treadmill (Hejtmanek et al., 2020; Huffman & Ekstrom, 2020). Using an omnidirectional treadmill may then present a solution to this issue, however, Huffman et al.'s (2020) model of idiothetic navigation contributions suggests that exploration of a space on an omnidirectional treadmill may provide the user with reduced idiothetic information relative to free and untethered ambulation. Consequently it may not capture free and naturalistic motility in the way that the immersive VR system employed in this thesis does.

The second potential issue when comparing the two platforms relates to the level of control afforded to participants when exploring the VEs. The controls on the desktop PC version of the task present the navigator with only two degrees of freedom when moving through the environment, i.e. forwards and backwards translation, and left/right yaw

rotation. This contrasts with the immersive VR system, in which participants can explore the space with six degrees of freedom, i.e. they can move their perspective across the three axes in space and rotate their view along those same three axes due to its 1:1 mapping to the navigator's movements. This discrepancy means that it is considerably easier to look around the environment on the immersive VR platform, as viewpoint rotations are mapped 1:1 to head turns. Ruddle et al. (1999) reported that participants do make a greater number of viewpoint shifts on immersive VR platforms than on desktop PC platforms. As participants can more easily apprehend the spatial relationships between landmarks, this may then uniquely benefit performance in the Allocentric condition, as observed in Experiment 2. Furthermore, a visual scan of the environment is a core component of reorientation, which in the vMWM literature is typically a marker of successful place learning (Kallai et al., 2005). Commins et al. (2020) did, however, report that freer access to rotational movements made little difference to vMWM performance in a comparison between a desktop PC vMWM and a non-ambulatory immersive VR equivalent. This suggests that easier access to rotational movement alone may not be the source of the differences.

Whilst it is important to acknowledge the procedural issues that may potentially lead to the observed results in Experiment 2, it is important that future work does address how motility and landmarks influence human navigation, and how this relates to contemporary theories of human navigation. Huffman & Ekstrom (2020) proposed a model that predicts that idiothetic self-motion cues are of greater utility in smaller spaces compared to larger spaces, and are more likely to support behaviours that rely on egocentric spatial representations more than allocentric representations. This model may provide an explanation for the cross-platform differences described above due to the differing environmental scales employed across the two versions of the task.

Huffman & Ekstrom's (2020) model may also provide an explanation for the cross-platform differences related to the disruptive influence of unreliable landmark cues in the Egocentric condition. Experiment 5 demonstrated that when participants had access to idiothetic self-motion cues in the immersive VR platform, their placement accuracy did not differ based on whether unreliable landmarks were present or not. In contrast, Experiments 3 and 4 indicated that the unreliable landmarks disrupt the use of egocentric information when participants did not have access to idiothetic self-motion cues, on the desktop PC platform. As success in the Egocentric condition is reliant upon the reliable recapitulation

of path information (i.e. distance and direction), then access to idiothetic self-motion cues may then strengthen a participant's representation of this path. Indeed, this egocentric representation is underpinned by path integration, a navigator's ability to use idiothetic self-motion cues to update their position. This additional information may be sufficiently salient to the navigator that it attenuates any disruptive influence of the unreliable landmarks.

The data from Experiment 2 does remain partly inconsistent with Huffman & Ekstrom's (2020) model. Whilst the immersive VR advantage to allocentric cue use may be as a consequence of the differences in scale across the two platforms, the model also predicts that behaviours dependent upon allocentric cue use may not benefit from motility as much as behaviours reliant upon egocentric information. Whilst Experiment 2 cannot disentangle the two components of the model due to its design, the role that motility plays in supporting the use of allocentric cues in navigational behaviour should be investigated further, to validate Huffman & Ekstrom's (2020) model. Following Huffman & Ekstrom's (2019a) earlier work, Steel et al. (2020) discussed which types of information are more likely to be used by a navigator, and in which contexts. As navigation is reliant upon such a broad range of component behaviours, it seems reasonable that these behaviours may then rely on different sources of information. Additionally, recent theories suggest that spatial representations are amodal (Huffman & Ekstrom, 2019a; Wolbers et al., 2011), so while different forms of navigation (e.g. motile, passive visual) may provide different sensory inputs, learning from one modality does appear to transfer across to others (Hejtmanek et al., 2020). This indicates a need within the literature to interrogate how different types of sensory input support the construction of spatial representations, so contributions from motility or visual flow can be fully understood.

4.1.3 The role of landmarks and motility in large-scale search

Much of the literature examining human search behaviour is based on the visual search literature, in which participants explore an array presented on a 2D monitor. This differs from our daily search behaviour as routine large-scale search is conducted under conditions in which we are motile. Moving through space means that one's viewpoint and perspective of the search environment changes regularly, and one also accrues idiothetic self-motion cues. These characteristics of large-scale search differ greatly from the task

demands in the 2D visual search literature (Gilchrist et al., 2001; Smith & De Lillo, 2022). Addressing this is the core reason why the experiments reported in Chapter 3 employed an immersive VR system to explore search, as it more closely captures the demands of everyday search due to the necessity to employ spatial information from a large-scale environment.

In Chapter 3 there were no direct comparisons between desktop PC and immersive VR versions of the probabilistic cueing task, as Experiments 7 and 8 were both conducted on an immersive VR system. Previous work has directly compared search when participants are motile using an immersive VR platform, or static, and moving through space using a joystick (Ruddle & Lessels, 2006, 2009). Ruddle & Lessels (2006, 2009) reported differences across the two platforms, as participants searched more efficiently under motile conditions compared to search conducted via a joystick on the desktop PC platform. This was indicated by participants making fewer revisits to previously inspected locations, suggesting that the access to idiothetic self-motion cues provides motile participants with a richer representation of space such that they could reliably monitor where they had already explored in a given trial. If the probabilistic cueing task reported in Chapter 3 was to be ported to a desktop PC platform, it would then be expected that participants would be less effective at focusing their search in the target rich region of space as they would potentially develop a less robust representation of the trial environment. This could cause particular difficulties in an adaptation of Experiment 8, as participants were seemingly unable to learn the probabilistic distribution of the target location, potentially as a result of being unable to integrate their perspectives from the two starting positions into integrated spatial representations. Further difficulties in developing a spatial representation from the absence of self-motion cues may then prevent participants from learning the statistical distribution of the target locations.

One of the core reasons for participants failing to acquire the statistical contingency underpinning the distribution of the target in Experiment 8 may have been that participants did not have sufficient visual information to successfully reorient themselves within the VE at the start of each trial. This is consistent with the results of Smith et al.'s (2010) Experiment 3, which also employed a sparse environment, and the inconsistency with Jiang et al.'s (2014) findings, which took place in a visually rich real-world scene. Reorientation is fundamentally easier in a visually rich space as there are a greater number of cues to support the navigator (Julian et al., 2018). This suggests that landmarks are necessary

for probabilistic cueing to be observed when the target rich region is fixed in allocentric coordinates. To interrogate this fully it is important to understand what properties are required from the landmarks to support probabilistic learning under these conditions.

Jiang et al.'s (2014) study was conducted in an environment in which there was a rich array of supplementary visual information around the outside of the arena. This could be used to reorient the participant at the start of each trial, and would then allow the participant to more rapidly learn that the target appears in a region of space more often than others. The rich visual scene may also provide participants with beacon type cues (i.e. specific landmarks that participants associate with the rich region of space), that may then support the demarcation of the target-rich region from the sparse region. This type of cue was employed by Smith et al. (2010) who manipulated the featural properties of the search array in their Experiment 5, such that each half of the search array was presented to participants in a different colour. Under these conditions participants focused their search in the target rich region of space. This manipulation does present participants with a binary choice of colours, and as a consequence does not require a spatial solution (e.g. search can be focused on the green items and not the red items). Evidence from these studies does suggest that landmarks may support allocentric probabilistic cueing, however, it is not clear from the current literature how landmarks are used to support the learning.

To address this, the minimal conditions under which probabilistic cueing can be observed in an allocentric reference frame could be explored by replicating Experiment 8 and incorporating supplementary landmarks. Manipulating the landmark locations (e.g. behind or in front of the starting position, or orthogonal to this axis) would then provide detail as to how this visual information is used. For example, by having a landmark aligned with the cueing axis, this might present participants with a beacon that they can use to demarcate the two regions in the array. In contrast, a landmark that is in front or behind a starting position may not have that same utility for demarcating the two regions as it would be equidistant from each. Instead, the landmark would be useful for reorienting participants and may then facilitate the development of a stable spatial representation of the environment.

A further manipulation could be conducted in which the featural properties of the array are varied, but not in a fashion that demarcates the two regions, as with the manipulation

that Smith et al. (2010) employed in their Experiment 5. This could be achieved by having different coloured columns that are repeated across the two sides of the array. The only difference would be the array's spatial distribution, however, by more clearly distinguishing the columns from each other, the pattern of each half of the search array should be more salient than an array of columns of a singular colour. This approach should render the two halves of the array more discriminable from each other, supporting search behaviour. Indeed, increasing salience of local landmarks has been shown to increase the precision of spatial representations in immersive VR (Zhou & Mou, 2019). This may then facilitate the acquisition of the spatial contingency underpinning the target's distribution, as the unique layout of columns in each side of the array would provide a stable cue.

Finally, within the 2D visual search literature a number of behavioural phenomena are described that have not been explored to any great extent in the large-scale search literature. Recent work has explored contextual cueing (Li et al., 2016, 2018) and feature versus conjunction search (Kristjánsson et al., 2022). Interrogating these behaviours in controlled large-scale spaces will begin to detail how search interacts with the components that underpin spatial cognition such as contributions from allocentric and egocentric reference frames.

4.2 Conclusion

There were two core aims for the research presented within this thesis. The first, was to identify whether fully motile immersive VR represented a suitable experimental tool for investigating both navigation and search behaviour, and the second was to identify whether motility impacts established behavioural effects previously identified in either navigation or search. Results from experiments in Chapters 2 and 3 indicate that immersive VR represents a reliable tool for measuring the focal behaviours, as the immersive VR place learning task replicated results reported by Merhav & Wolbers (2019), and the probabilistic cueing task replicated findings reported by Smith et al. (2010). Experiment 1 did highlight that there may be some parameters that can influence the sensitivity of an immersive VR assay of place learning, however, the reliability of results from the immersive VR place learning task reported in Experiments 2 and 5 do indeed suggest that the platform can be used as a reliable assay of allocentric and egocentric cue use. As Experiments 7 and 8 replicated results from Smith et al.'s (2010) Experiments 2 and

3, this provides further evidence of immersive VR platform utility. The translation of tasks to novel contexts presents a platform from which further manipulations can then be conducted, as the use of a VE presents a level of experimental control that would otherwise be impossible in a real-world context. For example one can easily investigate the role of landmarks within probabilistic cueing by modifying the task with a few additional lines of code. An equivalent real-world manipulation would present a time-consuming logistical challenge. The flexibility of the immersive VR platform then presents researchers with a valuable tool for examining behaviour in the future. It is important, however, to note that experiments reported in Chapter 2 do suggest that there are behavioural differences across similar tasks presented on immersive VR and desktop PC platforms. The core difference between the two platforms is that participants are fully motile when using an immersive VR platform, whereas on a desktop PC platform they are static. As participants are fully motile then behaviour should be more similar to that of freely moving rodents that informed a large swathe of navigational theory (e.g. the cognitive map - O'Keefe & Nadel, 1978) and presents a more naturalistic tool for interrogating navigational behaviour. It is important, however, to note that there were some differences between the tasks deployed on each of the two platforms that may present confounds for the conclusion that navigation is fundamentally different with motility Huffman & Ekstrom (2020). The difficulty in equating tasks across platforms presents a challenge for researchers, however, it is vital that influential theories of spatial behaviour are comprehensively tested across a range of conditions and platforms, including with motile participants, to ensure that these theories actually do capture a realistic portrayal of human behaviour.

References

- Ackerman, C. M., & Courtney, S. M. (2012). Spatial relations and spatial locations are dissociated within prefrontal and parietal cortex. *Journal of Neurophysiology*, *108*(9), 2419–2429.
URL <http://jn.physiology.org/cgi/doi/10.1152/jn.01024.2011>
- Aghajan, Z. M., Acharya, L., Moore, J. J., Cushman, J. D., Vuong, C., & Mehta, M. R. (2015). Impaired spatial selectivity and intact phase precession in two-dimensional virtual reality. *Nature Neuroscience*, *18*(1), 121–128.
- Antonova, E., Parslow, D., Brammer, M., Dawson, G. R., Jackson, S. H., & Morris, R. G. (2009). Age-related neural activity during allocentric spatial memory. *Memory*, *17*(2), 125–143.
- Antonova, E., Parslow, D., Brammer, M., Simmons, A., Williams, S., Dawson, G. R., & Morris, R. (2011). Scopolamine disrupts hippocampal activity during allocentric spatial memory in humans: An fMRI study using a virtual reality analogue of the Morris Water Maze. *Journal of Psychopharmacology*, *25*(9), 1256–1265.
- Anwyl-Irvine, A. L., Massonnié, J., Flitton, A., Kirkham, N., & Evershed, J. K. (2020). Gorilla in our midst: An online behavioral experiment builder. *Behavior Research Methods*, *52*(1), 388–407.
- Armitage, J., & Eerola, T. (2020). Reaction Time Data in Music Cognition: Comparison of Pilot Data From Lab, Crowdsourced, and Convenience Web Samples. *Frontiers in Psychology*, *10*(January), 1–6.
- Astur, R. S., Ortiz, M. L., & Sutherland, R. J. (1998). A characterization of performance by men and women in a virtual morris water task: A large and reliable sex difference. *Behavioural Brain Research*, *93*(1-2), 185–190.
URL <http://linkinghub.elsevier.com/retrieve/pii/S0166432898000199>
- Bartneck, C., Duenser, A., Moltchanova, E., & Zawieska, K. (2015). Comparing the similarity of responses received from studies in Amazon’s Mechanical Turk to studies conducted online and with direct recruitment. *PLoS ONE*, *10*(4), 1–23.
- Bartsch, T., Schönfeld, R., Müller, F. J., Alfke, K., Leplow, B., Aldenhoff, J., Deuschl, G., & Koch, J. M. (2010). Focal Lesions of Human Hippocampal CA1 Neurons in Transient Global Amnesia Impair Place Memory. *Science*, *328*(5984), 1412–1415.
URL <https://www.science.org/doi/10.1126/science.1188160>
- Biss, R. K., Campbell, K. L., & Hasher, L. (2013). Interference from previous distraction disrupts older adults’ memory. *Journals of Gerontology - Series B Psychological Sciences and Social Sciences*, *68*(4), 558–561.
- Blacker, K. J., Courtney, S. M., Tzourio-Mazoyer, N., Spitzer, B., & Nee, D. E. (2016). Distinct neural substrates for maintaining locations and spatial relations in working

- memory. *Frontiers in Human Neuroscience*, 10(NOV2016), 1–17.
 URL <http://journal.frontiersin.org/article/10.3389/fnhum.2016.00594/full>
- Blacker, K. J., Weisberg, S. M., Newcombe, N. S., & Courtney, S. M. (2017). Keeping track of where we are: Spatial working memory in navigation. *Visual Cognition*, 25(7-8), 691–702.
- Blodgett, H. C., & McCutchan, K. (1947). Place versus response learning in the simple T-maze. *Journal of Experimental Psychology*, 37(5), 412–422.
 URL <http://link.springer.com/10.3758/BF03206427><http://doi.apa.org/getdoi.cfm?doi=10.1037/h0059305>
- Bohbot, V. D., Copara, M. S., Gotman, J., & Ekstrom, A. D. (2017). Low-frequency theta oscillations in the human hippocampus during real-world and virtual navigation. *Nature Communications*, 8, 1–7.
- Bohbot, V. D., Kalina, M., Stepankova, K., Spackova, N., Petrides, M., & Nadel, L. (1998). Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. *Neuropsychologia*, 36(11), 1217–1238.
- Bostelmann, M., Lavenex, P., & Banta Lavenex, P. (2020). Children five-to-nine years old can use path integration to build a cognitive map without vision. *Cognitive Psychology*, 121(January), 101307.
 URL <https://doi.org/10.1016/j.cogpsych.2020.101307>
- Brady, T. F., & Chun, M. M. (2007). Spatial Constraints on Learning in Visual Search: Modeling Contextual Cuing. *Journal of Experimental Psychology: Human Perception and Performance*, 33(4), 798–815.
- Brandt, T., Schautzer, F., Hamilton, D. A., Brüning, R., Markowitsch, H. J., Kalla, R., Darlington, C., Smith, P., & Strupp, M. (2005). Vestibular loss causes hippocampal atrophy and impaired spatial memory in humans. *Brain*, 128(11), 2732–2741.
- Brunyé, T. T. (2018). Modulating spatial processes and navigation via transcranial electrical stimulation: A mini review. *Frontiers in Human Neuroscience*, 11(January), 1–8.
 URL <http://journal.frontiersin.org/article/10.3389/fnhum.2017.00649/full>
- Brunyé, T. T., Holmes, A., Cantelon, J., Eddy, M. D., Gardony, A. L., Mahoney, C. R., & Taylor, H. A. (2014). Direct current brain stimulation enhances navigation efficiency in individuals with low spatial sense of direction. *NeuroReport*, 25(15), 1175–1179.
- Brunyé, T. T., Hussey, E. K., Gardony, A. L., Holmes, A., & Taylor, H. A. (2018). Targeted Right Medial Temporal Lobe tDCS and Associative Spatial and Non-Spatial Memory. *Journal of Cognitive Enhancement*, 2(3), 287–297.
 URL <http://link.springer.com/10.1007/s41465-018-0072-5>
- Buckley, M. G., & Smith, A. D. (2013). Evidence for spatial navigational impairments in hydrocephalus patients without spina bifida. *Brain and Cognition*, 83(1), 132–141.
 URL <http://dx.doi.org/10.1016/j.bandc.2013.07.010>
- Burgess, N. (2006). Spatial memory: how egocentric and allocentric combine. *Trends in Cognitive Sciences*, 10(12), 551–557.
- Burgess, N. (2008). Spatial cognition and the brain. *Annals of the New York Academy of Sciences*, 1124, 77–97.
- Burgess, N., Spiers, H. J., & Paleologou, E. (2004). Orientational manoeuvres in the dark: Dissociating allocentric and egocentric influences on spatial memory. *Cognition*, 94(2), 149–166.

- Cabeza, R., Anderson, N. D., Locantore, J. K., & McIntosh, A. R. (2002). Aging gracefully: Compensatory brain activity in high-performing older adults. *NeuroImage*, *17*(3), 1394–1402.
- Ceccanti, M., Coriale, G., Hamilton, D. A., Carito, V., Coccorello, R., Scalese, B., Ciafrè, S., Codazzo, C., Messina, M. P., Chaldakov, G. N., & Fiore, M. (2018). Virtual Morris task responses in individuals in an abstinence phase from alcohol. *Canadian Journal of Physiology and Pharmacology*, *96*(2), 128–136.
URL <http://www.nrcresearchpress.com/doi/10.1139/cjpp-2017-0013>
- Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, *9*(2), 129–136.
- Chrastil, E. R., Sherrill, K. R., Hasselmo, M. E., & Stern, C. E. (2015). There and back again: Hippocampus and retrosplenial cortex track homing distance during human path integration. *Journal of Neuroscience*, *35*(46), 15442–15452.
URL <http://www.jneurosci.org/cgi/doi/10.1523/JNEUROSCI.1209-15.2015>
- Chrastil, E. R., & Warren, W. H. (2013). Active and passive spatial learning in human navigation: Acquisition of survey knowledge. *Journal of Experimental Psychology: Learning Memory and Cognition*, *39*(5), 1520–1537.
- Chrastil, E. R., & Warren, W. H. (2014). From cognitive maps to cognitive graphs. *PLoS ONE*, *9*(11).
- Chrastil, E. R., & Warren, W. H. (2015). Active and passive spatial learning in human navigation: Acquisition of graph knowledge. *Journal of Experimental Psychology: Learning Memory and Cognition*, *41*(4), 1162–1178.
- Chua, K. P., & Chun, M. M. (2003). Implicit scene learning is viewpoint dependent. *Perception and Psychophysics*, *65*(1), 72–80.
URL <http://link.springer.com/10.3758/BF03194784>
- Chun, M. M., & Jiang, Y. (1998). Contextual Cueing: Implicit Learning and Memory of Visual Context Guides Spatial Attention. *Cognitive Psychology*, *36*(1), 28–71.
URL <http://www.ncbi.nlm.nih.gov/pubmed/9679076>
http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=9679076
<http://linkinghub.elsevier.com/retrieve/doi/10.1006/cogp.1998.0681>
- Chun, M. M., & Jiang, Y. (2003). Implicit, Long-Term Spatial Contextual Memory. *Journal of Experimental Psychology: Learning Memory and Cognition*, *29*(2), 224–234.
- Coats, R. O., Snapp-Childs, W., Wilson, A. D., & Bingham, G. P. (2013). Perceptuo-motor learning rate declines by half from 20s to 70/80s. *Experimental Brain Research*, *225*(1), 75–84.
URL <https://doi.org/10.1007/s00221-012-3349-4>
- Commins, S., Duffin, J., Chaves, K., Leahy, D., Corcoran, K., Caffrey, M., Keenan, L., Finan, D., & Thornberry, C. (2020). NavWell: A simplified virtual-reality platform for spatial navigation and memory experiments. *Behavior Research Methods*, *52*(3), 1189–1207.
URL <http://link.springer.com/10.3758/s13428-019-01310-5>
- Cornwell, B. R., Salvatore, G., Colon-Rosario, V., Latov, D. R., Holroyd, T., Carver, F. W., Coppola, R., Manji, H. K., Zarate, C. A., & Grillon, C. (2010). Abnormal hippocampal functioning and impaired spatial navigation in depressed individuals: Evidence from whole-head magnetoencephalography. *American Journal of Psychiatry*, *167*(7), 836–844.

- Cuevas, H. M., Huthmann, A., Knudsen, A., & Wei, C. (2001). Performance differences in a navigation task among users presented with a north-up versus track-up orientation map display. *Proceedings of the Human Factors and Ergonomics Society Annual Meeting*, 45(23), 1666–1670.
- Dandurand, F., Shultz, T. R., & Onishi, K. H. (2008). Comparing online and lab methods in a problem-solving experiment. *Behavior Research Methods*, 40(2), 428–434.
- Daugherty, A. M., Bender, A. R., Yuan, P., & Raz, N. (2016). Changes in Search Path Complexity and Length during Learning of a Virtual Water Maze: Age Differences and Differential Associations with Hippocampal Subfield Volumes. *Cerebral Cortex*, 26(6), 2391–2401.
- Daugherty, A. M., Haacke, E. M., & Raz, N. (2015). Striatal iron content predicts its shrinkage and changes in verbal working memory after two years in healthy adults. *Journal of Neuroscience*, 35(17), 6731–6743.
- Daugherty, A. M., & Raz, N. (2017). A virtual water maze revisited: Two-year changes in navigation performance and their neural correlates in healthy adults. *NeuroImage*, 146, 492–506.
URL <http://dx.doi.org/10.1016/j.neuroimage.2016.09.044>
- De Araújo, D. B., Baffa, O., & Wakai, R. T. (2002). Theta oscillations and human navigation: A magnetoencephalography study. *Journal of Cognitive Neuroscience*, 14(1), 70–78.
- de Leeuw, J. R., & Motz, B. A. (2016). Psychophysics in a Web browser? Comparing response times collected with JavaScript and Psychophysics Toolbox in a visual search task. *Behavior Research Methods*, 48(1), 1–12.
- De Lillo, C., & James, F. C. (2012). Spatial working memory for clustered and linear configurations of sites in a virtual reality foraging task. *Cognitive Processing*, 13(1 SUPPL).
- De Lillo, C., Kirby, M., & James, F. C. (2014). Spatial working memory in immersive virtual reality foraging: Path organization, traveling distance and search efficiency in humans (Homo sapiens). *American Journal of Primatology*, 76(5), 436–446.
- Dienes, Z. (2014). Using Bayes to get the most out of non-significant results. *Frontiers in Psychology*, 5(July), 1–17.
URL <http://journal.frontiersin.org/article/10.3389/fpsyg.2014.00781/abstract>
- Diersch, N., & Wolbers, T. (2019). The potential of virtual reality for spatial navigation research across the adult lifespan. *Journal of Experimental Biology*, 222.
- Doeller, C. F., & Burgess, N. (2008). Distinct error-correcting and incidental learning of location relative to landmarks and boundaries. *Proceedings of the National Academy of Sciences of the United States of America*, 105(15), 5909–5914.
URL <http://www.ncbi.nlm.nih.gov/pubmed/18413609><http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=PMC2311326>
- Doeller, C. F., King, J. A., & Burgess, N. (2008). Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. *Proceedings of the National Academy of Sciences of the United States of America*, 105(15), 5915–5920.
URL <http://www.pnas.org/cgi/doi/10.1073/pnas.0801489105>
- Dong, Z., Bai, Y., Wu, X., Li, H., Gong, B., Howland, J. G., Huang, Y., He, W., Li, T., & Wang, Y. T. (2013). Hippocampal long-term depression mediates spatial reversal learning in

- the Morris water maze. *Neuropharmacology*, 64, 65–73.
 URL <http://dx.doi.org/10.1016/j.neuropharm.2012.06.027>
- Driscoll, I., Hamilton, D. A., Yeo, R. A., Brooks, W. M., & Sutherland, R. J. (2005). Virtual navigation in humans: The impact of age, sex, and hormones on place learning. *Hormones and Behavior*, 47(3), 326–335.
 URL https://ac-els-cdn-com.plymouth.idm.oclc.org/S0018506X04002624/1-s2.0-S0018506X04002624-main.pdf?_tid=92aff689-93f9-47f2-856e-4970ce76c0eb&acdnat=1528494477_0ccc3968897d1c4981adbb64057ddf87
- Druker, M., & Anderson, B. (2010). Spatial probability aids visual stimulus discrimination. *Frontiers in Human Neuroscience*, 4(August), 1–10.
- Dudchenko, P. A., Goodridge, J. P., Seiterle, D. A., & Taube, J. S. (1997). Effects of repeated disorientation on the acquisition of spatial tasks in rats: Dissociation between the appetitive radial arm maze and aversive water maze. *Journal of Experimental Psychology: Animal Behavior Processes*, 23(2), 194–210.
- Duncan, J., & Humphreys, G. W. (1989). Visual Search and Stimulus Similarity. *Psychological Review*, 96(3), 433–458.
 URL <http://doi.apa.org/getdoi.cfm?doi=10.1037/0033-295X.96.3.433>
- Ekstrom, A. D., & Isham, E. A. (2017). Human spatial navigation: representations across dimensions and scales. *Current Opinion in Behavioral Sciences*, 17, 84–89.
 URL <http://dx.doi.org/10.1016/j.cobeha.2017.06.005>
- Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., & Fried, I. (2003). Cellular networks underlying human spatial navigation. *Nature*, 425(6954), 184–188.
 URL <http://www.nature.com/articles/nature01964>
- Fenton, A. A., Arolfo, M. P., & Bures, J. (1994). Place navigation in the morris water maze under minimum and redundant extra-maze cue conditions. *Behavioral and Neural Biology*, 62(3), 178–189.
 URL <https://link.springer.com/article/10.3758/BF03330589>
- Ferguson, T. D., Livingstone-Lee, S. A., & Skelton, R. W. (2019). Incidental learning of allocentric and egocentric strategies by both men and women in a dual-strategy virtual Morris Water Maze. *Behavioural Brain Research*, 364(September 2018), 281–295.
 URL <https://doi.org/10.1016/j.bbr.2019.02.032>
- Fields, A. W., & Shelton, A. L. (2006). Individual skill differences and large-scale environmental learning. *Journal of Experimental Psychology: Learning Memory and Cognition*, 32(3), 506–515.
- Fjell, A. M., & Walhovd, K. B. (2010). Structural brain changes in aging: Courses, causes and cognitive consequences. *Reviews in the Neurosciences*, 21(3), 187–222.
 URL <https://doi.org/10.1515/REVNEURO.2010.21.3.187>
- Folley, B. S., Astur, R. S., Jagannathan, K., Calhoun, V. D., & Pearlson, G. D. (2010). Anomalous neural circuit function in schizophrenia during a virtual Morris water task. *NeuroImage*, 49(4), 3373–3384.
 URL <http://dx.doi.org/10.1016/j.neuroimage.2009.11.034>
- Foo, P., Warren, W. H., Duchon, A., & Tarr, M. J. (2005). Do humans integrate routes into a cognitive map? Map- Versus landmark-based navigation of novel shortcuts. *Journal of Experimental Psychology: Learning Memory and Cognition*, 31(2), 195–215.

- Foulsham, T., Chapman, C., Nasiopoulos, E., & Kingstone, A. (2014). Top-down and bottom-up aspects of active search in a real-world environment. *Canadian Journal of Experimental Psychology*, 68(1), 8–19.
- Furman, A. J., Clements-Stephens, A. M., Marchette, S. A., & Shelton, A. L. (2014). Persistent and stable biases in spatial learning mechanisms predict navigational style. *Cognitive, Affective and Behavioral Neuroscience*, 14(4), 1375–1391.
- Gallagher, M., & Nicolle, M. M. (1993). Animal models of normal aging: Relationship between cognitive decline and markers in hippocampal circuitry. *Behavioural Brain Research*, 57(2), 155–162.
- Gallistel, C. R. (1990). *The organization of learning*. The MIT Press.
- Garthe, A., Behr, J., & Kempermann, G. (2009). Adult-generated hippocampal neurons allow the flexible use of spatially precise learning strategies. *PLoS ONE*, 4(5).
- Gazova, I., Laczó, J., Rubinova, E., Mokrisova, I., Hyncicova, E., Andel, R., Vyhnalek, M., Sheardova, K., Coulson, E. J., & Hort, J. (2013). Spatial navigation in young versus older adults. *Frontiers in Aging Neuroscience*, 5(DEC), 1–8.
- Geinisman, Y., Detolledo-Morrell, L., Morrell, F., & Heller, R. E. (1995). Hippocampal markers of age-related memory dysfunction: Behavioral, electrophysiological and morphological perspectives. *Progress in Neurobiology*, 45(3).
- Geiser, C., Lehmann, W., & Eid, M. (2008). A note on sex differences in mental rotation in different age groups. *Intelligence*, 36(6), 556–563.
URL <https://www.sciencedirect.com/science/article/pii/S0160289608000032>
- Geng, J. J., & Behrmann, M. (2002). Probability cuing of target location facilitates visual search implicitly in normal participants and patients with hemispatial neglect. *Psychological Science*, 13(6), 520–525.
- Geng, J. J., & Behrmann, M. (2005). Spatial probability as an attentional cue in visual search. *Perception and Psychophysics*, 67(7), 1252–1268.
URL <http://www.springerlink.com/index/10.3758/BF03193557>
- Gilchrist, I. D., North, A., & Hood, B. (2001). Is visual search really like foraging? *Perception*, 30(12), 1459–1464.
- Gould, S. J. J., Cox, A. L., Brumby, D. P., & Wiseman, S. (2015). Home is Where the Lab is: A Comparison of Online and Lab Data From a Time-sensitive Study of Interruption. *Human Computation*, 2(1), 45–67.
- Graziano, A., Petrosini, L., & Bartoletti, A. (2003). Automatic recognition of explorative strategies in the Morris water maze. *Journal of Neuroscience Methods*, 130(1), 33–44.
- Hamilton, D. A., Kodituwakku, P., Sutherland, R. J., & Savage, D. D. (2003). Children with Fetal Alcohol Syndrome are impaired at place learning but not cued-navigation in a virtual Morris water task. *Behavioural Brain Research*, 143(1), 85–94.
- Hartley, T., Maguire, E. A., Spiers, H. J., & Burgess, N. (2003). The well-worn route and the path less traveled: Distinct neural bases of route following and wayfinding in humans. *Neuron*, 37(5), 877–888.
- Hegarty, M., Montello, D. R., Richardson, A. E., Ishikawa, T., & Lovelace, K. (2006). Spatial abilities at different scales: Individual differences in aptitude-test performance and spatial-layout learning. *Intelligence*, 34(2), 151–176.

- Hegarty, M., Richardson, A. E., Montello, D. R., Lovelace, K., & Subbiah, I. (2002). Development of a self-report measure of environmental spatial ability. *Intelligence*, 30(5), 425–447.
URL <http://www.sciencedirect.com/science/article/pii/S0160289602001162>
- Hejtmanek, L., Starrett, M., Ferrer, E., & Ekstrom, A. D. (2020). How much of what we learn in virtual reality transfers to real-world navigation? *Multisensory Research*, 33(4-5), 479–503.
URL https://brill.com/view/journals/msr/33/4-5/article-p479_6.xml
- Henriksen, S. P., & Midtbø, T. (2015). Investigation of map orientation by the use of low-cost virtual reality equipment. In *Cartography-Maps Connecting the World*, (pp. 75–88). Springer.
- Hessels, R. S., Hooge, I. T., Snijders, T. M., & Kemner, C. (2014). Is there a limit to the superiority of individuals with ASD in visual search? *Journal of Autism and Developmental Disorders*, 44(2), 443–451.
- Hilbig, B. E. (2016). Reaction time effects in lab versus Web-based research: Experimental evidence. *Behavior Research Methods*, 48(4), 1718–1724.
URL <http://dx.doi.org/10.3758/s13428-015-0678-9>
- Hort, J., Laczó, J., Vyhnálek, M., Bojar, M., Bureš, J., & Vlček, K. (2007). Spatial navigation deficit in amnesic mild cognitive impairment. *Proceedings of the National Academy of Sciences of the United States of America*, 104(10), 4042–4047.
- Howard, L. R., Javadi, A. H., Yu, Y., Mill, R. D., Morrison, L. C., Knight, R., Loftus, M. M., Staskute, L., & Spiers, H. J. (2014). The hippocampus and entorhinal cortex encode the path and euclidean distances to goals during navigation. *Current Biology*, 24(12), 1331–1340.
URL <http://dx.doi.org/10.1016/j.cub.2014.05.001>
- Huber, B., & Gajos, K. Z. (2020). Conducting online virtual environment experiments with uncompensated, unsupervised samples. *PLoS ONE*, 15(1), 1–17.
URL <http://dx.doi.org/10.1371/journal.pone.0227629>
- Huffman, D. J., & Ekstrom, A. D. (2019a). A Modality-Independent Network Underlies the Retrieval of Large-Scale Spatial Environments in the Human Brain. *Neuron*, 104(3), 611–622.e7.
URL <https://doi.org/10.1016/j.neuron.2019.08.012>
- Huffman, D. J., & Ekstrom, A. D. (2019b). Which way is the bookstore? A closer look at the judgments of relative directions task. *Spatial Cognition and Computation*, 19(2), 93–129.
URL <https://doi.org/10.1080/13875868.2018.1531869>
- Huffman, D. J., & Ekstrom, A. D. (2020). An important step toward understanding the role of body-based cues on human spatial memory for large-scale environments. *Journal of Cognitive Neuroscience*, 33(2), 167–179.
URL https://www.mitpressjournals.org/doi/abs/10.1162/jocn_a_01653
- Huygelier, H., Schraepen, B., van Ee, R., Vanden Abeele, V., & Gillebert, C. R. (2019). Acceptance of immersive head-mounted virtual reality in older adults. *Scientific Reports*, 9(1), 1–12.
- Iaria, G., Palermo, L., Committeri, G., & Barton, J. J. (2009). Age differences in the formation and use of cognitive maps. *Behavioural Brain Research*, 196(2), 187–191.

- Iddon, J. L., Morgan, D. J., Loveday, C., Sahakian, B. J., & Pickard, J. D. (2004). Neuropsychological profile of young adults with spina bifida with or without hydrocephalus. *Journal of Neurology, Neurosurgery and Psychiatry*, *75*(8), 1112–1118.
- Iglói, K., Zaoui, M., Berthoz, A., & Rondi-Reig, L. (2009). Sequential egocentric strategy is acquired as early as allocentric strategy: Parallel acquisition of these two navigation strategies. *Hippocampus*, *19*(12), 1199–1211.
- Jeffreys, H. (1961). *Theory of probability*. Clarendon Press Oxford, 3rd ed. ed.
- Jiang, Y. V., Capistrano, C. G., Esler, A. N., & Swallow, K. M. (2013). Directing attention based on incidental learning in children with autism spectrum disorder. *Neuropsychology*, *27*(2), 161–169.
URL <http://doi.apa.org/getdoi.cfm?doi=10.1037/a0031648>
- Jiang, Y. V., & Swallow, K. M. (2013). Spatial reference frame of incidentally learned attention. *Cognition*, *126*(3), 378–390.
URL <http://dx.doi.org/10.1016/j.cognition.2012.10.011>
- Jiang, Y. V., & Won, B. Y. (2015). Spatial scale, rather than nature of task or locomotion, modulates the spatial reference frame of attention. *Journal of Experimental Psychology: Human Perception and Performance*, *41*(3), 866–878.
- Jiang, Y. V., Won, B. Y., Swallow, K. M., & Mussack, D. M. (2014). Spatial reference frame of attention in a large outdoor environment. *Journal of Experimental Psychology: Human Perception and Performance*, *40*(4), 1346–1357.
- Julian, J. B., Keinath, A. T., Marchette, S. A., & Epstein, R. A. (2018). The Neurocognitive Basis of Spatial Reorientation. *Current Biology*, *28*(17), R1059–R1073.
URL <https://linkinghub.elsevier.com/retrieve/pii/S0960982218305293>
- Julian, J. B., Ryan, J., Hamilton, R. H., & Epstein, R. A. (2016). The Occipital Place Area Is Causally Involved in Representing Environmental Boundaries during Navigation. *Current Biology*, *26*(8), 1104–1109.
URL <http://dx.doi.org/10.1016/j.cub.2016.02.066>
- Kallai, J., Makany, T., Karadi, K., & Jacobs, W. J. (2005). Spatial orientation strategies in Morris-type virtual water task for humans. *Behavioural Brain Research*, *159*(2), 187–196.
- Kalová, E., Vlček, K., Jarolímová, E., & Bureš, J. (2005). Allothetic orientation and sequential ordering of places is impaired in early stages of Alzheimer's disease: Corresponding results in real space tests and computer tests. *Behavioural Brain Research*, *159*(2), 175–186.
- Karatekin, C., & Asarnow, R. F. (1998). Components of visual search in childhood-onset schizophrenia and attention-deficit/hyperactivity disorder. *Journal of abnormal child psychology*, *26*(5), 367–380.
- Kelly, R. L. (2013). *The Lifeways of Hunter-Gatherers: The Foraging Spectrum*. Cambridge University Press.
- Kim, H., Park, J. Y., & Kim, K. K. (2018a). Spatial learning and memory using a radial arm maze with a head-mounted display. *Psychiatry Investigation*, *15*(10), 935–944.
URL <http://psychiatryinvestigation.org/journal/view.php?doi=10.30773/pi.2018.06.28.3%0Ahttp://www.ncbi.nlm.nih.gov/pubmed/30301309>
- Kim, H. K., Park, J., Choi, Y., & Choe, M. (2018b). Virtual reality sickness questionnaire (VRSQ): Motion sickness measurement index in a virtual reality environment. *Applied Ergonomics*, *69*(January), 66–73.
URL <https://doi.org/10.1016/j.apergo.2017.12.016>

- Klein, R. M., & MacInnes, W. J. (1999). Inhibition of return is a foraging facilitator in visual search. *Psychological Science*, *10*(4), 346–352.
- Kober, S. E., Kurzman, J., & Neuper, C. (2012). Cortical correlate of spatial presence in 2D and 3D interactive virtual reality: An EEG study. *International Journal of Psychophysiology*, *83*(3), 365–374.
URL <http://dx.doi.org/10.1016/j.ijpsycho.2011.12.003>
- Kolarik, B. S., Shahlaie, K., Hassan, A., Borders, A. A., Kaufman, K. C., Gurkoff, G., Yonelinas, A. P., & Ekstrom, A. D. (2016). Impairments in precision, rather than spatial strategy, characterize performance on the virtual Morris Water Maze: A case study. *Neuropsychologia*, *80*, 90–101.
URL <http://dx.doi.org/10.1016/j.neuropsychologia.2015.11.013>
- Korthauer, L. E., Nowak, N. T., Moffat, S. D., An, Y., Rowland, L. M., Barker, P. B., Resnick, S. M., & Driscoll, I. (2016). Correlates of virtual navigation performance in older adults. *Neurobiology of Aging*, *39*, 118–127.
URL <http://dx.doi.org/10.1016/j.neurobiolaging.2015.12.003>
- Kovesdi, C. R., & Barton, B. K. (2013). The role of non-verbal working memory in pedestrian visual search. *Transportation Research Part F: Traffic Psychology and Behaviour*, *19*, 31–39.
URL <http://dx.doi.org/10.1016/j.trf.2013.03.005>
- Kozhevnikov, M., & Hegarty, M. (2001). A dissociation between object manipulation spatial ability and spatial orientation ability. *Memory and Cognition*, *29*(5), 745–756.
- Kozhevnikov, M., Motes, M. A., Rasch, B., & Blajenkova, O. (2006). Perspective-taking vs. mental rotation transformations and how they predict spatial navigation performance. *Applied Cognitive Psychology*, *20*(3), 397–417.
- Kraut, R., Olson, J., Banaji, M., Bruckman, A., Cohen, J., & Couper, M. (2004). Psychological Research Online: Report of Board of Scientific Affairs' Advisory Group on the Conduct of Research on the Internet. *American Psychologist*, *59*(2), 105–117.
- Kristjánsson, T., Draschkow, D., Pálsson, Á., Haraldsson, D., Jónsson, P. Ö., & Kristjánsson, Á. (2022). Moving foraging into three dimensions: feature-versus conjunction-based foraging in virtual reality. *Quarterly Journal of Experimental Psychology*, *75*(2), 313–327.
- Kruschke, J. K. (2010). Bayesian data analysis. *Wiley Interdisciplinary Reviews: Cognitive Science*, *1*(5), 658–676.
- Laczó, J., Andel, R., Vyhnalek, M., Matoska, V., Kaplan, V., Nedelska, Z., Lerch, O., Gazova, I., Moffat, S. D., & Hort, J. (2015). The effect of TOMM40 on spatial navigation in amnesic mild cognitive impairment. *Neurobiology of Aging*, *36*(6), 2024–2033.
URL <http://dx.doi.org/10.1016/j.neurobiolaging.2015.03.004>
- Laczó, J., Andel, R., Vyhnalek, M., Vlcek, K., Magerova, H., Varjassyova, A., Tolar, M., & Hort, J. (2010). Human analogue of the morris water maze for testing subjects at risk of Alzheimer's Disease. *Neurodegenerative Diseases*, *7*(1-3), 148–152.
URL <https://www.karger.com/Article/FullText/289226>
- Laczó, J., Markova, H., Lobellova, V., Gazova, I., Parizkova, M., Cerman, J., Nekovarova, T., Vales, K., Klovrczova, S., Harrison, J., Windisch, M., Vlcek, K., Svoboda, J., Hort, J., & Stuchlik, A. (2017). Scopolamine disrupts place navigation in rats and humans: a translational validation of the Hidden Goal Task in the Morris water maze and a real maze for humans. *Psychopharmacology*, *234*(4), 535–547.
URL <http://dx.doi.org/10.1007/s00213-016-4488-2>

- Laczó, J., Vlček, K., Vyhnálek, M., Vajnerová, O., Ort, M., Holmerová, I., Tolar, M., Anđel, R., Bojar, M., & Hort, J. (2009). Spatial navigation testing discriminates two types of amnesic mild cognitive impairment. *Behavioural Brain Research*, *202*(2), 252–259.
- Laczó, M., Wiener, J. M., Kalinova, J., Matuskova, V., Vyhnalek, M., Hort, J., & Laczó, J. (2021). Spatial navigation and visuospatial strategies in typical and atypical aging. *Brain Sciences*, *11*(11).
URL <https://osf.io/mx52y/>
- Lange, K., Kühn, S., & Filevich, E. (2015). "Just another tool for online studies" (JATOS): An easy solution for setup and management of web servers supporting online studies. *PLoS ONE*, *10*(6), 1–14.
- Learmonth, A. E., Newcombe, N. S., Sheridan, N., & Jones, M. (2008). Why size counts: Children's spatial reorientation in large and small enclosures: Paper. *Developmental Science*, *11*(3), 414–426.
- Lee, M. D., & Wagenmakers, E.-J. (2014). *Bayesian Cognitive Modeling*. Cambridge University Press, 1st ed. ed.
- Li, C. L., Aivar, M. P., Kit, D. M., Tong, M. H., & Hayhoe, M. M. (2016). Memory and visual search in naturalistic 2D and 3D environments. *Journal of Vision*, *16*(8), 1–20.
- Li, C. L., Aivar, M. P., Tong, M. H., & Hayhoe, M. M. (2018). Memory shapes visual search strategies in large-scale environments. *Scientific Reports*, *8*(1), 1–11.
URL <http://dx.doi.org/10.1038/s41598-018-22731-w>
- Liang, M., Starrett, M. J., & Ekstrom, A. D. (2018). Dissociation of frontal-midline delta-theta and posterior alpha oscillations: A mobile EEG study. *Psychophysiology*, *55*(9), e13090.
URL <http://doi.wiley.com/10.1111/psyp.13090>
- Lind, S. E., Williams, D. M., Raber, J., Peel, A., & Bowler, D. M. (2013). Spatial navigation impairments among intellectually high-functioning adults with autism spectrum disorder: Exploring relations with theory of mind, episodic memory, and episodic future thinking. *Journal of Abnormal Psychology*, *122*(4), 1189–1199.
- Linn, M. C., & Petersen, A. C. (1985). Emergence and characterization of sex differences in spatial ability: a meta-analysis. *Child development*, *56*(6), 1479–1498.
- Livingstone-Lee, S. A., Murchison, S., Zeman, P. M., Gandhi, M., van Gerven, D., Stewart, L., Livingston, N. J., & Skelton, R. W. (2011). Simple gaze analysis and special design of a virtual Morris water maze provides a new method for differentiating egocentric and allocentric navigational strategy choice. *Behavioural Brain Research*, *225*(1), 117–125.
URL <http://dx.doi.org/10.1016/j.bbr.2011.07.005>
- Livingstone-Lee, S. A., Zeman, P. M., Gillingham, S. T., & Skelton, R. W. (2014). Navigational strategy may be more a matter of environment and experience than gender. *Learning and Motivation*, *45*(1), 30–43.
URL <http://dx.doi.org/10.1016/j.lmot.2013.09.003>
- Luo, X., Guo, J., Li, D., Liu, L., Chen, Y., Zhu, Y., Johnstone, S. J., Wang, Y., Song, Y., & Sun, L. (2021). Atypical developmental trajectories of early perception among school-age children with attention deficit hyperactivity disorder during a visual search task. *Child Development*, *92*(6), e1186–e1197.
- Lustig, C., & Jantz, T. (2015). Questions of age differences in interference control: When and how, not if? *Brain Research*, *1612*, 59–69.

- M. Aghajan, Z., Schuette, P., Fields, T. A., Tran, M. E., Siddiqui, S. M., Hasulak, N. R., Tchong, T. K., Eliashiv, D., Mankin, E. A., Stern, J., Fried, I., & Suthana, N. (2017). Theta Oscillations in the Human Medial Temporal Lobe during Real-World Ambulatory Movement. *Current Biology*, 27(24), 3743–3751.e3.
URL <https://doi.org/10.1016/j.cub.2017.10.062>
- Machado, M. L., Lefèvre, N., Philoxene, B., Le Gall, A., Madeleine, S., Fleury, P., Smith, P. F., & Besnard, S. (2019). New software dedicated to virtual mazes for human cognitive investigations. *Journal of Neuroscience Methods*, 327(October 2018), 108388.
URL <https://doi.org/10.1016/j.jneumeth.2019.108388>
- Maguire, E. A., Gadian, D. G., Johnsrude, I. S., Good, C. D., Ashburner, J., Frackowiak, R. S., & Frith, C. D. (2000). Navigation-related structural change in the hippocampi of taxi drivers. *Proceedings of the National Academy of Sciences of the United States of America*, 97(8), 4398–4403.
- Maguire, E. A., Woollett, K., & Spiers, H. J. (2006). London taxi drivers and bus drivers: A structural MRI and neuropsychological analysis. *Hippocampus*, 16(12), 1091–1101.
URL https://onlinelibrary.wiley.com/doi/10.1002/hipo.20233http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=17598147
- Marchette, S. A., Bakker, A., & Shelton, A. L. (2011). Cognitive mappers to creatures of habit: Differential engagement of place and response learning mechanisms predicts human navigational behavior. *Journal of Neuroscience*, 31(43), 15264–15268.
URL <http://www.jneurosci.org/cgi/doi/10.1523/JNEUROSCI.3634-11.2011>
- Marchette, S. A., Vass, L. K., Ryan, J., & Epstein, R. A. (2014). Anchoring the neural compass: Coding of local spatial reference frames in human medial parietal lobe. *Nature Neuroscience*, 17(11), 1598–1606.
- Masters, M. S., & Sanders, B. (1993). Is the gender difference in mental rotation disappearing? *Behavior Genetics*, 23(4), 337–341.
URL <https://doi.org/10.1007/BF01067434>
- Maya, C., Rosetti, M. F., Pacheco-Cobos, L., & Hudson, R. (2019). Human Foragers: Searchers by Nature and Experience. *Evolutionary Psychology*, 17(2), 147470491983972.
URL <http://journals.sagepub.com/doi/10.1177/1474704919839729>
- McAvan, A. S., Du, Y. K., Oyao, A., Doner, S., Grilli, M. D., & Ekstrom, A. D. (2021). Older Adults Show Reduced Spatial Precision but Preserved Strategy-Use During Spatial Navigation Involving Body-Based Cues. *Frontiers in Aging Neuroscience*, 13(April), 1–14.
- Meng, L. (2005). Egocentric design of map-based mobile services. *The Cartographic Journal*, 42(1), 5–13.
- Merhav, M., & Wolbers, T. (2019). Aging and spatial cues influence the updating of navigational memories. *Scientific Reports*, 9(1), 1–10.
URL <http://dx.doi.org/10.1038/s41598-019-47971-2>
- Moffat, S. D., & Resnick, S. M. (2002). Effects of age on virtual environment place navigation and allocentric cognitive mapping. *Behavioral Neuroscience*, 116(5), 851–859.
URL <http://www.ncbi.nlm.nih.gov/pubmed/12369805>
- Montello, D. R. (1993). Scale and multiple psychologies of space. *Lecture Notes in Computer Science (including subseries Lecture Notes in Artificial Intelligence and Lecture Notes in Bioinformatics)*, 716 LNCS, 312–321.
URL https://link.springer.com/chapter/10.1007/3-540-57207-4_21http://link.springer.com/10.1007/3-540-57207-4_21

- Morey, R. D., & Rouder, J. N. (2018). *BayesFactor: Computation of Bayes Factors for Common Designs [Computer Software]*.
URL <https://cran.r-project.org/web/packages/BayesFactor/index.html>
- Morris, R. G. (1981). Spatial localization does not require the presence of local cues. *Learning and Motivation, 12*(2), 239–260.
- Morris, R. G. (1984). Developments of a water-maze procedure for studying spatial learning in the rat. *Journal of Neuroscience Methods, 11*(1), 47–60.
- Morris, R. G., Garrud, P., Rawlins, J. N. P., & O'Keefe, J. (1982). Place navigation impaired in rats with hippocampal lesions. *Nature, 297*(5868), 681–683.
- Morris, R. G. M., Schenk, F., Tweedie, F., & Jarrard, L. E. (1990). Ibotenate Lesions of Hippocampus and/or Subiculum: Dissociating Components of Allocentric Spatial Learning. *European Journal of Neuroscience, 2*(12), 1016–1028.
URL <https://onlinelibrary.wiley.com/doi/10.1111/j.1460-9568.1990.tb00014.x>
- Munion, A. K., Stefanucci, J. K., Rovira, E., Squire, P., & Hendricks, M. (2019). Gender differences in spatial navigation: Characterizing wayfinding behaviors. *Psychonomic Bulletin and Review, 26*(6), 1933–1940.
- Murphy, A., & Glennerster, A. (2021). Route selection in non-Euclidean virtual environments. *PLoS ONE, 16*(4 April), 1–23.
URL <http://dx.doi.org/10.1371/journal.pone.0247818>
- Nazareth, A., Weisberg, S. M., Margulis, K., & Newcombe, N. S. (2018). Charting the development of cognitive mapping. *Journal of Experimental Child Psychology, 170*, 86–106.
URL <https://doi.org/10.1016/j.jecp.2018.01.009>
- Nedelska, Z., Andel, R., Laczó, J., Vlcek, K., Horinek, D., Lisy, J., Sheardova, K., Bureš, J., & Hort, J. (2012). Spatial navigation impairment is proportional to right hippocampal volume. *Proceedings of the National Academy of Sciences of the United States of America, 109*(7), 2590–2594.
- Negen, J., Bird, L., & Nardini, M. (2019). An adaptive cue selection model of allocentric spatial reorientation. *bioRxiv*, (pp. 59–66).
- Negen, J., Bird, L. A., King, E., & Nardini, M. (2020). The Difficulty of Effectively Using Allocentric Prior Information in a Spatial Recall Task. *Scientific Reports, 10*(1), 1–10.
- Newcombe, N. S. (2018). Individual variation in human navigation. *Current Biology, 28*(17), R1004–R1008.
URL <http://dx.doi.org/10.1016/j.cub.2018.04.053>
- Newman, M. C., & Kaszniak, A. W. (2000). Spatial memory and aging: Performance on a human analog of the Morris water maze. *Aging, Neuropsychology, and Cognition, 7*(2), 86–93.
- Newman, P. M., & McNamara, T. P. (2021). A comparison of methods of assessing cue combination during navigation. *Behavior Research Methods, 53*(1), 390–398.
- Nosek, B. A., Banaji, M. R., & Greenwald, A. G. (2002). E-Research: Ethics, Security, Design, and Control in Psychological Research on the Internet. *Journal of Social Issues, 58*(1), 161–176.
URL <https://onlinelibrary.wiley.com/doi/10.1111/1540-4560.00254>

- O'Keefe, J. (1976). Place units in the hippocampus of the freely moving rat. *Experimental Neurology*, 51(1), 78–109.
URL <https://linkinghub.elsevier.com/retrieve/pii/0014488676900558>
- O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, 34(1), 171–175.
URL <http://www.ncbi.nlm.nih.gov/pubmed/5124915><https://linkinghub.elsevier.com/retrieve/pii/0006899371903581>
- O'Keefe, J., & Nadel, L. (1978). *The Hippocampus as a Cognitive Map*. Oxford University Press.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113.
- Packard, M. G., & McGaugh, J. L. (1996). Inactivation of Hippocampus or Caudate Nucleus with Lidocaine Differentially Affects Expression of Place and Response Learning. *Neurobiology of Learning and Memory*, 65(1), 65–72.
URL <https://linkinghub.elsevier.com/retrieve/pii/S1074742796900076>
- Padilla, L. M., Creem-Regehr, S. H., Stefanucci, J. K., & Cashdan, E. A. (2017). Sex differences in virtual navigation influenced by scale and navigation experience. *Psychonomic Bulletin and Review*, 24(2), 582–590.
- Palan, S., & Schitter, C. (2018). Prolific.acA subject pool for online experiments. *Journal of Behavioral and Experimental Finance*, 17, 22–27.
URL <https://doi.org/10.1016/j.jbef.2017.12.004>
- Park, J. L., Dudchenko, P. A., & Donaldson, D. I. (2018). Navigation in real-world environments: New opportunities afforded by advances in mobile brain imaging. *Frontiers in Human Neuroscience*, 12(September), 1–12.
URL <https://www.frontiersin.org/article/10.3389/fnhum.2018.00361/full>
- Pashler, H., & Wagenmakers, E. J. (2012). Editors' Introduction to the Special Section on Replicability in Psychological Science: A Crisis of Confidence? *Perspectives on Psychological Science*, 7(6), 528–530.
- Paízková, M., Andel, R., Lerch, O., Marková, H., Gažová, I., Vyhnálek, M., Hort, J., & Laczó, J. (2016). Homocysteine and Real-Space Navigation Performance among Non-Demented Older Adults. *Journal of Alzheimer's Disease*, 55(3), 951–964.
URL <https://www.medra.org/servlet/aliasResolver?alias=iospress&doi=10.3233/JAD-160667>
- Paízková, M., Lerch, O., Moffat, S. D., Andel, R., Mazancova, A. F., Nedelska, Z., Vyhnálek, M., Hort, J., & Laczó, J. (2018). The effect of Alzheimer's disease on spatial navigation strategies. *Neurobiology of Aging*, 64, 107–115.
URL <https://doi.org/10.1016/j.neurobiolaging.2017.12.019><https://linkinghub.elsevier.com/retrieve/pii/S0197458017304165>
- Peer, M., Brunec, I. K., Newcombe, N. S., & Epstein, R. A. (2021). Structuring Knowledge with Cognitive Maps and Cognitive Graphs. *Trends in Cognitive Sciences*, 25(1), 37–54.
URL <https://doi.org/10.1016/j.tics.2020.10.004>
- Pellicano, E., Smith, A. D., Cristino, F., Hood, B. M., Briscoe, J., & Gilchrist, I. D. (2011). Children with autism are neither systematic nor optimal foragers. *Proceedings of the National Academy of Sciences of the United States of America*, 108(1), 421–426.
URL <http://www.pnas.org/cgi/doi/10.1073/pnas.1014076108>

- Peters, M., Laeng, B., Latham, K., Jackson, M., Zaiyouna, R., & Richardson, C. (1995). A redrawn vanderberg and kuse mental rotations test - different versions and factors that affect performance.
- Possin, K. L., Sanchez, P. E., Anderson-Bergman, C., Fernandez, R., Kerchner, G. A., Johnson, E. T., Davis, A., Lo, I., Bott, N. T., Kiely, T., Fenesy, M. C., Miller, B. L., Kramer, J. H., & Finkbeiner, S. (2016). Cross-species translation of the Morris maze for Alzheimer's disease. *Journal of Clinical Investigation*, *126*(2), 779–783.
- Prados, J., & Trobalon, J. B. (1998). Locating an invisible goal in a water maze requires at least two landmarks. *Psychobiology*, *26*(1), 42–48.
- R Core Team (2020). R: A language and environment for statistical computing. URL <https://www.R-project.org/>.
- Ramzaoui, H., Faure, S., & Spotorno, S. (2018). Alzheimers disease, visual search, and instrumental activities of daily living: a review and a new perspective on attention and eye movements. *Journal of Alzheimer's Disease*, *66*(3), 901–925.
- Ravassard, P., Kees, A., Willers, B., Ho, D., Aharoni, D., Cushman, J., Aghajan, Z. M., & Mehta, M. R. (2013). Multisensory control of hippocampal spatiotemporal selectivity. *Science*, *340*(6138), 1342–1346.
- Raz, N., Lindenberger, U., Rodrigue, K. M., Kennedy, K. M., Head, D., Williamson, A., Dahle, C., Gerstorf, D., & Acker, J. D. (2005). Regional brain changes in aging healthy adults: General trends, individual differences and modifiers. *Cerebral Cortex*, *15*(11), 1676–1689.
- Reinecke, K., & Gajos, K. Z. (2015). LabintheWild: Conducting Large-Scale Online Experiments With Uncompensated Samples. In *Proceedings of the 18th ACM Conference on Computer Supported Cooperative Work and Social Computing*, (pp. 1364–1378). New York, NY, USA: ACM. URL <https://dl.acm.org/doi/10.1145/2675133.2675246>
- Ring, M., Gaigg, S. B., de Condappa, O., Wiener, J. M., & Bowler, D. M. (2018). Spatial navigation from same and different directions: The role of executive functions, memory and attention in adults with autism spectrum disorder. *Autism Research*, *11*(5), 798–810.
- Rodgers, M. K., Sindone, J. A., & Moffat, S. D. (2012). Effects of age on navigation strategy. *Neurobiology of Aging*, *33*(1), 202.e15–202.e22. URL <http://dx.doi.org/10.1016/j.neurobiolaging.2010.07.021>
- Rogers, N., SanMartin, C., Ponce, D., Henríquez, M., Valdés, J., & Behrens, M. (2017). Virtual spatial navigation correlates with the moca score in amnesic mild cognitive impairment patients. *Journal of the Neurological Sciences*, *381*(2017), 116–117. URL <https://doi.org/10.1016/j.jns.2017.08.365><https://linkinghub.elsevier.com/retrieve/pii/S0022510X17308626>
- Rosetti, M. F., Pacheco-Cobos, L., & Hudson, R. (2016). An Experimental Method For Investigating Human Searching Behavior In Large, Open Areas. *Current Psychology*, *35*(3), 325–334.
- Rösler, A., Mapstone, M. E., Hays, A. K., Mesulam, M. M., Rademaker, A., Gitelman, D. R., & Weintraub, S. (2000). Alterations of visual search strategy in Alzheimer's disease and aging. *Neuropsychology*, *14*(3), 398–408.
- Rouder, J. N., Speckman, P. L., Sun, D., Morey, R. D., & Iverson, G. (2009). Bayesian t tests for accepting and rejecting the null hypothesis. *Psychonomic Bulletin and Review*, *16*(2), 225–237.

- Ruddle, R. A., & Lessels, S. (2006). For efficient navigational search, humans require full physical movement, but not a rich visual scene. *Psychological Science*, *17*(6), 460–465.
- Ruddle, R. A., & Lessels, S. (2009). The benefits of using a walking interface to navigate virtual environments. *ACM Transactions on Computer-Human Interaction*, *16*(1), 1–18.
URL <http://portal.acm.org/citation.cfm?doid=1502800.1502805>
- Ruddle, R. A., Payne, S. J., & Jones, D. M. (1999). Navigating large-scale virtual environments: What differences occur between helmet-mounted and desk-top displays? *Presence: Teleoperators and Virtual Environments*, *8*(2), 157–168.
URL <https://direct.mit.edu/pvar/article/8/2/157-168/18224>
- Ruddle, R. A., Volkova, E., & BüLthoff, H. H. (2011a). Walking improves your cognitive map in environments that are large-scale and large in extent. *ACM Transactions on Computer-Human Interaction*, *18*(2), 1–20.
- Ruddle, R. A., Volkova, E., Mohler, B., & BüLthoff, H. H. (2011b). The effect of landmark and body-based sensory information on route knowledge. *Memory and Cognition*, *39*(4), 686–699.
- Saunders, D. R., Bex, P. J., & Woods, R. L. (2013). Crowdsourcing a normative natural language dataset: A comparison of amazon mechanical turk and in-lab data collection. *Journal of Medical Internet Research*, *15*(5).
- Sauter, M., Draschkow, D., & Mack, W. (2020). Building, hosting and recruiting: A brief introduction to running behavioral experiments online. *Brain Sciences*, *10*(4), 1–11.
- Schachter, S. C. (2000). *The Quantification and Definition of Handedness: Implications for Handedness Research*, (pp. 155–174). Dordrecht: Springer Netherlands.
URL https://doi.org/10.1007/0-306-46884-0_6
- Schinazi, V. R., Nardi, D., Newcombe, N. S., Shipley, T. F., & Epstein, R. A. (2013). Hippocampal size predicts rapid learning of a cognitive map in humans. *Hippocampus*, *23*(6), 515–528.
- Schöberl, F., Zwergal, A., & Brandt, T. (2020). Testing Navigation in Real Space: Contributions to Understanding the Physiology and Pathology of Human Navigation Control. *Frontiers in Neural Circuits*, *14*(March), 1–14.
- Schoenfeld, R., Foreman, N., & Leplow, B. (2014). Ageing and spatial reversal learning in humans: Findings from a virtual water maze. *Behavioural Brain Research*, *270*, 47–55.
URL <http://dx.doi.org/10.1016/j.bbr.2014.04.036>
- Schoenfeld, R., Lehmann, W., & Leplow, B. (2010a). Effects of age and sex in mental rotation and spatial learning from virtual environments. *Journal of Individual Differences*, *31*(2), 78–82.
- Schoenfeld, R., Moenich, N., Mueller, F. J., Lehmann, W., & Leplow, B. (2010b). Search strategies in a human water maze analogue analyzed with automatic classification methods. *Behavioural Brain Research*, *208*(1), 169–177.
URL <http://dx.doi.org/10.1016/j.bbr.2009.11.022>
- Schoenfeld, R., Schiffelholz, T., Beyer, C., Leplow, B., & Foreman, N. (2017). Variations of the Morris water maze task to comparatively assess human and rodent place navigation. *Neurobiology of Learning and Memory*, *139*, 117–127.
URL <http://dx.doi.org/10.1016/j.nlm.2016.12.022>

- Segen, V., Avraamides, M., Slattery, T., Colombo, G., & Wiener, J. M. (2021). Comparable performance on a spatial memory task in data collected in the lab and online. *PLoS ONE*, *16*(11 November), 1–12.
URL <http://dx.doi.org/10.1371/journal.pone.0259367>
- Seidler, R. D. (2006). Differential effects of age on sequence learning and sensorimotor adaptation. *Brain Research Bulletin*, *70*(4-6), 337–346.
- Sheardova, K., Laczó, J., Vyhnaek, M., Mokrišová, I., Nedelska, Z., Gazova, I., Telensky, P., Andel, R., & Hort, J. (2013). Anxiety but not depression affects self-reported spatial navigation difficulties irrespective of the realspace navigation performance in individuals at risk of Alzheimer's disease. *Alzheimer's & Dementia*, *9*(4), 790–791.
- Shirama, A., Kato, N., & Kashino, M. (2017). When do individuals with autism spectrum disorder show superiority in visual search? *Autism*, *21*(8), 942–951.
- Simons, D. J., & Wang, R. F. (1998). Perceiving real-world viewpoint changes. *Psychological Science*, *9*(4), 315–320.
- Singmann, H., Bolker, B., Westfall, J., & Aust, F. (2016). *afex: Analysis of Factorial Experiments [Computer Software]*. R package version 0.16-1.
URL <https://CRAN.R-project.org/package=afex>
- Sisk, C. A., Interrante, V., & Jiang, Y. V. (2021). Location probability learning in 3-dimensional virtual search environments. *Cognitive Research: Principles and Implications*, *6*(1).
URL <https://doi.org/10.1186/s41235-021-00284-3>
- Skelton, R. W., Bukach, C. M., Laurance, H. E., Thomas, K. G., & Jacobs, W. J. (2000). Humans with traumatic brain injuries show place-learning deficits in computer-generated virtual space. *Journal of Clinical and Experimental Neuropsychology*, *22*(2), 157–175.
- Skelton, R. W., Ross, S. P., Nerad, L., & Livingstone, S. A. (2006). Human spatial navigation deficits after traumatic brain injury shown in the arena maze, a virtual Morris water maze. *Brain Injury*, *20*(2), 189–203.
- Small, S. A., Schobel, S. A., Buxton, R. B., Witter, M. P., & Barnes, C. A. (2011). A pathophysiological framework of hippocampal dysfunction in ageing and disease. *Nature Reviews Neuroscience*, *12*(10), 585–601.
URL <http://dx.doi.org/10.1038/nrn3085>
- Smith, A. D. (2015). Spatial navigation in autism spectrum disorders: A critical review. *Frontiers in Psychology*, *6*(JAN), 1–8.
- Smith, A. D., & Buckley, M. G. (2012). Spatial navigational impairments in hydrocephalus. *Cognitive Processing*, *13*(1 SUPPL), 329–332.
- Smith, A. D., & De Lillo, C. (2022). Sources of variation in search and foraging: A theoretical perspective. *Quarterly Journal of Experimental Psychology*, *75*(2), 197–231.
- Smith, A. D., Gilchrist, I. D., & Hood, B. M. (2005). Children's search behaviour in large-scale space: Developmental components of exploration. *Perception*, *34*(10), 1221–1229.
- Smith, A. D., Hood, B. M., & Gilchrist, I. D. (2008). Visual search and foraging compared in a large-scale search task. *Cognitive Processing*, *9*(2), 121–126.
- Smith, A. D., Hood, B. M., & Gilchrist, I. D. (2010). Probabilistic Cuing in Large-Scale Environmental Search. *Journal of Experimental Psychology: Learning Memory and Cognition*, *36*(3), 605–618.

- Sosa, Y., Teder-Sälejärvi, W. A., & McCourt, M. E. (2010). Biases of spatial attention in vision and audition. *Brain and Cognition*, 73(3), 229–235.
URL <http://dx.doi.org/10.1016/j.bandc.2010.05.007>
- Srivastava, P., Rimzhim, A., Vijay, P., Singh, S., & Chandra, S. (2019). Desktop VR Is Better Than Non-ambulatory HMD VR for Spatial Learning. *Frontiers in Robotics and AI*, 6(July), 1–15.
- Stackman, R. W., Clark, A. S., & Taube, J. S. (2002). Hippocampal spatial representations require vestibular input. *Hippocampus*, 12(3), 291–303.
- Steel, A., Robertson, C. E., & Taube, J. S. (2020). Current promises and limitations of combined virtual reality and functional magnetic resonance imaging research in humans: A commentary on huffman and ekstrom (2019). *Journal of Cognitive Neuroscience*, 33(2), 159–166.
URL <https://direct.mit.edu/jocn/article/33/2/159-166/95532http://www.ncbi.nlm.nih.gov/pubmed/33054553>
- Tales, A., Bayer, A. J., Haworth, J., Snowden, R. J., Philips, M., & Wilcock, G. (2011). Visual search in mild cognitive impairment: A longitudinal study. *Journal of Alzheimer's Disease*, 24(1), 151–160.
- Taube, J. S., Valerio, S., & Yoder, R. M. (2013). Is navigation in virtual reality with fMRI really navigation? *Journal of Cognitive Neuroscience*, 25(7), 1008–1019.
URL https://www.apa.org/ptsd-guideline/ptsd.pdf%0Ahttps://www.apa.org/about/offices/directorates/guidelines/ptsd.pdfhttps://www.mitpressjournals.org/doi/abs/10.1162/jocn_a_00386
- Thornberry, C., Cimadevilla, J. M., & Commins, S. (2021). Virtual Morris water maze: Opportunities and challenges. *Reviews in the Neurosciences*, 32(8), 887–903.
URL <https://www.degruyter.com/document/doi/10.1515/revneuro-2020-0149/html>
- Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, 55(4), 189–208.
URL <https://pdfs.semanticscholar.org/0874/a64d60a23a20303877e23caf8e1d4bb446a4.pdfhttp://doi.apa.org/getdoi.cfm?doi=10.1037/h0061626>
- Tolman, E. C., Ritchie, B. F., & Kalish, D. (1946a). Studies in spatial learning. I. Orientation and the short-cut. *Journal of Experimental Psychology*, 36(1), 13–24.
URL <http://doi.apa.org/getdoi.cfm?doi=10.1037/0096-3445.121.4.429http://content.apa.org/journals/xge/36/1/13>
- Tolman, E. C., Ritchie, B. F., & Kalish, D. (1946b). Studies in spatial learning. II. Place learning versus response learning. *Journal of Experimental Psychology*, 36(3), 221–229.
URL <http://content.apa.org/journals/xge/36/3/221>
- Török, Á., Peter Nguyen, T., Kolozsvári, O., Buchanan, R. J., & Nadasdy, Z. (2014). Reference frames in virtual spatial navigation are viewpoint dependent. *Frontiers in Human Neuroscience*, 8(SEP), 1–10.
- Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, 12(1), 97–136.
- Unity (2019). Unity professional software (version 2019.2.12f1) [computer software].
URL <https://unity3d.com/get-unity/download/archive>
- Vadillo, M. A., Linszen, D., Orgaz, C., Parsons, S., & Shanks, D. R. (2020). Unconscious or underpowered? Probabilistic cuing of visual attention. *Journal of Experimental Psychology: General*, 149(1), 160–181.

- Valve Software (2019). Steam vr plugin (version 2.5.0) [computer software].
URL https://github.com/ValveSoftware/steamvr_unity_plugin
- van der Ham, I. J., Claessen, M. H., Evers, A. W., & van der Kuil, M. N. (2020). Large-scale assessment of human navigation ability across the lifespan. *Scientific Reports*, *10*(1), 1–12.
URL <http://dx.doi.org/10.1038/s41598-020-60302-0>
- Vandenberg, S. G., & Kuse, A. R. (1978). Mental rotations, a group test of three-dimensional spatial visualization. *Perceptual and Motor Skills*, *47*(2), 599–604.
- Vorhees, C. V., & Williams, M. T. (2006). Morris water maze: procedures for assessing spatial and related forms of learning and memory. *Nature Protocols*, *1*(2), 848–858.
URL <http://www.nature.com/articles/nprot.2006.116>
- Vorhees, C. V., & Williams, M. T. (2014). Assessing spatial learning and memory in rodents. *ILAR Journal*, *55*(2), 310–332.
- Vouros, A., Gehring, T. V., Szydlowska, K., Janusz, A., Tu, Z., Croucher, M., Lukasiuk, K., Konopka, W., Sandi, C., & Vasilaki, E. (2018). A generalised framework for detailed classification of swimming paths inside the Morris Water Maze. *Scientific Reports*, *8*(1), 1–15.
URL <http://dx.doi.org/10.1038/s41598-018-33456-1>
- Voyer, D., Voyer, S., & Bryden, M. P. (1995). Magnitude of sex differences in spatial abilities: A meta-analysis and consideration of critical variables. *Psychological Bulletin*, *117*, 250–270.
URL </record/1995-20087-001>
- Walthev, C., & Gilchrist, I. D. (2006). Target location probability effects in visual search: An effect of sequential dependencies. *Journal of Experimental Psychology: Human Perception and Performance*, *32*(5), 1294–1301.
- Wang, R. F., & Simons, D. J. (1999). Active and passive scene recognition across views. *Cognition*, *70*(2), 191–210.
URL <https://linkinghub.elsevier.com/retrieve/pii/S0010027799000128>
- Wang, R. F., & Spelke, E. S. (2002). Human spatial representation: Insights from animals. *Trends in Cognitive Sciences*, *6*(9), 376–382.
- Warren, W. H., Rothman, D. B., Schnapp, B. H., & Ericson, J. D. (2017). Wormholes in virtual space: From cognitive maps to cognitive graphs. *Cognition*, *166*, 152–163.
URL <http://dx.doi.org/10.1016/j.cognition.2017.05.020>
- Weiler, M. D., Bernstein, J. H., Bellinger, D., & Waber, D. P. (2002). Information processing deficits in children with attention-deficit/hyperactivity disorder, inattentive type, and children with reading disability. *Journal of Learning Disabilities*, *35*(5), 449–462.
- Weisberg, S. M., Badgio, D., & Chatterjee, A. (2018). Feel the way with a vibrotactile compass: Does a navigational aid aid navigation? *Journal of Experimental Psychology: Learning Memory and Cognition*, *44*(5), 667–679.
- Weisberg, S. M., Newcombe, N. S., & Chatterjee, A. (2019). Everyday taxi drivers: Do better navigators have larger hippocampi? *Cortex*, *115*(10), 280–293.
URL <https://linkinghub.elsevier.com/retrieve/pii/S0010945219300371>
- Weisberg, S. M., Schinazi, V. R., Newcombe, N. S., Shipley, T. F., & Epstein, R. A. (2014). Variations in cognitive maps: Understanding individual differences in navigation. *Journal of Experimental Psychology: Learning Memory and Cognition*, *40*(3), 669–682.

- Weniger, G., Ruhleder, M., Lange, C., Wolf, S., & Irle, E. (2011). Egocentric and allocentric memory as assessed by virtual reality in individuals with amnesic mild cognitive impairment. *Neuropsychologia*, *49*(3), 518–527.
URL <http://dx.doi.org/10.1016/j.neuropsychologia.2010.12.031>
- Wiener, J. M., Büchner, S. J., & Hölscher, C. (2009). Taxonomy of human wayfinding tasks: A knowledge-based approach. *Spatial Cognition and Computation*, *9*(2), 152–165.
- Wiener, J. M., Carroll, D., Moeller, S., Bibi, I., Ivanova, D., Allen, P., & Wolbers, T. (2020). A novel virtual-reality-based route-learning test suite: Assessing the effects of cognitive aging on navigation. *Behavior Research Methods*, *52*(2), 630–640.
- Wiener, J. M., de Condappa, O., Harris, M. A., & Wolbers, T. (2013). Maladaptive bias for extrahippocampal navigation strategies in aging humans. *Journal of Neuroscience*, *33*(14), 6012–6017.
URL <http://www.jneurosci.org/cgi/doi/10.1523/JNEUROSCI.0717-12.2013>
- Wiener, J. M., Kmecova, H., & de Condappa, O. (2012). Route repetition and route retracing: Effects of cognitive aging. *Frontiers in Aging Neuroscience*, *4*(MAY), 1–7.
- Witmer, B. G., & Kline, P. B. (1998). Judging perceived and traversed distance in virtual environments. *Presence: Teleoperators and Virtual Environments*, *7*(2), 144–167.
- Wolbers, T., & Hegarty, M. (2010). What determines our navigational abilities? *Trends in Cognitive Sciences*, *14*(3), 138–146.
- Wolbers, T., Klatzky, R. L., Loomis, J. M., Wutte, M. G., & Giudice, N. A. (2011). Modality-independent coding of spatial layout in the human brain. *Current Biology*, *21*(11), 984–989.
URL <http://dx.doi.org/10.1016/j.cub.2011.04.038>
- Wolbers, T., & Wiener, J. M. (2014). Challenges for identifying the neural mechanisms that support spatial navigation: The impact of spatial scale. *Frontiers in Human Neuroscience*, *8*(AUG), 1–12.
URL <http://journal.frontiersin.org/article/10.3389/fnhum.2014.00571/abstract>
- Wolfer, D. P., & Lipp, H.-P. (2000). Dissecting the behaviour of transgenic mice: is it the mutation, the genetic background, or the environment? *Experimental Physiology*, *85*(6), 627–634.
- Wolfer, D. P., Madani, R., Valenti, P., & Lipp, H. P. (2001). Extended analysis of path data from mutant mice using the public domain software Wintrack. *Physiology and Behavior*, *73*(5), 745–753.
- Wolfer, D. P., Stagljar-Bozicevic, M., Errington, M. L., & Lipp, H. P. (1998). Spatial memory and learning in transgenic mice: Fact or artifact? *News in Physiological Sciences*, *13*(3), 118–123.
- Woolley, D. G., Laeremans, A., Gantois, I., Mantini, D., Vermaercke, B., Op De Beeck, H. P., Swinnen, S. P., Wenderoth, N., Arckens, L., & D'Hooge, R. (2013). Homologous involvement of striatum and prefrontal cortex in rodent and human water maze learning. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(8), 3131–3136.
- Yoder, R. M., Clark, B. J., Brown, J. E., Lamia, M. V., Valerio, S., Shinder, M. E., & Taube, J. S. (2011). Both visual and idiothetic cues contribute to head direction cell stability during navigation along complex routes. *Journal of Neurophysiology*, *105*(6), 2989–3001.

- Zhao, J., Sensibaugh, T., Bodenheimer, B., McNamara, T. P., Nazareth, A., Newcombe, N. S., Minear, M., & Klippel, A. (2020). Desktop versus immersive virtual environments: effects on spatial learning. *Spatial Cognition and Computation*, 20(4), 328–363.
URL <https://doi.org/10.1080/13875868.2020.1817925>
- Zhao, M., & Warren, W. H. (2015a). Environmental stability modulates the role of path integration in human navigation. *Cognition*, 142, 96–109.
URL <http://dx.doi.org/10.1016/j.cognition.2015.05.008>
- Zhao, M., & Warren, W. H. (2015b). How You Get There From Here: Interaction of Visual Landmarks and Path Integration in Human Navigation. *Psychological Science*, 26(6), 915–924.
- Zhong, J. Y., Magnusson, K. R., Swarts, M. E., Clendinen, C. A., Reynolds, N. C., & Moffat, S. D. (2017). The application of a rodent-based morris water maze (MWM) protocol to an investigation of age-related differences in human spatial learning. *Behavioral Neuroscience*, 131(6), 470–482.
- Zhou, R., & Mou, W. (2019). The effects of cue placement on the relative dominance of boundaries and landmark arrays in goal localization. *Quarterly Journal of Experimental Psychology*, 72(11), 2614–2631.