

**Testing the acquisition and use of navigation strategies in humans
using a virtual environment**

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Statement of Authorship

All research undertaken in this thesis was conducted with the approval of the Human Research Ethics Committee of the University of Sydney under the Project Title “Neuropsychological applications of virtual reality” and the Project number 2015/347.

The work detailed here involved the collaboration with, or assistance from, the following individuals:

Dr. Ian N. Johnston who provided considerable supervisory support in each of the experiments detailed here and with the construction and preparation of the component chapters of this thesis.

Mr. Stephen J. Rogers who developed the software program used for the construction of the virtual mazes used in the experiments detailed here and provided technical support.

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Prof. Frans Verstraten who provided supervisory support and advice on the direction of this research project.

I, Blake John Segula do here certify that to the best of my knowledge, the content of this thesis is my own work. I further certify that the intellectual content of this thesis is the product of my own work and that all assistance received in preparing this thesis and sources have been acknowledged. This thesis has not been submitted for any degree or other purposes.

I also acknowledge with the submission of this thesis that, if my candidature is successful, the thesis will be lodged with the librarian of the University of Sydney and made available for use.

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Abstract

Navigation is the area of spatial cognition related to how people move through space. Agents represent this space using reference frames fixed relative to the agent (egocentric) or the environment (allocentric).

Research into how reference frames are used and interact has revealed many variables that can affect navigation. The thesis aim was to assess some of these variables and observe the important, modulatory roles of environment structure and complexity. For this a virtual Morris water maze analogue was designed to flexibly assess allocentric, intrinsic information-based and sequential response-based navigation.

This research focussed on four facets of the interaction between environment and navigation: 1) How different reference systems knowledge develops over time in an environment; 2) What information drives improvements in navigation; 3) How reference systems interact when they suggest competing responses; 4) The relationship between the preceding points and environmental complexity.

The results showed successful allocentric navigation after little training. Successful self-referential knowledge took longer to develop. Allocentric knowledge was centred on landmarks, overshadowing other cues, while egocentric knowledge was idiothetic. Conflict tests showed a strong preference for allocentric navigation that related to training maze complexity. A simpler training maze produced more egocentric navigators with relatively accurate route knowledge.

These results provide further evidence for the multiple types of spatial navigation information that can be acquired and utilised, and demonstrate the importance of consideration of environment design for navigation research. The strong correspondence between these results

and the real world navigation of human and non-human animals also suggest this virtual reality setup as a promising way to assess navigation in future.

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Introduction

The study of spatial cognition involves research into how humans and other animals represent, perceive and interact with the space around them. As it is an area of cognition that is defined by its relating to these contents of thought spatial cognition can, under different circumstances, be seen to involve a great many psychological processes (Waller & Nadel, 2013). These include, but are not limited to, how mental representations of space are constructed and utilised, how spatial features of an environment are encoded in, and retrieved from, memory and how agents move through space. This last process, commonly referred to as spatial navigation, is the subdomain of spatial cognition that is of most interest to the research undertaken here. Spatial reference frames are a key part of many aspects of spatial cognition, including navigation. They involve how space is represented by an agent and is centred upon a referent of some type, where within a reference frame the features of an environment are defined spatially by their position with respect to the referent (Waller & Nadel, 2013). Different reference frames are identified by what, and what type, of referent they use. Broadly, reference frames centred on the agent or parts of the agent's body are referred to as egocentric, while reference frames entirely independent of the agent are referred to as allocentric. While navigation depends on the spatial reference systems used by a navigator on a given task, how space is represented is not the major area of focus. This distinguishes navigation research from research into spatial updating, which involves updating the positions of environmental features in accordance with movement of the navigator (Chrastil & Warren, 2012). In humans, tests of spatial updating generally involve placing participants in the centre of an environment where all members of a small set of objects can be view simultaneously so that the spatial relationships between them can be easily observed. Navigation research by contrast typically takes place in a much larger environment where

observers are exposed to features sequentially (Chrastil & Warren, 2012). What will be looked at in the work to follow is how navigation can be observed to change depending on the different spatial reference frames employed by a navigator.

Navigation is an ability that involves the interaction of multiple, distinct neural and cognitive systems and types of knowledge and memory. A great deal of research has been undertaken to study these many different features; however, as a result of this there exist many different definitions for the same key terms. Problems can therefore occur in cases where relationships between these features are potentially incorrectly posited as a result of different groups applying the same terms in different ways. The core focus of the research that will be described here is the distinction between the allocentric and the egocentric. This is a distinction that here pertains to both the types of spatial reference frames developed and utilised by navigators and the types of knowledge that are acquired. Therefore before proceeding to look at what is currently known about how human and non-human animals navigate, how these two areas will be conceptualised and used here will be clearly defined.

The knowledge that underpins navigation through an environment can be classified simply into three distinct types: route, survey and graph (Chrastil, 2013). Survey and graph knowledge inform the construction of allocentric reference frames while route knowledge is egocentric. Survey knowledge is generally conceived of as involving a map-like, observer independent representation and involves the learning of distances and angles between environmental features (Chrastil, 2013). Methods of navigation that utilise observer-independent reference frames are commonly referred to as allocentric strategies. Survey knowledge is generally thought to store metric distance information between environmental features and one of the key contributors to the acquisition of this information is locomotion (Chrastil & Warren,

2013). The information derived from the motor commands that control, and the proprioceptive feedback from, locomotion is referred to as podokinetic information. Graph knowledge is thought to play the intermediary role between survey and route knowledge, representing the environment as a network of edge-connected location nodes (Chrastil, 2013). Node connections do not contain any distance or angle information, instead serving to facilitate the construction of novel paths through the environment. This distinction between knowledge types can potentially cause confusion when attempting to draw conclusions from results. Given the multiple different definitions of terms in the literature, it is important to keep their use distinct and consistent when referring to them.

Underpinning these knowledge types are distinct categories of learning. These categories are divided by the features of the environment they involve and differences observed in the circumstances and rate of their acquisition. Place learning, which is the process of acquiring the ability to recognise and situate a location in the environment, is one of the most important of these categories as it is a necessary, but not sufficient, component of survey knowledge (Chrastil, 2013). Chrastil (2013) suggests that survey maps are likely composed of multiple instances of this type of learning. Landmarks play an important role in place learning, serving as distal environmental cues that provide navigators with relational information about their position relative to other features of the environment (Vorhees & Williams, 2014). There are a variety of different aspects of an environmental stimulus that might see it adopted for use as a landmark. Contrast in the appearance of an environmental feature plays a role in this process, as the more visually unique an object is relative to its environment the more likely it is to be used as a landmark (Chan, Baumann, Bellgrove, & Mattingley, 2012). This perceptual salience can come as a result of the landmark's features or its relative spatial position (Caduff & Timpf, 2008). For

spatial position, objects at important decision points are more likely to be used as landmarks (Chan et al., 2012). Other important factors include the stability of the object, which affects how reliable it is perceived to be. The salience of a landmark appears to be the result of the combination of the properties of the feature, the surrounding environment and the point of view, and cognitive processing, of the observer (Caduff & Timpf, 2008). Prior experience of a navigator with an environment also plays a role in what features are used to make decisions. In general therefore it appears that whether an object is used as a landmark depends on the context in which it is encountered and the goals of the navigator.

Features of an environment can also serve as beacons, and are used as such when they are highly reliable predictors of an important location. Following a beacon involves the utilisation of a minimal allocentric reference frame where the navigator's focus is only on their position relative to the beacon. Landmarks that come to be used as beacons differ from those that are instead used as proximal environmental cues in that they are exclusively associated with a given location, while proximal cues serve as providers of associational information, for example where to turn on a route, and are generally less reliable due to their typically been transient in nature (Chan et al., 2012).

Spatial integration is another, less common allocentric learning process observed in many species which involves the combination of multiple learned landmark relationships. In the simplest cases the navigator learns a pair of associations, one between two landmarks, A and B, and the other between landmark A and the goal, after which they are able to use their landmark-landmark association to compute the probable location of the goal when only landmark B is present (Leising & Blaisdell, 2009). Theoretically, since vectors can be learned between landmarks and locations using associative processes, it may be possible for navigators to use

spatial integration to build more complex spatial representations by combining these lower-level landmark-goal associations. However it is not currently clear when or if this occurs.

While survey and graph knowledge are the two key components of allocentric navigation, route knowledge, which involves the procedural learning of an ordered, circumstance-specific (Kallai, Makany, Karadi, & Jacobs, 2005) sequence of turns that are represented via a ground-level perspective (Chrastil, 2013), is the key area of interest for egocentric navigation as it will be looked at here. Like survey knowledge, route knowledge has its own category of learning that serves as a key component of its development. Response learning is generally thought of in contrast to place learning and involves the navigator acquiring the correct behavioural response to make when exposed to a particular feature of the environment (Chrastil, 2013). Response learning is the less flexible of the two as it cannot be used to build an understanding of the larger spatial layout. Instead learned response behaviours are typically, when necessary, chained together to construct a route that can be followed to a known location (Chrastil, 2013).

Path integration, also sometimes referred to here as dead reckoning, is one of the most fundamental learning mechanisms that support navigation and is another major component of egocentric navigation. It is observed in vertebrates and invertebrates (Biegler, 2000), and involves an animal recording the direction and distance it has travelled relative to some prior reference point (Collett & Graham, 2004). Different animals can gauge their travelled distance in different ways; bees appear to use optic flow (Cheng, 2000; Srinivasan, Zhang, Berry, Cheng, & Zhu, 1999), ants use proprioception (Wohlgemuth, Ronacher, & Wehner, 2001), while dogs, hamsters and humans use idiothetic information (Etienne & Jeffery, 2004). Mammalian idiothetic information is provided by the visual, vestibular and proprioceptive systems (Etienne & Jeffery, 2004). The salient features visible while navigating in a familiar environment can also

be used by animals to reset their internal path integrator (Collett & Graham, 2004). This is important as evidence across multiple species suggests that the systems for the distance and direction calculations used for path integration have an internal source of error that accumulates as the animal travels. In non-human animals path integration is usually studied using homing in the context of foraging; however, it appears to only play an important role in cases where it can be combined with other learned strategies and with familiar spatial cues in the environment. More generally, research that aims to test path integration needs to be careful to ensure that no external frame of reference is in use, a process that typically includes removing all possible extrinsic cues from the environment (Etienne & Jeffery, 2004). Complicating this process, non-human animals can use a wide variety of environmental cues in order to orient themselves in an environment including the earth's magnetic field (Chan et al., 2012).

In general, tests that aim to measure the exclusive use of either an egocentric or allocentric strategy need to be designed to minimise or exclude cues that could facilitate navigation that utilises an undesired strategy type. On tests for egocentric navigation this means distal cues are removed while allocentric tests remove proximal cues. As the separable employment of allocentric and egocentric strategies is a key area of focus of the work that it is to follow the design of these sorts of tests is an important consideration. One very fruitful way to gain an understanding of how to separate different types of strategies is to look at the many ways these strategies have been observed to be developed and utilised in both humans and non-human animals.

Non-human navigation

Within the broad field of spatial navigation there are three key avenues of study that are very informative about the aspects of human navigation that are of interest here. Whether navigation can be generally considered to involve the use of simple or complex cognitive mechanisms is one of the most common questions within the field of spatial navigation research. Framing this debate within the consideration of allocentric and egocentric strategy use, egocentric navigation, which depends on relatively simple reference frames and follows more universally observed rules of associative learning, is representative of these simpler mechanisms. The degree to which more complex allocentric reference frames are necessary to explain how navigation has been observed to proceed is the crux of the issue, with some arguing that theories based around the development of external, or in some cases map-like, spatial representations depend on observations that themselves can be explained by simpler cognitive processes. Related to this discussion is the consideration of to what extent the acquisition of the information that underpins navigation follows the rules of associative learning that are observed in many other areas of cognition. One of the most common ways to assess how different learned strategies and environmental features compete and interact during navigation is to test for evidence of blocking between them. Blocking is observed when a novel stimulus is trained in the presence of a previously learned stimulus that can, to some variable extent, predict the location of the goal of interest (Kelly & Gibson, 2007). In these cases, much less is learned about the novel stimulus than would have been if the familiar, predictive stimulus were absent (Kelly & Gibson, 2007). Another similar behavioural phenomenon is overshadowing. To test for overshadowing a participant is trained in the presence of multiple stimuli, and it is observed when testing their navigation that the stimuli that are relatively less salient, where salience is task-dependent, are

less effective at guiding behaviour than the more salient stimuli and less effective than they would have been if the participant had been trained with the less salient stimuli alone (Kelly & Gibson, 2007). Both blocking and overshadowing are examples of cue competition and are fundamental principles of associative learning. The final, and most relevant to the work undertaken here, avenue of interest looks at how different navigation systems interact to guide navigation and the acquisition of spatial information. This area can be seen to combine considerations from the previous two, most commonly when looking at how the rules of associative learning are manifested in environments where both allocentric and egocentric navigation strategies are acquired and utilised.

Before considering how people learn and utilise different navigation strategies, it can be very informative to look at what has been observed in research into the navigation abilities of non-human animals. Many aspects of non-human animals' spatial navigation have been found to be very informative and predictive about human navigation, from the most common rodent studies to the strategies observed in invertebrate honeybees and ants (Wang & Spelke, 2002). The flexibility of non-human animal navigation research has also allowed researchers to manipulate and more closely examine the neural underpinnings of different systems of navigation. This can be seen in research into the role played by the hippocampus in navigation, with O'Keefe and Nadel (1978) most famously utilising extensive research into many different species of non-human animals to construct their theory of the hippocampus as the home of the cognitive map.

Pigeons.

Pigeons are one of the most common species of animal studied in psychology. One of the key areas of interests in this research is how pigeons use landmarks to delineate locations and navigate. Pigeons appear to use a vector-sum model to encode a target location relative to a landmark (Cheng, Spetch, Kelly, & Bingman, 2006). This involves learning a distance and direction vector from the landmark to the goal. Learning according to this model weights proximal cues more heavily when multiple landmarks are present, such that movement of a proximal cue produces a greater shift in search location than does equivalent change of a distal cue. This vector sum model has been observed in a variety of species, including rats, humans, pigeons and insects (Leising & Blaisdell, 2009).

Pigeons' spatial cognition has also been observed to follow some of the rules of associative learning when acquiring information about landmarks in an environment (Cheng et al., 2006) including showing spatial blocking and overshadowing effects (Leising & Blaisdell, 2009; Spetch, 1995). This landmark overshadowing can, in both pigeons and humans, be dependent upon both the absolute position of a landmark and the positions of other associated landmarks in the environment (Spetch, 1995). Pigeons have also been shown to be capable of reasoning about the location of a target using spatial integration between landmarks (Leising & Blaisdell, 2009). A similar ability has been observed in rats (Chamizo, Roderigo, & Mackintosh, 2006).

Unlike humans, pigeons are not able to demonstrate a transfer of learning about spatial relationships between novel feature arrays. That is, pigeons trained with multiple different landmark arrays that share the same arrangement and the same relationship to a target location

do not show preferential search according to this repeating relationship when tested on a novel array (Spetch, Cheng, & MacDonald, 1996). Pigeons and humans also differ in the way that array manipulation controls search. When the landmarks in an array have their positions expanded or contracted people adjust their search to maintain relative spatial relationships, while pigeons search in positions that maintain the absolute distances to individual landmarks (Spetch et al., 1996). When searching for a target location they appear to use all landmarks in an array equally to guide their behaviour (Cheng et al., 2006).

Touch-screens are sometimes used for landmark tests in pigeons as they allow for the automatic manipulation of the presented landmarks and highly accurate recording of search behaviour. As touch screen tests also present a 2-dimensional, small scale environment and have the requirement that locations be selected rather than navigated to, they can be used to assess the generality of pigeons' spatial cognitive processes. There are, for example, some landmark search results on touch-screens that show pigeons producing the same search patterns as observed in open-field experiments (Cheng et al., 2006).

Insects.

Unlike with pigeons the search patterns seen in honeybees as a result of manipulations of landmark arrays are more similar to those observed in humans, although honeybees appear to achieve the same results by matching the perceived size of the array on their retina with the size that had been experienced previously (Spetch et al., 1996). While bees are capable of learning a target location with reference to a landmark array and utilising the angles between the component landmarks when searching, they appear to give more weight to one preferred landmark, such that they preferentially search for the target in locations their favoured landmark

suggests (Capaldi, Robinson, & Fahrbach, 1999; Cheng, 1999a, 2000; Collett, 1996). They can also, when necessary, learn the position of a target with reference to the gap between landmarks in an array (Cheng, 1999b).

Generally bees use vector or route following to navigate to a target location, while the sun and other major landmarks in the environment are used to determine their direction of travel. These landmarks are typically recognised by colour and are beacons in to when located, while distance travelled is measured by the visual flow of objects on the bee's retina (Cheng, 2000; Srinivasan et al., 1999; Srinivasan, 2014). When a location has been arrived at but the target has not been found, bees utilise landmark matching which involves flying in a particular direction attempting to arrange nearby landmarks in to a familiar position on their retina. The distance and direction information to these landmarks are computed separately (Cheng & Spetch, 1998). These processes of attempting to match a current scene to a remembered view of the environment are together known as snapshot matching, which is a method of navigation utilised by honeybees and many other species of insect (Cheng & Graham, 2013). As bees are required to navigate over relatively large distances, their matching process is thought to likely rely on large environmental features. Together these results support the idea that bees are capable of navigating allocentrically; however, there is still no agreement on whether honeybees can or do navigate using cognitive maps (Cheeseman et al., 2014a; Cheeseman et al., 2014b; Cheung et al., 2014).

Similar to honeybees there are many species of ant that also make use of the snapshots when searching for a familiar location. However, while honeybees are capable of adjusting their search in response to positional changes in a landmark array, ants' search becomes random unless changes to the array are matched by changes to the landmark's size. When this condition

is met, search centres on the location from which the view of the array on the retina matches the view previously experienced, regardless of the fact that the distances to the landmarks have changed (Cheng & Graham, 2013). Ants also appear to make use of the way distal environmental features are arranged against the sky as a visual, directional cue to guide navigation to and from their nests (Graham & Cheng, 2009).

In general, how ants use distal environmental features can depend on the system of navigation they are employing. When ants are attempting to navigate using a familiar route they are observed to move in a way that positions landmarks in a previously experienced arrangement relative to their current heading direction but do not attend to the retinal size of the landmark as they do when using snapshot matching (Cheng & Graham, 2013). These differences support the more general idea that ants use their spatial knowledge on a more case-by-case basis, using landmarks and the like as cues that inform them when to perform a particular response (Wehner, 2003).

Path integration is another primary method of navigation for ants, as it is for many other species. A common way it is observed is in the ability of ants to take direct paths back to familiar locations following a circuitous, and often random, journey to their current position (Wang & Spelke, 2002). This involves the construction of a global vector that incorporates information across the entirety of the ant's journey. Ants also make use of a local vector system, where larger routes are composed of smaller segments that are selectively initiated in response to the ants' experience with a particular visual landmark. These distinct systems, global path integration and local, landmark associated response vectors, are differentially engaged based on the information available in the environment at a given point on the journey (M. Collett, Collett, Bisch, & Wehner, 1998). This method of use is in contrast to the idea that ant spatial knowledge is

combined to create a more allocentric representation, an idea for which there appears to be no convincing evidence (Cheng & Graham, 2013; Wehner, 2003).

Non-human Primates.

While non-human primates are very close to humans evolutionarily they are, as in many other areas of psychological research, not typically the focus of attempts to use animal models to understand human navigation. This is in part due to the dual observations that many of the brain areas that underpin navigation have their function conserved between mammalian species, meaning informative research can be undertaken in more flexible model animals such as rodents, and that many of the spatial abilities of humans can be seen in, and predicted from, other species. However, the research that has been undertaken has shown many similarities between humans and non-human primates in the ways that they navigate. Bonobos, like humans, are able to use both egocentric and allocentric spatial representations (Rosati, 2015). When tested on a plus maze equivalent, bonobos also preferentially navigate to the allocentric location. Chimpanzees also appear able to form allocentric representations of space, demonstrating that they can make use of novel shortcuts between learned foraging locations (Rosati, 2015). Capuchin monkeys are also capable of learning to take detours through virtual mazes as a spatial strategy when trained under circumstances that punish the taking of direct paths through the environment. This ability to learn detours was taken as evidence that capuchin monkeys preferentially employed navigation strategies instead of learning multiple separate routes for each maze (Pan et al., 2011).

Non-human primates also, like humans and other mammals, have their navigation through an environment affected by their familiarity with it (Dolins, Klimowicz, Kelley, & Menzel, 2014). Non-human primates have been observed to utilise short and direct routes when

navigating to familiar feeding locations for example (Di Fiore & Suarez, 2007). However, Di Fiore and Suarez (2007) found when examining the long-term navigation behaviour of spider and woolly monkeys that novel paths are rarely taken between familiar locations. Instead travel was usually observed along a network of repeatedly utilised routes. The study of navigation in non-human primates also runs across some of the same difficulties that can occur in real-world experiments into human spatial abilities. Studies that attempt to look at primate navigation in more free-ranging environments can come across difficulty determining which features of the world are playing an important role in the animal's navigation (Dolins et al., 2014). On the other hand smaller scale studies in captive primates are often constrained in what they can say about how navigation proceeds in their wild counterparts. Primate researchers have been able to circumvent these concerns to an extent using virtual reality software, an approach that is also often utilised in human research. Chimpanzees tested in virtual environments were observed to be able to utilise landmarks as both positive and negative cues, where features in the latter group are taken as indicators that a wrong decision has been made while navigating. In general, Dolins et al. (2014) observed that chimpanzees and humans appear to show the same learning and behavioural responses when navigating in virtual environments.

Rodents.

Two of the most common animal species studied in spatial navigation research are mice and rats. This can be seen to be related to the belief that there exists a great deal of overlap between mammalian species in how shared brain areas function (O'Keefe & Nadel, 1978). As a result of this expectation of shared function between mammals, rodents immediately suggest themselves as a convenient model for navigation study for the same conveniences that sees them utilised in many other areas of psychological research. The idea that mammalian navigation is

underpinned by an allocentric cognitive map based in the hippocampus motivated researchers for decades after it was first posited (O'Keefe & Nadel, 1978), a trend that also served to motivate research using rodents as they allow for neural manipulations of this shared brain structure that are either not possible or more difficult in other animals. Shared hippocampal function between rodents and humans can then be combined to construct theories about how navigation proceeds in humans (Redish & Ekstrom, 2013).

As a result of the large number of studies making use of them, there is a great deal of evidence regarding how rodents utilise both allocentric and egocentric reference frames to navigate. These navigation behaviours can be, depending on the timing and circumstances, either flexible or very habitual. Observations of these habitual responses include rats running into walls when traversing familiar paths that have been shortened or have had barriers placed along them (Leising & Blaisdell, 2009). Rats have also been observed to ignore food placed along a well-traversed path as result of their habitual execution of the response behaviour to travel the path in its entirety. Rats are also capable of flexible, goal-oriented behaviour as evidenced by their successful performance in T and Y mazes and when navigating in large enclosures. In general it appears that whether a rat uses a more flexible place or a habitual response strategy depends on the information available at and around the goal location and how much training has taken place (Leising & Blaisdell, 2009). Rodents are generally thought to show a shift from an early preference for utilising an allocentric reference frame to employing a more habitual response strategy as they become more familiar with an environment. This pattern of behaviour is most simply demonstrated when training rodents on a T-maze and testing the relationship between environment familiarity and their strategy preference using a conflict test. Navigators are first trained to find a target location that can be travelled to using either an allocentric strategy

involving determining the correct arm of the maze with reference to the arrangement of the surrounding room cues, or an egocentric strategy involving learning the correct turn behaviour when arriving at the intersection. During a conflict test rodents are started from the opposite side of the maze, a change which means the two different strategies now suggest opposite arms as the correct choice. Which arm is chosen under these circumstances can then be used as a measure of which strategy the navigator prefers to use. On the T-maze rodents show the shift described earlier, changing from preferring the place arm to choosing the response arm as they become more experienced navigating the maze (Packard & McGaugh, 1996). This shift represents the generally accepted progression from a more deliberate, effortful strategy to a habitually executed response that occurs as animals become more familiar with the environment they are navigating.

The Morris water maze (MWM) is one of the most popular tests of spatial navigation in rodent research, allowing researchers to look at both allocentric and egocentric navigation. It involves placing a rodent in pools of variable sizes filled with opaque water and observing how it learns to find its way to a hidden platform that allows it to escape the water (Morris, 1984). This platform location can be learned in a variety of different ways at the discretion of the experimenter. A rodent's spatial learning and preferential navigation strategy can then be probed by placing them in the pool from a familiar or unfamiliar location, and potentially with particular manipulations of the available information, and observing where they search for the platform. One of the key benefits of using a pool as a space for navigation is that it allows for the removal of proximal cues that may serve as confounds when attempting to assess allocentric navigation (Vorhees & Williams, 2014). A major motivator for the development of the MWM was the removal of proximal cues, including olfactory information left from previous trials, which become available to a rat when they enter a corridor on the radial arm maze (RAM). There are

many other benefits to the use of the MWM including the relatively little training required to observe learning, the removal of food deprivation as a motivator for behaviour, the ease of testing and the rapid and reliable learning that is observed (Vorhees & Williams, 2014).

In order to assess what has been learned during MWM training probe test trials are conducted. These involve removing the platform from the pool and observing where the rodent preferentially searches for it. When analysing the data acquired from a MWM task there are four common measures of probe test performance. These are, in no particular order, the amount of time spent in each of the pool's quadrants, the amount of time spent in a target zone centred on the platform's location, how close the rodent was to the platform averaged over the whole trial and the number of times the platform's location was swum over (Maei, Zaslavsky, Teixeira, & Frankland, 2009). Attempting to assess the sensitivity of these different measures, Maei et al. (2009) looked at how well each one could distinguish different populations of rodents with distinct genetic, pharmacological and neuroanatomical manipulations based on their MWM performance and found that mean proximity to the platform was the best able to differentiate the different conditions. Reversal learning is also a common feature of MWM testing with rodents trained to locate a platform location in the quadrant opposite to the one in which it had originally been positioned (Vorhees & Williams, 2006). Mice show an initial preference for swimming to the original location on training trials which suggests an inability to completely extinguish their prior learning. Rats on the other hand rapidly switch strategies to the new location, with a complete switch commonly observed within four training trials. The double-reversal task, where the platform is moved back to its original position following reversal learning is also used to reveal very subtle differences in performance between groups and to uncover hard-to-observe cognitive deficits (Vorhees & Williams, 2006).

Rats show a typical pattern of progression in their search behaviour on the MWM, moving from navigating using a thigmotaxis strategy, which involves searching while remaining in constant contact with the wall, to a pattern of weaving and circling while swimming some distance from the wall, a strategy that is usually successful (Vorhees & Williams, 2014). However, they are also capable of learning a variety of other spatial strategies, depending on the environmental variations used, that utilise both internal and external information. Rats appear to acquire these different strategies based in part on the availability of distal cues in the environment, choosing for example a simpler, beacon-based response in cases where only one navigable cue was available (Harvey, Brant, & Commins, 2009). Rodents also appear to estimate distance and direction in similar ways to people on the MWM (Koppen et al., 2013).

There are potential methodological concerns that need to be addressed depending on how an experimenter wants to use the MWM. Pool size is an obvious one as it is an important variable that affects the slope of the observed learning curve. Larger pools produce shallower curves that allow time for evidence of deficits in performance to be revealed while smaller pools produce steeper curves which, in some cases, allow rodents to solve the task without the use of any spatial cues. However, pools that are too large can run in to the opposite problem of being too difficult for rodents to show any learning on. The size of the platform relative to the size of the pool is also an important consideration, wherein the larger this ratio the more difficult the task (Vorhees & Williams, 2014). There are conventions for how the pool and platform should be sized, however depending on the goals of the experimenter they can be variables that need to be given consideration. Where rodents are started in the maze also often needs to be considered. Multiple start locations are often used to stop rodents learning an egocentric strategy; however, this can cause problems. Using different quadrant-based locations raises the problem of some

locations potentially being closer to the platform than others (Vorhees & Williams, 2006). Attempting to avoid this concern by restricting the possible start quadrants can also run the risk of allowing rodents to circumvent the acquisition of allocentric strategies in favour of different egocentric responses for different start points (Vorhees & Williams, 2006). Another facet of MWM environment design that does not perhaps get as much attention as it deserves is the number and arrangement of the distal environmental cues, with the possibilities ranging from a single cue on each wall (Hamilton, Driscoll, & Sutherland, 2002) to unique arrangements of distinct wall textures and landmarks (Jacobs, Laurance, & Thomas, 1997). In general according to Vorhees and Williams (2006) many of the commonly perceived flaws of the MWM result from the use of inappropriately small mazes, poorly designed protocols that do not assess learning or poor control tests that measure non-spatial explanations of the observed results.

The RAM is another of the more popular rodent tests of navigation. The maze is composed of a variable number of arms that radiate out from a central hub. The variability in the number of arms allows for the construction of tests that assess different types of memory (Vorhees & Williams, 2014). The standard RAM uses eight arms and assesses working memory. The arms of the maze are baited and the rodents are required to visit each arm only once, with revisits counted as evidence of their failure to recall prior search behaviour. This task therefore tests working memory, which involves the brief retention of acquired information in order to guide relatively immediate behaviour, as the arms are rebaited between trials. Experiments that vary this number of arms typically aim to assess working and reference memory, which refers to information that is acquired and kept across multiple trials, in combination. During tests in these experiments only some of the arms are baited, and this is consistent between trials, so visits to unbaited arms are considered reference memory errors while revisiting an arm is still a working

memory error (Vorhees & Williams, 2014). Rats are able to recall the arms they have visited on a RAM task using both intrinsic information, which includes vestibular and kinaesthetic information, and extrinsic information, such as the visual cues in the environment. These different types of information appear to be integrated such that disagreement between them in the spatial arrangement they suggest produces erroneous behaviour (Brown & Moore, 1997).

Pigeons have been observed to perform similarly to rats when tested on a bird-equivalent version of the radial arm maze and in many situations have been found to utilise similar mechanisms to solve navigation tasks (Leising & Blaisdell, 2009).

Labyrinthine mazes are another test type that can be employed to assess egocentric learning in rodents as they allow for the complete removal of distal cues when used in the dark (Vorhees & Williams, 2014). The star maze is another, more complicated, rodent maze that allows for the assessment of their ability to navigate using either allocentric information or a sequential egocentric strategy that encodes an ordered sequence of choice point behaviours (Fouquet et al., 2013).

Environmental landmarks, as an integral component of place learning, play a key role in how rodents acquire and utilise allocentric navigation strategies. How rodents utilise these landmarks is variable, depending on a variety of different environmental factors. The distance of a given landmark to the navigation target and its relationship to the other landmarks in the environment are two such factors. Rats trained with a landmark array on the MWM with one landmark either closer or further from the platform than the others showed more accuracy in the closer group than the further one when tested with only the variable landmark present, but poorer performance in the closer group when tested on configurations composed of only the remaining landmarks (Chamizo, Manteiga, Rodrigo, & Mackintosh, 2006). Here it can be seen that the

position of a landmark can affect both what is learned about it and about other landmarks nearby, an example of landmark learning following the associative principle of overshadowing. More generally, on the MWM rats appear to be able to better delineate the platform's location relative to a landmark when it is nearer the platform than when it is further away (Chamizo & Rodrigo, 2004). Landmark use is also affected by perceived reliability, where rats trained on the MWM with static landmark and platform positions show less accurate search than those trained with the landmark and platform changing position between training sessions but remaining in the same spatial relationship (Roberts & Pearce, 1998). Here the uncertainty of the platform's location relative to everything else in the environment but the landmark grants a stronger associative power to the unstable landmark than is acquired in the stable condition. Research in rats also suggests that the geometric stability of a landmark relative to other environmental features plays an important role in determining whether any given landmark will be used to guide navigation (Biegler & Morris, 1996). Landmark arrays can also be relatively insensitive to loss of information, an effect typically achieved by the removal of some number of array members. For example rats trained on the MWM with four distinct landmarks present could still accurately locate the platform on probe tests when half of them were removed (Prados & Trobalon, 1998). Landmark arrangements in rats also appear to be learned in relation to other environmental cues. When rats are trained on an arrangement of landmarks that are clustered near to or far from the pool on a MWM task only changes to the nearer configuration impair their performance; however, when a salient directional cue is included during training the same rearrangements result in no observable quadrant search preference (Civile, Chamizo, Mackintosh, & McLaren, 2014). Civile et al. (2014) suggest this is a result of the added directional cue providing orientation information that is used in conjunction with the other landmarks, such that if the

landmarks no longer align with the orientation cue they lose their connection to the information learned during training and are therefore no longer used to guide navigation.

How well rodent spatial navigation adheres to the principles of associative learning can also be seen when looking at extrinsic cues more generally. For example rats learning to navigate through a maze containing both intra and extra maze cues can have their learning about the latter overshadowed by the presence of the former (March, Chamizo, & Mackintosh, 1992). A similar effect is observed in the MWM, where training rats with a beacon attached to the platform overshadows rat learning about the other cues in the room (Roberts & Pearce, 1999). In some cases a navigational cue can, by its nature, be considered so much more salient than other features of a new environment that it is preferentially attended to and learned about, even when its unreliability produces worse performance than would result without it. This was observed in rats trained on a water maze task in the presence of a prominent light cue which was either stable or moved between trials, where this movement meant it was not predictive of the target location (Martin, Walker, & Skinner, 2003). The unstable light was observed to produce significantly worse performance than the stable condition, which itself produced equivalent performance to a no light group (Martin et al., 2003). It has also been observed that vector-based learning and place learning can, in some cases, function as learning systems that are both cooperative and also associatively competitive (Kosaki, Poulter, Austen, & McGregor, 2015). Kosaki et al. (2015) trained rats on a variation of the MWM where both intra and extra maze cues were present but the platform and the intramaze cues were moved between training sessions such that they maintained the same relationship. Under these conditions it was found that rats were able to rapidly learn and re-learn each new inter-session relationship between the platform and the distal cues. This was in spite of the fact that the intramaze landmarks already perfectly predict the

platform location, but was only observed when the extramaze cues were salient. When the distal cues were not salient the intramaze landmarks overshadowed their learning (Kosaki et al., 2015). Hence it can be seen that the two systems can be both cooperative and competitive. Rats trained in a triangular MWM pool with a pair of proximal cues in the base and distal cues around the room are also perfectly able to learn the platform location with reference to both while also possessing the ability to successfully locate the platform when only one type of cue was available (McGregor, Good, & Pearce, 2004). The addition of a beacon to the same environment during training also had no effect on the rats' ability to locate the target when they were tested with only the proximal cues present, and these results together suggest a lack of an overshadowing interaction between the different cue types. Therefore while it can be seen that rodent navigation is consistent in many ways with associative learning mechanisms (Chamizo, 2003) the relationship between them is far from simple.

There is, however, debate around whether what is typically considered navigation driven by place learning is not instead the employment of a directional strategy. Directional navigation differs from place navigation in that movement is not directed to a particular location delineated by the arrangement of external cues but rather in the direction of a feature or features of the environment. Typically the two are separated in testing by shifting the navigable environment along a single axis when wanting to test strategy use. After the shift the absolute location remains the same but the direction strategy, which for example may involve heading towards the area of the environment nearest a given cue, leads to a different position. Looking at this difference on an open field maze it was found that rats forced to use one of the three response, direction and place strategies could acquire only the first two, and showed no evidence of place navigation even after three hundred training trials (Skinner et al., 2003). Experiments that

separate out direction and place strategies tend to produce results that suggest the ability of rats to show place navigation is dependent upon their having distinct starting points and initial heading directions when tested from different maze positions (Skinner et al., 2003; Whyte, Martin, & Skinner, 2009). However, it may also be the case that rats are not learning place navigation under these conditions. Rather, they could be using the different directions of movement that result from these different positions to guide their search, in essence learning that different start positions necessitate different behaviour instead of constructing a proper allocentric representation of space (Skinner, Horne, Murphy, & Martin, 2010).

These concerns extend to the MWM task suggesting that, as it is typically implemented, it is unlikely to actually serve as a test of pure place navigation in rodents. Attempting to separate place and directional navigation by shifting the pool position found the same preference for directional responding as has been observed in various other mazes (Hamilton, Akers, Weisend, & Sutherland, 2007). Multiple experiments attempting to find evidence of place navigation by varying different procedural parameters, including the length of the training period (Hamilton et al., 2008; Hamilton et al., 2007), the variability of the platform location and the position of the pool, observed true place strategy use only when the different pool positions varied along multiple axes while the platform location was invariant (Hamilton et al., 2008). When the platform's location varied as the position of the pool did, directional navigation was observed, as it was as a result of all the other manipulations. Rats using directional navigation also learn the platform location faster than place navigators, a finding that Hamilton et al. (2008) interpret as indicating that directional behaviours are the more readily learned. Alongside the position of the pool, the presence of the pool wall also appears to be an important determiner of whether place navigation is observed on the MWM. The typical design of the MWM fills the pool only part

way meaning that alongside the external distal cues introduced by the experimenter the bare walls above the pool can also serve as navigational cues. Removing the walls as cues has also been found to produce place navigation (Hamilton et al., 2008), where in such cases rats show a progressive shift in preferential strategy use from place navigation early in training, to an equal division of place and directional navigation to preferring the directional response (Hamilton, Akers, et al., 2009). Together these results suggest that on the standard MWM rats learn to navigate to a particular region of the pool relative to the distal cues, with the pool wall serving as an important provider of distance information (Hamilton et al., 2008).

However, there also exist procedural concerns that further complicate how rodent allocentric navigation is understood. For example rats appear to be unable to solve a plus-maze with reference to the distal environmental cues when there are multiple start locations that they are unable to differentiate between (Horne, Martin, Harley, & Skinner, 2007). Horne et al. (2007) suggest this is a result of discernibly different start locations improving the rat's sensitivity to distal cues. Task complexity can also play an important role in how rats are observed to navigate. Rats trained from a fixed starting point to look in multiple search locations for a reward in an open-field maze tend to show place navigation, whereas training on a simpler, 4-arm-plus maze produces predominantly directional behaviour (Ruprecht, Taylor, Wolf, & Leising, 2014). In the open-field maze, which was designed to serve as an appetitive version of the MWM, rats continued to show preferential place navigation after extended training and reaching asymptotic performance, an observation that the authors take as evidence that the test variation used was quite complex (Ruprecht et al., 2014).

The complex interactions between place and directional strategies serve as an informative example of how different methods of allocentric navigation can interact, with their differential

engagement dependent upon the constraints and opportunities provided by the environment. These interactions can also be seen in rodents at the level of allocentric and egocentric spatial reference systems. When rats are trained to find a target location that is delineated by a fixed spatial reference to distal cues and a constant behavioural response, both place and response learning are observed to occur (Gibson & Shettleworth, 2005; Packard & McGaugh, 1996). These results suggest that the place and response systems do not overshadow each other in such environments, although they do compete on conflict tests. Rodents can, however, show blocking between strategies, with rats trained to preferentially use a response strategy not developing an allocentric strategy at a later time when it is possible to do so (Gibson & Shettleworth, 2005). Together this evidence supports the idea that navigators can acquire information about the environment that underpins multiple different strategies. This runs contrary to the associative idea that only one type of learning should occur. However, that is not to say that there is no inhibitory interaction occurring. It has been observed that lesioning the region of the brain that underpins one reference system leads to better observed performance on the undamaged one (Packard & Goodman, 2013). Consolidation of one system's learning can also be improved by the inhibition of the other system after training. The differential engagement of these systems can also depend on the spacing of training trials, with longer inter-trial intervals encouraging preferential response navigation while shorter intervals encourage place navigation (Packard & Goodman, 2013). These two systems also show evidence of cue competition, with rats learning less on a learning task that facilitates both strategy types when the response behaviour to-be-learned matched a response behaviour they had been taught previously (Gibson & Shettleworth, 2005).

While strategy types are often transitioned between as rodents become more familiar with an environment that is not to say that one replaces the other. Rats trained to a response behaviour on an environment are still able to utilise an allocentric strategy when the maze is shifted in space in such a way as to make it obvious the rats position has changed either immediately upon entering the maze or after first attempting the incorrect response strategy, an observation that supports the idea that the two strategies co-exist and can be conditionally employed (Cassel, Kelche, Lecourtier, & Cassel, 2012). These different types of behaviour can also interact in ways that affect a rat's navigation behaviour within the same journey. Rats trained on a foraging task where route and landmark cue information are available were able to return to the learned target location when only cue type was available and when both were available (Tamara & Timberlake, 2011). In cases where the two cue types were put in conflict, initial heading followed the egocentric strategy while subsequent search was based on locations suggested by the allocentric cues. However this pattern of behaviour was dependent on the starting position used for the test trial, with novel positions producing the allocentric preference, while familiar ones produced no preference for either. Research in mice also suggests that the distance travelled during navigation can play a role in how these two strategy types interact. Mice that have been trained to navigate to and from a particular nest location and then tested on their ability to return to the nest when it has been moved to a novel location show different patterns of strategy use based on how far they needed to travel, with longer distances producing a shift from early self-referential navigation to utilising distal cues when they got closer to the nest (Alyan & Jander, 1997). When only a short distance needed to be travelled mice instead only used an egocentric strategy. This distance relationship is also evident in rats tested on the MWM (Tamara, Leffel, & Timberlake, 2010). Looking at their strategic preference when required to navigate to a familiar location from

a novel start point, Tamara et al. (2010) observed that rats searched equally at the locations suggested by both strategies when they had been trained to find a shorter distance platform but predominantly used allocentric information when trained with a longer distance platform. The rats could learn to use self-referential cues to find the long distance platform when trained without any landmarks present; however, adding landmarks that were not predictive of the platform's location impaired this learning, a result the authors take as suggesting that rats have a tendency to use landmark information when navigating long distances (Tamara et al., 2010). When navigating in the water maze with a beacon attached to the platform rats also appear to show a pattern of alternately and independently employing allocentric and egocentric strategies. On such a water maze rats' navigation behaviour is separated into two distinct parts. The first is an initial swim behaviour the trajectory of which is directed by the distal cues surrounding the pool. This is followed by a homing behaviour that is directed towards the beacon associated with the platform. The independence of these stages is suggested by the observation that altering the distal cues only impairs the initial trajectory part of their navigation while removing the beacon cue disrupts the homing behaviour only (Hamilton, Rosenfelt, & Whishaw, 2004).

Similar to the observations made by researchers looking into place learning the understanding of how allocentric and egocentric strategies interact is also complicated by procedural concerns. Making part of a maze task more complex by requiring rats to solve a spatial working memory dependent problem at one point in a maze results in their persevering with place navigation at other stages where it is not necessary (Gardner et al., 2013). There is also evidence to suggest that whether a training environment uses escape or reward as motivation can affect strategy preference. When rats were trained to solve a water T-maze task, they showed a shift from preferential response to preferential direction strategy use over the training period, a

change opposite to the one typically observed on appetitive tests (Whyte et al., 2009). When these two different motivation types were directly compared on a plus maze, it was observed that they resulted in opposite linear changes in strategy preference with rats on the submerged environment shifting from a response to a direction preference while land maze rats showed the opposite trend (Asem & Holland, 2013). In general it is likely to be the case that which of these two strategies is better for a rat to use when solving a maze will depend on a variety of factors, including the experimental conditions (Cole, Clipperton, & Walt, 2007).

Human navigation research

Taking these observations about the navigation abilities of different non-human animals together it can be seen that there is a great deal of variety in the behavioural manifestations of navigation and how it proceeds. These many different behaviours are in turn underpinned by cognitive systems that are generally well conserved between species. This conservation allows researchers to construct predictions and theories about how those aspects of human navigation that are currently not well understood might function. The research that will be described here was undertaken in an attempt to do just that, utilising prior human and rodent research together to look more closely at how people acquire and utilise different spatial navigation strategies.

Consistent with the patterns of navigation behaviour observed in rodents, humans appear to acquire and make use of information that is centred on both allocentric and egocentric reference frames. This can be seen when looking at the neural activation of the basal ganglia and the hippocampus, the regions of the brain thought to underpin response and place learning respectively (Iaria, Petrides, Dagher, Pike, & Bohbot, 2003). As people learn their way around and then are required to navigate through an environment there looks to be a balanced

engagement of both systems, with stable biases within individuals for one system or the other which were observed to be predictive of their navigation behaviours (Furman, Clements-Stephens, Marchette, & Shelton, 2014). The authors take these results as suggesting that both systems are present in parallel during human navigation, facilitating a variety of navigational behaviours, where the biases indicate preferences for, rather than unilateral dominance by, a particular system (Furman et al., 2014).

However, while there is a great deal of research that shows patterns and trends in the ways that people, on average, learn and prefer to navigate it also appears to be the case that the rates at which different types of spatial information are acquired can vary dramatically between individuals. People tested on their ability to acquire metric knowledge of a novel route over several learning trials were observed to mostly either develop this knowledge after one training session or to never come to acquire it (Ishikawa & Montello, 2006). Only a minority of the participants showed a gradual development of knowledge consistently with exposure to the route. While how well these results can be said to generalise to other types of spatial knowledge acquired under different learning circumstances is not known it can be useful to keep in mind this variability within people in how navigation may proceed. These differences can be also be seen in the results of Furman et al. (2014) discussed earlier, with different navigation biases between individuals reflected in differential activation of the hippocampus and basal ganglia.

As has been mentioned previously there is a great deal of overlap between the navigation behaviours observed in rodents and those observed in humans. The overlap in how these two groups navigate allocentrically is of particular interest here in part due to the difficulties separating place and directional navigation that are found in rodent research. There is for example evidence to suggest that at least some aspects of the rodent preference for directional

navigation are observed in humans. When comparing directional and place navigation on a virtual MWM task, it has been observed that people showed the same preference for directional responding as is observed in rats on the same task (Hamilton, Johnson, Redhead, & Verney, 2009). Similar to the rat results completely removing the pool wall was again able to shift the navigator's preferences to place navigation; however, participants appeared to show more difficulty solving this variant of the task, another observation in line with prior research. This increased difficulty manifested as fewer participants showing a direct trajectory when moving to the platform location on a probe test, which the authors take as evidence supporting the more complex nature of place navigation (Hamilton, Johnson, et al., 2009). However, as was observed in the rodent literature, it can be difficult to draw conclusions about the difficulty of implementing a particular strategy that extend beyond the particular circumstances of the environment used to observe navigation.

When people have learned a location by its' relationship to an array of environmental landmarks they appear to act in such a way as to preserve this learned relationship by adjusting their search distances from the landmarks when the array expands or contracts (Spetch et al., 1996). How much information an array of landmarks provides to people navigating an environment has been observed to scale with the number of them available, depending on the circumstances. This was observed in an experiment looking at the boundary superiority effect, which refers to the preference navigators show for learning key locations with reference to the boundary of the surrounding environment. In an experiment by Mou and Zhou (2013) people were trained to find objects in a virtual environment with a circular boundary and a variable number of landmarks present as potential cues. In this environment the effect of removing the boundary on performance was negatively correlated with the number of landmarks, such that the

more landmarks available the more information they provided together and therefore the less important the boundary became for localisation (Mou & Zhou, 2013). The number of landmarks available in an environment also appears to have a positive correlation with the willingness of people to utilise them for navigation (Andersen, Dahmani, Konishi, & Bohbot, 2012). There exist many different types of information that can be acquired about a landmark array, with relative distance and angular information of most interest here. These two features are generally assigned different levels of importance. People appear to make more use of distance information, which is defined as the distance ratios between the landmarks in the array, but distance and direction information can also interact, with the degree of the angles formed between salient locations in the environment and the landmarks also affecting learning (Waller, Loomis, Golledge, & Beall, 2000). Similar to honeybees people can in some cases also show a selective accuracy for the location of particular landmarks based on their preference for some aspect of the landmark's identity (Smith, 1984). People are also capable of learning complex spatial relationships between locations and features of the environment when they are necessary to solve spatial problems. Participants that were trained to locate a target amongst a number of possible locations in an environment with a pair of landmarks present were able to learn to solve test trials where one of the landmarks was removed (Sturz, Cooke, & Bodily, 2011). To do this, participants had to use the observed spatial relationships between the different landmarks and vector algebra to infer the location of the missing landmark and from this the location of the goal.

However, while people are capable of learning about and utilising the spatial relationships between members of a landmark array, there is evidence to suggest that they have difficulty constructing a coherent, consistent representation of the spatial environment they

inhabit without experience navigating through and to its multiple constituent parts. For example, Hamilton et al. (2002) trained people in a virtual MWM (vMWM) task to find a platform that was located in one half of the pool (region 1) while being granted different degrees of access to the other half (region 2). When asked to find the platform from a starting point in region 2, their success was dependent on whether they had had the opportunity to experience moving to the target from this region. Here the ability to observe the environmental cues from within region 2, or to move within the region but without the opportunity to move from one region to the other, were not enough to make up for the absence of the apparently key experience of moving between regions. These results match those seen in rats, who were observed to require unrestricted viewing and swimming access to the non-platform half of the pool in order to successfully find the platform when started from within that region (Sutherland, Chew, Baker, & Linggard, 1987).

Human use of egocentric navigation systems can be seen to relate even more strongly to the behaviours observed in rodents and other non-human animals. This is not particularly surprising as the most common methods of egocentric navigation, path integration and stimulus-response learning, are both fairly ubiquitous. Route learning, which involves the chaining together of many of these stimulus-response behaviours, is of particular interest here. People are able to construct these navigation routes in environments that are completely independent of any distinguishing external features. However this is a process that requires some cognitive effort. People trained to learn a route through a series of rooms where access to the next room in the sequence was dependent upon choosing the correct door from the two presented were able to solve this task even when there were no visual cues to identify the rooms; however, the inclusion of a backcounting task during training blocked their ability to do so (Tlauka & Wilson, 1994). Visual features that help distinguish the different rooms, or both the rooms and the correct door

do, however, lead to better performance than is observed by pure route learning alone, at least over short training periods (Waller & Lipka, 2007).

People, similar to rats, also show an interaction between their experience with an environment and their preferred navigation strategy. This similarity includes humans showing the same typical shift from allocentric to egocentric navigation as a result of increasing environment familiarity (Iaria et al., 2003; Schmitzer-Torbert, 2007). However, this shift is dependent on the environment being complex enough for a human that there is a period during training wherein participants do not yet have enough experience to develop an adequate response strategy (Schmitzer-Torbert, 2007). Relatively successful navigation, where success is relative here due to the fact that the paths from a start to a target location are not yet stable, during this period appears to be driven by the use of place navigation (Schmitzer-Torbert, 2007). However, it needs to be noted that the design of Schmitzer-Torbert's (2007) environment, where environmental features are presented as textures on the wall of a labyrinthine maze, differs from the presentation of more open environments where all allocentric cues are visible at all times. The similar shift from allocentric to egocentric navigation under these different circumstances supports the generality of this relationship between environment familiarity and strategy use. People tested on a virtual version of the RAM also show approximately the same pattern of transition in their use of navigation strategies with an approximately half-half split between allocentric and egocentric navigators observed at the start of training ending up with a majority of response navigators by the end of the experiment (Andersen et al., 2012; Iaria et al., 2003). Evidence for the ability of people to acquire both types of knowledge within the same environment can be seen in participants who were trained to learn a route through a virtual environment and were able to by the end of training solve both repeat tests that required simple

recapitulation of the route and retrace tests that required correctly navigating the learned route in reverse (Wiener, Kmecova, & de Condappa, 2012). As repeat tests are thought to depend on egocentric knowledge while retrace tests rely on allocentric knowledge, Wiener et al. (2012) concluded that participants were able to acquire both during the same training period.

The ability of rats to flexibly utilise egocentric and allocentric frames of reference when solving navigation tasks due to their apparent coexistence is also one they share with humans. While people tend to show a preference for the adoption of one strategy or the other when both are equally viable (Furman et al., 2014) they are easily able to utilise their non-preferred frame when instructed to and without impairment in their spatial abilities, even in cases when switching was unpredictable or required from trial to trial (Gramann, Muller, Eick, & Schonebeck, 2005). However, in some cases people can also have a preferred strategy that they employ regardless of how well it fits with the demands of the task at hand (Etchamendy & Bohbot, 2007). Comparing how well participants performed on a RAM test to a wayfinding task, Etchamendy and Bohbot (2007) observed that some people would spontaneously and inflexibly develop a preferred strategy that would be sub-optimal on one of the two tests. Only a subset of people showed the willingness or ability to flexibly switch between optimal strategies although the members of this set were also the most efficient navigators on both tests.

Looking at the behaviour of people on navigation tasks where the optimal strategy is not immediately apparent it has been found that there is tendency for navigators to default to utilising the simplest of the many strategies they may have acquired. When attempting to find the correct path at an intersection people were observed to navigate via simpler response strategies when they were available, despite their maladaptivity (Condappa & Wiener, 2014; Wiener, de Condappa, Harris, & Wolbers, 2013). A shift to a more cognitively demanding allocentric

strategy was only observed after the inadequacy of their first choice became apparent via environmental feedback. This may suggest a more general pattern of preferring to utilise the least demanding strategy that is generally observed to be accurate. Considering human navigation in this way it might be expected that the described shift moves from an easier egocentric to a more demanding allocentric strategy (Condappa & Wiener, 2014; Wiener et al., 2013) and that which is more demanding may also vary as a function of familiarity with the environment and the constraints it imposes on navigation.

However, the observation that spatial learning involves the acquisition of multiple, redundant sources of information in parallel conflicts with the predictions of associative theory where cues are expected to compete for associative strength (Gibson & Shettleworth, 2005). There is evidence to suggest that spatial learning is unique in how, and to what extent, these common rules of learning are followed. That these rules are not always observed to be followed in spatial learning is one of the clearest demonstrations of this. For example beacon learning, which is commonly observed to result in less learning about distal environmental cues, does not overshadow the learning of an environment's geometry, a result that suggests there are unique components, or interactions, of spatial learning that operate under their own unique conditions (Gibson & Shettleworth, 2005). It has also been observed that participants tested on a vMWM show no evidence of blocking occurring when they are explicitly instructed to explore the environment (Hardt, Hupbach, & Nadel, 2009). When Hardt et al. (2009) attempted to replicate a study that showed blocking in human participants (Hamilton & Sutherland, 1999) the addition of instructions encouraging exploration of the environment also attenuated blocking effects. While performance on the traditional MWM probe trial was mixed, performance on the location accuracy probe (LAP) test showed a clear lack of blocking (Hardt et al., 2009). The aim of using

the LAP is to remove the contamination of spatial strategy and test performance from the assessment of spatial knowledge by informing participants of the missing platform on test trials and asking them to go the location they believed it would be if it were present (Hardt et al., 2009). Hardt et al. (2009) point out that it can be potentially difficult to tell what exactly the traditional probe trial is measuring, with possibilities including spatial strategy, spatial knowledge and potentially pathological perseverance. However, when considering how different types of knowledge interact it is important to distinguish between interactions observed during learning and those observed during performance. Under this distinction blocking and overshadowing can be seen as good measures of strategy interaction that occurs during learning (Gibson & Shettleworth, 2005).

The information that underpins the use of these multiple different strategies can also interact in a time-dependent manner, such that earlier knowledge can in some cases modulate what is acquired later. Prior allocentric learning can, for example, interact with egocentric information that is acquired after it. In an experiment demonstrating this phenomenon people were first shown a regular or distorted map of an environment. They were then walked through the environment blindfolded so that only egocentric information was acquired (Lafon, Vidal, & Berthoz, 2009). The path participants reproduced when asked to do so was consistent with the map they had been shown, such that those who saw the regular map drew the correct path while those who saw the distorted map drew a path that was distorted in the same manner. Participants who were not shown a map beforehand also reproduced the correct path. Distorted map participants also showed more inaccuracy when asked to point from later points in the learned path to the origin while walking through the environment. As distorted map participants could point correctly to the origin when closer to it the authors suggest this distance dependent effect is

evidence of a shift from using kinaesthetic to allocentric information to update position as navigation proceeds (Lafon et al., 2009).

It is also important to consider when attempting to look at navigation strategy use the distinction between tasks that involve different strategies that produce their own distinct behavioural responses and tasks where the different strategies produce congruent output (Kosaki et al., 2015). The rodent T-maze provides a clear example of the first group, as the allocentric strategy of moving to the arm suggested by the room cues and the egocentric strategy of producing a learned turn response at the intersection are entirely independent and involved in the execution of separate behaviours. An example of the second system can be seen in the beacon version of the MWM where correctly navigating to the platform is a behaviour that results from the combination of an initial movement trajectory based on the distal room cues and a homing response towards the beacon (Hamilton et al., 2004). It might be expected in cases where different strategies with separate outputs are put in conflict that degraded learning of one knowledge system should produce improved performance in the other. When different strategies produce congruent output, the question changes to whether the presence of other strategies might affect the strength of learning acquired for any given system (Kosaki et al., 2015).

Taken altogether these results paint a complicated picture of the way that allocentric and egocentric navigation strategies are acquired and interact in humans. The aim of this study was to attempt to look more closely at these interactions utilising an experimental paradigm that also allowed comparisons to be drawn directly to the wealth of non-human animal research that has been conducted. With this aim in mind the MWM immediately suggests itself as one of the few rat spatial navigation tests that can be ported with little to no alteration for use in humans (Jacobs et al., 1997). Typically people appear to use three key search behaviours on a vMWM; a pattern

of approach-withdraw exploration near the platform, thigmotaxis, and visual scan, where a participant stops moving and rotates around to scan the environment (Kallai et al., 2005). This pattern of search behaviour is quite similar to that employed by rats in the analogue water maze. Successful navigators preferentially employ the visual scan, while poor navigators prefer to use thigmotaxis (Vorhees & Williams, 2014). One of the key considerations when designing a navigation test and interpreting the observed behaviour is the spatial scale of the environment in which navigation takes place. For most navigation research the two relevant spatial scales are vista and environmental (Wolbers & Wiener, 2014). Vista scale spaces are environments where all relevant spatial features can be fully understood from one location without moving, while environmental scale spaces require movement to fully experience. Examples of vista spaces would be T and Y mazes and the MWM while examples of environmental spaces are multi-floor buildings and towns. Navigating environmental spaces typically involves travel through multiple, distinct vista spaces and the integration of information across time and space. Target locations are also positioned so as to be located beyond a participant's sensory horizon when they enter the environment (Wolbers & Wiener, 2014). The most important point to draw from this distinction is the importance of keeping the scale of the environment in mind when attempting to assess a particular facet of navigation and when attempting to relate observations from different findings together.

Another important point of consideration for the design of a new spatial test is the complexity of the presented environment. As was discussed previously the design of the MWM that is now generally considered standard resulted from different experimenters varying the size of the pool and pool to platform size ratio and observing the resultant learning curves and navigation behaviours (Vorhees & Williams, 2014). While there are many mazes and test types

administered to non-human animals that could be used to assess human spatial navigation it is important to ensure that human versions of these tasks are made complex enough to motivate the spatial learning that is hypothesised. The rodent star maze provides an example of the problems that can arise when these concerns are not considered, with people trained on it appearing to be able reach asymptotic performance within an average of three training trials (Igloi, Zaoui, Berthoz, & Rondi-Reig, 2009). As Igloi et al. (2009) were aiming to assess parallel learning of allocentric and egocentric information, but only administered their first test trial long after participants had reached asymptotic performance, it may very well have been the case that information was acquired sequentially but within the relatively large training window before testing. As has been shown in the MWM more complex environments that produce shallower learning curves provide an experimenter with more time to observe changes in behaviour and strategy use (Vorhees & Williams, 2014). When considering what navigation behaviours or strategies can be employed on a task it can also be important to have some idea of what types of knowledge about the goal location, the navigated environment, and the paths through it, can be acquired. What behaviours and strategies the chosen task constrains the participant from applying is also important to consider (Wiener, Büchner, & Hölscher, 2009).

Using virtual reality to study human navigation: methodological constraints.

Another fundamental question that needs to be considered when designing an experiment to look at spatial navigation is how the environment will be presented to participants. For modern researchers to answer this question often the first issue that needs to be addressed is whether to make use of a real world space or to construct a virtual environment. While real world environments might generally be expected to produce patterns of behaviour that better reflect how people navigate on a daily basis there are a variety of possible benefits that come from

investigating navigation using virtual reality. Virtual environments can in some cases better facilitate the isolation of the different processes that come together to produce navigation (Loomis, Blascovich, & Beall, 1999). They also allow for the easy manipulation of environmental features, large and small, that might be utilised for navigation. This allows virtual reality to address one of the key arguments against the use of real-world environments, which is that can be difficult or impossible to remove or modify large features (Kelly & Gibson, 2007). It can also be the case in some more impaired populations that real-world navigation tasks may be too demanding to be utilised (Kelly & Gibson, 2007), or it may be that such tasks are too difficult for them to perform adequately on. Most spatial navigation research focuses on participants acquiring information about a novel environment over a single experimental session; however, virtual representations of real-world spaces can also allow researchers the ability to flexibly look at how people navigate through environments they have become familiar with over very long timescales. One such experiment looking at how residents of the city of Tübingen performed on route and survey navigation tests administered in a virtual 3D model of their city (Meilinger, Frankenstein, & Bulthoff, 2013). The authors found that tests of different navigation abilities in this environment showed no systematic relationship between them in the performance and types of error they produced (Meilinger et al., 2013). They take these results as evidence that when navigating or reasoning spatially about familiar environments people make use of many different and independent spatial reference frames (Meilinger et al., 2013). Virtual environments have also been used to study spatial navigation in non-human animals, allowing for tests of behaviour that would not be possible with real-world tasks (Kelly & Gibson, 2007).

The mechanism by which people search through space appears to be much the same in virtual environments as in real ones, an observation that further supports the idea that the spatial

mechanisms used in both environments are similar (Sturz, Bodily, Katz, & Kelly, 2009). The ability of virtual environments to produce the same behaviour as observed in the real world has also been found to extend beyond the standard populations of university students and young adults. Volunteer participants aged 40 years and older were tested on their ability to flexibly navigate a virtual recreation of a real-world, complex building through which they had previously learned a fixed route (Koenig, Crucian, Dalrymple-Alford, & Dunser, 2011). These participants showed an optimality in the paths they took that did not differ from those who were required to navigate from the same novel locations within the real-world building (Koenig et al., 2011). Further support for the idea that tests in virtual environments can produce real-world patterns of behaviour comes from looking at the relationship between rat and human spatial navigation research. Virtual environments testing humans on virtual versions of rodent mazes have been shown to produce learning curves similar to those observed in rodents (Shore, Stanford, MacInnes, Klein, & Brown, 2001). Similar observations have also been made by researchers using the vMWM (Hamilton, Johnson, et al., 2009), a result that is of particular relevance here.

One of the common concerns that crops up in the literature regarding experiments that deviate from the real world experience of walking through an environment involves the potential importance of active navigation on human spatial ability. When considering this interaction there are typically two types of navigation that are delineated. Active navigation is generally defined as having both physical and cognitive components. Podokinetic information, and vestibular information from head movement makeup the physical component and are together commonly referred to as idiothetic information. The cognitive component refers to the decision making involved in navigating and to what extent attention is allocated to the spatial properties of the

environment (Chrastil & Warren, 2012, 2013). In contrast passive navigation involves providing participants with only visual information about movement through an environment (Chrastil & Warren, 2013). Podokinetic information is one of the primary sources of information underpinning the acquisition of metric survey knowledge, with people tested on their ability to find a novel shortcut between familiar locations performing best when the environment had been learned by having the participant walk through it (Chrastil & Warren, 2013). Participants trained to learn a route through a real or virtual environment were able to recapitulate that route on a later real-world test equally well when the virtual group controlled their view and movement through the world using their bodies, with translation information provided via a treadmill and movement direction by head rotation (Larrue et al., 2014). However, participants trained on the virtual environment with no body-based control, or with only translational information performed more poorly on the route recapitulation test, but not on pointing tests to within-route locations, suggesting that it was only on tests of allocentric knowledge that idiothetic information was important (Larrue et al., 2014).

Idiothetic information is also thought to help people keep track of their position in space and with the acquisition of spatial relationships and accurate path integration. The evidence also suggests that idiothetic information builds up over time and tends to reveal its importance more when looking at performance in more complex environments (Chrastil & Warren, 2012).

Idiothetic information from locomotion also provides better distance approximations (A. R. Richardson & Waller, 2007). This distance information can also aid the formation and recapitulation of route knowledge, facilitating correct turning responses in cases where distance varies between the sections of the route by creating a more accurate representation of the length of different route segments (Ruddle, Volkova, Mohler, & Bulthoff, 2011). That this

improvement observed by Ruddle et al. (2011) was relative to performance where participants could make use of rotational, but not translational, body movement further supports the important role idiothetic information provided by locomotion plays in many forms of navigation.

Taken together these observations would appear to stress the importance of matching the vehicle of virtual movement to real world locomotion as closely as possible, and researchers have come up with many ways to do just that. There is evidence to suggest for example that this idiothetic information, and its associated improvement in navigation performance, can be acquired by having participants walk in place, with the inferred pace of their steps used to drive movement in the virtual environment (Williams, Bailey, Narasimham, Li, & Bodenheimer, 2011). Williams et al. (2011) achieved this using a Wii-Fit balance board. Real walking within a constrained physical space can also be achieved using redirected walking, where participants are induced to veer imperceptibly as they move so as to stay within the confines of the designated area (Hodgson, Bachmann, & Waller, 2011). However, it is important to consider both the physical and cognitive components of active navigation and, more importantly, how different types of knowledge interact with these components and can complicate the idea that locomotion is always necessary to observe perfectly accurate navigation performance in a virtual environment. The most relevant example for the work that is to follow involves how people appear to acquire graph knowledge. Unlike survey knowledge, graph knowledge (Chrastil & Warren, 2013), is improved by allowing people to make decisions about where they navigate in the environment (Chrastil & Warren, 2015). Chrastil and Warren (2015) speculate this result may have been the result of decision making encouraging people to attend to the relevant spatial features of an environment and to develop predictions about the results of their choices. The success or failure of these predictions could then be used to progressively update people's

representation of graph space (Chrastil & Warren, 2015). A similar mechanism is thought to underpin some the improvement active navigation has on the development of route knowledge (Chrastil & Warren, 2012). However, for route knowledge it is more likely that active attention to the environment is important as opposed to specific attention to the spatial properties (Chrastil & Warren, 2012). All of this is not to say, however, that more accurate metric information cannot affect the route and graph knowledge acquired, as local metric information can for example help people determine the length of possible paths between locations (Chrastil & Warren, 2015). Looking more generally it appears to be the case that the benefits of active exploration are observed in cases where the environment and the navigation tasks encourage or depend on the acquisition of the information active navigation provides (Dalgarno, Bennett, & Harper, 2010). Therefore, it can be seen that consideration of active navigation further stresses the importance of correctly matching experimental methodology to the navigation strategy or strategies under observation.

How immersed a person feels by the virtual environment is another variable that has been observed to play an important role in people's navigation behaviour. Participants tested on their navigation ability in the same environment presented in either 2 or 3 dimensions showed better performance on the latter, alongside higher subjective ratings of presence and dedication of cortical resources to the navigation task, as measured by EEG (Slobounov, Ray, Johnson, Slobounov, & Newell, 2015). The visual fidelity of a virtual environment can also affect the level of real world correspondence observed in a person's behaviour and performance, with higher fidelity improving correspondence regardless of whether navigation is active or passive (Wallet et al., 2011). The virtual environment's visual realism also plays an important role in how well observed behaviour matches that seen in the real world, and how well participants

perform on tests of navigational ability more generally (Meijer, Geudeke, & van den Broek, 2009). People have also been observed to improve their spatial updating ability when asked to navigate through more visually rich, naturalistic environments (Riecke, Sigurdarson, & Milne, 2012). The visual detail provided in the environment used here was motivated at least in part by these observations of the effect that immersion can have on navigation behaviour.

When using a virtual environment consideration also needs to be given to how the environment will be experienced by participants. The standard method is to have participants sit in front of a desktop computer monitor and navigate through the environment using keyboard or joystick controls if the experimenters are testing active navigation. However, this method presents a relatively limited and artificial field of view to participants, where the artificiality comes as a result of the lack of environmental constancy. That the view of the virtual world this type of arrangement provides is completely independent of the rotation of the participant's head provides a clear example of this disconnect. It is possible that limiting the field of view of the presented environment can affect navigation performance, however, this may not be a factor except in cases where the view is extremely constrained (A. E. Richardson & Collaer, 2011). One possible way to address these concerns is to construct a panoramic display that surrounds the participant with multiple monitors rendering the virtual environment and providing a more naturalistic presentation. Typically, participants tested in such a set-up will be seated in an interactive chair with rotation sensors so they can update their view and movement direction using the position of their bodies. Such set-ups tend to produce better performance on tests of spatial cognition than the standard desktop system, with participant results also better correlating with other measures of spatial orientation ability (Meng, Zhang, & Yang, 2014). Researchers have also looked at the effects of different monitor display types and sizes. Larger displays and

stereoscopic presentation using 3D displays and 3D glasses do not improve performance on survey knowledge dependent tasks, while large screens can in some cases increase the likelihood of participants developing simulator sickness (Dahmani, Ledoux, Boyer, & Bohbot, 2012). However, larger displays have also been observed to improve navigation performance when compared to smaller monitors where the perceived size of the projected image, the resolution and the refresh rate are matched between them (Tan, Gergle, Scupelli, & Pausch, 2006). This effect of display size was also independent of the degree of the environment's immersiveness.

Many of these more complicated display set-ups, however, can be prohibitively expensive and are also not very portable. This lack of portability is limiting in that it does not allow tests to be taken to people that cannot visit the premises in which these setups are housed, a group that often includes clinical populations. To address this portability concern some researchers utilise head-mounted displays (HMDs), which involve presenting a virtual environment to a participant with stereoscopic depth using a relatively lightweight and portable headset. Modern setups using HMDs require only the headset and a laptop, which can be carried around by the participant in a backpack if locomotion is used as the method of movement, to present the environment (Hodgson et al., 2015). The evidence regarding whether or not there is added utility to the use of HMDs to present virtual environments in a more realistic manner, where head rotation controls the participants' view of the world, is not currently conclusive. Research into the benefits of HMDs when their development was still in its relative infancy found no improvement in navigation performance as a result of the added proprioceptive information the headsets provided (Ruddle & Peruch, 2004). However, there exists the possibility that any benefits would have been disguised by the headset's relatively low resolution compared to the desktop monitor used as a point of comparison. The degree of the field of view

(FOV) presented may have also played a role. For virtual environments there are two distinct types of FOV to be considered. The display FOV is the angle subtended from the eye to the left and right edges of the display and depends on the size of the display and its distance from the user. The other is the geometric FOV, which is the horizontal angle of the visible part of the environment presented to the participant. In general it can be harmful to deviate from a 1:1 to ratio between these two FOVs, while increasing both together can improve participants performance on spatial navigation tasks (Tan, Czerwinski, & Robertson, 2006). The relatively recent development of HMDs with higher visual fidelity and larger FOV has allowed researchers to construct highly immersive virtual environments that allow for the testing of navigation behaviours in a wide-variety of locations with little to no external infrastructure required (Hodgson et al., 2015). In order to maximise the possible circumstances under which the experimental methodology described here could be utilised, and as a consequence of the modern development of many relatively inexpensive, high fidelity headsets, a HMD was used here as the vehicle of presentation of the virtual environment.

Aims

The aim of this research was to look at how spatial navigation strategies are acquired in humans, how this acquisition interacts with the development of environmental familiarity, how people, on average, prefer to employ the strategies they have acquired and how strategy preference relates to environment complexity. In order to allow for a relatively simple connection between this work and the behavioural data observed in rodents the vMWM was decided upon as an ideal environment to look into these areas of interest. This necessitated looking at navigation within a vista scale space which, combined with the freeform movement allowed by the use of a water maze, would have put an unwanted limit on the types of egocentric

strategies that participants could develop. To circumvent this while adhering to the requirements of a vista scale space a large, complex maze was used with the aim of maintaining the freedom of movement offered by the traditional MWM while also allowing for the potential development of sequential egocentric strategies. Taking in to consideration the potential importance of decision making on the development of particular types of spatial knowledge, participants in the experiments employed here were always entirely free to navigate however they preferred within the confines of this maze. The paths of the maze were composed of planks in order to keep all of the distal environmental cues visible at all times. These landmarks were expected to serve as cues that would have their salience delineated by their distinct features and contrast with the environment. As the maze was composed of interconnecting planks of uniform length the issue of participants' acquisition of metric distance information was not expected to be a concern as, if a map or graph-like representation of the maze was constructed by participants, the shortest paths could be found with perfect accuracy by simply counting the number of planks that would need to be traversed. Therefore, it was not expected for locomotion to be a necessary inclusion in the experimental design. Following these experimental specifications the research undertaken here was motivated by three key aims; to observe whether and how participants acquired allocentric and egocentric navigation strategies, to look more closely at what sources of information came to underpin these strategies, and to assess whether the information people acquired, and the complexity of the navigated environment, might interact to affect how navigation was preferentially undertaken.

Empirical Chapter 1

Experiment 1

The following experiments were designed to look at the nature and development of allocentric and egocentric navigation strategies in a novel virtual environment. This environment was designed to imitate the open, complex space of the MWM while also constraining the paths participants could take in order to potentially facilitate the development of a route-based strategy. A similar training structure to that used for the MWM was also utilised for these experiments, with participants trained to navigate from a fixed starting location to a fixed target location across multiple training trials.

A virtual training environment was designed so that participants could learn allocentric, egocentric or both, strategies to navigate. The environment resembled the standard water maze set up, with the addition of a hexagonal grid maze of planks positioned above the water. This maze was included to allow participants to potentially develop complex egocentric strategies as well as, or in place of methods of navigation based on distal environmental cues. Participants began each training trial in the maze from a fixed location and heading and were required to find a hidden treasure chest. The fixed nature of the starting position meant participants could learn a specific route across the plank system to the target location. Allocentric strategies could be learned by attending to the multiple landmarks arrayed beyond the boundary of the pool. Participants could learn to use the relationships between them as well as their individual identities. A fixed sky was also included that could serve as a crude orientation cue.

In order to test whether participants were capable of navigating with these strategies independently test environments were constructed as variations of the training trial environment

that contained features relevant to navigation by only one knowledge type. For the allocentric tests, the plank maze was removed and the starting position changed, as any egocentric strategies that developed were expected to be dependent upon the relationship between the start and the target. For the egocentric tests the landmarks and sky were removed as distal environmental features. These tests measuring the efficacy of participants' unimodal navigation were administered multiple times as participants were trained in the virtual maze.

The aim of this experiment was to observe the acquisition of allocentric and egocentric navigation strategies by people learning to navigate in a virtual maze environment. As training progressed, it was predicted that participants would become more efficient in navigating from the start to the target location. It was hypothesised that this would manifest first as a decrease in the time (latency) to find the target location, second as a decrease in the distance travelled, third as a decrease over training in the area of the maze participants searched, and fourth as a shift towards participants preferentially navigating via the same regions of the maze over multiple trials. In order to separately measure the acquisition of allocentric and egocentric information, participants were also tested on how well they could navigate entirely via reference to one strategy or the other. Here it was hypothesised that the ability to solve these tasks, or at least perform proficiently on them, would emerge with training.

Method

Participants

Twenty-nine undergraduates from the University of Sydney participated in this experiment in exchange for course credit. Potential participants older than the age of sixty-five or who had any prior history of schizophrenia were excluded from this study. Eight of the

participants were excluded from the analyses, five as a result of their developing simulator sickness. The other three failed to complete the experiment within the allocated one and a half hour time limit.

Materials

The virtual environments used in this experiment were scripted in, and generated by, Unity 3D software (Unity Technologies, Version 5.3.1). To flexibly construct different virtual environments a bespoke maze designer software was used (VR Maze Designer developed by Stephen J Rogers at the School of Psychology, University of Sydney, used with permission). The world was presented stereoscopically to participants using the Oculus Rift Development Kit 2 (DK2) (Oculus VR, Irvine, CA), a head-mounted virtual reality display. The DK2 tracked participants' head movements, and these were used to determine what part of the environment the view was oriented towards with an update rate of 1000 Hz. Participants controlled their virtual avatar using a Bluetooth controller (Samsung EI-GP20HNBEGWW Gamepad). The joystick of the controller was used to allow participants movement in their desired direction. The direction the participant was facing when tilting the joystick was used as the reference point for movement, such that tilting the joystick up moved the participant in the direction their head was pointing in the 2D plane. Participants were required to be standing for the duration of the experiment.

Design

This experiment made use of a within-subjects design. There were three within-subjects independent variables used here; training trials, allocentric test trials, and egocentric test trials. There were fifteen training trials. Distance travelled and latency to the target were recorded as

dependent variables per trial, while between trial route variability was recorded for the first and last blocks of five trials. There were three allocentric test trials, with each participant tested after five, ten and fifteen training trials. Participants' ability to approximate the target location on a test trial was recorded as the dependent variable. Three egocentric test trials were conducted at the same time as the allocentric test trials, with both test types administered in a counter-balanced order.

Procedure

Pre-training

Before the experiment proper began, participants were fitted for the headset and then placed into a virtual practice environment, which was identical to the training environment except that there was not a target location. Participants were instructed on the correct way to control the movement of their virtual avatar and on the relationship between their head orientation and their view of the environment. They were then told to practice moving freely around this environment within the constraints of the plank system to become familiarised with manoeuvring using the DK2 and the Bluetooth controller in sync. Once participants reported themselves to be sufficiently familiar with the controls, the program running the practice environment was terminated.

Training

The design of the training environment, visualized in Figure 1, was motivated by the Morris water maze. The pool was bounded by a grass terrain and surrounded by two concentric rings of eight landmarks each. The landmark layout can be seen in Figure 1, with each landmark in the distal ring positioned so as to be visible in the space between a pair of neighbouring

landmarks in the proximal ring. The landmarks were included to serve as precise, allocentric cues for participants to use to orient themselves and delineate locations within the maze. A static sky was also included above the terrain to provide a crude but stable orientation cue, with the sun clearly positioned in the NE quadrant and multiple clouds scattered in fixed positions above and around the maze. To constrain navigation within the pool and create the opportunity for egocentric paths to be learned a plank maze in the shape of a hexagonal grid was included above the pool, as can be seen in Figure 1. A variety of different grid sizes were tested during a pilot study. Similar criteria to those used for choosing the pool size in MWM experiments were used here with the maze size chosen that best balanced learnability with difficulty. To prevent the participants from using the hexagonal grid system as a visual orienting cue, only the planks connected to the last intersection that had been visited were made visible at any given time.

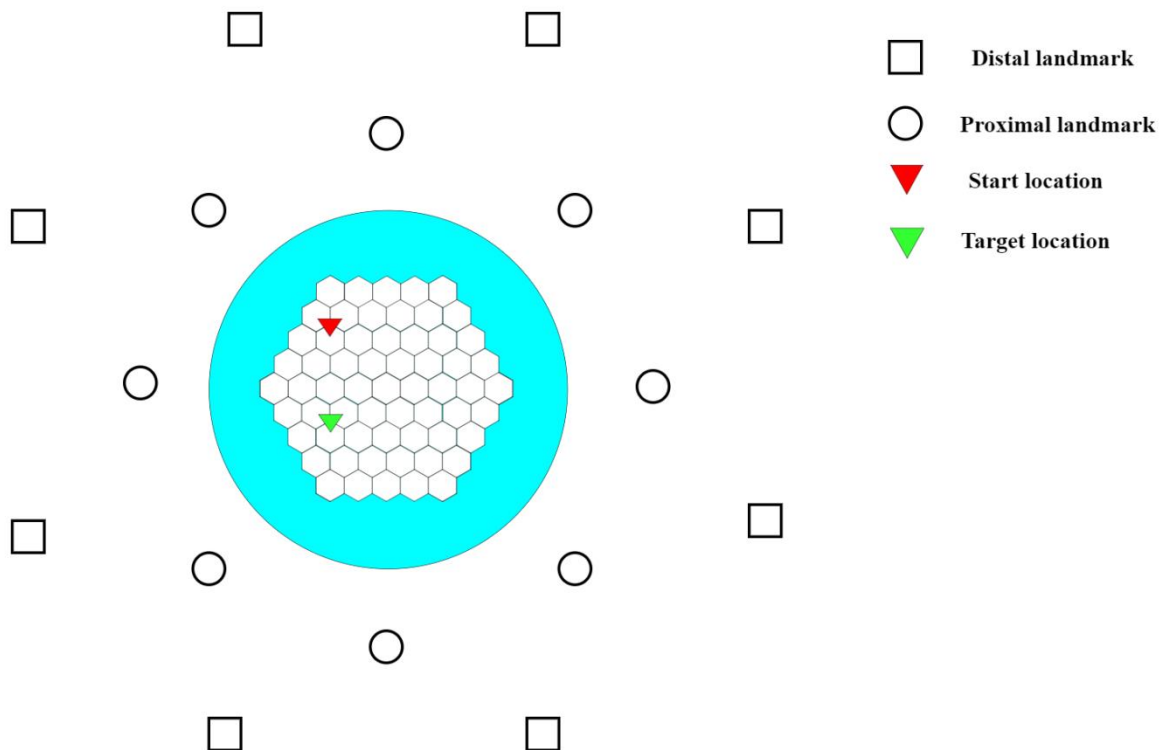


Figure 1. Schematic survey view of the training environment utilised in Experiment 1.

Participants were informed that they would be completing a set number of training trials, where in each trial they would be required to navigate through the environment from a starting location to a target location, where both locations were fixed and unchanging for the entirety of the training process. They were then told they would only have four minutes per trial to do this. If successful they would move on to the next trial and have to repeat the process. If unsuccessful they would be first teleported to the target location and given ten seconds to familiarise themselves with it before the next trial was begun. Finally, they were informed there would be test trials that would be used to measure their knowledge of the target location about which they would receive instruction later.

The start and target positions, along with the direction participants started out facing, were fixed and invariant. The start location was in the NW quadrant and the goal location was in the SW quadrant. As there was a time gap of approximately one second between the end of one trial and the beginning of another, participants needed to avoid any noticeable head movements to ensure that the direction they were facing at the start of each trial was fixed and constant within and between individuals. To ensure this did not cause any problems, participants were instructed to face their head to the floor of the room at the end of each training trial and to only lift it and begin the trial after receiving the instruction from the experimenter to do so.

The target was located on a plank intersection and was delineated by the appearance of a chest object during training. Participants were informed that a chest would appear to signify they had discovered the target location. They were also told that all movement of the joystick would need to cease at the end of a trial. The chest was programmed to not reveal itself until the participant had traversed more than halfway down one of the planks leading to it. The chest's appearance was accompanied by a short audio cue to indicate the successful completion of a

trial. The end of an unsuccessful trial was accompanied by a different audio cue. Teleportation to the target location at the end of an unsuccessful trial followed this cue once participants had released the joystick. This teleportation process was instantaneous, which meant participants were not given the opportunity to view any possible path between their last location and the target.

Allocentric test

The allocentric test environment was based on the training environment, with the difference that the plank maze, and the accompanying restrictions it placed on participants' movement, had been removed (see Figure 2). Thus, the only cues available to locate the target position by were the distal cues outside of the water pool. Moreover, the starting location for the allocentric test trials was different to the one used during training. Participants were instead started from one of three new start locations that were chosen on the basis that they fulfil two criteria: they needed to be the same distance to the target as the training start location, and they needed to be in one of the two pool quadrants that did not house either the start or the target location during training. A different starting location was used for each test time, with each only used once.

Participants were informed before the start of each test trial of the new environment conditions and that, with the absence of any cues delineating the target location, they would instead be expected to navigate to whatever location they believed the target to be given the available information, and to inform the experimenter when they had done so. As the allocentric test environment had no plank maze, they were further informed that the restrictions on their movement had been removed and that any apparent decrease in movement speed they

experienced was the result of the removal of the planks as an immediate frame of reference for their motion.

Once the participant had informed the experimenter they believed they had completed the trial the maze program was instructed to record their current position. This location was recorded as their approximation of the target's position and used to calculate the dependent variable used in the statistical analyses of test performance.

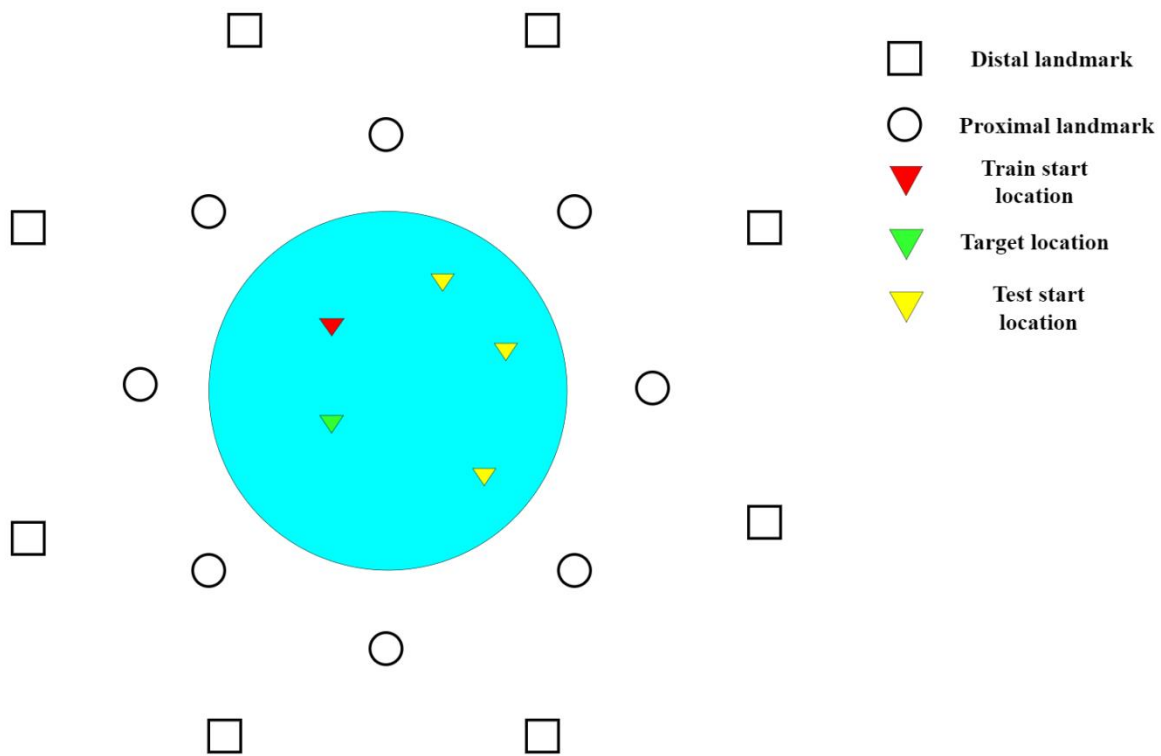


Figure 2. Schematic survey view of the allocentric test environment utilised in Experiment 1. For each participant all three test start locations were used once, one for each test trial time.

Egocentric test

For the egocentric tests, the boundary of the pool, the sky, and both rings of landmarks from the training environment were removed (see Figure 3). The plank maze system that was

available during training was present in these tests. Participants had to try to recall the route across the plank system from the start location to the hidden target location. The participants were informed before the start of each test trial of the new environment conditions, and that they would be expected to navigate to whatever location they believed to be the target location given the available information, and to inform the experimenter when they had done so. They were also informed that they would start these test trials in the same location and facing the same direction as they had done during training.

Once the participant had informed the experimenter they believed they had completed the trial the maze program was instructed to record their current position. This location was recorded as their approximation of the target's position and used to calculate the dependent variable used in the statistical analyses of test performance.

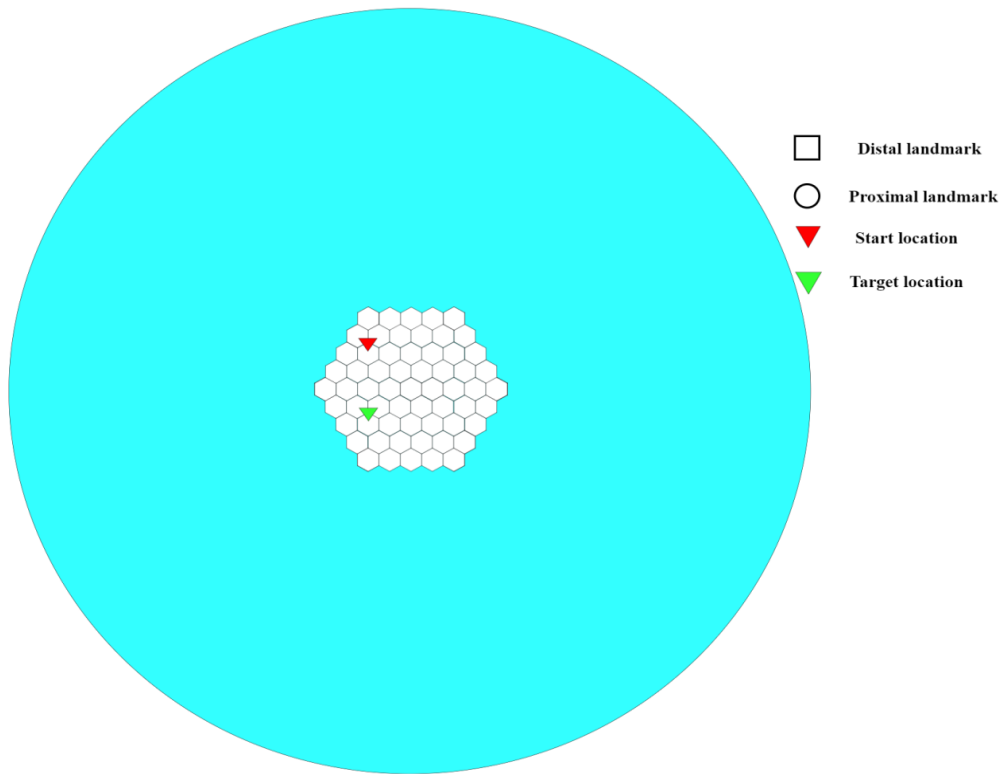


Figure 3. Schematic survey view of the egocentric test environment utilised in Experiment 1.

Statistics

Training

To assess learning about the environment across training the distance travelled and the latency to find the target location per participant per training trial were both recorded as dependent variables. Latency was recorded as the time from when participants were informed that they could begin the trial to the time that the cues delineating the discovery of the target location were triggered. Any trial where the participant failed to find the target was automatically given a latency score of four minutes, the time limit of the training trials. Distance travelled was recorded as the length of the path taken by a participant from the start to the end of a trial, with no modifications as a result of the trial ending due to the time limit or to finding the target

location. Both measures of learning were submitted to One Way Within-Subjects ANOVAs, with training trial number as the independent variable.

To measure the variability of the paths participants took during training all of the intersections traversed by each participant within a single block of training trials (where a block was defined as an unbroken sequence of five training trials) were recorded. For each trial every intersection was marked as visited or unvisited. Therefore, within a block each intersection was assigned to a frequency bin based on the number of trials it was visited on, ranging from zero visits to a maximum of five. Two blocks of interest (trials 1-5 and 11-15) were used for analysis. The number of intersections with zero visits was compared between blocks using a paired samples t-test. For each participant the scores of the non-zero bins were summed together creating a total score that represented the number of intersections visited by that participant one or more times during a training block. The non-zero bins for each participant were then assigned a percentage score by dividing each bin's frequency by the individual's total score. These percentages were then compared between blocks using a 2 (training block) x 5 (bins 1-5) Within-Subjects ANOVA. Alpha was set at $p = 0.05$.

Test

For egocentric and allocentric test trials, the accuracy of participants' approximations of the target location was calculated using the distance formula. These distance scores were used as the test trial dependent variables, and were calculated relative to the actual target location, and three other dummy locations. Each dummy location was located within the centre of one of the three, non-target pool quadrants (the target location was positioned so as to be in the centre of its own quadrant). These dummy locations were used to test whether the approximated target

locations were closer to the actual target than to other parts of the pool. For the allocentric tests, the distance scores from the target approximations were calculated with respect to the actual target location with respect to the distal cues outside the pool. For the egocentric tests, distance scores were calculated between the participants' approximation of the target location and where the target location would be in the hexagonal plank maze during training with respect to the start location.

The distance scores for the egocentric and allocentric test trials were analysed separately using a 3 (test time) x 4 (quadrant) Within-Subjects ANOVA to compare quadrant preference across the three test trials. In addition, a One Way Within-Subjects ANOVA was used to test whether there were changes in the distance scores to the target location specifically across the three trials. Planned contrasts were also used. First, distance scores to the target location were compared against the combined average scores for the remaining three locations. These difference scores were then separately calculated for each test time and were used for comparisons between the three times. Time 1's score was compared against the combined average of times 2 and 3, and time 2 was compared against time 3. Alpha was set at $p = 0.05$.

Results

Training

Visualised in Figure 4a it can be seen that participants, on average, showed a clear decrease in distance travelled per trial with more training. This observation is supported by statistical analysis, with a One-Way Within-Subjects ANOVA revealing a significant effect, $F(14, 280) = 13.67, p < .001$, of training trial number on distance travelled.

A similar trend can be observed in participants' time taken to find the target (see Figure 4b), with latency also decreasing with training trial number. This was supported statistically, with a One Way Within-Subjects ANOVA showing a significant effect, $F(14, 280) = 13.11, p < .001$, of trial number on latency.

Figure 4c-d visualizes the measure of variability in the areas of the maze participants traversed during training. Here it can be seen that the repetition of the use of particular unique intersections per participant increased from the start (trials 1-5) to the end (trials 11-15) of training, and that the number non-visited intersections increased from the first block to the last. Comparing the number of intersections with no visits between the two blocks using a paired-samples t-test revealed a significant, $t(20) = -7.87, p < .001$, increase by block 3. Looking at the percentage scores with a 2 (training block) x 5 (unique visits) Within-Subjects ANOVA, a significant, $F(4, 80) = 46.98, p < .001$, main effect of unique visits was found that was modulated by a significant, $F(4, 80) = 16.39, p < .001$, interaction effect. It can be seen in Figure 4d that the source of this interaction was likely the decrease in frequency of single intersection visits and an increase in the number visited four or five times.

Allocentric tests

Figure 4e shows the distance scores calculated with reference to the target location and the three other dummy quadrant locations, sorted by test time. Here it can be seen that participants appeared to show, from the first test time, a preference for approximating the target near the target location which was unchanged over training. This lack of change was demonstrated with a One Way Within-Subjects ANOVA using the distance scores to the target location as the dependent variable, which showed the effect of test time was not significant, $p >$

.05). A 3 (test time) x 4 (quadrant) Within-Subjects ANOVA did reveal a significant, $F(3, 60) = 90.94, p < .001$, main effect of quadrant but no main effect of test time and no interaction (p 's $> .05$). Planned contrasts compared target location distance scores to the combined distance scores for the other three pool quadrants, and revealed a significant, $F(1, 20) = 122.35, p < .001$, preference for the target location. There was no evidence of a relationship between test time and degree of preference for the target location (p 's $> .05$).

Egocentric tests

The distance scores for the egocentric test trials at each test time are shown in Figure 4f. They appear to show that participants developed a preference for approximating the target location closer to the actual target as a result of more training. A One Way Within-Subjects ANOVA looking at target location distance scores as a function of test time supported this interpretation, revealing a significant, $F(2, 40) = 9.77, p < .001$, effect of test time. A 3 x 4 Within-Subjects ANOVA revealed a significant, $F(3, 60) = 8.51, p < .001$, main effect of quadrant and no main effect of test time ($p > .05$). The interaction between test time and quadrant was significant, $F(6, 120) = 4.97, p < .001$. Planned contrasts comparing the target location distance scores to the combined distance scores for the other three locations showed a significant, $F(1, 20) = 11.02, p = .003$, preference for the target location. Further, they revealed that participants target location preference was significantly, $F(1, 20) = 7.91, p = .011$, stronger for the last two test times combined when compared to test time 1. There was also a significant, $F(1, 20) = 9.63, p = .006$, stronger preference for the target location at time 3 compared to time 2.

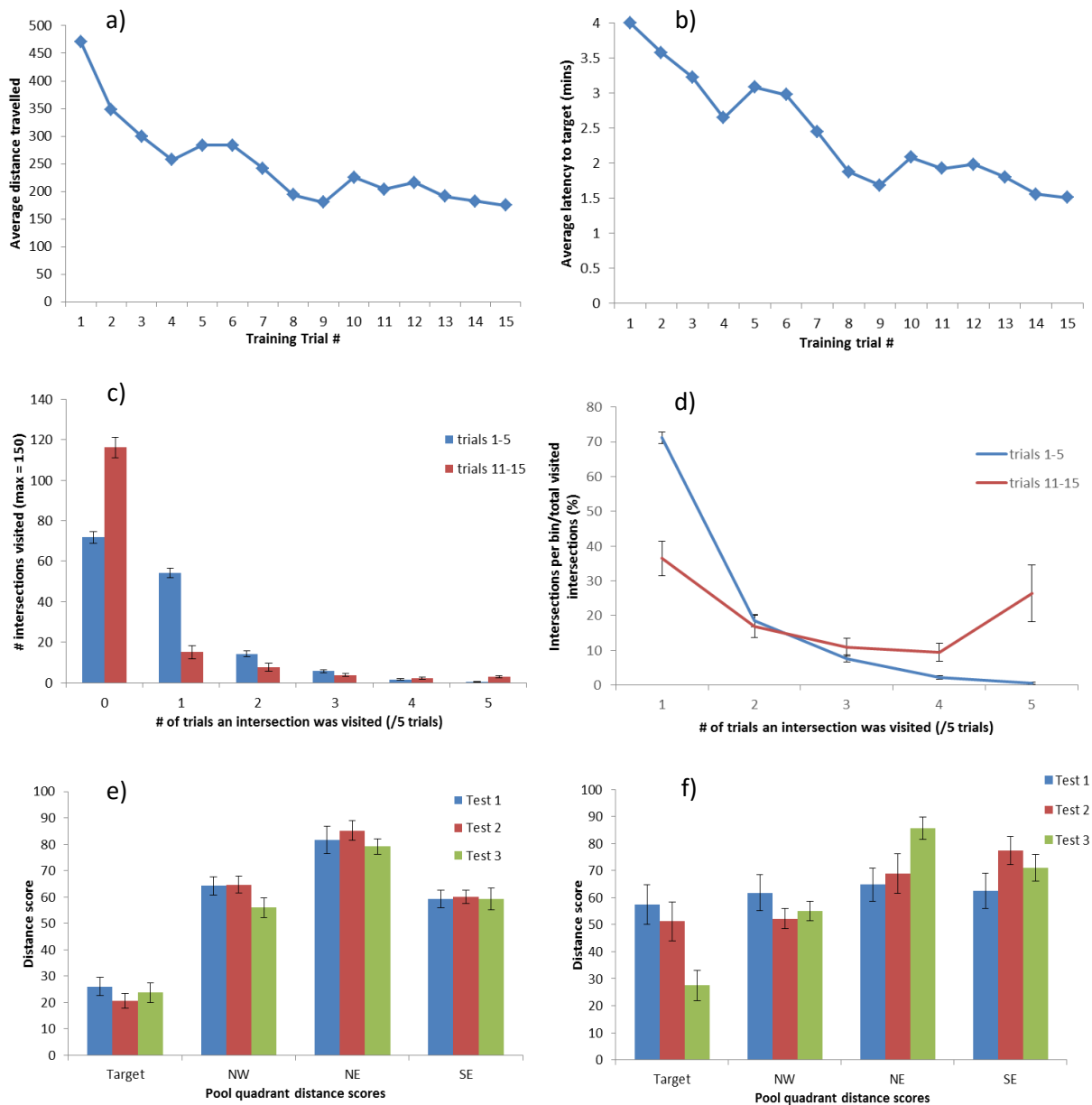


Figure 4. Training (a-d) and test (e-f) data collected from participants during Experiment 1. (a-b) Relationship between number of training trials completed and average distance travelled (a) or time spent (b) searching for the target location. (c) Number of trials, divided into frequency bins of 0-5, each intersection in the plank maze was visited during the first (trials 1-5) and last (trials 11-15) blocks of training trials. (d) To calculate percentage scores the frequency counts for each non-zero bin (1-5) were divided by the total number of intersections visited at least once in a block. Percentage scores were calculated for the first and last training blocks. (e-f) Average distance of participants' approximations of the target location from the actual target location (Target) and the centres of the remaining pool quadrants (NW, NE, SE) on the allocentric (e) and egocentric (f) test trials at each test time, calculated using the distance formula. Test 1=after 5 training trials; Test 2=after 10 training trials; Test 3=after 15 training trials. All error bars are \pm SEM.

Discussion

The results observed in Experiment 1 were consistent with the outcomes hypothesised. The decreases in latency to the target and the distance travelled through the maze during training provide clear evidence that participants were learning some sort of navigation strategy that could facilitate their successful movement to the target location. The area of the maze participants would search for the target also decreased over the training period while the number of intersections that were reused between trials while navigating increased. Together these results support the idea that participants learned to refine their approximations of the target location with training while also coming to prefer taking the same familiar paths while navigating. These observations provide clear support for the hypothesis that participants would be able to become more efficient navigators of the novel environment used here with training.

It was also found that participants were able to estimate a target location using two separable methods. Participants appear to acquire enough information to navigate with exclusive reference to the allocentric features of the environment by the end of the first training block, while egocentric knowledge takes until the end of training to develop such that it can guide relatively successful navigation. These trends match those observed in prior research, where people tend to show a shift in preferential strategy use from allocentric to egocentric with training (Andersen et al., 2012; Iaria et al., 2003; Schmitzer-Torbert, 2007). Participants, however, did not appear to be acquiring more precise allocentric information across training. This may have been a consequence of competition from the egocentric learning that the results suggest is taking place across the length of training or it may have been that the allocentric information provided by the environment was not sufficient to facilitate a more precise approximation of the target location. More information about what features specifically

underpinned participants' allocentric navigation would be necessary to potentially decide between these possibilities. The allocentric test results of Experiment 1 show that participants are at least able to navigate to the correct quadrant of the pool. However, it is not known how this was achieved. For instance, a similar level of performance could have been achieved by navigating with reference to the landmark array, to a single landmark or to the virtual sky which could serve as a crude orienting cue.

The question of what specifically participants are acquiring information about can also be applied to the egocentric test results which showed improvement over training but never a degree of precision that would suggest a precise route had been learned. It may have been the case that participants acquired the beginnings of a route that could not be completed before the end of training, a possibility that is supported by the decrease in path variability during the last five training trials. This would suggest that their egocentric knowledge was dependent upon the presence of the plank maze. Participants may also have solved the test without any use of a route, instead learning the approximate distance from the start to the target location and a direction of bearing relative to their heading position at the beginning of each training trial, which was fixed. This distance and bearing information could, unlike a route, be entirely self-referential and therefore independent of the presence of the plank maze, with participants using the time spent moving as a proxy for distance travelled. Distance information could also be maze-dependent and encoded as an approximation of the number of planks usually travelled from the start to the target location.

Experiment 2

This experiment aimed to understand more about the nature of the cues that the participants used while navigating in the allocentric and egocentric tests. The participants were tested on allocentric tests in the same manner as in Experiment 1. However, in this experiment they also received a second test in which the distal landmark cues around the maze were spatially randomised. The aim here was to test whether participants were attending to the spatial arrangement of the landmarks, whether they were learning to associate the target location with a single proximate landmark or if they were, in some capacity, utilising the arrangement of the sky as a crude orientation cue. If participants were relying on the spatial configuration of multiple cues to locate the target location, it was expected that randomising landmark position would randomise test performance, such that they would show no preference for approximating the target near its actual location. However, if participants were relying on a single proximate landmark to the target location, then they should show a clear preference for the quadrant in front of that landmark. Finally, if participants continued to preferentially approximate the target in the correct quadrant this would suggest some use was being made of the sky arrangement.

Two new egocentric tests were used in Experiment 2. The first test modified the version used in Experiment 1. However, in this test the length of the planks was doubled. This was changed to examine what system participants were using to approximate the distance that needed to be travelled across the plank system to locate the target. This distance could be measured in time or the number of planks taken to travel to the target. Therefore, with the planks lengthened there were two potential locations that participants would be expected to approximate the target. One location would be based on the number of planks that the participants would expect to need to traverse before they would reach the target location. This could be compared against an

alternative target location which would be the intersection that is the same metric distance and direction from the start to the target location as was the case during training.

The second egocentric test examined whether participants could rely on a system equivalent to dead reckoning to successfully guide navigation to the target location using only information about bearing from the start location and distance travelled. In this test all external cues (planks, landmarks, sky) were removed except the water surface, which could be used to provide visual information about velocity. This forced participants to use entirely self-referential information about the approximate distance and angle of bearing from the start to the target.

These new test types were motivated by several hypotheses about the results observed in Experiment 1. For the allocentric tests it was hypothesised that participants were making use of the specific arrangement of landmarks presented during training and would therefore produce random performance when tested with a randomised landmark array. However, if participants were selectively navigating with reference to a single landmark it was further hypothesised that they would prefer to approximate the target in the pool quadrant delineated by the cue that was previously closest to the target. The apparent lack of route learning that was observed in Experiment 1 led to the hypothesis that participants could be solving the egocentric test using entirely self-referential information. On the egocentric plank test used for this experiment this would be evident by a preference for approximating distance using travel time, which would mean target approximations would be closer to the time-based location. As participants would be expected to be using the same dead reckoning system on both egocentric tests it was further hypothesised that there would be no difference in the distance scores to the time-based location on the plank test and the target location on the no plank test.

Method

Participants

Thirty-four undergraduates from the University of Sydney participated in this experiment in exchange for course credit. Exclusion criteria were the same as Experiment 1. Twenty participants were excluded from the analyses, thirteen due to a lack of learning, and seven as a result of simulator sickness. The criteria for a participant not showing learning were the same as Experiment 1.

Materials

The materials used here were the same as those described in Experiment 1.

Design

This experiment used the same basic within-subjects design as that employed in Experiment 1; however, there were now two allocentric and two egocentric test types. Due to this increase in the number of tests the testing process for this experiment was modified, with the number of test phases reduced to two. Once a testing phase was begun, the four tests were administered in pairs, with a single training trial included to separate the two pairs. There were therefore 17 training trials, with test phases occurring after the first 5 trials and after the 17th trial. In each pair of tests, there was always one allocentric and one egocentric test. However, the order of the tests was counterbalanced within a pair, and between the test type pairs. Performance in the normal allocentric test maze (now allocentric-n) was compared against the randomised allocentric test maze (allocentric-r). Performance in the expanded plank egocentric

test (now egocentric-p) was compared against the egocentric with no plank maze test (egocentric-np).

Procedure

Pre-training

The pre-training process was the same as that described in Experiment 1.

Training

The training environment used in Experiment 2, which can be seen in Figure 5, was essentially the same as that used in Experiment 1 but with the variation that the boundary of the pool was now stretched beyond the horizon of the virtual environment. This was done to remove the ability of participants to potentially navigate with reference to the pool edge. In this experiment the start position was changed. To simplify potential route acquisition an extra plank was added to the edge of the maze and used as the starting position for training and egocentric test trials. The start location was in the NW quadrant and the target location was in the SW quadrant.

All other aspects of the training process were the same as that described in Experiment 1.

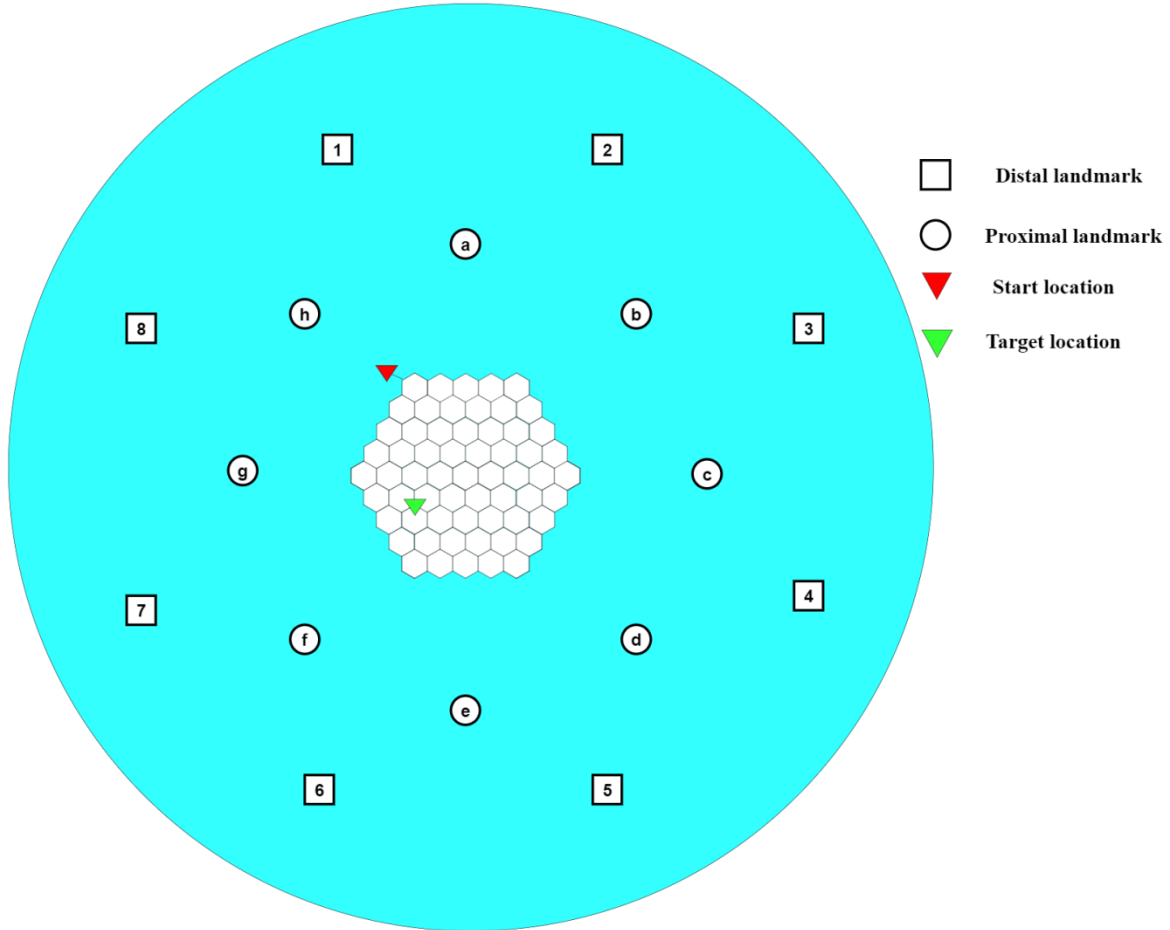


Figure 5. Schematic survey view of the training environment utilised in Experiment 2. a-h delineate the unique identity of each proximal landmark; 1-8 delineate the unique identity of each distal landmark.

Allocentric test

The allocentric-n test environment was the same as that used in Experiment 1; however, the pool boundary now extended beyond the horizon in the same manner as the training environment (see Figure 6a).

For the allocentric-r environment, the allocentric-n environment was used with the landmark locations changed according to a set of criteria: First, a landmark could only be moved

to a location within the ring (proximal or distal) it was originally a part of; Second, every landmark had to be moved to a new location; Third, a landmark had to have different immediate neighbours at its new location (and this applied to neighbours in both rings). The difference between the two landmark arrays can be seen by comparing Figures 6a and 6b. One important feature of this test is that the landmark that was closest to the target location during training, the statue of Christ the Redeemer, was now in the SE quadrant.

Both the allocentric-n and allocentric-r test trials had participants start in the middle of the pool. This new starting position was used to situate participants at a location equidistant to all four of the pool quadrants. For each participant the initial direction they were facing varied between test times, with the heading at the second test time determined by rotating the heading from the first test time 180°.

All other features of the allocentric test trials were the same as those described for Experiment 1.

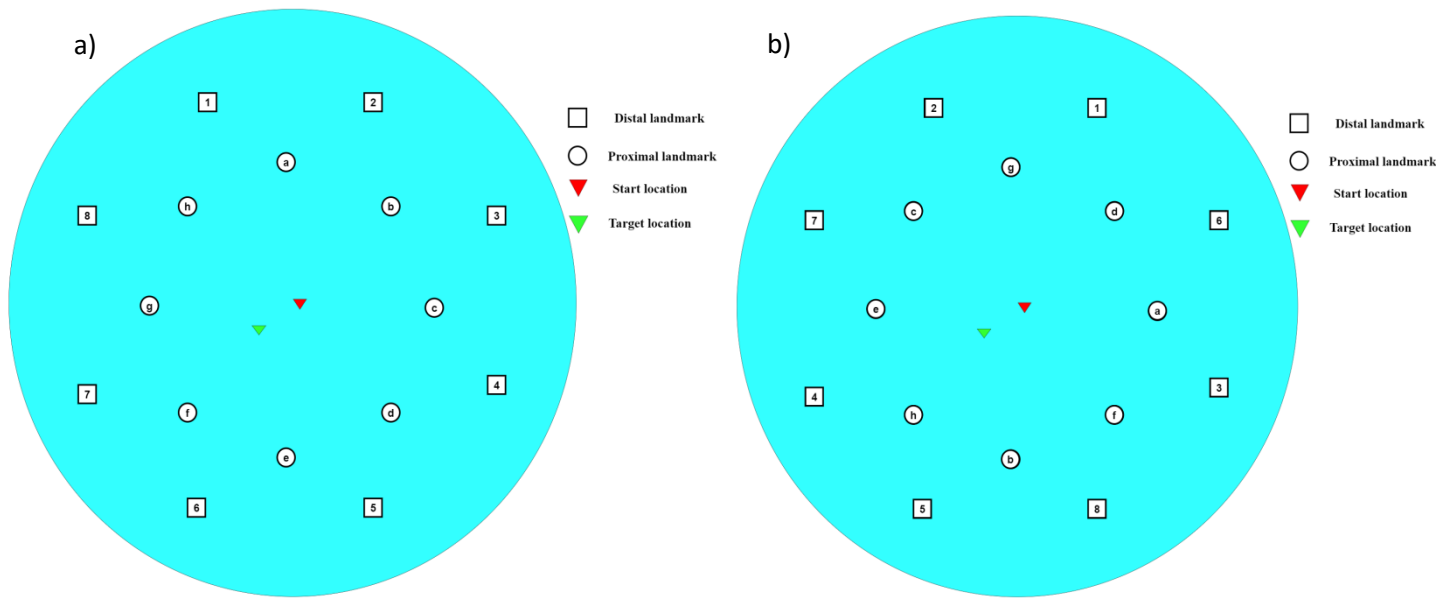


Figure 6. Schematic survey views of the allocentric normal (a) and randomised (b) testing environments utilised in Experiment 2. a-h delineate the unique identity of each proximal landmark; 1-8 delineate the unique identity of each distal landmark. All test trials were started at the test start location.

Egocentric test

For the egocentric-p test trials the environment differed from that used in Experiment 1 in that the size of the plank maze was increased relative to the one used in the training trials. The egocentric-p maze was therefore increased in the number of hexes per edge, as seen in Figure 7a. This change in maze size was done with the aim of removing the edge of the pool maze as a possible cue by which participants could navigate. The length of the planks was also doubled relative to those used in the training environment.

As can be seen in Figure 7b, the test environment for the egocentric-np test trials removed the plank maze altogether. Due to the removal of the plank maze in this test

environment, participants were informed before each trial that the restrictions on their movement had been removed and that any apparent decrease in movement speed they experienced was the result of the removal of the planks as an immediate frame of reference for their motion. They were further informed that changes in the perception of the movement of water beneath their feet could be used as a cue to indicate whether or not they were moving if necessary.

The basic aims and instructions for these experiments, as well as the trial starting positions, were the same as those used in Experiment 1.

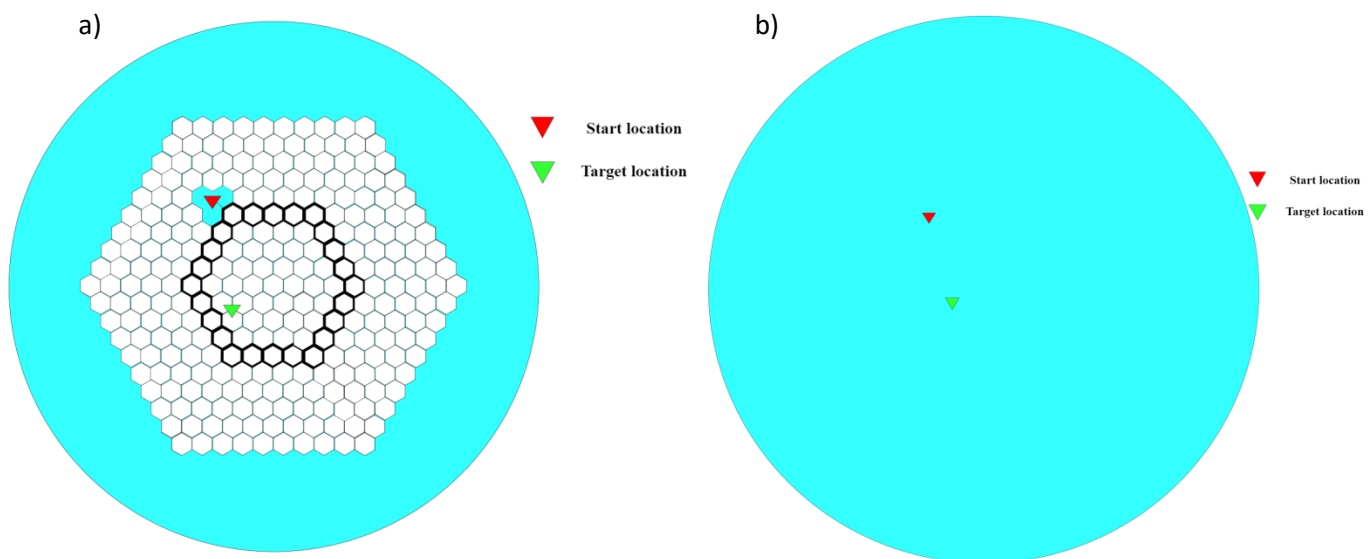


Figure 7. Schematic survey views of the egocentric plank (a) and no-plank (b) test environments used in Experiment 2. The black boundary in (a) delineates the extent and position of the training environment maze.

Statistics

Training

The dependent variables recorded and the analyses employed were the same as those described for Experiment 1.

Allocentric Tests

In addition to the analyses and variables described for Experiment 1, a 2 (test type) x 2 (test time) Within-Subjects ANOVA was also used to compare distance scores to the target location between the new and original test trials. The same planned contrasts from Experiment 1 were employed separately for both allocentric test types with the variation that, as there were only two test times, the difference scores were only compared between times 1 and 2. For the allocentric-r test another contrast was added that calculated the distance scores for the SE quadrant and compared this against the combined average scores for the remaining three locations. These difference scores were then calculated separately for each test time and used to look for a difference in these difference scores as a function of time. To compensate for the addition of a second contrast a Bonferroni correction was applied to the significance level, giving an alpha of $p = 0.025$.

Egocentric Tests

For the egocentric-p test trials, two distance scores were calculated using the distance formula. To calculate the time-based location the distance and angular deviation between the start and target locations during training were first calculated. The time-based location for the egocentric-p test was then set as the point in the new test environment that was the same distance and rotation from the new starting position that resulted from lengthening the maze planks. The plank-based location was set as the new location of the intersection to which the target was attached during training. These two distance score types were compared using a 2 (location) x 2 (test time) Within-Subjects ANOVA to compare location preference across the two test trials.

The same 2 x 4 Within-Subjects ANOVA, One Way Within-Subjects ANOVA and planned contrasts from the allocentric-n test were also used to analyse the egocentric-np distance scores.

The egocentric-p and np tests were compared using a 2 (test type) x 2 (test time) Within-Subjects ANOVA using the time-based distance scores for the egocentric-p tests and the target location based distance scores for the egocentric-np test.

Results

Training

Visualised in Figure 8a it can be seen that participants, on average, showed a clear decrease in distance travelled per trial with more training. This observation is supported by statistical analysis, with a One Way Within-Subjects ANOVA revealing a significant effect, $F(14, 182) = 4.22, p < .001$, of training trial number on distance travelled.

A similar trend can be observed in participants' latency to find the target (see Figure 8b), with latency also decreasing with training trial number. This was supported statistically, with a One Way Within-Subjects ANOVA showing a significant effect, $F(14, 182) = 5.28, p < .001$, of trial number on latency.

Figures 8c-d visualise the measures of variability in the areas of the maze participants traversed during training. Here it can be seen that the repetition of the use of particular unique intersections increased per participant from the start (trials 1-5) to the end (trials 11-15) of training, and that the number of intersections that were never visited by the participants increased from the first block to the last. Comparing the number of intersections with no visits between the two blocks using a paired-samples t-test revealed a significant, $t(13) = -7.68, p < .001$, increase by block 3.

Looking at the percentage scores with a 2 (training block) x 5 (unique visits) Within-Subjects ANOVA, a significant, $F(4, 52) = 36.21, p < .001$, main effect of unique visits was found that was modulated by a significant, $F(4, 52) = 4.65, p = .003$, interaction effect. It can be seen in Figure 8d that the source of this interaction is likely the decrease in frequency of single intersection visits and an increase in the number visited four or five times.

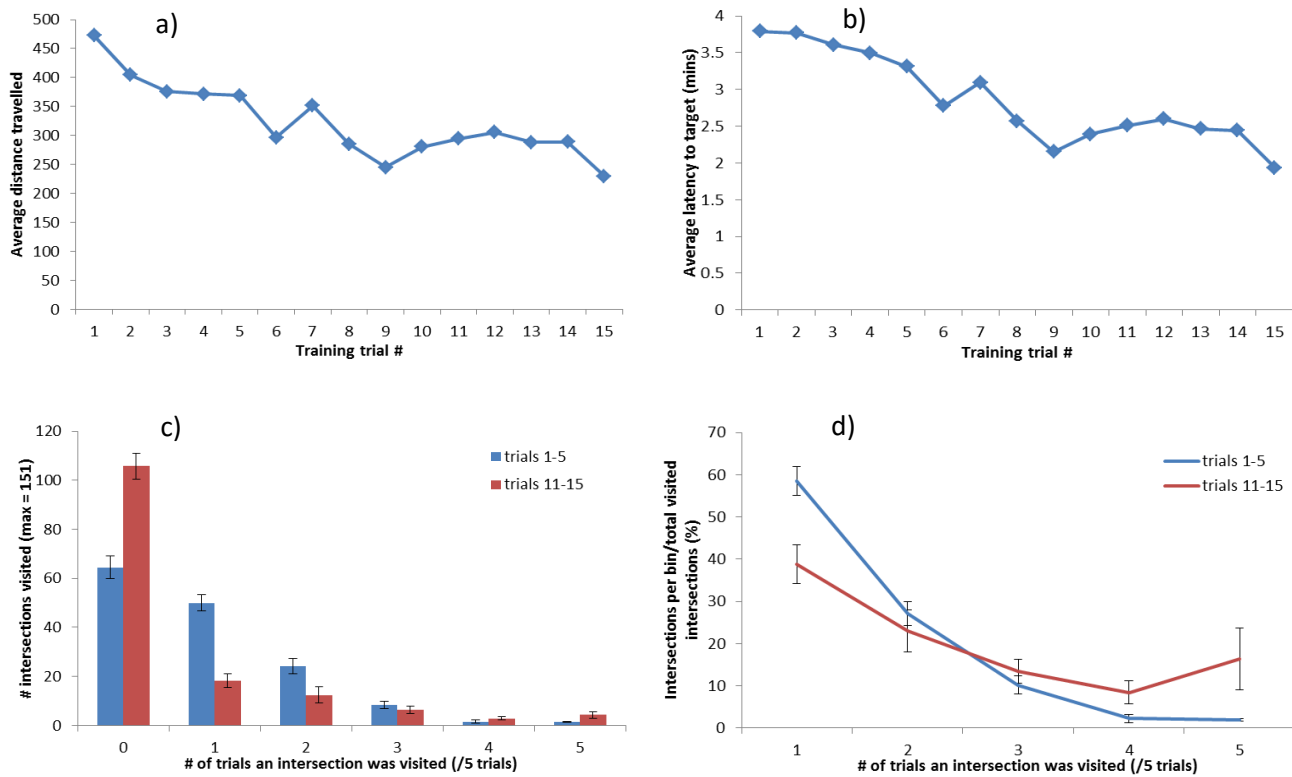


Figure 8. Training data collected from participants during Experiment 2. (a-b) Relationship between number of training trials completed and average distance travelled (a) or time spent (b) searching for the target location. (c) Number of trials, divided into frequency bins of 0-5, each intersection in the plank maze was visited during the first (trials 1-5) and last (trials 11-15) blocks of training trials. (d) To calculate percentage scores the frequency counts for each non-zero bin (1-5) were divided by the total number of intersections visited at least once in a block. Percentage scores were calculated for the first and last training blocks. All error bars are \pm SEM.

Allocentric tests

Looking at the distance score data for the allocentric-n test in Figure 9a participants appear to be showing a preference for approximating the target near the target location that is not related to test time. A 2 (test time) x 4 (quadrant) Within-Subjects ANOVA supported this apparent target location preference, finding a significant, $F(3, 39) = 104.02, p < .001$, effect of quadrant, but not of test time and no interaction between the two (p 's $> .05$). Planned contrasts revealed a significant, $F(1, 13) = 212.63, p < .001$, preference for the target location, but no interactions with test time. Comparing just the target location distance scores between the two test times using a One Way Within-Subjects ANOVA also showed that test time did not appear to be having an effect on this preference ($p > .05$).

The distance scores for the allocentric-r test trials, displayed in Figure 9b, appear to differ from those of the allocentric-n tests, showing no preference for the target location relative to the other quadrants. The results in Figure 9b also do not appear to show any preference for the SE quadrant. The 2 x 4 Within-Subjects ANOVA here revealed a significant, $F(3, 39) = 30.78, p < .001$, effect of test time, but no effect of quadrant and no interaction (p 's $> .05$). Planned contrasts found no significant preference for the target quadrant when compared to the combined distance scores for the other three locations, with no effect of test time (p 's $> .025$). There was also no preference for the SE quadrant and no interaction between this preference and test time (p 's $> .025$). A One Way Within-Subjects ANOVA comparing the target location distance scores across the test times also found no difference ($p > .05$).

Comparing the distance scores to the target location for the allocentric-n trials (see Figure 9a) with the allocentric-r trials (see Figure 9b), participants appeared to guess closer to the target

on the former compared to the latter regardless of test time, suggesting that they were preferentially making use of the landmark array when navigating. A 2 (test time) x 2 (test type) Within-Subjects ANOVA supported these observations, with a significant effect of test type, $F(1, 13) = 32.82, p < .001$, but no effect of test time and no interaction (p 's $> .05$).

Egocentric tests

The distance scores for the egocentric-p test, as shown in Figure 9c, appear to show participants were preferentially approximating their travel distance using time travelled. However, they do not appear to improve in their accuracy with training. A 2 (location) x 2 (test time) Within-Subjects ANOVA supports this observation revealing a significant, $F(1, 13) = 37.54, p < .001$, effect of location type but no interaction and no effect of test time (p 's $> .05$).

The data from the egocentric-np tests visualised in Figure 9d does not show any improvement in the target approximation accuracy with training. The 2 x 4 Within-Subjects ANOVA found the effect of quadrant was significant, $F(3, 39) = 9.81, p < .001$; however, there was no effect of test time found and the interaction was also not significant (p 's $> .05$). The planned contrasts also found no significant effects (p 's $> .05$), and a One Way Within-Subjects ANOVA also found no difference in the target location distance scores between test times ($p > .05$).

Comparing the egocentric-p and egocentric-np (see Figure 9c) results it can be seen that the average distance score to the target location on the egocentric-np test matched the distance scores to the time-based location on the egocentric-np test. A 2 (test type) x 2 (test time) Within-Subjects ANOVA supported this observation, finding no significant differences for test type or test time and no interaction (p 's $> .05$).

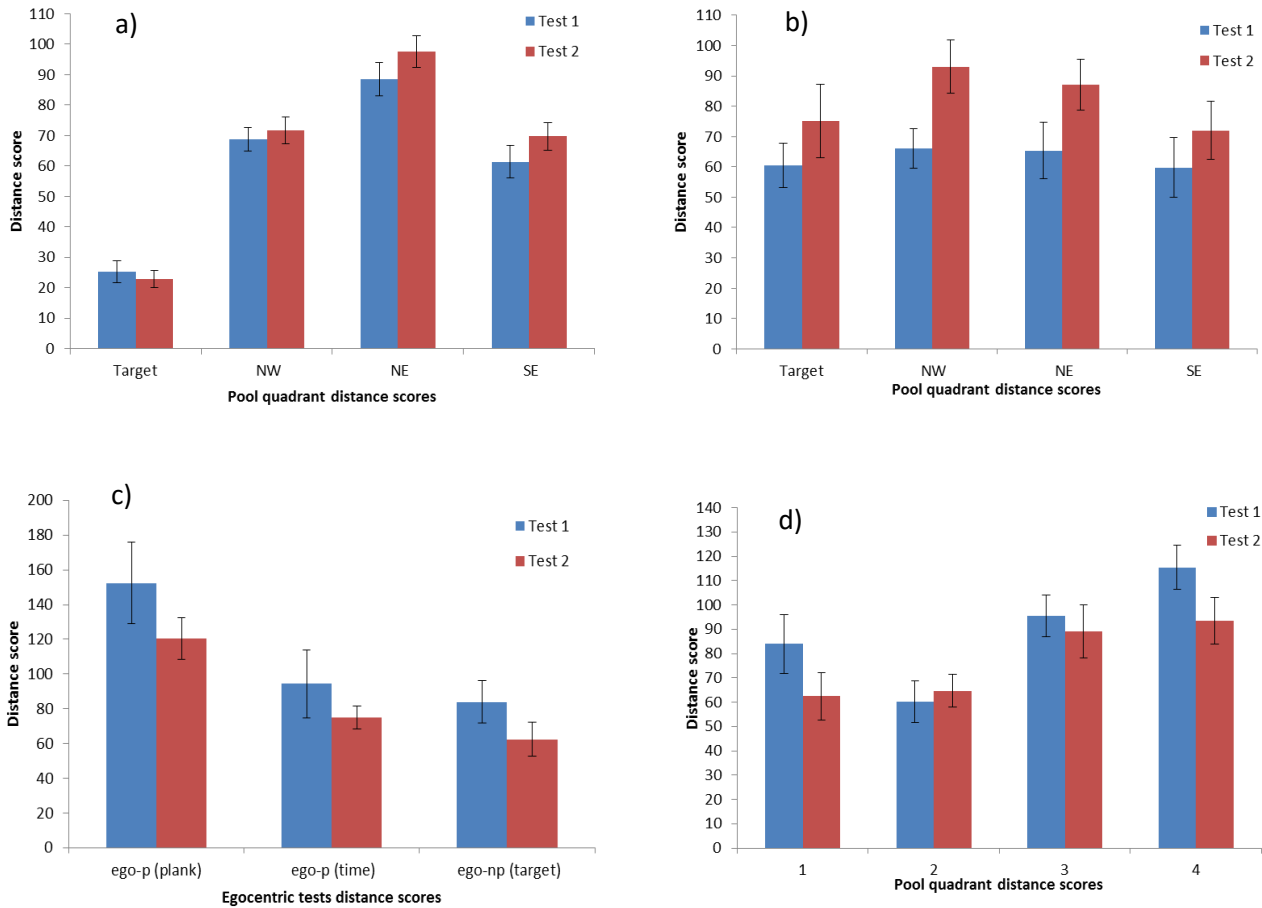


Figure 9. Test data collected from participants during Experiment 2. (a) Average distance of participants' approximations of the target location from the actual target location (Target) and the centres of the remaining pool quadrants (NW, NE, SE) calculated using the distance formula (distance score) at each allocentric-normal test time. (b) Average distance scores for the allocentric-random test relative to the target location and the centres of the remaining pool quadrants. (c) Average distance scores calculated for the egocentric plank (ego-p) and egocentric no-plank (ego-np) tests at each test time. On the ego-p test distance scores were calculated relative to two locations determined by expectations of where target approximations would be localised if participants were recording their travel distance using the number of planks traversed [ego-p (plank)] or time spent moving [ego-p (time)]. The ego-np (target) distance scores here are relative to the actual target location. (d) Average distance scores for the egocentric no-plank test relative to the target location and the centres of the remaining pool quadrants. Test 1=after 5 training trials; Test 2=after 15 training trials. All error bars are \pm SEM.

Discussion

The results of Experiment 2 appeared to suggest that either participants were not acquiring egocentric information from the modified training environment with training or that the new tests used were too difficult to solve, at least given the training time provided here. The distance scores relative to the two distance locations on the egocentric-p test show that participants look to be using time travelled as a way to encode the distance between the start and the target. This conclusion is further supported by the lack of any difference in results between the two egocentric results, which suggests they were solved using the same information. Together these results are consistent with the hypothesis that participants are acquiring dead reckoning-like information that was utilised in both tests; however, the lack of improvement with training is contrary to the results from Experiment 1.

The allocentric test results better fit expectations with participants showing an approximate understanding of the target location that did not become more refined with training. The results of the allocentric-r test suggest that participants make use of the relationships between landmarks when navigating allocentrically, an observation that was consistent with the initial hypotheses as randomising the landmark positions produced essentially random target approximations. This random preference behaviour does not fit with the idea that participants were selectively attending to only the landmark nearest the target. The lack of change on the allocentric-r test between test times further suggests that training had no effect on this preference, with participants using the same allocentric strategy for the duration of the experiment.

There were a large number of variables changed from Experiment 1 to Experiment 2. These included both the changes to the test environment, the testing structure and the testing environments. Therefore one possible explanation for the lack of improvement on the egocentric tests that will be pursued in the next experiment is that some aspects of learning became more difficult as a consequence of some unexpected interaction between the many changes made to the methodology of Experiment 1.

Experiment 3

As the results of Experiment 2 may have been the unintended consequence of methodological changes from Experiment 1 this experiment aimed to retest most of the key hypotheses of Experiment 2 while keeping as much consistency as possible between it and the successful methodology of Experiment 1. While the allocentric tests and hypotheses were kept the same as a result of the similarity in test performance between Experiments 1 and 2, the egocentric test structure was modified to focus only on assessing whether participants acquire and use plank maze independent, self-referential information to solve the egocentric tests. The egocentric test results from Experiment 2 support this idea, showing that participants are likely approximating distance travelled using some internal representation of time spent navigating. However, the lack of evidence for improvement on the egocentric tests complicates the interpretation of the results. For this experiment the plank length on the egocentric-p test was returned to that used in the training environment. By simplifying this test it was expected that one possible complication of Experiment 2, that participants were confused by the new maze structure, could be removed. The simpler environment also meant the two egocentric tests

differed only on the presence or absence of the plank maze. Therefore any observed differences between them would necessarily be due to some role, either complementary or inhibitory, played by the maze. The hypothesis that the plank maze does not provide any extra navigable information during the egocentric tests was continued for this experiment.

Method

Participants

Twenty-six undergraduates from the University of Sydney participated in this experiment in exchange for course credit. Exclusion criteria were the same as Experiment 1. Thirteen of the participants were excluded from the analyses, eight as a result of simulator sickness, and five due to a lack of learning. The criteria for a participant not showing any learning were the same as Experiment 1.

Materials

The materials used here were the same as those described for Experiment 1.

Design

This experiment used the same basic within-subjects design as that employed in Experiment 2.

Procedure

Pre-training

The pre-training process was the same as that described in Experiment 1.

Training

The training environment used in Experiment 3 was essentially the same as that used in Experiment 2 but with the variation that the starting position was changed to the one used in Experiment 1. The plank added for the new start position in Experiment 2 was removed.

All other aspects of the training process were the same as that described in Experiment 1.

Allocentric test

The allocentric-n and allocentric-r test trials were the same as those described in Experiment 2. The environment designs with the start positions changed can be seen in Figure 10a-b.

Egocentric test

For the egocentric-p test trials the environment differed from that used in Experiment 2 in that the length of the planks was the same as that used in the training trials. This change in plank length was done with the aim of simplifying the egocentric-p test in case the increased lengths had made the task too difficult to solve. The new variations of the egocentric tests can be seen in Figure 10c-d.

All other features of the egocentric test trials were the same as Experiment 2.

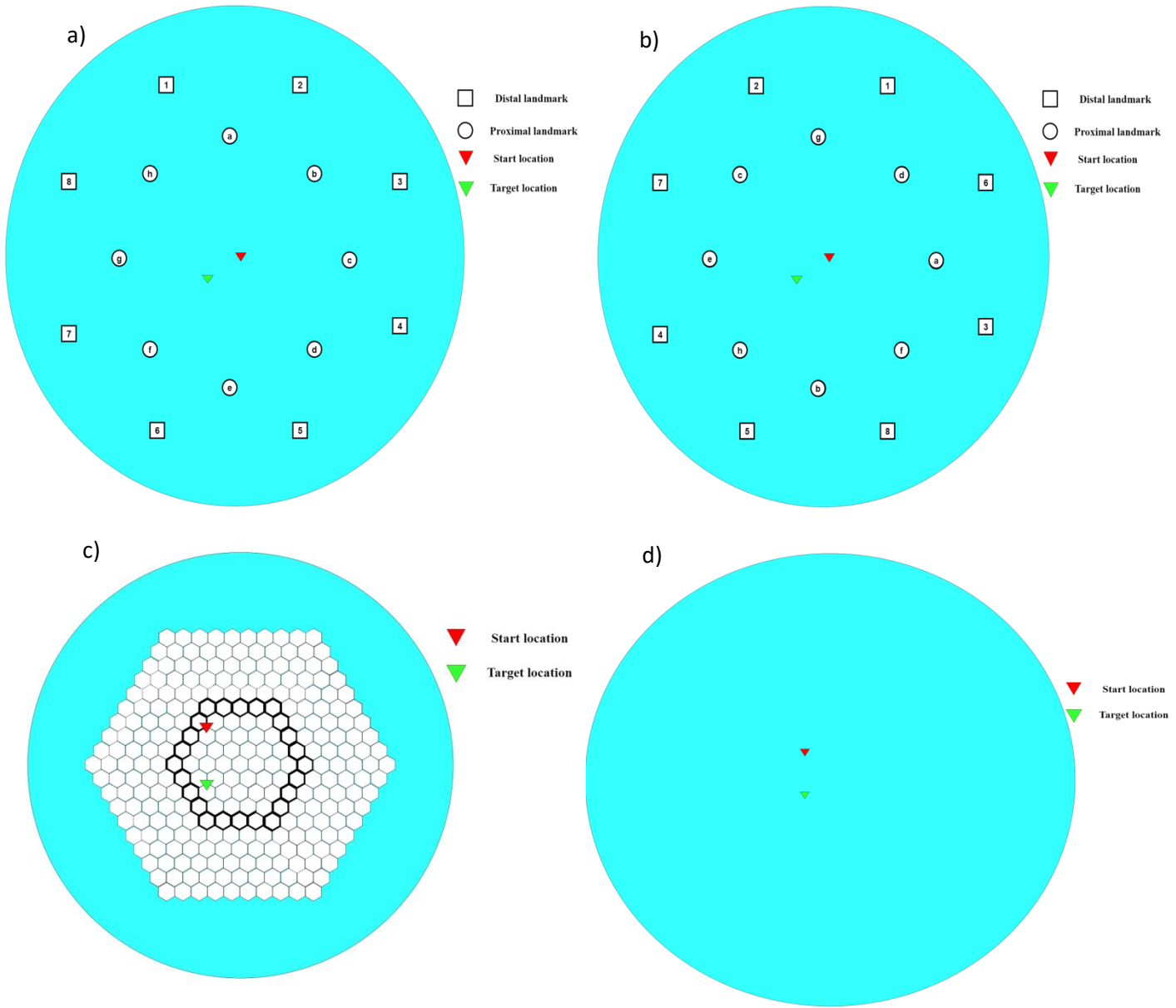


Figure 10. Schematic survey views of the four test environments, allocentric normal (a) and randomised (b), egocentric plank (c) and no-plank (d), used in Experiment 3. All test trials were started at the test start location. (c) Black boundary delineates the extent and position of the training environment maze.

Statistics

Training

The dependent variables recorded and the analyses employed were the same as those described for Experiment 1.

Test

The analyses for the egocentric test results were changed to be more in line with those used for the allocentric tests in Experiment 2. For both egocentric tests the distance scores were analysed separately using a 2 (test time) x 4 (quadrant) Within-Subjects ANOVA to compare quadrant preference between the two test times. A One Way Within-Subjects ANOVA was also used to specifically compare the target quadrant distance scores between test times. A 2 (test type) x 2 (test time) Within-Subjects ANOVA was also added to compare distance scores to the target location between the two egocentric test types. Planned contrasts comparing target location distance scores to the averaged scores for the remaining quadrants were also used for both test types, as was the test for the interaction between this difference and test time.

The rest of the dependent variables recorded and the analyses employed were the same as those described for Experiment 2.

Results

Training

Figure 11a shows a clear decrease in distance travelled per trial as training progressed. A One Way Within-Subjects ANOVA revealed that the relationship between training trial number and distance travelled is significant, $F(14, 168) = 4.57, p < .001$.

Latency to the target, seen in Figure 11b, shows the same improvement with training. This relationship was also found to be significant, $F(14, 168) = 4.62, p < .001$, using a One Way Within-Subjects ANOVA.

Training path variability is visualised in Figure 11c-d, showing an increase in intersections repeatedly visited at the end of training (trials 11-15) compared to at the start of it (trials 1-5). The number of unvisited intersections, as measured with a paired samples t-test, increased significantly, $t(12) = -6.56, p < .001$, from the first block to the last, supporting this observation. A 2 (training block) x 5 (unique visits) Within-Subjects ANOVA comparing percentage scores revealed a significant, $F(4, 48) = 25.25, p < .001$, main effect of unique visits and a significant, $F(4, 48) = 9.66, p < .001$, interaction between the independent variables that is likely a result of a relative increase in intersections with four or five visits (see Figure 11d).

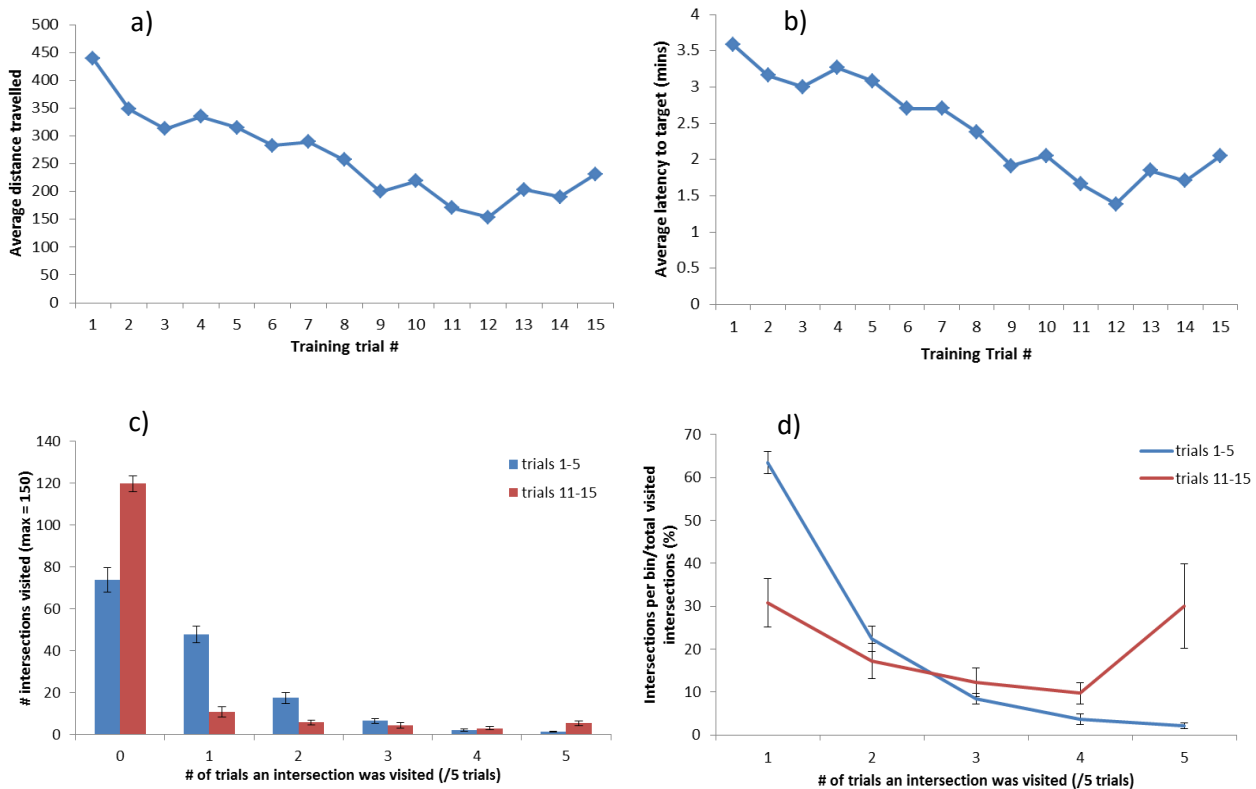


Figure 11. Training data collected from participants during Experiment 3. (a-b) Relationship between number of training trials completed and average distance travelled (a) or time spent (b) searching for the target location. (c) Number of trials, divided into frequency bins of 0-5, each intersection in the plank maze was visited during the first (trials 1-5) and last (trials 11-15) blocks of training trials. (d) To calculate percentage scores the frequency counts for each non-zero bin (1-5) were divided by the total number of intersections visited at least once in a block. Percentage scores were calculated for the first and last training blocks. All error bars are \pm SEM.

Allocentric tests

Visualizing the allocentric-n test distance scores in Figure 12a, the results show participants approximate the target near the target location but do not improve in their accuracy with more training. This target location preference was shown by a 2 (test time) \times 4 (quadrant) Within-Subjects ANOVA with a significant, $F(3, 36) = 36.92, p < .001$, effect of quadrant and

no effect test time and no interaction (p 's $> .05$). A significant, $F(1, 12) = 83.88, p < .001$, preference for the target location compared to the other three quadrants, with no relationship to test time ($p > .05$) was revealed by planned contrasts. Comparing just the target location distance scores between the two test times using a One Way Within-Subjects ANOVA also showed that test time did not appear to be having an effect on this preference ($p > .05$).

The distance scores for the allocentric-r test trials, displayed in Figure 12b, show no preference for the target location relative to the other quadrants; however, a preference for the SE quadrant appears to develop by the end of training. A significant, $F(3, 36) = 3.42, p = .027$, effect of quadrant was observed with the 2 x 4 Within-Subjects ANOVA alongside a significant, $F(3, 36) = 7.68, p < .001$, interaction, but no effect of test time ($p > .05$). No significant preference for the target quadrant, when compared to the combined distance scores for the other three locations, was found via analysis with planned contrasts and there was no effect of test time (p 's $> .025$). However, contrasts did reveal a significant, $F(1, 12) = 13.45, p = .003$, preference for the SE quadrant when compared to the combined distance scores for the other three quadrants. A significant, $F(1, 12) = 10.96, p = .006$, interaction between this preference and test time was also found. A One Way Within-Subjects ANOVA found no difference in target location distance scores between the test times ($p > .05$).

Comparing the results show in Figure 12a to those in Figure 12b, it can be seen that participants look to be approximating the target closer to its actual location on the allocentric-n test trials. This observation was supported by a significant, $F(1, 12) = 20.20, p = .001$, effect of test type when comparing the two on a 2 (test time) x 2 (test type) Within-Subjects ANOVA. There was no effect of test time and no interaction (p 's $> .05$).

Egocentric tests

The distance scores for the egocentric-p test, as visualized in Figure 12c, show participants developing a preference for the target location over the training period. A 2 (test time) x 4 (quadrant) Within-Subjects ANOVA revealed a significant, $F(3, 36) = 16.24, p < .001$, effect of quadrant and a significant, $F(3, 36) = 4.05, p = .014$, interaction but no effect of test time. Planned contrasts comparing target location distance scores to the combined scores for the other three quadrants found a significant, $F(1, 12) = 12.29, p = .004$, preference for the target location and a significant, $F(1, 12) = 7.88, p = .016$, interaction between this preference and test time, with a stronger preference at test time 2 compared to time 1. A One Way Within-Subjects ANOVA looking at target location distance scores as a function of test time also showed the same significant, $F(1, 12) = 6.16, p = .029$, improvement at test time 2 as that seen in Experiment 1.

The data from the egocentric-np tests shown in Figure 12d also shows target approximation improving with more training. The 2 x 4 Within Subjects ANOVA found a significant, $F(3, 36) = 23.75, p < .001$, effect of quadrant and a significant, $F(3, 36) = 4.19, p = .012$, interaction between quadrant and test time, but no effect of test time ($p = .059$). The planned contrasts showed a significant, $F(1, 12) = 15.47, p = .002$, preference for the target location compared to the other three quadrants, but no test time interaction ($p = 0.073$) The One-Way Within Subjects ANOVA looking at the difference between distance scores to the target location as a result of different test times, however, did also find a significant, $F(1, 12) = 7.73, p = .017$, difference with test time 2 showing a smaller scores than time 1.

Comparing these two tests on their target location distance scores, the pattern of change as a function of test time seen in Figures 12c (for egocentric-p) and Figure 12d (for egocentric-np) looks to be the same for both of them, a result that would suggest that the information underpinning egocentric navigation on this experiment is mostly plank maze independent. A 2 (test time) x 2 (test type) Within-Subjects ANOVA supported this, finding a significant, $F(1, 12) = 17.50, p = .001$, effect of test time but not of test type, and no interaction (p 's > .05).

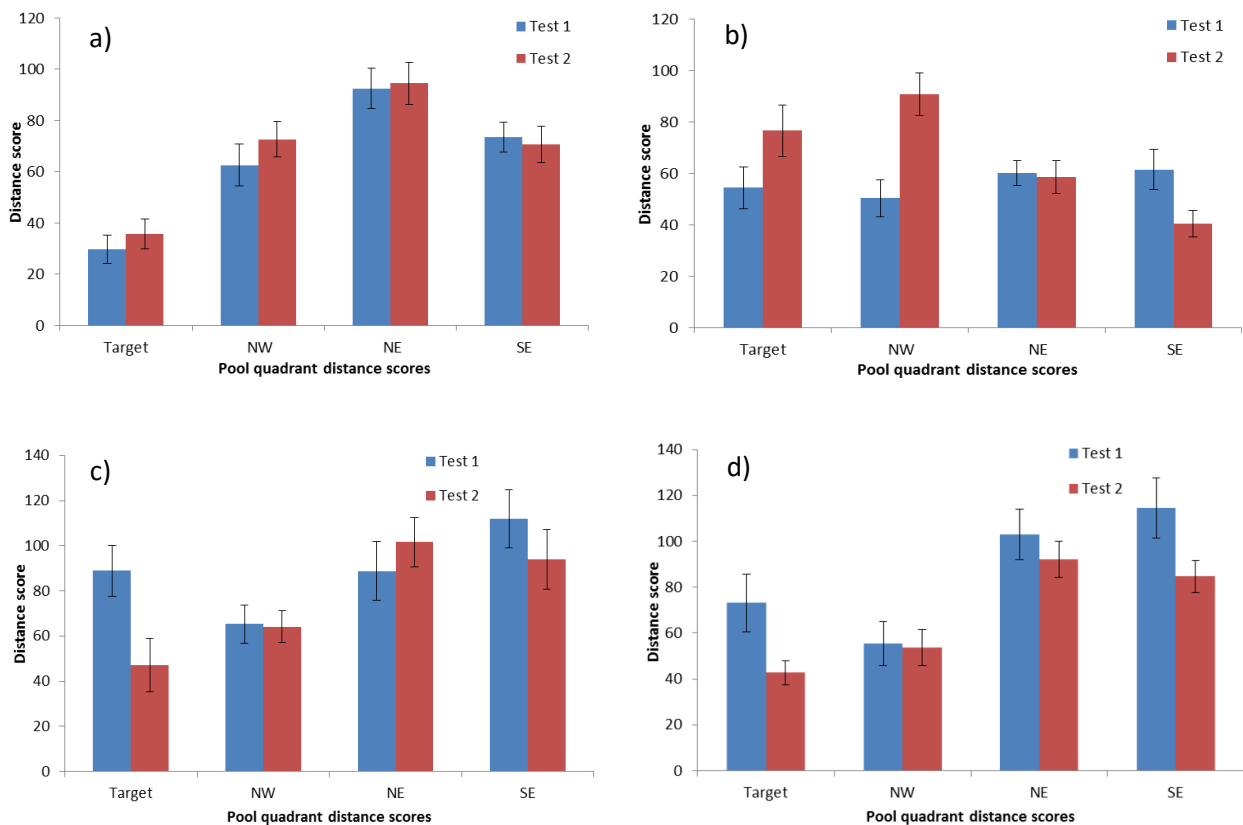


Figure 12. Test data collected from participants during Experiment 3. (a-d) Average distance of participants' approximations of the target location from the actual target location (Target) and the centres of the remaining pool quadrants (NW, NE, SE) on the allocentric normal (a) and randomised (b), and egocentric plank (c) and no-plank (d) test trials at each test time, calculated using the distance formula. Test 1=after 5 training trials; Test 2=after 15 training trials. All error bars are ± SEM.

General Discussion

The results of these experiments help to answer questions about how familiarity with an environment affects the different strategies that people can employ to guide their navigation and what information it is that underpins these methods. Across all three experiments it was clear from the data on participants' travel time, path length and search variability that information supporting progressively more precise and reliable navigation was acquired over the training period. In Experiment 1 it was observed that participants were able to learn to estimate the location of a target using separable allocentric and egocentric methods. These methods had different rates of acquisition, with the allocentric available by the time of the first test trial while the egocentric appeared to take until the end of training to be able to guide navigation. Experiment 2 looked at the possible sources of information that underpinned these separate methods. Allocentric tests showed that participants were likely using some relationship between multiple landmarks in the environment. The egocentric tests appeared to show that the distance between the start and the target was likely recorded by participants as the time taken to travel between the two. Experiment 3 aimed to simplify and retest the key hypotheses of Experiment 2. The allocentric results suggested, contrary to those of Experiment 2, that participants were, at least by the end of training, selectively navigating with reference to only a single landmark. The egocentric tests focussed on measuring whether the information participants acquired was entirely self-referential or was to some extent dependent upon the presence of the plank maze. The results revealed that participants did not appear to be acquiring any maze dependent information.

Together the allocentric test results from these three experiments show that people rapidly acquire a representation of the location of the target location that is accurate to at least

the correct quadrant and is, at least at the first test time, dependent upon a relationship between multiple landmarks. All three experiments also consistently show that participants do not improve on their approximations of the target location over the training period, a result that suggests that there is no more allocentric information acquired after the first training block. There are multiple possible explanations for this lack of improvement. The limited precision of the allocentric estimates may have been the result of participants only requiring fairly broad knowledge to narrow the search space to an area that could be searched within the time limit. The array of landmarks may also have been insufficient to allow for any more learning than was demonstrated here. It may have also been the case that the egocentric learning that is observed to proceed across the entire training period modulated how much allocentric information participants acquired. Finally, it might have been that allocentric learning proceeded along a decelerated curve, with the bulk of the learning occurring in the first five training trials. If this were the case then any later learning that did take place might have been too weak to detect statistically.

The results from the allocentric-r tests in Experiments 2 and 3 put forward competing explanations about what allocentric information participants are using to guide navigation. In Experiment 2 there is no evidence for a preference to approximate the target in any particular quadrant and this randomised performance as a result of randomising the position of the landmarks suggests some aspect of the relationship between these features is important for navigation. In Experiment 3 participants developed with training a systematic bias towards approximating the target location in the quadrant delineated by the landmark nearest the target. This result suggests that a preference for navigating with reference to a single landmark was developed. It is difficult to say conclusively why this pattern of behaviour developed only in

Experiment 3. However, it may relate to the more general concern that some combination of the changes made to the protocol of Experiment 2 increased the complexity of the task. This increased complexity may have in turn affected learning and strategy use, a result that is observed in rats where the typical preference for directional strategy use when navigating is not shown when they are trained in a complex environment (Gardner et al., 2013; Ruprecht et al., 2014). That the changes to the methodology for Experiment 3 resulted in participants showing evidence of egocentric learning supports this idea that the difficulty of the training environment may have affected information acquisition. That participants in both experiments failed to show a preference for the target quadrant strongly suggests that the sky was not made use of as an orienting cue. Due to the consistent design of the skybox attention to the position of the sun would allow participants to clearly distinguish at least one pool quadrant, after which the identities of the remaining regions could likely be determined by fairly simple inference. While participants appear to shift to a single landmark strategy across training they are still able to correctly approximate the target location using an array strategy and do not improve in their accuracy as a result of changing strategies. This suggests that the shift to the single landmark strategy is a result of its ability to maintain a relatively accurate approximation of the target while improving the simplicity of the navigator's strategy, a result that fits with the observation that navigators across many species prefer to shift to a less cognitively demanding method of navigation as they become more familiar with an environment (Hamilton, Akers, et al., 2009; Iaria et al., 2003; Schmitzer-Torbert, 2007). Together these results show that landmarks are clearly the only source of information participants used to navigate allocentrically and that adequate and equivalent performance can be achieved attending to either a single landmark or to the relationships between them.

The egocentric test results from Experiments 1 and 3 show that participants improve in their ability to correctly approximate the target location using egocentric knowledge with training. The improvement observed by the end of training in Experiment 1 suggested that the knowledge participants were acquiring was not of a learned route from the start to the target. This was taken to suggest that participants were instead approximating the target by learning about the travel distance and the degree of angular deviation between the start and the target. Experiment 2 showed that time spent travelling, rather than the number of planks traversed, was the likely measure of distance. This supported the possibility that participants' egocentric information was entirely self-referential and maze independent. The equivalent performance observed on the plank and no-plank tests in Experiment 3 appeared to confirm this hypothesis that participants were developing relatively accurate idiothetic knowledge across training.

Together the results from these experiments show that people are capable of acquiring both allocentric and egocentric navigation strategies in the virtual environment utilised here. Allocentric strategies were landmark-based while egocentric strategies were more akin to dead reckoning behaviour. While it can be seen that these strategies are not mutually exclusive here no consideration was given to how they might be interacting during training or how they might interact when they suggest different behavioural responses.

Empirical Chapter 2

Experiment 4

Experiments 1-3 aimed to look at the availability of allocentric and egocentric navigation strategies on a constrained-path analogue of the MWM, how availability interacted with a person's familiarity with an environment and what sources of information underpinned these strategies. Experiment 1 showed that participants were able to acquire both allocentric and egocentric strategies over the training period. In the virtual environment used here it was further observed that allocentric performance improved faster than did egocentric. The information that underpinned allocentric navigation was found to be landmark based, with participants appearing to shift to a simpler single-landmark strategy with more training. Egocentric information did not appear to be route-based but was instead more akin to dead reckoning, with participants able to learn to approximate the target location with same degree of success with or without the plank maze. However, it could not be determined from these experimental data which strategy participants were preferentially utilising in the training environment when the cues for both were available.

One way to test this preference that will be looked at in the following experiments involves testing how participants respond when their learned strategies are put in conflict. A standard example of this conflict test protocol involves the T-maze used to train rats. The rats are first trained to navigate from a fixed starting arm of the maze to one of the two arms that can be chosen at a choice point where one arm is baited with a food reward. Due to the fixed starting point rats can solve this task either allocentrically, by navigating to the arm nearest a cue or cues in the surrounding room, or egocentrically, by learning to make a right or left hand turn at the

choice point. To put these two strategies in conflict the rats are started from the opposite side of the maze, and this novel starting point means the environmental cues and the learned turn behaviour suggest different arms of the maze. Preferential strategy use is then indexed by which arm the rat chooses. One of the most famous experiments that utilised such a conflict test was conducted by Packard and McGaugh (1996). They looked at how rats' preferred navigation strategy changes as they become more familiar with an environment and found that there was a shift from a place to a response based strategy across training (Packard & McGaugh, 1996). The conflict test also helped demonstrate that these two strategies were underpinned by different areas of the brain, as selective inhibition of the hippocampus or basal ganglia impaired the rats' ability to use a place or response strategy, respectively.

Experiment 4 aimed to apply a conflict test to the complex training environment utilised for Experiments 1-3. The results observed in these prior experiments showed that participants' egocentric knowledge was likely represented as a travel time and angular rotation relative to the fixed start location of the training trials. As the hex grid presented a more complex maze than a standard T-maze the conflict test was structured so that following the learned rotation from the test starting point would send participants to a different quadrant of the maze than the one delineated by the landmark array. The starting position was also chosen to keep any salient inter-maze features, including the travel distances to different edges, constant.

The focus of Experiments 1-3 was on the interaction between familiarity with an environment and the availability of different navigation strategies. To this end, the tests used to probe participant knowledge looked at these strategies separately. Experiment 4 served as an approximate test of how the different types of knowledge participants gained in Experiment 3 (and to a lesser extent Experiments 1 and 2) interact. For rats on the T-maze, it is generally

observed that the preference for making an egocentric response during a conflict trial emerges as the turn behaviour executed during training becomes habitual. Therefore in addition to the allocentric and egocentric tests in Experiment 3 participants were also tested in an environment where both strategy types were supported but suggested different search locations in order to look at the distribution of strategy preference by the end of training. As prior research tends to show a shift with training from an allocentric to an egocentric preference it was hypothesised that most participants' initial response on the test trial would be to employ an egocentric strategy. Participants' confidence in their initial behaviour was also of interest and it was further hypothesised that confidence would be observable as time spent searching in each strategy suggested location, where more confidence would result in a stronger skew in favour of the strategy initially employed.

Method

Participants

Forty-three undergraduates from the University of Sydney participated in this experiment in exchange for course credit. Exclusion criteria were the same as Experiment 1. Twenty-four of the participants were excluded from the analyses, sixteen as a result of simulator sickness, and eight due to a lack of learning. The criteria for a participant not showing any learning were the same as Experiment 1.

Materials

The materials used here were the same as those described for Experiment 1.

Design

This experiment used a within-subjects design, similar to that employed in Experiment 3. All participants received 15 training trials. There were two test times following the 5th and 15th training trials. In order to avoid overloading participants with too many tests, of the four tests from Experiment 3 the allocentric-r test was removed for this experiment. In addition, all participants received one conflict test, which occurred after the 15th training trial and before the last allocentric and egocentric tests. As only one conflict test was administered participants received one block of three test trials after 5 training trials and a second block of four test trials after 15 training trials. For the new conflict test the quadrant first entered by a participant was recorded as a measure of their preferred strategy. Time spent in each quadrant was also recorded as a measure of a participants' search confidence.

Procedure

Pre-training

The pre-training process was the same as that described in Experiment 1.

Training

The training process and environment were the same as that described in Experiment 3.

Allocentric test

Following the 5th and 15th training trials, all participants received the allocentric-n test used in Experiments 2 and 3.

Egocentric test

After the 5th and 15th training trials, all participants received both egocentric tests used in Experiment 3.

Conflict test

In order to have both types of navigation cue available the conflict test trial used the same environment as the training trials. This similarity was also expected to reduce the chance that participants might determine that they were involved in a different type of trial. The aim of the conflict test was to put participants in a situation where both strategy types would appear equally viable and, given participants' egocentric knowledge is theorised to be relative to the fixed training starting position, the conflict test's starting point needed to appear similar enough to facilitate successful egocentric navigation. The way the chosen starting point and the training trial start point were matched can be seen in Figure 13. Both points are in the same relationship to their nearest edges of the maze, and the participant is oriented in both such that the initial view of the plank maze is matched with respect to the arrangement of the distal landmarks and such that the same behavioural response leads to an approximately identical region of the plank maze. Figure 13 also shows how the two strategies are separated, with different choices leading to the clearly distinct quadrants demarcated in the figure.

The instructions given before the start of the conflict test were the same as those given before the start of each training trial in order to maintain the belief in participants that they were not being tested. Any questions raised by a participant regarding the change in start location were addressed with the reminder that all necessary instructions were imparted before each trial, and that the answers to any other questions should be determined at their own discretion.

The conflict test trial was programmed to have no visual or audio indicators of the discovery of the target location. For this test this was done to remove the possibility of errant strategy learning resulting from the novel start position. The four minute time limit for training trials was also used here to maintain the appearance of a regular training trial and to allow time to observe participants' search behaviours.

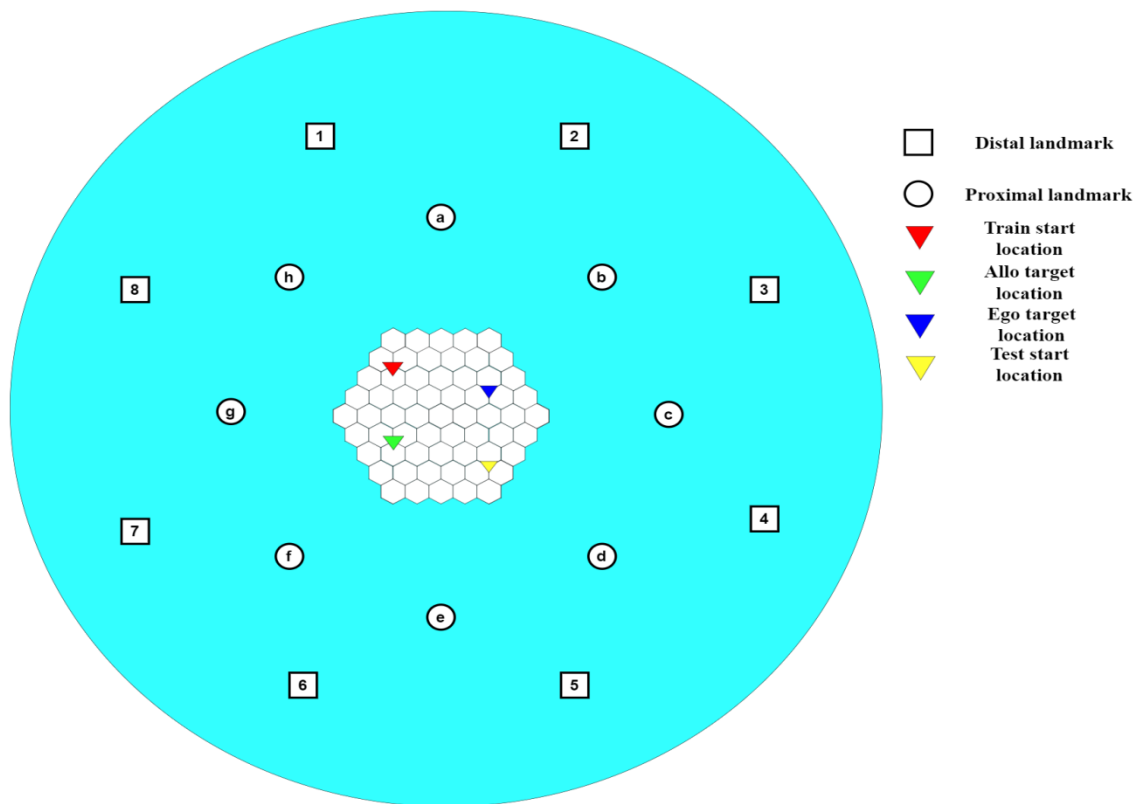


Figure 13. Schematic survey view of the conflict test environment used in Experiment 4. Conflict test trial was started at the test start location. Ego target represents the location in the maze participants utilising an optimal egocentric strategy would be expected to believe the target to be positioned. Allo target represents the location in the maze participants utilising an optimal allocentric strategy would be expected to believe the target to be positioned.

Statistics

Training

The dependent variables recorded and the analyses employed were the same as those described for Experiment 1.

Test

For the conflict test, the first non-start quadrant a participant entered was recorded as a measure of their initial navigation strategy. As no participants made the egocentric choice a binomial test was used to compare the observed proportion of allocentric navigators to the expected proportion of 0.5. Time spent in each pool quadrant across the test trial period was used to measure to what extent participants' search was motivated by either strategy. Four quadrant percentage scores were generated based on how much of the total trial time was spent in each and these were compared using a One Way Between-Subjects ANOVA. A paired-samples t-test was employed to specifically compare the percentage scores between the allocentric and egocentric quadrants.

For the allocentric test trials, the removal of the allocentric-r test type meant the analyses employed for the allocentric-n tests were the same as those used in Experiment 1. The distance scores to each quadrant at each test time were analysed together using a 2 (test time) x 4 (quadrant) Within-Subjects ANOVA to compare quadrant preference between the two test times. A One Way Within-Subjects ANOVA was also used to assess whether there was any change in the target location distance scores between the two test times. The same planned contrasts were also used, first comparing the target location distance scores to the combined average scores for

the three dummy quadrants independent of test time and then testing whether any difference between these two groups was modulated by test time.

The analyses and data collected for the egocentric tests were the same as those described for Experiment 3. The distance scores for both tests were analysed separately in a 2 (test time) x 4 (quadrant) Within-Subjects ANOVA in order to look at quadrant preference and how it might relate to test time. A One Way Within-Subjects ANOVA was also utilised to compare the target location distance scores between the two test times. As two egocentric test types were used, potential differences in target location approximation between them were tested for using a 2 (test type) x 2 (test time) Within-Subjects ANOVA. Planned contrasts were also used to compare the target location distance scores against the averaged scores for the remaining three quadrants and to see if this difference interacted with test time.

Results

Training

It can be seen in Figure 14a that participants learned to take shorter paths to the target with more training. Using a One Way Within-Subjects ANOVA this apparent relationship between path length and training was found to be significant, $F(14, 252) = 6.36, p < .001$.

Participants also became quicker to find the target with more training (see Figure 14b). This relationship was also significant, $F(14, 252) = 5.37, p < .001$, as measured by a One Way Within-Subjects ANOVA.

As can be seen in Figure 14c-d, participants showed an increase in the repetition of the regions of the maze they visited from the start (trials 1-5) to the end (trials 11-15) of training. A

paired-samples t-test showed participants were visiting significantly, $t(18) = -6.30, p < .001$, fewer intersections by the last training block compared to the first. Comparing percentage scores with a 2 (training block) x 5 (unique visits) Within-Subjects ANOVA found a significant, $F(4, 72) = 158.55, p < .001$, main effect of unique visits and a significant, $F(4, 72) = 11.18, p < .001$, interaction that, looking at Figure 14d, is likely a result of a decrease in the number of intersections with only one unique visit by the end of training.

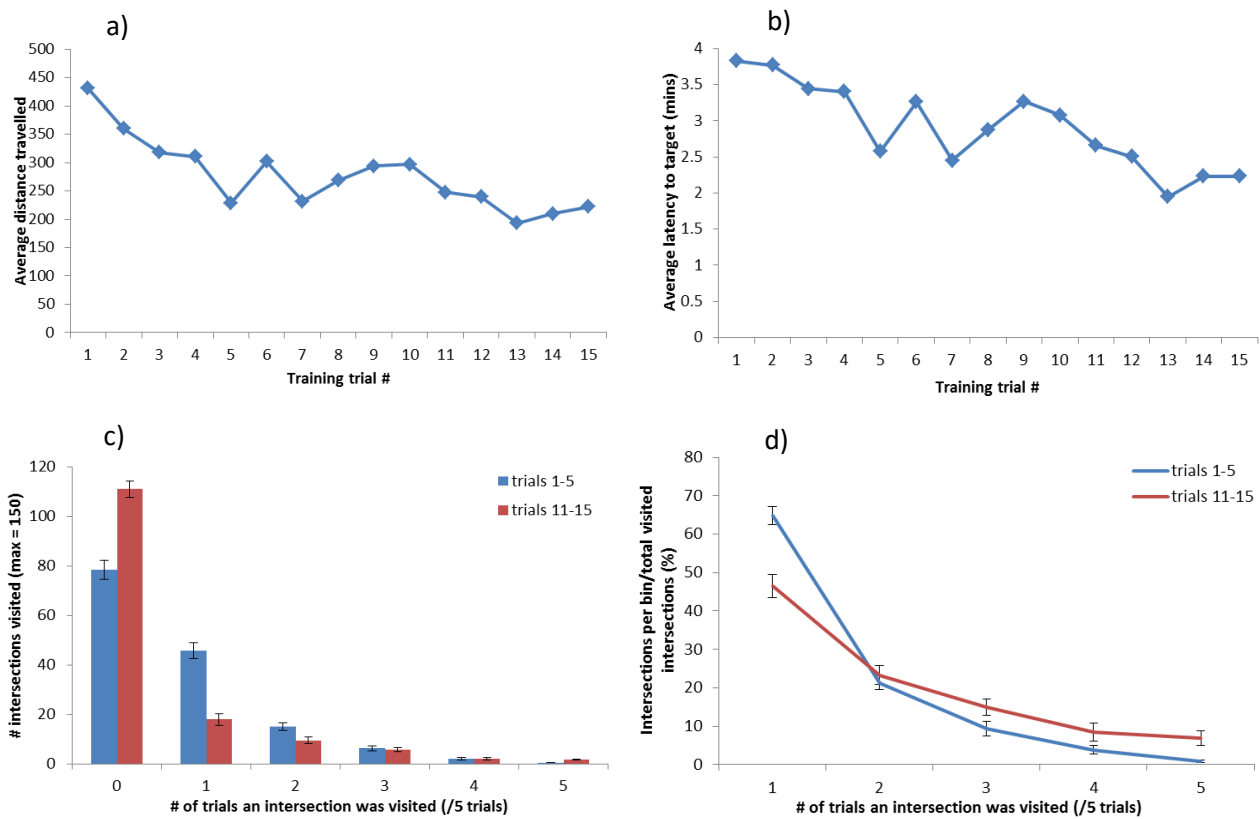


Figure 14. Training data collected from participants during Experiment 4. (a-b) Relationship between number of training trials completed and average distance travelled (a) or time spent (b) searching for the target location. (c) Number of trials, divided into frequency bins of 0-5, each intersection in the plank maze was visited during the first (trials 1-5) and last (trials 11-15) blocks of training trials. (d) To calculate percentage scores the frequency counts for each non-zero bin (1-5) were divided by the total number of intersections visited at least once in a block. Percentage scores were calculated for the first and last training blocks. All error bars are \pm SEM.

Allocentric tests

The allocentric-n results, shown in Figure 15a, show an early preference for approximating the target location correctly that does not improve with training. A 2 (test time) x 4 (quadrant) Within Subjects ANOVA supported this observation, with a significant, $F(3, 54) = 237.40, p < .001$, effect of quadrant but no effect test time and no interaction (p 's $> .05$). Planned contrasts comparing target location preference to the combined preference for the remaining locations found a significant, $F(1, 18) = 374.27, p < .001$, preference for the target location, with no effect of test time ($p > .05$). Comparing the test times on just the target location preference using a One Way Within-Subjects ANOVA also showed no effect of test time ($p > .05$).

Egocentric tests

Looking at the distance scores for the egocentric-p test in Figure 15b participants look to be developing a preference for approximating the target near the target location over the training period. A 2 (test time) x 4 (quadrant) Within-Subjects ANOVA found significant effects of quadrant, $F(3, 54) = 29.47, p < .001$, and test time, $F(1, 18) = 5.09, p = .037$, along with a significant, $F(3, 54) = 3.78, p = .015$, interaction. Comparing the target location distance scores to the combined scores for the other three quadrants using planned contrasts revealed a significant, $F(1, 18) = 13.65, p = .002$, preference for the target location but no interaction between this preference and test time ($p = .068$). Directly comparing the target location distance scores between test times with a One Way Within-Subjects ANOVA showed a significant, $F(1, 18) = 7.69, p = .013$, improvement in approximating the target location by test time 2.

Target approximation also looks to improve on the egocentric-np test with training, as can be seen in Figure 15c. A significant, $F(3, 54) = 15.96, p < .001$, effect of quadrant and a

significant, $F(1, 18) = 5.98, p = .025$, effect of test time were found with the 2 x 4 Within-Subjects ANOVA; however, the interaction was not significant ($p > .05$). Looking at the target location preference compared to the other three quadrants using planned contrasts found a significant, $F(1, 18) = 10.46, p = .005$, preference for the target location, an effect that was not modulated by test time ($p > .05$). A One Way Within-Subjects ANOVA found a significant, $F(1, 18) = 6.41, p = .021$, difference between test times when comparing them on target location distance scores.

Comparing target location distance scores between test types looking at Figures 15b and 15c reveals that both show the same change as a function of test time. This observation was supported by a 2 (test time) x 2 (test type) Within-Subjects ANOVA which reported a significant, $F(1, 18) = 15.60, p = .001$, effect of test time but not of test type, and no interaction (p 's $> .05$).

Conflict test

Looking at Figure 15d, there was a clear, overwhelming preference for participants to initially navigate with reference to the allocentric features of the environment and to search for the target in the quadrant these features delineate (as seen in Figure 15e). A binomial test comparing the proportion of observed allocentric navigators of 1.0 to the expected distribution of 0.5 indicated that significantly, $p < .001$, more participants navigated allocentrically than was expected. A One Way Between-Subjects ANOVA comparing the percentages of total test time spent in each quadrant found a significant, $F(3, 72) = 226.03, p < .001$, difference between them. Comparing these percentages between the egocentric and allocentric delineated quadrants using

a paired-samples t-test revealed a significant, $t(18) = 23.26, p < .001$, preference for the allocentric quadrant.

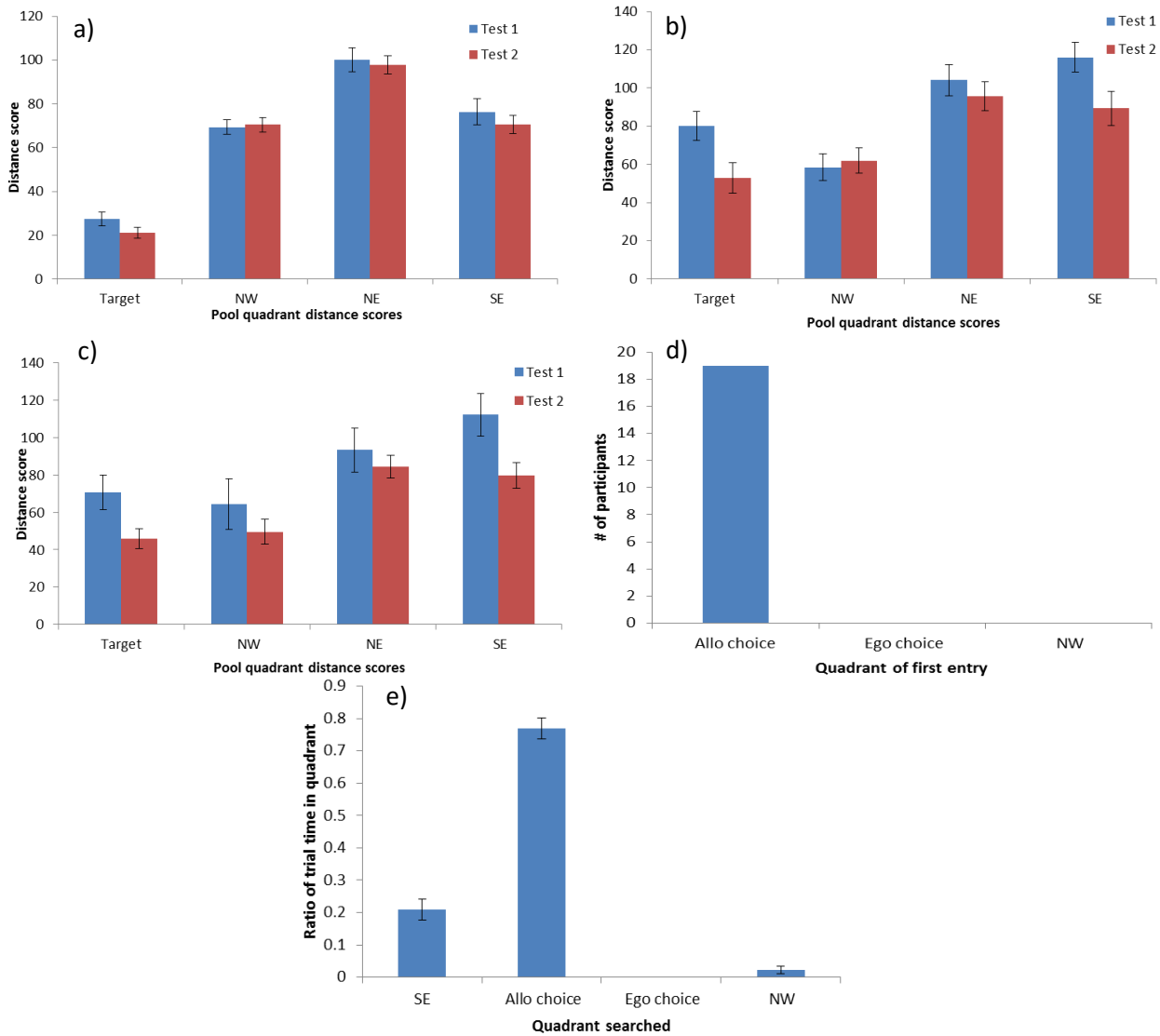


Figure 15. Test data collected from participants during Experiment 4. (a) Average distance of participants' approximations of the target location from the actual target location (Target) and the centres of the remaining pool quadrants (NW, NE, SE) calculated using the distance formula (distance score) on the allocentric normal test at each test time. (b-c) average distance scores to the actual target location and the three pool quadrants for the egocentric-plank (b) and no-plank (c) test trials at each test time. Test 1=after 5 training trials; Test 2=after 15 training trials. (d) Number of participants that initially employed an allocentric (allo choice), egocentric (ego choice) or other (NW) navigation strategy on the conflict test trial. (e) Participants' search behaviour was indexed as the average fraction of the total conflict test trial time participants were recorded as been located in each of the four pool quadrants. Here quadrants were delineated as: suggested by an allocentric strategy (allo choice), suggested by an egocentric strategy (ego choice), the conflict test starting quadrant (SE) and the training trial starting quadrant (NW). All error bars are \pm SEM.

Discussion

The results of Experiment 4 suggest that participants overwhelmingly prefer to navigate allocentrically by the end of the training period. The distribution of where participants spent most of the time during the conflict test further supported this preference, with search focussed almost exclusively in the allocentric quadrant. Participants also appeared to have great confidence in their chosen strategy as it was persevered with by all participants for the duration of the conflict test trial despite the absence of the target. As participants did not know the delineators of the target location were absent it would be expected that, if they had doubts about their chosen strategy, their inability to find the target might encourage them to search according to a different one. This did not occur for any participants. However, it may have been the case that participants' allocentric preference was a result of some bias introduced in the experimental methodology. This possibility is suggested by the ability of participants to solve the allocentric-n test after only five training trials. Looking at the pattern of results on the egocentric tests participants did not tend to show a preference for approximating the target near the correct location until the end of training. Therefore it might be the case that training participants in an environment that facilitates the acquisition of more reliable egocentric knowledge affects the extent to which allocentric navigation is preferred.

Experiment 5

Experiment 5 was motivated by the overwhelming preference for allocentric navigation observed in the conflict test of Experiment 4. As was mentioned previously, this result may have been a consequence of participants not developing a more reliable egocentric response strategy.

One possible explanation for this complete absence of any egocentric strategy preference may be the complexity of the training environment used in Experiments 1-4. It may have been the case that the great variety in the number of possible search locations and in the number of paths that could be taken to reach the target location made the development of a reliable egocentric strategy too difficult, at least within the training time of earlier experiments. However, that is not to say that a more reliable egocentric strategy, if one could be developed, would necessarily produce less of an allocentric strategy preference. It may also be the case that the distal cues of the environment are too distinct to be ignored in the execution of any but the simplest egocentric responses such as those seen when solving a T-maze conflict test. Experiment 5 therefore aimed to test whether the complexity of the learned egocentric strategy had any effect on participants' preferential navigation behaviour.

In order to simplify the egocentric strategy that participants were likely to learn the maze in the training environment was made easier to navigate. The maze was therefore redesigned with the aim of encouraging the acquisition of route knowledge. This knowledge was expected to be easier to utilise while also being more accurate and less susceptible to error than the dead reckoning system participants appeared to be employing in Experiments 1-4. The key change made to the training maze was the removal of the hex grid design in order to remove the large amount of variability in the number and length of the possible paths from start to target. It was replaced with a maze with only one possible, fixed length path between the two locations. To keep this path simple enough to potentially learn a route through only a small number of choice points were included. It was hypothesised that, keeping the number of training trials constant, having participants learn to navigate this simpler maze would lead to their developing more accurate and reliable egocentric knowledge. It was hypothesised that this in turn would produce a

twofold effect, resulting in improved performance on the egocentric-p relative to the egocentric-np test and in a more even split of allocentric and egocentric navigators on a conflict test.

Method

Participants

Thirty-seven undergraduates from the University of Sydney participated in this experiment in exchange for course credit. Exclusion criteria were the same as Experiment 1. Nineteen of the participants were excluded from the analyses, eleven as a result of simulator sickness, and eight due to a lack of learning. The criteria for a participant not showing any learning were the same as Experiment 1.

Materials

The materials used here were the same as those described for Experiment 1.

Design

The test structure of this experiment was varied from the one used for Experiments 1-4, with test time removed as an independent variable. The same four test types as in Experiment 4 were employed here but only at the end of the training period. The administration of this block of test trials followed the same protocol as Experiment 4.

All other details of the experiment's design were the same as those detailed for Experiment 4.

Procedure

Pre-training

The pre-training process was the same as that described in Experiment 1.

Training

The design of the training environment, visualized in Figure 16, was conceived with the aim of making the maze more conducive to the development of route-based egocentric knowledge. To achieve this, a simpler training environment was used where simplicity was considered to be related to the number of turns in the longest path from the start to the target location, the number of possible paths between the two points and the average length of dead-end paths. The hex grid design was replaced with a maze with only one possible, fixed length path with a set number of choice points between the start and target locations. In order to minimise the time taken to reveal a dead-end path the wrong choices at any intersection were only one plank long, meaning mistakes were made immediately apparent to participants. The maze also needed to not be so simple in its design that it could be solved trivially by the learning of a directional response from the start point. As can be seen in Figure 16 this problem was avoided by constructing a circuitous path that precluded the use of a simple directional bearing strategy as a result of the inclusion of several changes in the path's direction of bearing. To allow for more flexibility in the design of this path sections of the maze that contained no choice points were included, with the expectation that the lack of choice points would mean these regions would have no effect on the overall difficulty of learning a route through the path. One dead-end path section that did not immediately reveal itself as such was included as the equivalent of the non-baited arm in a T-maze. This arm was necessary to allow the same maze to be used in both

training and the conflict test. Therefore the two environments were matched in all aspects but the rotation of the maze. These arms were designed to be exact mirrors of each other, with the exception that only one contained the target location. This was to avoid participants potentially choosing the egocentric arm on the conflict test as a result of their association of a particular path structure with the incorrect option. As a result of this the paths from the start location to the ends of both arms were identical with the exception of the turn at the intersection from which they branch.

The transitions between training trials were changed to remove the transferring of participants to the target location following the end of an unsuccessful trial. Instead new trials were begun immediately regardless of the previous trial's outcome. This was to address the concern that moving participants to the target location after a failed trial might encourage a biased use of the allocentric cues. As a simplified training environment was used for this experiment the expectation was that most participants would be able to eventually discover the target location under their own power.

All other environmental features and training protocols were the same as those described in Experiment 3.

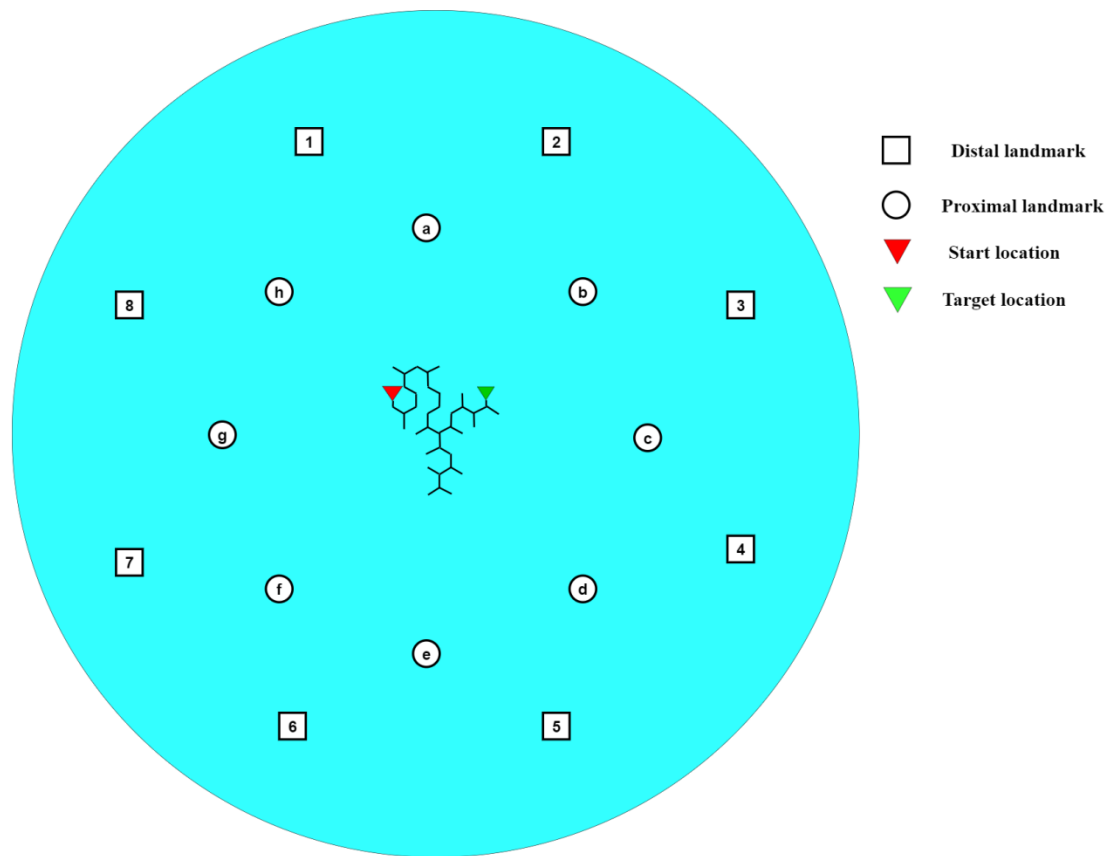


Figure 16. Schematic survey view of the training environment used in Experiment 5. Of note are the greatly simplified design compared to Experiments 1-4 and the meandering nature of the path meant to throw off the learning of a simple directional bearing strategy.

Allocentric test

The allocentric test trial was the same as in Experiment 4.

Egocentric test

The egocentric test trials were the same as those described in Experiment 4. This includes the test environment for the egocentric-p test, meaning that participants were tested in a hex grid maze environment even though they were not trained on one. The hex maze structure was preserved to avoid participants solving the test trivially using knowledge of the fact that in the

training maze the target location could be approximated to within two locations simply by knowing that it was located at the end of the path. The egocentric test environments can be seen in Figure 17.

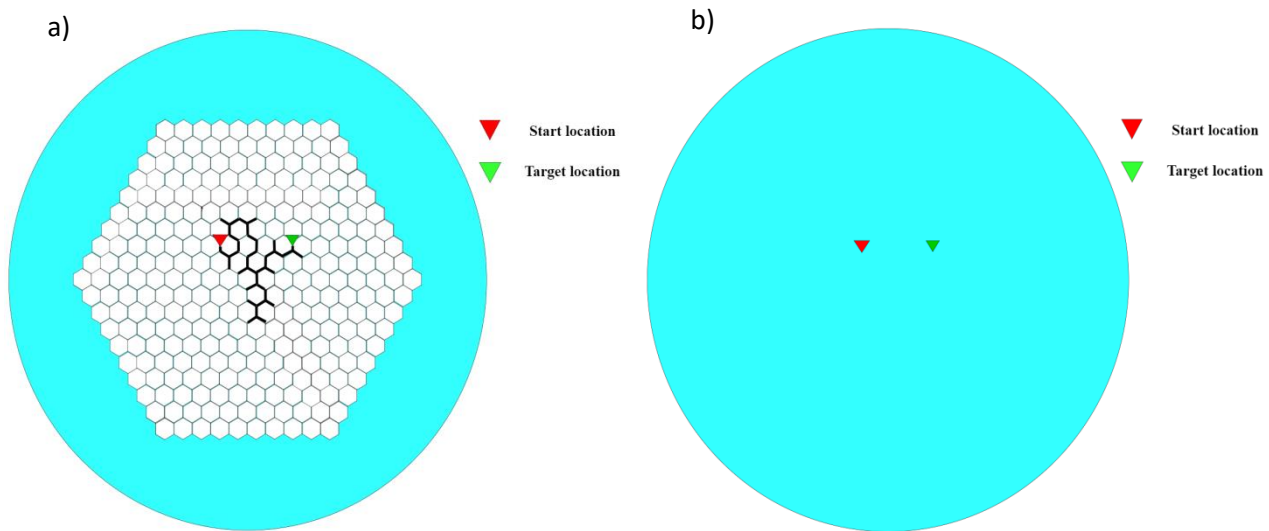


Figure 17. Schematic survey views of the egocentric plank (a) and no-plank (b) test environments used in Experiment 5. (a) Black boundary delineates the extent and position of the training environment maze.

Conflict test

In order to put the two strategy types in conflict a new test environment was constructed that followed the same basic principles as a T-maze. The training maze was mirrored so that participants now started on the opposite side of the environment and the two main branches of the maze could be used to delineate a participant's preferred strategy. Looking at Figure 18 and comparing the conflict test maze to that shown in Figure 16 it can be seen that following the correct sequence of turns from the start to the target learned during training now takes a participant to the opposite arm to that suggested by the allocentric cues.

As the probable target location, which would likely be the end of either maze branch, is more clearly delineated than in Experiment 4 the conflict test protocol was modified to remove the four minute time limit allowing participants to continue on the test trial until they had reached a termination location. Four such locations were defined, with two on either branch positioned on the two branches of the final choice point (see Figure 18). Once one of these termination locations was reached the trial was ended.

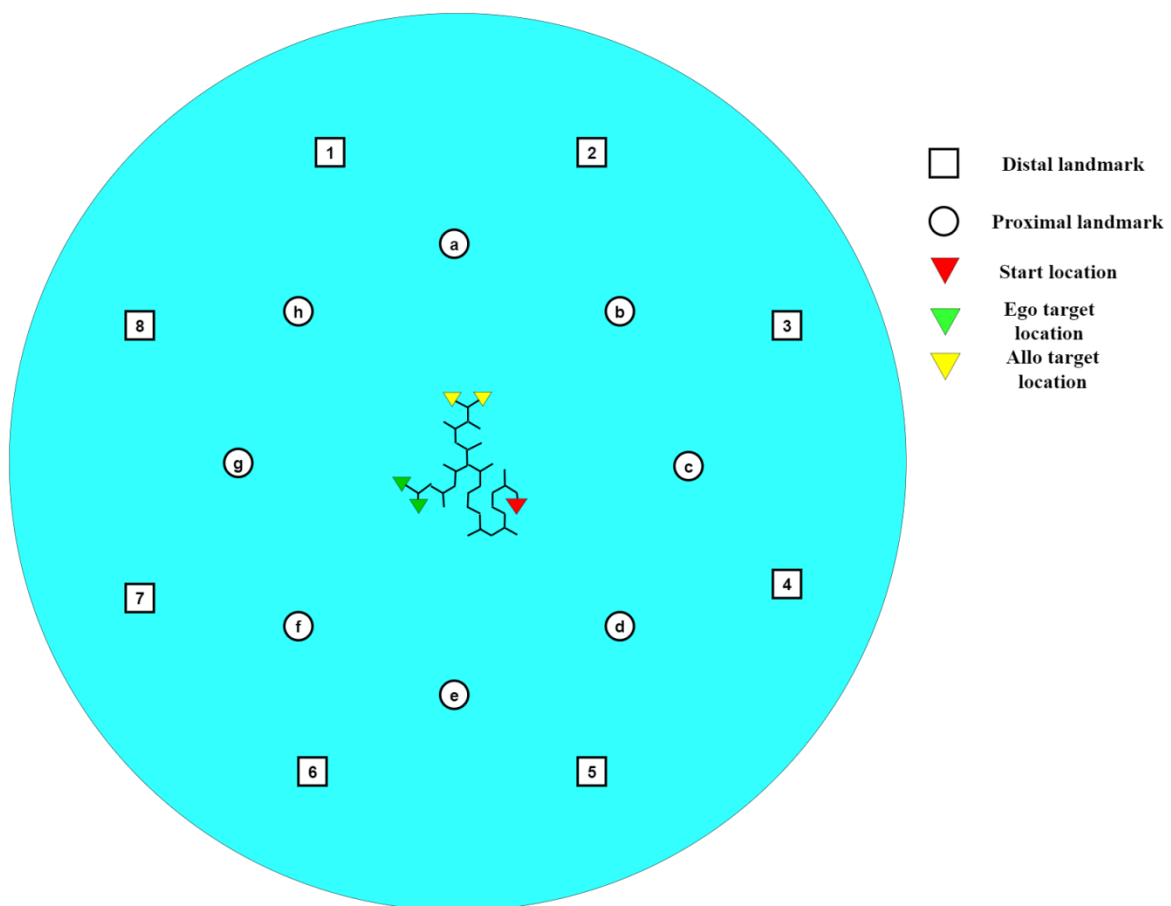


Figure 18. Schematic survey view of the conflict test environment used in Experiment 5. Conflict test trial was started at the test start location. Ego targets represent the pair of locations in the maze participants utilising an optimal egocentric strategy would be expected to believe the target to be positioned. Allo targets represent the locations in the maze participants utilising an optimal allocentric strategy would be expected to believe the target to be positioned.

Statistics

Training

The dependent variables recorded and the analyses employed were the same as those described for Experiment 1.

Test

For the conflict test strategy choice was indexed by the arm in which the termination point a participant reached was located. While there were four termination points programmed into the test trial only two were ever reached, one for each arm, and therefore only arm choice was analysed. A chi-square test was used to compare the frequency with which each arm was chosen. The expected value used here was set based on the expectation that simplifying the training environment would produce an equal distribution of allocentric and egocentric choices. It was therefore expected that all participants would make the allocentric choice and the chi-square test was designed to reflect this. The distance travelled from the start to the termination point was also recorded. An independent samples t-test was used to compare the average path length of allocentric against egocentric choice participants.

For the allocentric and egocentric test trials, due to the use of only one test time a One Way Within-Subjects ANOVA was used to compare distance scores between pool quadrants. For this experiment, contrasts only tested preference for the target location against the combined average for the remaining three dummy quadrants due to the removal of test time as a variable.

These contrasts were tested for each test type. A One Way Within-Subjects ANOVA was also used to compare target location distance scores between the two egocentric tests.

Results

Training

Over the course of training participants, as shown in Figure 19a, decreased the distance of the paths they took through the environment. A One Way Within-Subjects ANOVA found this relationship between training and travel distance to be significant, $F(14, 238) = 17.68, p < .001$.

As can be seen in Figure 19b, participants also became faster to find the target as a result of more training. This relationship was found, using a One-Way Within Subjects ANOVA, to be significant, $F(14, 210) = 27.30, p < .001$.

Figure 19c-d shows that participants developed a preference for making repeated use of particular unique intersections from the start (trials 1-5) to the end (trials 11-15) of training. Looking at the change in the number of unvisited intersections using a paired-samples t-test found a significant, $t(17) = -6.68, p < .001$, decrease when comparing the last training block to the first. Analysing the percentage scores using a 2 (training block) x 5 (unique visits) Within-Subjects ANOVA revealed a significant, $F(4, 68) = 84.04, p < .001$, main effect of unique visits and a significant, $F(4, 68) = 46.62, p < .001$, interaction. The data visualised in Figure 19d suggests these effects are a result of the increase in the number of intersections visited five times by the last training block.

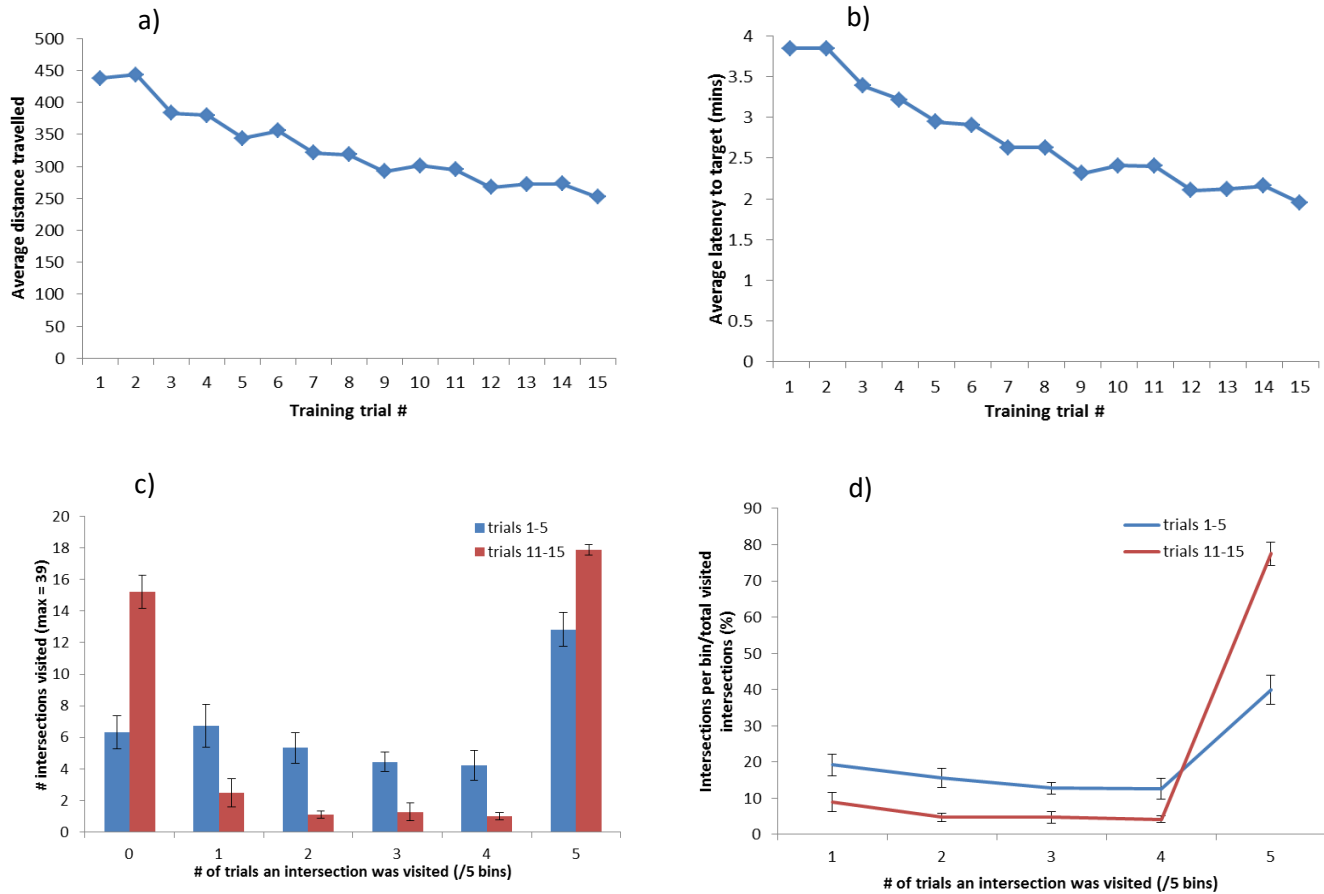


Figure 19. Training data collected from participants during Experiment 5. (a-b) Relationship between number of training trials completed and average distance travelled (a) or time spent (b) searching for the target location. (c) Number of trials, divided into frequency bins of 0-5, each intersection in the plank maze was visited during the first (trials 1-5) and last (trials 11-15) blocks of training trials. (d) To calculate percentage scores the frequency counts for each non-zero bin (1-5) were divided by the total number of intersections visited at least once in a block. Percentage scores were calculated for the first and last training blocks. All error bars are \pm SEM.

Allocentric tests

As can be seen in Figure 20a, participants on the allocentric-n test preferentially approximated the target near its training location. A One Way Within-Subjects ANOVA with

pool quadrant as the independent variable supported this observation, finding a significant, $F(3, 51) = 52.99, p < .001$, effect of quadrant. Planned contrasts comparing target location preference to the combined preference for the remaining quadrants revealed a significant, $F(1, 17) = 134.34, p < .001$, preference for the target location.

Egocentric tests

The distance scores for the egocentric-p test, visualised in Figure 20a, appear to show that participants failed to develop an egocentric representation of the target location by the end of training. This observation was supported by a One Way Within-Subjects ANOVA which found no effect of quadrant on distance scores ($p > .05$). Similarly, planned contrasts comparing the target location distance scores to the combined scores for the other three quadrants found no preference for the target quadrant ($p > .05$).

Figure 20a also shows that participants did appear to be preferentially approximating the target near its actual location on the egocentric-np test. A One-Way Within-Subjects ANOVA supported this, finding a significant, $F(3, 51) = 14.21, p < .001$, effect of quadrant. This interpretation was further supported by a planned contrast comparing target quadrant preference to the averaged distance scores of the other three quadrants which revealed a significant, $F(1, 17) = 5.49, p = .031$, preference for the target location.

The target location distance scores for the different egocentric tests, as can be seen in Figure 20a, appear quite similar, suggesting no difference in participants' ability to correctly locate the target on one test compared to the other. A One Way Within-Subjects ANOVA comparing the two tests on their target location distance scores supports this observation, finding no effect of test type on the distance scores ($p > .05$).

Conflict test

It can be seen in Figure 20b that participants appeared to prefer to navigate with reference to the allocentric features on the conflict test. Those participants who did make the egocentric choice, however, look to have taken much shorter paths to their terminations (see Figure 20c). Comparing the frequency of arm choice using a chi-square test, however, found there was no significant difference in the strategy participants preferred to employ ($p = .059$). An independent samples t-test comparing path lengths as a function of conflict choice found that egocentric choice participants took significantly, $t(16) = 2.71$, $p = .015$, shorter paths to their termination point.

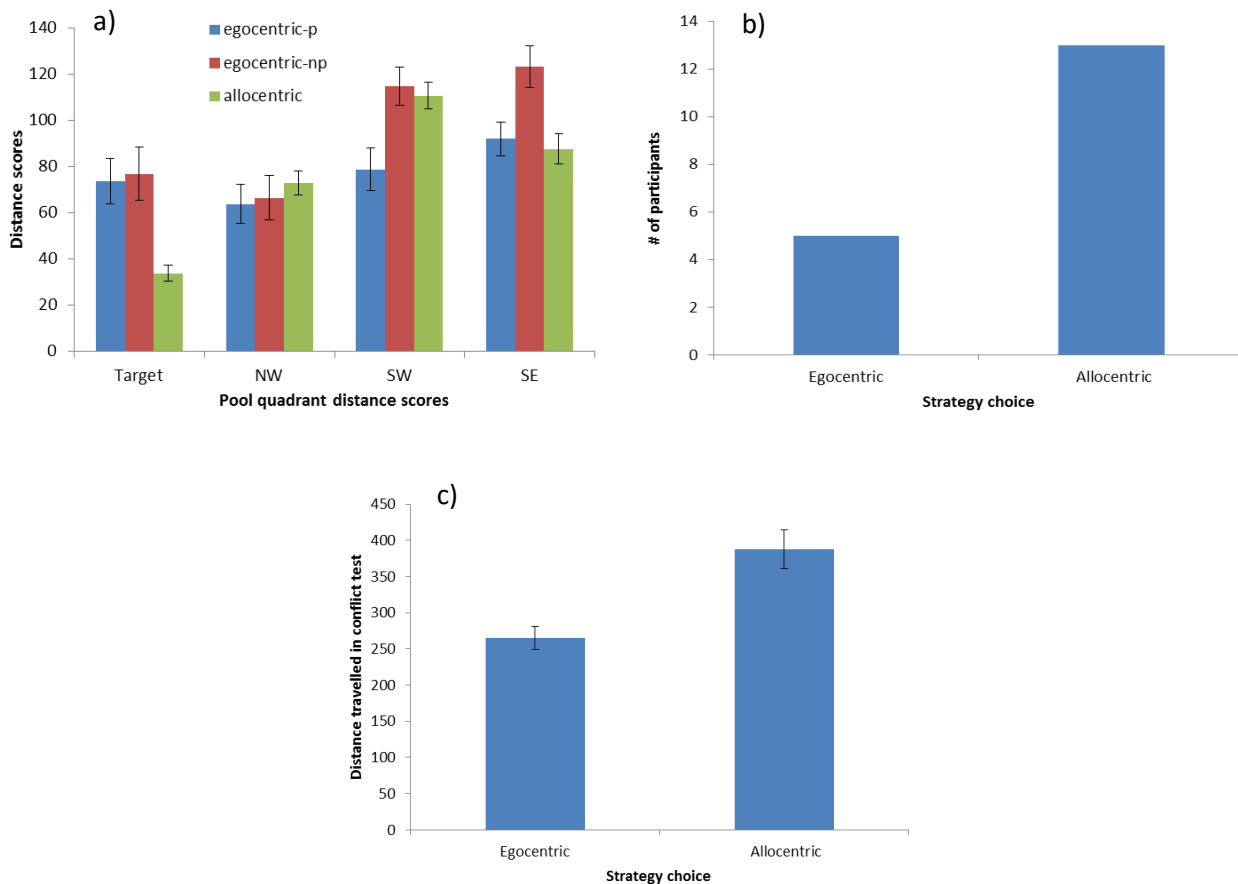


Figure 20. Test data collected from participants during Experiment 5. (a) Average distance of participants' approximations of the target location from the actual target location (Target) and the centres of the remaining pool quadrants (NW, SW, SE) on the egocentric plank (egocentric-p), egocentric no-plank (egocentric-np) and allocentric (allocentric) test trials, calculated using the distance formula. (b) Number of participants that employed an egocentric (egocentric) or allocentric (allocentric) navigation strategy on the conflict test trial. (c) The length of the paths taken on the conflict test by participants separated by whether an egocentric or allocentric choice was made on the conflict test. All error bars are \pm SEM.

General Discussion

The aim of these experiments was to answer the question of how participants behave when the two distinct navigation strategies they have acquired the ability to separably employ are put in to conflict. Together they suggest that, for the environment and training process used here,

the degree to which participants preferentially employ one strategy or the other depends on the complexity of the environment they are required to navigate. Training data from both experiments clearly showed that participants acquired the ability to navigate through the environment more accurately as they became more familiar with it. Both experiments also demonstrated that participants were capable of acquiring information about the distal features of the environment that could facilitate relatively successful allocentric navigation. In Experiment 4 participants revealed an overwhelming preference for allocentric navigation following the training and testing protocol established by Experiments 1-3. Participants also all demonstrated great confidence in their chosen strategy, persevering in their search of the quadrant delineated by the distal environmental cues despite the conflict test been run under extinction conditions. Experiment 5 found that simplifying the process of constructing a reliable egocentric strategy produced a shift towards an equal distribution of strategy preference on the conflict test. Consistent with the idea that these participants had learned the correct route through the maze those that made the egocentric choice took much shorter paths to their predicted target location than did the allocentric navigators who made more errors. Taken together these results suggest that people can have their preferential strategies affected by the complexity of the environment they are navigating.

One possible explanation for the results of Experiment 4 ruled out by the data from Experiment 5 was that the completely different view of the distal landmarks participants were presented with at the start of the trial immediately alerted them to their new position. If this were the case participants, if they held the implicit assumption that the position of the target was fixed relative to the landmarks and not the maze, they would therefore proceed to navigate allocentrically and indeed never even think to check the quadrant suggested by an egocentric

strategy. That some participants in Experiment 5 exposed to a similar, starkly different view of the environment still preferentially employed an egocentric strategy on the conflict test suggests that people are capable of ignoring the change in their position. For Experiment 4 this suggests that participants were likely still attending to the arrangement of the landmarks at the beginning of each training trial. The conflict test can therefore be said to show that participants, at least in the early stages of a training trial, were selectively attending to the distal cues of the environment when determining how and where they should navigate.

The results of Experiment 5 also appear to provide information about how participants who preferentially utilise different strategies when navigating are acquiring knowledge during training. Egocentric-choice participants made far fewer errors, on average, navigating the path to their chosen location than did allocentric navigators. As the paths to both the egocentric and allocentric target locations both during training and the conflict test were identical from start to finish, with the exception of the turn on to one arm or the other, these shorter paths suggest that allocentric navigators had acquired less information about the correct route. This relative lack of learning may be a possible explanation for their preferred navigation strategy, although it might also be the case that these participants resolved to navigate allocentrically and therefore attended less to learning an accurate route.

Of concern regarding the data from Experiment 5 is that the results of the egocentric tests appear to suggest that participants were not acquiring egocentric knowledge that could reliably guide them to the target location. This result does not fit well with the idea that at least some participants were acquiring highly accurate routes through the environment. However, it may be the case that this result, at least for the egocentric-p test, is a consequence of the design of the test environment. Prior to the start of this experiment there was concern about the structure of the

egocentric-p test. Running it using the training environment maze with the distal cues removed would allow for the straightforward assessment of successful route learning. However, it would have also made the maze trivially easy to solve by any participant who realised that the end of the path was reached once they arrived at a pair of dead end choices. Provided they chose the correct arm at the main path intersection, a savvy participant could therefore be accurate to within one intersection choice in their approximation of the target without any route knowledge. Several possible ways to address this concern were considered, the most straightforward of which, and the one that would help make the results from Experiment 5 more comparable to those from earlier experiments, was to test participants in the full hex grid maze in the egocentric-p test. However, this change carried the implicit assumption that participants would have acquired some form of knowledge about how to navigate the non-choice point regions of the maze. Without this knowledge participants would likely be unable to navigate successfully at intersections they had not previously experienced as requiring a choice. One possible way to structure the egocentric-p test in the future that could avoid these concerns would be to measure the number of errors participants made navigating a test environment that contained the training maze. Those who were using a non-spatial strategy but had not learned a route would be expected to make more choice point errors than those who had followed a correctly learned route even though they appeared to guess the target location correctly.

The egocentric-np test environment does not suffer from the same problem. That may be the explanation for why participants appeared to be capable of approximating the target in the correct quadrant on this test. This observation, combined with the lack of an observable difference in the average accuracy of target approximations between the two egocentric tests suggests that participants were likely making use of learned directional information but did not

have accurate information about the distance between the start and target locations. If this were the case it would suggest that unlike with earlier experiments participants were not solving both these tasks using the same information, with participants on the egocentric-p test likely attempting to navigate via a learned route that contained no idiothetic information. Initial attempts to navigate with reference to such a strategy would likely lead participants astray and, separated from the starting location as the initial reference point for any dead reckoning based strategy, where the target was eventually approximated would be essentially random, which is what was observed.

Taken together these results appear to show that in the virtual environments used here there is a relationship between the complexity of the training maze and the navigation strategy that is preferentially employed on a conflict test. There is also evidence to suggest that some participants are capable of acquiring a route-based strategy on the simpler training environment of Experiment 5. These results also suggest that people can, in some cases, come to completely ignore distal environmental cues, even while navigating a long route.

General Discussion

Taken altogether these results can be seen to advance our understanding of how it is that people come to acquire and make preferential use of allocentric and egocentric navigation strategies. The results of Experiments 1-3 revealed that participants were capable of acquiring information that could drive relatively successful navigation that used only entirely allocentric or entirely egocentric information. Allocentric knowledge was seen to be landmark-dependent and appeared to be related to the complexity of training, with more difficulty producing an array-based strategy while less difficulty produced a single landmark strategy. Egocentric knowledge was observed to be independent of the structure of the maze and was instead based entirely on internal information. Experiments 4 and 5 followed up on these observations and found that participants, when both types of strategy were available, showed a preference for navigating allocentrically, the strength of which was dependent upon the complexity of the environment they were required to navigate. The more complex training environment of Experiment 4 produced a universal allocentric preference, while a preference in some participants for egocentric navigation emerged from the simpler environment of Experiment 5.

The observed pattern of results on the standard allocentric test was remarkably consistent across all five experiments. In each experiment participants showed the ability to quickly acquire a representation of the target's location relative to the distal cues of the environment that was never observed to improve with training. Research in both humans and rodents (Andersen et al., 2012; Iaria et al., 2003; Packard & McGaugh, 1996) has tended to show that there is a general preference for navigators to navigate allocentrically during the early stages of training. While participants in the experiments described here were not tested on their early strategy preferences it can be seen that their rapid development of a relatively accurate allocentric representation is a

result that would be consistent with a preference for allocentric navigation. That participants could acquire this relatively accurate representation within five training trials further suggests that the development of this representation was not overly difficult. Research in both rodents and humans has suggested that, rather than place information, what navigators are developing on the MWM is a directional strategy (Hamilton, Johnson, et al., 2009). While the separation of direction from place navigation was not a focus of the research here a key component of the theorised direction strategy in the MWM is the presence of the pool wall which serves as an important source of distance information. However, the unique design of the environments used here meant no walls were available to be used in this way. In order to remove the possibility that the boundary of the pool may have served a similar purpose in Experiment 1 the edges of the pool were extended beyond the visible horizon from Experiment 2 onwards with no observable effect on allocentric test performance. Therefore, while the distinction between direction and place navigation was not explicitly tested here it appears to be the case that a directional strategy, at least as they are typically observed to be employed on more traditional MWM experiments, was not acquired here. Returning to the considerations of difficulty raised earlier, directional strategy use is generally observed to be the simpler strategy for navigators to use on the MWM (Hamilton et al., 2008; Skinner et al., 2003). Some researchers have even observed that, at least in rodents, place learning can be too difficult to observe at all (Skinner et al., 2003), while requiring that people use a place strategy on the vMWM results in generally poorer navigation (Hamilton, Johnson, et al., 2009). As a directional strategy does not appear to be the likely explanation for the allocentric test results observed here, however, it may also be the case that the difficulty of place learning is related to the availability of distal cues in the environment. The sixteen landmarks used here may have provided more information to navigators than the four

distal cues, one for each wall, that are commonly used in more traditional MWM experiments (Hamilton, Johnson, et al., 2009). This could be seen to fit with the observation that people are more likely to utilise landmarks to navigate when more of them are present in the environment (Andersen et al., 2012).

The results from the allocentric-r tests revealed that participants' allocentric strategies were based entirely on knowledge acquired about the identities and the arrangement of the landmarks surrounding the maze. As a result of this preferential landmark learning participants were unable to accurately approximate the target location when the positions of the landmarks were randomised. This was despite the presence of the skybox which, if its arrangement had been attended to, would have likely allowed participants to solve the test as accurately as they had the non-randomised variant. A similar result has been observed in rats, where randomisation of the landmark array surrounding a RAM produced degraded performance, an observation the authors interpret as indicating that the rats were making use of the topographical relationships between the surrounding cues (Suzuki, Augerinos, & Black, 1980). The lack of learning about the arrangement of the sky as an orienting cue could be taken to suggest that it had a relatively low level of salience, either as a result of its own intrinsic properties or as a consequence of the greater salience of the many landmarks in the environment. As the allocentric-r test was administered twice per participant the lack of any improvement on the test with training suggests that the uncertainty induced by the first test, which can be seen in the essentially random distribution of participants' target approximations, did not motivate any re-evaluation of the allocentric knowledge acquired. If therefore participants were not attending to the sky as a result of the greater salience of the landmarks it may be said that poor allocentric-r performance was a result of overshadowing. Overshadowing, as discussed previously, can be observed in a variety

of different ways in spatial learning across many different species, with cues closer to the target location generally able to reduce learning about more distal cues (Chamizo, Manteiga, et al., 2006; March et al., 1992; Roberts & Pearce, 1999). This overshadowing has been observed to interact with feature salience, with Kosaki et al. (2015) finding that extramaze cues on the MWM are still learned about even when intramaze cues are perfectly predictive of the target location provided the extramaze cues are made sufficiently salient. This would suggest that, despite participants showing the ability to acquire multiple types of spatial knowledge about the environment, at least some of the learning observed in these experiments was subject to the principles of associative learning.

However, the finding that participants developed a preference for a single landmark strategy does not explain why participants appeared to, on average, come to preferentially favour navigating with reference to the Christ the Redeemer landmark. It may have been the case that the perceptual salience of the landmark, which refers to how much a feature captures the navigator's attention (Caduff & Timpf, 2008), played a role as it was not a factor that was controlled for here. Of the landmarks surrounding the target quadrant it may therefore have been that the statue was the most salient to participants. Therefore if the landmarks had been deliberately chosen according to the evaluations of participants to be of equal salience within the context of the training environment, and it is important to stress the context here as salience is also seen to be related to a feature's contrast with the environment (Chan et al., 2012), it may be the case that the single landmark strategy would no longer develop, or that it would develop without the uniform preference for any one particular feature.

The difference in patterns of performance on the allocentric-r test between Experiments 2 and 3 was suggested to be a consequence of the differences in the complexity of the training

trials between the two experiments. Participants in Experiment 3 showed a shift to a single landmark strategy with training. As Experiments 3 and 4 shared the same training environment it seems likely then that participants in the latter experiment made the same shift to the simpler, but no more accurate, strategy. This would therefore suggest that participants on the Experiment 4 conflict test were likely making use of this simple, single landmark strategy. This conclusion can be considered in relation to findings that people, in situations where the optimal strategy is ambiguous, default to employing the least demanding, relatively reliable strategy they know (Condappa & Wiener, 2014; Wiener et al., 2013). If a similar approach to strategy selection was followed here that would suggest that in Experiments 1, 3 and 4, the single landmark strategy was the easiest participants could reliably employ. This allocentric preference at the end of the training period is contrary to the results observed by Wiener et al. (2013) where participants showed a preference for egocentric spatial reasoning. As people tend to show a shift from place to response strategies with training (Andersen et al., 2012; Iaria et al., 2003; Schmitzer-Torbert, 2007) it may also be the case that the pattern of behaviour observed here is a consequence of the limited training time afforded to participants. If this were the case it would be expected that extending the training period might have resulted in the development of a simpler egocentric strategy and a preference for egocentric navigation. Results from Experiment 1 not published here provide tentative support for the possibility that a simpler egocentric strategy could be developed by participants with more training. For participants who were able to complete Experiment 1's standard training and testing trials well within the set time limit another ten training trials, and four test trials, were administered. This was done to provide a general idea of how the observed learning trends might extend beyond the amount of training that could be provided for the average participant. The few participants who completed the extra trials were

observed to develop perfect accuracy on the egocentric test and no variability in the paths they took to the target during training, a pair of results that in combination strongly suggest that a complete route from the start to the target had been learned. However, the constraints of these data, which include the small number of participants, the selection bias that results from only being able to test the best performing students and the limitation that these extra trials could only be administered during Experiment 1, need to be kept in mind when attempting to draw conclusions. Therefore, all that can be said is that there exists tentative evidence to suggest that, with more training, participants may be able to acquire a highly accurate route strategy. The conflict test results from Experiment 5 also show that some participants trained in a simpler version of the mazes used in Experiments 1-4 can come to prefer to navigate egocentrically. However, it is also the case that the difference in complexity between Experiment 5 and Experiment 4 may play a key role in why a complete preference for allocentric navigation was observed in the latter experiment. Rats, for example, have been observed to preferentially navigate with reference to place information even after extensive training and reaching asymptotic test performance when required to navigate a complex variant of the open-field maze (Ruprecht et al., 2014).

Considering the allocentric-r test results from a different perspective it might also have been the case that in randomising the distal cues by changing their positions but not their identities a sub-optimal navigation strategy was encouraged. How this might happen in theory can be seen in a paper by Newman et al. (2007). They observed that people navigating a city environment are capable of using pure layout information, which includes the arrangement of streets and positions of buildings but not their identities, to navigate between locations when the identities of all the features that compose that environment have changed. However, when the

identities of only a select few key buildings were changed participants' navigation performance degraded (Newman et al., 2007). This suggests that, when available, the identities of these salient features may be preferentially relied upon to the extent that they are utilised even under circumstances where the navigator is in possession of knowledge that would allow her to solve the task optimally. A preference for learning about and utilising a particular type of navigation cue, even under circumstances where it is suboptimal to do so, has also been observed in rats. When trained to find a platform on the MWM that was a long distance from the starting location rats preferentially make use of landmark information regardless of whether it is predictive of the platform and despite their possessing the ability to find the platform using an egocentric strategy when forced to do so (Tamara et al., 2010). Rats will also preferentially learn about and navigate with reference to a salient light cue on the MWM regardless of whether it is predictive of the platform location (Martin et al., 2003) and, more generally, have also been observed to make preferential use of ambiguous geometric cues despite the presence of more predictive feature information (Cheng, 1986). It has also been observed that some people will inflexibly persevere with a preferred strategy in cases where it is sub-optimal to do so (Etchamendy & Bohbot, 2007). While it needs to be kept in mind that Newman et al. (2007) used an environmental scale space and therefore were likely to have been assessing different facets of navigation, if the potential conclusions from their research are generalizable to the environments used here it may have been the case that a preferential use of landmark identities on the allocentric-r test adversely affected how participants navigated. As has been pointed out previously, if participants had attended to the arrangement of the skybox during training they would have been able to correctly identify the target quadrant in the allocentric-r test and, like the use of layout information observed by Newman et al. (2007), might have been more willing to attend to, or make use of, this source of

information in a completely randomised environment. Random performance even under these circumstances would further strengthen the hypothesis that the presence of landmarks was strongly overshadowing the acquisition of any other allocentric information. This consideration of sub-optimal strategies relates to both the multi and single landmark strategies used to solve the allocentric-r test as both fail to locate the correct quadrant in circumstances under which it is possible to do so. It may have also been the case that participants interpreted the allocentric-r environment as an entirely new space, separate from the other environments they had been trained and tested in. In this scenario the randomised performance would be a consequence of participants not transferring any knowledge they had acquired during training to the new environment. However, this is unlikely to have been the case here. No participant was ever recorded as questioning whether they were present in a new space on the allocentric-r test. Participants treating the allocentric-r environment as a new space would also not explain why the systematic preference to approximate the target near the Christ the Redeemer landmark was observed in Experiment 3.

The results observed on the egocentric tests were less consistent between experiments than the allocentric test results. However, it can be reasonably concluded that participants were, at least in Experiments 1-4, acquiring angular direction and time-based distance information about the spatial relationship between the start and target locations. Experiment 5 revealed that by simplifying the training process participants were capable of acquiring a route-based strategy that they could come to preferentially employ over an allocentric strategy. Of particular interest in the egocentric strategies of Experiments 1-4 is the preference for participants to develop a strategy that was entirely dependent upon idiothetic information. The distance component of idiothetic information in particular is generally thought of as been strongly related to the

podokinetic information provided by locomotion (Chrastil & Warren, 2012; A. R. Richardson & Waller, 2007). The absence of this source of idiothetic information does not preclude the acquisition of distance information; however, it is interesting to note that participants developed, whether deliberately or otherwise, this entirely self-referential egocentric strategy despite the presence of the plank maze. Due to their uniform length the planks of the maze could theoretically have served as integer based approximations of travel distance that might have been easier to keep track of than an internal approximation of time. As participants were acquiring and making use of distance information in these experiments it might be interesting to look at the effect of locomotion as the method for controlling movement on the knowledge that they develop. Differences in egocentric test performance, or lack thereof, could potentially be informative as to whether the travel time-based approximations of distance used here were a suboptimal proxy adopted out of necessity or an ideal way to measure distance in environments like the ones used here. As has been discussed previously the allocentric preference that participants displayed in Experiment 4, and by extension were likely to have developed in Experiments 1-3, was likely the result of the relative ease with which the strategy could be acquired and reliably employed. Therefore if locomotion was observed to improve participants' ability to acquire distance information it might also be seen to have a knock-on effect on how people preferentially navigate.

There are multiple possible explanations for the appearance of preferential egocentric navigators in Experiment 5. One explanation suggested by research into egocentric strategy use in rodents is that the egocentric-choice navigators were simply executing a habitual behavioural response they had acquired with training. While this is a possibility it is worth noting that it would suggest people are capable of following a habitual behaviour for the, on average, two

minutes of travel time necessary to move from the start to the target location while ignoring the entirely novel views of the environment to which they were exposed. A similar degree of exclusion of external information while executing a habitual navigation response has been observed in rats, where they have been seen to run in to walls or past food when traversing familiar paths that have been shortened or had their target locations moved (Leising & Blaisdell, 2009). However, whether people can develop habitual navigation responses that extreme is not yet known as it does not appear that much research has looked in to it. That egocentric-choice navigators appear to have been unaffected by the entirely new views of the environment presented to them is a point that needs to be stressed. This is because unlike with the training environments of Experiments 1-4, due to the constrained and simplified maze used in Experiment 5, participants would have had no experience navigating within, to, or from most of the quadrant in which the conflict test trial was started. These results also contradict the idea that allocentric navigation strategies are employed in situations where the navigators are started from an unfamiliar place in the environment (Tamara & Timberlake, 2011); however, this finding may relate only to rats. People have been shown to be capable of developing route based strategies that are entirely independent of environmental information; however, it is a cognitively effortful process typically seen when distinguishing features of the navigated world are removed (Tlauka & Wilson, 1994). If route navigators were found to be navigating without any awareness of the change in their position this strategy would necessarily have developed in a way that excluded external information.

The observation that all participants preferred to not only make the initial choice to follow an allocentric strategy but to never shift in their quadrant of search for the entirety of the conflict test appears to strongly suggest that participants in Experiments 1-4 were of the belief

that the target location was fixed relative to the distal features of the environment. If participants conceptualised the target as relative to the external environment it would not be expected that they would ever think to search the quadrant suggested by their egocentric knowledge as such a possibility would not make sense in the context of an allocentric reference frame. However, Experiment 5, and the appearance of some participants who preferentially employed an egocentric strategy, suggests that this preference to localise the target relative to the distal environmental cues is one that may, under certain circumstances, be affected by the nature of the environment in which people are trained. There is precedence for this idea, with people trained to navigate in a vMWM equivalent that selectively biased them towards one strategy or the other observed to preferentially navigate using the method promoted by their training environment when tested in a maze in which both were equally efficient (Livingstone-Lee, Zeman, Gillingham, & Skelton, 2014). However, in that experiment participants were trained in the bias environments to localise the target relative to distal or proximal environmental cues (Livingstone-Lee et al., 2014) and were therefore in either case of the belief that the target was fixed relative to some landmark feature. It may have been that a similar biasing effect occurred in Experiment 5 as a result of the constrained number of possible ways that the target location could be reached. Unlike Experiments 1-4 where the target location could be approached from three different directions the target in Experiment 5 was always only ever experienced as coming at the end of the plank at the end of the maze. This variation between the two maze types might have had the effect of biasing some participants towards the belief that the target was fixed to a particular plank in the maze. In turn this conceptualisation of the target location might have promoted the acquisition of a maze-dependent strategy during training which resulted in the more accurate route knowledge seen in the egocentric-choice navigators.

More generally, it can be seen that the results observed across all five experiments show clearly that people were able to, and did, acquire different types of information across training. This acquisition appeared to occur across different timescales for allocentric and egocentric information; however, the early acquisition of relatively accurate allocentric knowledge was not found to block participants from later developing a separately employable and reliable egocentric strategy. This development appeared to be in spite of the fact that early accuracy on the allocentric test trials suggests acquisition of another, separate strategy would be unnecessary. The allocentric-r results of Experiment 3 further show that participants may have also been refining their allocentric knowledge into a simpler navigation strategy in parallel with their acquisition of egocentric knowledge. However, while both allocentric and egocentric information was seen to develop here the results observed also, as expected, contradict those of Igloi et al. (2009) that were interpreted as showing the simultaneous acquisition of allocentric and sequential egocentric information. Here it can be seen that with a more complex task sequential egocentric knowledge is only observed to develop in some participants under particular environmental conditions and is, more typically, not observed at all. Relatively accurate allocentric knowledge, however, was observed to consistently develop within five training trials. The differences in the results between the experiments reported here and those of Igloi et al. (2009) can be seen to help stress the importance of taking the complexity of the training environment into consideration when attempting to answer questions regarding the acquisition of spatial knowledge. These observations can be seen to be in contrast to the main principles of associative learning that would suggest that the later acquisition of information would not be expected to occur. However, the acquisition of information in parallel in the training environments used here does not mean that associative mechanisms were not affecting how

learning proceeded in ways that were not tested for. While the conflict tests looked at which strategy is preferentially employed, how the two strategies combined during training is an alternative avenue of possible interaction that was not looked at here. This interaction can be conceived of as proceeding in one of two ways; either the two systems are combined to produce one congruent output or they are separate producers of incongruent behaviours. Congruent behaviour can be seen in how the traditional MWM is observed to be solved, with navigation to the platform the result of information about the distal environmental cues and the perceived distance between the navigator and the pool boundary (Hamilton et al., 2008; Kosaki et al., 2015). The plus maze demonstrates incongruent behaviour as the place and response strategies are independent and unrelated (Kosaki et al., 2015). As Kosaki et al. (2015) point out, the distinction between these two possibilities is important as they predict different interactions. If the two systems combine, it needs to be considered whether the presence of multiple strategies is affecting the strength of learning acquired for each separate component system, while incongruent behaviour would suggest that degrading the learning of one system should produce improved performance in the other (Kosaki et al., 2015). Therefore it may be fruitful in the future to look for differences in how learning proceeds in the same environment under circumstances where one type of knowledge or the other can no longer be acquired. Having participants perform concurrent distractor tasks that make the acquisition of a particular type of knowledge more difficult may be one possible way to achieve this inhibition of a navigation system temporarily. Improved performance on the unimpaired system would be consistent with the findings of Packard and Goodman (2013), who observed that rats could acquire distinct place and response strategies in a given environment but also had their learning affected by the

selective inhibition of the neural correlates of one system or the other, such that lesioning improved the performance of the undamaged system.

Another aspect that might be important to consider is the potential leeway granted to participants by the fixed time limit of the training trials, a factor that might have interacted with the accuracy of the knowledge developed. The timescale that the development of spatial knowledge followed might also have been affected. As participants were not informed of the number of trials they would need to complete any motivation to complete a given trial faster would have likely been almost entirely self-generated. Therefore while faster and more efficient navigation was an obvious consequence of training that is not to say that it was necessarily an intentional goal in all cases. This might have interacted specifically with how participants developed allocentric knowledge. As was observed across Experiments 1-4, participants were able to localise the target to the correct pool quadrant within five training trials using only the landmarks in the environment. However, lacking any external motivation to better approximate the target location, participants would not be expected to exert any, or extra, effort to improve on how accurate this localisation was. This hypothesis that participants navigated with the aim of minimising the effort exerted fits with prior observations about how people preferentially employ navigation strategies (Condappa & Wiener, 2014; Wiener et al., 2013). It is also consistent with the gradual shift towards simpler, habitual strategies with training that is observed in both humans and rodents (Iaria et al., 2003; Packard & McGaugh, 1996; Schmitzer-Torbert, 2007). Taken altogether this suggests that a simple, relatively accurate strategy of navigating to, and searching within, the pool quadrant delineated by the landmark array was likely the first developed. With more training this strategy would likely lead to the repeated execution of similar behavioural responses. The turn from the starting position to face the target quadrant would be a

simple example of this. These behaviours would become more learned and familiar with repetition and, as they would be necessarily fixed relative to a constant starting position, likely formed the basis of the egocentric navigation strategy observed at the end of training. Participants could also simplify their allocentric strategy further still by learning to attend to only a single landmark as the quadrant delineator. If learning were to proceed in broadly this fashion it might be expected that the level of accuracy on the allocentric tests demonstrated here would not be reflective of the accuracy that participants could develop with sufficient motivation to do so. Providing this motivation would also move future experiments more in line with the navigation that is undertaken by people in the real world, where there are typically outcomes valued by the individual that result from their finding more efficient ways to navigate through an environment. A simple way this could be implemented under the current experimental protocol would be to reduce the time limit available to participants as they became better able to find the target location. This would remove the motivation gap in the current methodology where participants have reached a level of performance that means they are unlikely to feel pressured by the possibility of failure but lack any reason to attempt to solve a given trial faster.

Another aspect of navigation during training that might be informative to look at is how search and the acquisition of spatial knowledge interact with how deliberate navigation is required to be. In both the experiments used here and the traditional MWM navigators are able to happen upon the goal of their navigation by chance or as a result of the exhaustive searching of some constrained area of the environment. This allows for the possibility that navigation can proceed, from moment to moment, relatively aimlessly and still result in a successful trial. In the MWM experimenters can require rodents' search to be more deliberate by adding a timing element to the appearance of the platform such that it only appears after a certain amount of time

has been spent in the correct location (Buresova, Krekule, Zahalka, & Bures, 1985). Both the amount of time that needs to be spent in the correct location and the size of the target zone are variables that can be manipulated (Buresova et al., 1985). A similar timing element could be added to the appearance of the visual and audio cues that indicate the successful discovery of the target location to remove the ability of participants to simply happen across it during search. Such a change would be expected to shift how a person makes decisions about their navigation within a trial as an active commitment would need to be made to wait in any given location.

While the multiple tests used here were informative as to how different strategies and sources of information operated independently, real world navigation typically allows for the combination of multiple different types of information either simultaneously or in stages. A clear example of the latter can be seen on the more traditional MWM where rats appear to find the platform by utilising first the distal room cues followed by their position relative to the pool wall as a gauge of distance (Hamilton et al., 2008; Kosaki et al., 2015). There are several ways this sort of dual process navigation could be tested for in humans. Eye-trackers included in a HMD can be used to observe where participants are directing their attention in real time during training trials, and how which features of the world are overtly attended to changes over time could be used as a proxy measure of strategy engagement. Hamilton, Johnson et al. (2009) looked at how people directed their attention during trials on their vMWM environment, finding a similar trend of behaviour to that seen in rats, with overt attention directed first to room cues and then to the pool wall. Andersen et al. (2012) also used eye tracking to measure the relationship between attention directed to landmarks in the environment and the number of them available. Programming of virtual environments also allows experimenters more control over how navigation might be tested during a training trial. Environmental features could be distorted,

removed, or repositioned within a trial to tease apart the effect that particular manipulations have on different stages of navigation. An experiment employing a similar idea in rodents on the MWM found that manipulation of the information cues in the environment at different times only impaired performance if it occurred when that information source was likely to be in use by the rat's two-stage navigation system (Hamilton et al., 2004).

The most consistent observation in the results described here was the ability of participants to acquire, unprompted, different types of spatial information that were able to support relatively accurate navigation independently. It can be seen in reviewing these results together that there are a great many possible factors that can and do influence the navigation behaviours that people display. Here these included the amount of training required and the motivation provided to participants to improve their performance, the number and relative salience of the distal environmental cues, the information provided by the tools used to control movement, the simplicity of the strategies the environment could support, the complexity of the environment and the frames of reference suggested by environmental design. These results can be seen to further explicate how these factors, many of which have been observed previously in human or rodent research, interact with navigation. This strong correspondence with navigation behaviours observed previously in combination with the new insights provided suggests that the experimental methodology developed here may be a promising tool for use in future navigation research.

References

- Alyan, S., & Jander, R. (1997). Interplay of directional navigation mechanisms as a function of near-goal distance: Experiments with the house mouse. *Behavioural Processes*, 41(3), 245-255. doi: <http://dx.doi.org/10.1016/S0376-6357%2897%2900051-X>
- Andersen, N. E., Dahmani, L., Konishi, K., & Bohbot, V. D. (2012). Eye tracking, strategies, and sex differences in virtual navigation. *Neurobiology of Learning and Memory*, 97(1), 81-89. doi: <http://dx.doi.org/10.1016/j.nlm.2011.09.007>
- Asem, J. S., & Holland, P. C. (2013). Immediate response strategy and shift to place strategy in submerged T-maze. *Behavioral Neuroscience*, 127(6), 854-859. doi: <http://dx.doi.org/10.1037/a0034686>
- Biegler, R. (2000). Possible uses of path integration in animal navigation. *Animal Learning & Behavior*, 28(3), 257-277. doi: <http://dx.doi.org/10.3758/BF03200260>
- Biegler, R., & Morris, R. (1996). Landmark stability: Further studies pointing to a role in spatial learning. *The Quarterly Journal of Experimental Psychology B: Comparative and Physiological Psychology*, 49B(4), 307-345.
- Brown, M. F., & Moore, J. A. (1997). In the dark II: Spatial choice when access to extrinsic spatial cues is eliminated. *Animal Learning & Behavior*, 25(3), 335-346.
- Buresova, O., Krekule, I., Zahalka, A., & Bures, J. (1985). On-demand platform improves accuracy of the Morris water maze procedure. *Journal of neuroscience methods*, 15(1), 63-72.
- Caduff, D., & Timpf, S. (2008). On the assessment of landmark salience for human navigation. *Cognitive Processing*, 9(4), 249-267.
- Capaldi, E., Robinson, G., & Fahrbach, S. (1999). Neuroethology of spatial learning: the birds and the bees. *Annual Review of Psychology*, 50(1), 651-682.
- Cassel, R., Kelche, C., Lecourtier, L., & Cassel, J.-C. (2012). The match/mismatch of visuo-spatial cues between acquisition and retrieval contexts influences the expression of response vs. place

- memory in rats. *Behavioural Brain Research*, 230(2), 333-342. doi: <http://dx.doi.org/10.1016/j.bbr.2012.02.021>
- Chamizo, V. (2003). Acquisition of knowledge about spatial location: Assessing the generality of the mechanism of learning. *The Quarterly Journal of Experimental Psychology B: Comparative and Physiological Psychology*, 56B(1), 102-113. doi: <http://dx.doi.org/10.1080/02724990244000205>
- Chamizo, V., Manteiga, R., Rodrigo, T., & Mackintosh, N. (2006). Competition between landmarks in spatial learning: The role of proximity to the goal. *Behavioural Processes*, 71(1), 59-65. doi: <http://dx.doi.org/10.1016/j.beproc.2005.11.003>
- Chamizo, V., Roderigo, T., & Mackintosh, N. (2006). Spatial Integration With Rats. *Learning & Behavior*, 34(4), 348-354. doi: <http://dx.doi.org/10.3758/BF03193198>
- Chamizo, V., & Rodrigo, T. (2004). Effect of absolute spatial proximity between a landmark and a goal. *Learning and Motivation*, 35(2), 102-114. doi: <http://dx.doi.org/10.1016/S0023-9690%2803%2900059-6>
- Chan, E., Baumann, O., Bellgrove, M. A., & Mattingley, J. B. (2012). From objects to landmarks: The function of visual location information in spatial navigation. *Frontiers in Psychology*, 3, 304. doi: <http://dx.doi.org/10.3389/fpsyg.2012.00304>
- Cheeseman, J. F., Millar, C. D., Greggers, U., Lehmann, K., Pawley, M. D., Gallistel, C. R., . . . Menzel, R. (2014a). Reply to Cheung et al.: The cognitive map hypothesis remains the best interpretation of the data in honeybee navigation. *Proceedings of the National Academy of Sciences of the United States of America*, 111(42), E4398. doi: <http://dx.doi.org/10.1073/pnas.1415738111>
- Cheeseman, J. F., Millar, C. D., Greggers, U., Lehmann, K., Pawley, M. D., Gallistel, C. R., . . . Menzel, R. (2014b). Way-finding in displaced clock-shifted bees proves bees use a cognitive map. *PNAS Proceedings of the National Academy of Sciences of the United States of America*, 111(24), 8949-8954. doi: <http://dx.doi.org/10.1073/pnas.1408039111>
- Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition*, 23(2), 149-178.

- Cheng, K. (1999a). Landmark-based spatial search in honeybees. I. Use of elements and interlandmark angles. *Animal Cognition*, 2(2), 73-78. doi: <http://dx.doi.org/10.1007/s100710050026>
- Cheng, K. (1999b). Landmark-based spatial search in honeybees. II. Using gaps and blocks. *Animal Cognition*, 2(2), 79-90. doi: <http://dx.doi.org/10.1007/s100710050027>
- Cheng, K. (2000). How honeybees find a place: Lessons from a simple mind. *Learning & Behavior*, 28(1), 1-15.
- Cheng, K., & Graham, P. (2013). Spatial memory: Place learning, piloting, and route knowledge *Handbook of spatial cognition* (pp. 137-153). Washington, DC: American Psychological Association; US.
- Cheng, K., & Spetch, M. L. (1998). Mechanisms of landmark use in mammals and birds *Spatial representation in animals* (pp. 1-17). New York, NY: Oxford University Press; US.
- Cheng, K., Spetch, M. L., Kelly, D. M., & Bingman, V. P. (2006). Small-scale spatial cognition in pigeons. *Behavioural Processes*, 72(2), 115-127. doi: <http://dx.doi.org/10.1016/j.beproc.2005.11.018>
- Cheung, A., Collett, M., Collett, T. S., Dewar, A., Dyer, F., Graham, P., . . . Zeil, J. (2014). Still no convincing evidence for cognitive map use by honeybees. *Proceedings of the National Academy of Sciences of the United States of America*, 111(42), E4396-4397. doi: <http://dx.doi.org/10.1073/pnas.1413581111>
- Chrastil, E. R. (2013). Neural evidence supports a novel framework for spatial navigation. *Psychonomic Bulletin & Review*, 20(2), 208-227. doi: <http://dx.doi.org/10.3758/s13423-012-0351-6>
- Chrastil, E. R., & Warren, W. H. (2012). Active and passive contributions to spatial learning. *Psychonomic Bulletin & Review*, 19(1), 1-23. doi: <http://dx.doi.org/10.3758/s13423-011-0182-x>
- 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. doi: <http://dx.doi.org/10.1037/a0032382>

- 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.
- Civile, C., Chamizo, V., Mackintosh, N., & McLaren, I. (2014). The effect of disrupting configural information on rats' performance in the Morris water maze. *Learning and Motivation*, 48, 55-66. doi: <http://dx.doi.org/10.1016/j.lmot.2014.07.001>
- Cole, M. R., Clipperton, A., & Walt, C. (2007). Place versus response learning in rats. *Learning & Behavior*, 35(4), 214-224. doi: <http://dx.doi.org/10.3758/BF03206427>
- Collett, M., Collett, T. S., Bisch, S., & Wehner, R. (1998). Local and global vectors in desert ant navigation. *Nature*, 394(6690), 269-272.
- Collett, T. S. (1996). Insect navigation en route to the goal: multiple strategies for the use of landmarks. *Journal of Experimental Biology*, 199(1), 227-235.
- Collett, T. S., & Graham, P. (2004). Animal Navigation: Path Integration, Visual Landmarks and Cognitive Maps. *Current Biology*, 14(12), R475-R477. doi: <http://dx.doi.org/10.1016/j.cub.2004.06.013>
- Condappa, O., & Wiener, J. M. (2014). Human place and response learning: Navigation strategy selection, pupil size and gaze behavior. *Psychological Research* Dec(Pagination), No Pagination Specified. doi: <http://dx.doi.org/10.1007/s00426-014-0642-9>
- Dahmani, L., Ledoux, A.-A., Boyer, P., & Bohbot, V. D. (2012). Wayfinding: The effects of large displays and 3-D perception. *Behavior Research Methods*, 44(2), 447-454.
- Dalgarno, B., Bennett, S., & Harper, B. (2010). The importance of active exploration, optical flow, and task alignment for spatial learning in desktop 3D environments. *Human-Computer Interaction*, 25(1), 25-66. doi: <http://dx.doi.org/10.1080/07370020903586670>
- Di Fiore, A., & Suarez, S. A. (2007). Route-based travel and shared routes in sympatric spider and woolly monkeys: cognitive and evolutionary implications. *Animal Cognition*, 10(3), 317-329.

- Dolins, F. L., Klimowicz, C., Kelley, J., & Menzel, C. R. (2014). Using virtual reality to investigate comparative spatial cognitive abilities in chimpanzees and humans. *American Journal of Primatology*, 76(5), 496-513.
- Etchamendy, N., & Bohbot, V. D. (2007). Spontaneous navigational strategies and performance in the virtual town. *Hippocampus*, 17(8), 595-599.
- Etienne, A. S., & Jeffery, K. J. (2004). Path Integration in Mammals. *Hippocampus*, 14(2), 180-192. doi: <http://dx.doi.org/10.1002/hipo.10173>
- Fouquet, C., Babayan, B. M., Watilliaux, A., Bontempi, B., Tobin, C., & Rondi-Reig, L. (2013). Complementary roles of the hippocampus and the dorsomedial striatum during spatial and sequence-based navigation behavior. *PLoS ONE*, 8(6), e67232.
- 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 & Behavioral Neuroscience*, 14(4), 1375-1391. doi: <http://dx.doi.org/10.3758/s13415-014-0279-6>
- Gardner, R. S., Uttaro, M. R., Fleming, S. E., Suarez, D. F., Ascoli, G. A., & Dumas, T. C. (2013). A secondary working memory challenge preserves primary place strategies despite overtraining. *Learning & Memory*, 20(11), 648-656. doi: <http://dx.doi.org/10.1101/lm.031336.113>
- Gibson, B. M., & Shettleworth, S. J. (2005). Place Versus Response Learning Revisited: Tests of Blocking on the Radial Maze. *Behavioral Neuroscience*, 119(2), 567-586. doi: <http://dx.doi.org/10.1037/0735-7044.119.2.567>
- Graham, P., & Cheng, K. (2009). Ants use the panoramic skyline as a visual cue during navigation. *Current Biology*, 19(20), R935-R937.
- Gramann, K., Muller, H. J., Eick, E.-M., & Schonebeck, B. (2005). Evidence of Separable Spatial Representations in a Virtual Navigation Task. *Journal of Experimental Psychology: Human Perception and Performance*, 31(6), 1199-1223. doi: <http://dx.doi.org/10.1037/0096-1523.31.6.1199>

- Hamilton, D. A., Akers, K. G., Johnson, T. E., Rice, J. P., Candelaria, F. T., & Redhead, E. S. (2009). Evidence for a shift from place navigation to directional responding in one variant of the Morris water task. *Journal of Experimental Psychology: Animal Behavior Processes*, *35*(2), 271-278. doi: <http://dx.doi.org/10.1037/a0013260>
- Hamilton, D. A., Akers, K. G., Johnson, T. E., Rice, J. P., Candelaria, F. T., Sutherland, R. J., . . . Redhead, E. S. (2008). The relative influence of place and direction in the Morris water task. *Journal of Experimental Psychology: Animal Behavior Processes*, *34*(1), 31-53. doi: <http://dx.doi.org/10.1037/0097-7403.34.1.31>
- Hamilton, D. A., Akers, K. G., Weisend, M. P., & Sutherland, R. J. (2007). How do room and apparatus cues control navigation in the Morris water task? Evidence for distinct contributions to a movement vector. *Journal of Experimental Psychology: Animal Behavior Processes*, *33*(2), 100-114. doi: <http://dx.doi.org/10.1037/0097-7403.33.2.100>
- Hamilton, D. A., Driscoll, I., & Sutherland, R. J. (2002). Human place learning in a virtual Morris water task: Some important constraints on the flexibility of place navigation. *Behavioural Brain Research*, *129*(1-2), 159-170. doi: <http://dx.doi.org/10.1016/S0166-4328%2801%2900343-6>
- Hamilton, D. A., Johnson, T. E., Redhead, E. S., & Verney, S. P. (2009). Control of rodent and human spatial navigation by room and apparatus cues. *Behavioural Processes*, *81*(2), 154-169. doi: <http://dx.doi.org/10.1016/j.beproc.2008.12.003>
- Hamilton, D. A., Rosenfelt, C. S., & Wishaw, I. Q. (2004). Sequential control of navigation by locale and taxon cues in the Morris water task. *Behavioural Brain Research*, *154*(2), 385-397. doi: <http://dx.doi.org/10.1016/j.bbr.2004.03.005>
- Hamilton, D. A., & Sutherland, R. J. (1999). Blocking in human place learning: Evidence from virtual navigation. *Psychobiology*, *27*(4), 453-461.
- Hardt, O., Hupbach, A., & Nadel, L. (2009). Factors moderating blocking in human place learning: The role of task instructions. *Learning & Behavior*, *37*(1), 42-59. doi: <http://dx.doi.org/10.3758/LB.37.1.42>

- Harvey, D. R., Brant, L., & Commins, S. (2009). Differences in cue-dependent spatial navigation may be revealed by in-depth swimming analysis. *Behavioural Processes*, 82(2), 190-197. doi: <http://dx.doi.org/10.1016/j.beproc.2009.06.008>
- Hodgson, E., Bachmann, E., & Waller, D. (2011). Redirected walking to explore virtual environments: Assessing the potential for spatial interference. *ACM Transactions on Applied Perception*, 8(4), 1-22. doi: <http://dx.doi.org/10.1145/2043603.2043604>
- Hodgson, E., Bachmann, E. R., Vincent, D., Zmuda, M., Waller, D., & Calusdian, J. (2015). WeaVR: a self-contained and wearable immersive virtual environment simulation system. *Behavior Research Methods*, 47(1), 296-307.
- Horne, M. R., Martin, G. M., Harley, C. W., & Skinner, D. M. (2007). Where am I? Distal cues use requires sensitivity to start location change in the rat. *Journal of Experimental Psychology: Animal Behavior Processes*, 33(2), 92-99. doi: <http://dx.doi.org/10.1037/0097-7403.33.2.92>
- Iaria, G., Petrides, M., Dagher, A., Pike, B., & Bohbot, V. D. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: variability and change with practice. *Journal of neuroscience*, 23(13), 5945-5952.
- Igloi, 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. doi: <http://dx.doi.org/10.1002/hipo.20595>
- Ishikawa, T., & Montello, D. R. (2006). Spatial knowledge acquisition from direct experience in the environment: Individual differences in the development of metric knowledge and the integration of separately learned places. *Cognitive Psychology*, 52(2), 93-129. doi: <http://dx.doi.org/10.1016/j.cogpsych.2005.08.003>
- Jacobs, W., Laurance, H. E., & Thomas, K. G. (1997). Place learning in virtual space I: Acquisition, overshadowing, and transfer. *Learning and Motivation*, 28(4), 521-541. doi: <http://dx.doi.org/10.1006/lmot.1997.0977>

- 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. doi: <http://dx.doi.org/10.1016/j.bbr.2004.10.015>
- Kelly, D. M., & Gibson, B. M. (2007). Spatial navigation: Spatial learning in real and virtual environments. *Comparative Cognition & Behavior Reviews*, 2(1), 111-124.
- Koenig, S., Crucian, G., Dalrymple-Alford, J., & Dunser, A. (2011). Assessing navigation in real and virtual environments: a validation study. *International Journal on Disability and Human Development*, 10(4), 325-330. doi: <http://dx.doi.org/10.1515/IJDHD.2011.050>
- Koppen, J. R., Winter, S. S., Loda, E. L., Apgar, B. P., Grimelli, D., Hamilton, D. A., & Wallace, D. G. (2013). Analysis of movement kinematics on analogous spatial learning tasks demonstrates conservation of direction and distance estimation across humans (*Homo sapiens*) and rats (*Rattus norvegicus*). *Journal of Comparative Psychology*, 127(2), 179-193. doi: <http://dx.doi.org/10.1037/a0030162>
- Kosaki, Y., Poulter, S. L., Austen, J. M., & McGregor, A. (2015). Dorsolateral striatal lesions impair navigation based on landmark-goal vectors but facilitate spatial learning based on a "cognitive map.". *Learning & Memory*, 22(3), 179-191.
- Lafon, M., Vidal, M., & Berthoz, A. (2009). Selective influence of prior allocentric knowledge on the kinesthetic learning of a path. *Experimental Brain Research*, 194(4), 541-552. doi: <http://dx.doi.org/10.1007/s00221-009-1728-2>
- Larrue, F., Sauzeon, H., Wallet, G., Foloppe, D., Cazalets, J.-R., Gross, C., & N'Kaoua, B. (2014). Influence of body-centered information on the transfer of spatial learning from a virtual to a real environment. *Journal of Cognitive Psychology*, 26(8), 906-918. doi: <http://dx.doi.org/10.1080/20445911.2014.965714>
- Leising, K. J., & Blaisdell, A. P. (2009). Associative basis of landmark learning and integration in vertebrates. *Comparative Cognition & Behavior Reviews*, 4, 80-102. doi: <http://dx.doi.org/10.3819/ccbr.2009.40010>

- 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*, 30-43. doi: <http://dx.doi.org/10.1016/j.lmot.2013.09.003>
- Loomis, J. M., Blascovich, J. J., & Beall, A. C. (1999). Immersive virtual environment technology as a basic research tool in psychology. *Behavior research methods, instruments, & computers*, *31*(4), 557-564.
- Maei, H. R., Zaslavsky, K., Teixeira, C. M., & Frankland, P. W. (2009). What is the most sensitive measure of water maze probe test performance? *Frontiers in Integrative Neuroscience*, *3*, 4. doi: <http://dx.doi.org/10.3389/neuro.07.004.2009>
- March, J., Chamizo, V., & Mackintosh, N. (1992). Reciprocal overshadowing between intra-maze and extra-maze cues. *The Quarterly Journal of Experimental Psychology B: Comparative and Physiological Psychology*, *45B*(1), 49-63.
- Martin, G. M., Walker, K. M., & Skinner, D. M. (2003). A single unstable visual cue impairs spatial learning in a water maze. *Learning and Motivation*, *34*(1), 87-103. doi: <http://dx.doi.org/10.1016/S0023-9690%2802%2900502-7>
- McGregor, A., Good, M. A., & Pearce, J. M. (2004). Absence of an Interaction Between Navigational Strategies Based on Local and Distal Landmarks. *Journal of Experimental Psychology: Animal Behavior Processes*, *30*(1), 34-44. doi: <http://dx.doi.org/10.1037/0097-7403.30.1.34>
- Meijer, F., Geudeke, B. L., & van den Broek, E. L. (2009). Navigating through virtual environments: Visual realism improves spatial cognition. *CyberPsychology & Behavior*, *12*(5), 517-521. doi: <http://dx.doi.org/10.1089/cpb.2009.0053>
- Meilinger, T., Frankenstein, J., & Bulthoff, H. H. (2013). Learning to navigate: Experience versus maps. *Cognition*, *129*(1), 24-30. doi: <http://dx.doi.org/10.1016/j.cognition.2013.05.013>
- Meng, F., Zhang, W., & Yang, R. (2014). The development of a panorama manifestation virtual reality system for navigation and a usability comparison with a desktop system. *Behaviour & Information Technology*, *33*(2), 132-142. doi: <http://dx.doi.org/10.1080/0144929X.2013.857432>

- Morris, R. (1984). Developments of a water-maze procedure for studying spatial learning in the rat. *Journal of neuroscience methods*, *11*(1), 47-60.
- Mou, W., & Zhou, R. (2013). Defining a boundary in goal localization: Infinite number of points or extended surfaces. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *39*(4), 1115-1127. doi: <http://dx.doi.org/10.1037/a0030535>
- Newman, E. L., Caplan, J. B., Kirschen, M. P., Korolev, I. O., Sekuler, R., & Kahana, M. J. (2007). Learning your way around town: How virtual taxicab drivers learn to use both layout and landmark information. *Cognition*, *104*(2), 231-253. doi: <http://dx.doi.org/10.1016/j.cognition.2006.05.013>
- O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*: Oxford: Clarendon Press.
- Packard, M. G., & Goodman, J. (2013). Factors that influence the relative use of multiple memory systems. *Hippocampus*, *23*(11), 1044-1052.
- 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.
- Pan, J., Kennedy, E. H., Pickering, T., Menzel, C. R., Stone, B. W., & Frigaszy, D. M. (2011). Development of maze navigation by tufted capuchins (*Cebus apella*). *Behavioural Processes*, *86*(2), 206-215.
- Prados, J., & Trobalon, J. B. (1998). Locating an invisible goal in a water maze requires at least two landmarks. *Psychobiology*, *26*(1), 42-48.
- Redish, A. D., & Ekstrom, A. (2013). Hippocampus and related areas: What the place cell literature tells us about cognitive maps in rats and humans *Handbook of spatial cognition* (pp. 15-34). Washington, DC: American Psychological Association; US.
- Richardson, A. E., & Collaer, M. L. (2011). Virtual navigation performance: The relationship to field of view and prior video gaming experience. *Perceptual and Motor Skills*, *112*(2), 477-498. doi: <http://dx.doi.org/10.2466/22.24.PMS.112.2.477-498>

- Richardson, A. R., & Waller, D. (2007). Interaction with an immersive virtual environment corrects users' distance estimates. *Human Factors*, 49(3), 507-517.
- Riecke, B. E., Sigurdarson, S., & Milne, A. P. (2012). Moving through virtual reality without moving? *Cognitive Processing*, 13 Suppl 1, S293-297. doi: <http://dx.doi.org/10.1007/s10339-012-0491-7>
- Roberts, A. D., & Pearce, J. M. (1998). Control of spatial behavior by an unstable landmark. *Journal of Experimental Psychology: Animal Behavior Processes*, 24(2), 172-184. doi: <http://dx.doi.org/10.1037/0097-7403.24.2.172>
- Roberts, A. D., & Pearce, J. M. (1999). Blocking in the Morris swimming pool. *Journal of Experimental Psychology: Animal Behavior Processes*, 25(2), 225-235. doi: <http://dx.doi.org/10.1037/0097-7403.25.2.225>
- Rosati, A. G. (2015). Context influences spatial frames of reference in bonobos (*Pan paniscus*). *Behaviour*, 152(3-4), 375-406. doi: <http://dx.doi.org/10.1163/1568539X-00003189>
- Ruddle, R. A., & Peruch, P. (2004). Effects of proprioceptive feedback and environmental characteristics on spatial learning in virtual environments. *International Journal of Human-Computer Studies*, 60(3), 299-306. doi: <http://dx.doi.org/10.1016/j.ijhcs.2003.10.001>
- Ruddle, R. A., Volkova, E., Mohler, B., & Bulthoff, H. H. (2011). The effect of landmark and body-based sensory information on route knowledge. *Memory & Cognition*, 39(4), 686-699. doi: <http://dx.doi.org/10.3758/s13421-010-0054-z>
- Ruprecht, C. M., Taylor, C., Wolf, J. E., & Leising, K. J. (2014). Task complexity modifies the search strategy of rats. *Behavioural Brain Research*, 258, 208-217. doi: <http://dx.doi.org/10.1016/j.bbr.2013.10.009>
- Schmitzer-Torbert, N. (2007). Place and response learning in human virtual navigation: Behavioral measures and gender differences. *Behavioral Neuroscience*, 121(2), 277-290. doi: <http://dx.doi.org/10.1037/0735-7044.121.2.277>

- Shore, D. I., Stanford, L., MacInnes, W., Klein, R. M., & Brown, R. E. (2001). Of mice and men: Virtual Hebb-Williams mazes permit comparison of spatial learning across species. *Cognitive, Affective & Behavioral Neuroscience*, 1(1), 83-89. doi: <http://dx.doi.org/10.3758/CABN.1.1.83>
- Skinner, D. M., Etchegary, C. M., Ekert-Maret, E. C., Baker, C. J., Harley, C. W., Evans, J. H., & Martin, G. M. (2003). An analysis of response, direction and place learning in an open field and T maze. *Journal of Experimental Psychology: Animal Behavior Processes*, 29(1), 3-13. doi: <http://dx.doi.org/10.1037/0097-7403.29.1.3>
- Skinner, D. M., Horne, M. R., Murphy, K. E., & Martin, G. M. (2010). Rats' orientation is more important than start point location for successful place learning. *Journal of Experimental Psychology: Animal Behavior Processes*, 36(1), 110-116. doi: <http://dx.doi.org/10.1037/a0015773>
- Slobounov, S. M., Ray, W., Johnson, B., Slobounov, E., & Newell, K. M. (2015). Modulation of cortical activity in 2D versus 3D virtual reality environments: An EEG study. *International Journal of Psychophysiology*, 95(3), 254-260. doi: <http://dx.doi.org/10.1016/j.ijpsycho.2014.11.003>
- Smith, C. (1984). The relationship between the pleasingness of landmarks and the judgement of distance in cognitive maps. *Journal of Environmental Psychology*, 4(3), 229-234.
- Spetch, M. L. (1995). Overshadowing in landmark learning: Touch-screen studies with pigeons and humans. *Journal of Experimental Psychology: Animal Behavior Processes*, 21(2), 166-181. doi: <http://dx.doi.org/10.1037/0097-7403.21.2.166>
- Spetch, M. L., Cheng, K., & MacDonald, S. E. (1996). Learning the configuration of a landmark array: I. Touch-screen studies with pigeons and humans. *Journal of Comparative Psychology*, 110(1), 55-68. doi: <http://dx.doi.org/10.1037/0735-7036.110.1.55>
- Srinivasan, M., Zhang, S., Berry, J., Cheng, K., & Zhu, H. (1999). Honeybee navigation: linear perception of short distances travelled. *Journal of Comparative Physiology A*, 185(3), 239-245.
- Srinivasan, M. V. (2014). Going with the flow: a brief history of the study of the honeybee's navigational 'odometer'. *Journal of Comparative Physiology A-Sensory Neural & Behavioral Physiology*, 200(6), 563-573. doi: <http://dx.doi.org/10.1007/s00359-014-0902-6>

- Sturz, B. R., Bodily, K. D., Katz, J. S., & Kelly, D. M. (2009). Evidence against integration of spatial maps in humans: Generality across real and virtual environments. *Animal Cognition*, *12*(2), 237-247. doi: <http://dx.doi.org/10.1007/s10071-008-0182-z>
- Sturz, B. R., Cooke, S., & Bodily, K. D. (2011). Solving for two unknowns: An extension of vector-based models of landmark-based navigation. *Journal of Experimental Psychology: Animal Behavior Processes*, *37*(3), 368-374. doi: <http://dx.doi.org/10.1037/a0022938>
- Sutherland, R., Chew, G., Baker, J., & Linggard, R. (1987). Some limitations on the use of distal cues in place navigation by rats. *Psychobiology*, *15*(1), 48-57.
- Suzuki, S., Augerinos, G., & Black, A. H. (1980). Stimulus control of spatial behavior on the eight-arm maze in rats. *Learning and Motivation*, *11*(1), 1-18. doi: <http://dx.doi.org/10.1016/0023-9690%2880%2990018-1>
- Tamara, C., Leffel, J., & Timberlake, W. (2010). Egocentric and allocentric search: Effects of platform distance and environmental cues. *Animal Cognition*, *13*(3), 565-581. doi: <http://dx.doi.org/10.1007/s10071-009-0307-z>
- Tamara, C., & Timberlake, W. (2011). Route and landmark learning by rats searching for food. *Behavioural Processes*, *86*(1), 125-132. doi: <http://dx.doi.org/10.1016/j.beproc.2010.10.007>
- Tan, D. S., Czerwinski, M. P., & Robertson, G. G. (2006). Large Displays Enhance Optical Flow Cues and Narrow the Gender Gap in 3-D Virtual Navigation. *Human Factors*, *48*(2), 318-333. doi: <http://dx.doi.org/10.1518/001872006777724381>
- Tan, D. S., Gergle, D., Scupelli, P., & Pausch, R. (2006). Physically large displays improve performance on spatial tasks. *ACM Transactions on Computer-Human Interaction (TOCHI)*, *13*(1), 71-99.
- Tlauka, M., & Wilson, P. N. (1994). The effect of landmarks on route-learning in a computer-simulated environment. *Journal of Environmental Psychology*, *14*(4), 305-313. doi: <http://dx.doi.org/10.1016/S0272-4944%2805%2980221-X>
- 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.

- Vorhees, C. V., & Williams, M. T. (2014). Assessing spatial learning and memory in rodents. *Ilar Journal*, 55(2), 310-332. doi: <http://dx.doi.org/10.1093/ilar/ilu013>
- Waller, D., & Lippa, Y. (2007). Landmarks as beacons and associative cues: Their role in route learning. *Memory & Cognition*, 35(5), 910-924. doi: <http://dx.doi.org/10.3758/BF03193465>
- Waller, D., Loomis, J. M., Golledge, R. G., & Beall, A. C. (2000). Place learning in humans: The role of distance and direction information. *Spatial Cognition and Computation*, 2(4), 333-354. doi: <http://dx.doi.org/10.1023/A:1015514424931>
- Waller, D., & Nadel, L. (2013). Handbook of spatial cognition *Handbook of spatial cognition* (pp. x, 309). Washington, DC: American Psychological Association; US.
- Wallet, G., Sauzeon, H., Pala, P. A., Larrue, F., Zheng, X., & N'Kaoua, B. (2011). Virtual/real transfer of spatial knowledge: Benefit from visual fidelity provided in a virtual environment and impact of active navigation. *Cyberpsychology, Behavior, and Social Networking*, 14(7-8), 417-423. doi: <http://dx.doi.org/10.1089/cyber.2009.0187>
- Wang, R. F., & Spelke, E. S. (2002). Human spatial representation: Insights from animals. *Trends in Cognitive Sciences*, 6(9), 376-382. doi: <http://dx.doi.org/10.1016/S1364-6613%2802%2901961-7>
- Wehner, R. (2003). Desert ant navigation: how miniature brains solve complex tasks. *Journal of Comparative Physiology A*, 189(8), 579-588.
- Whyte, J. T., Martin, G. M., & Skinner, D. M. (2009). An assessment of response, direction and place learning by rats in a water T-maze. *Learning and Motivation*, 40(4), 376-385. doi: <http://dx.doi.org/10.1016/j.lmot.2009.06.001>
- Wiener, J. M., Büchner, S. J., & Hölscher, C. (2009). Taxonomy of human wayfinding tasks: A knowledge-based approach. *Spatial Cognition & Computation*, 9(2), 152-165.
- Wiener, J. M., de Condappa, O., Harris, M. A., & Wolbers, T. (2013). Maladaptive bias for extrahippocampal navigation strategies in aging humans. *The Journal of Neuroscience*, 33(14), 6012-6017. doi: <http://dx.doi.org/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, 7. doi: <http://dx.doi.org/10.3389/fnagi.2012.00007>
- Williams, B., Bailey, S., Narasimham, G., Li, M., & Bodenheimer, B. (2011). Evaluation of walking in place on a Wii Balance Board to explore a virtual environment. *ACM Transactions on Applied Perception*, 8(3), 1-14. doi: <http://dx.doi.org/10.1145/2010325.2010329>
- Wohlgemuth, S., Ronacher, B., & Wehner, R. (2001). Ant odometry in the third dimension. *Nature*, 411(6839), 795.
- 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, 571.

Appendix

Appendix 1

SPSS Data Output – Experiment 1

Appendix 1.1.1: Distance travelled One Way Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
trial	Sphericity Assumed	1872553.767	14	133753.841	13.674	.000
	Greenhouse-Geisser	1872553.767	5.900	317359.077	13.674	.000
	Huynh-Feldt	1872553.767	8.646	216573.196	13.674	.000
	Lower-bound	1872553.767	1.000	1872553.767	13.674	.001
Error(trial)	Sphericity Assumed	2738753.930	280	9781.264		
	Greenhouse-Geisser	2738753.930	118.009	23208.103		
	Huynh-Feldt	2738753.930	172.926	15837.748		
	Lower-bound	2738753.930	20.000	136937.696		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
250.250	17.303	214.158	286.343

2. trial

Measure: MEASURE_1

trial	Mean	Std. Error
1	471.574	15.257
2	348.524	23.826
3	299.852	25.229
4	256.857	28.363
5	283.238	25.492
6	283.505	27.383
7	241.767	28.182
8	194.020	27.861
9	180.501	26.852
10	225.702	32.215
11	203.860	28.647

12	216.247	31.697
13	191.127	25.434
14	182.031	28.569
15	174.949	27.435

Appendix 1.1.2: Latency to target One Way Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
trial	Sphericity Assumed	181.203	14	12.943	13.107	.000
	Greenhouse-Geisser	181.203	5.147	35.207	13.107	.000
	Huynh-Feldt	181.203	7.142	25.371	13.107	.000
	Lower-bound	181.203	1.000	181.203	13.107	.002
Error(trial)	Sphericity Assumed	276.494	280	.987		
	Greenhouse-Geisser	276.494	102.937	2.686		
	Huynh-Feldt	276.494	142.844	1.936		
	Lower-bound	276.494	20.000	13.825		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
2.423	.141	2.129	2.717

2. trial

Measure: MEASURE_1

trial	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	4.000	.000	4.000	4.000
2	3.575	.191	3.177	3.972
3	3.223	.251	2.699	3.747
4	2.646	.278	2.066	3.226
5	3.079	.272	2.511	3.647
6	2.975	.263	2.427	3.524
7	2.444	.296	1.827	3.060
8	1.873	.275	1.300	2.446
9	1.686	.235	1.196	2.175
10	2.081	.286	1.485	2.676
11	1.920	.265	1.367	2.473
12	1.983	.288	1.383	2.584
13	1.801	.264	1.251	2.351
14	1.556	.237	1.061	2.051
15	1.506	.242	1.002	2.010

Appendix 1.2.1: Allocentric test 3 x 4 Within Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	582.931	2	291.466	1.245	.299
	Greenhouse-Geisser	582.931	1.439	405.147	1.245	.291
	Huynh-Feldt	582.931	1.520	383.479	1.245	.293
	Lower-bound	582.931	1.000	582.931	1.245	.278
Error(test)	Sphericity Assumed	9365.802	40	234.145		
	Greenhouse-Geisser	9365.802	28.776	325.470		
	Huynh-Feldt	9365.802	30.402	308.063		
	Lower-bound	9365.802	20.000	468.290		

quad	Sphericity Assumed	111732.640	3	37244.213	90.939	.000
	Greenhouse-Geisser	111732.640	1.742	64140.375	90.939	.000
	Huynh-Feldt	111732.640	1.894	58990.582	90.939	.000
	Lower-bound	111732.640	1.000	111732.640	90.939	.000
Error(quad)	Sphericity Assumed	24572.983	60	409.550		
	Greenhouse-Geisser	24572.983	34.840	705.309		
	Huynh-Feldt	24572.983	37.882	648.680		
	Lower-bound	24572.983	20.000	1228.649		
test * quad	Sphericity Assumed	1128.305	6	188.051	.881	.511
	Greenhouse-Geisser	1128.305	3.340	337.832	.881	.465
	Huynh-Feldt	1128.305	4.090	275.883	.881	.481
	Lower-bound	1128.305	1.000	1128.305	.881	.359
Error(test*quad)	Sphericity Assumed	25604.874	120	213.374		
	Greenhouse-Geisser	25604.874	66.797	383.325		
	Huynh-Feldt	25604.874	81.796	313.034		
	Lower-bound	25604.874	20.000	1280.244		

Appendix 1.2.2: Allocentric test planned contrasts

Tests of Within-Subjects Contrasts							
Measure: MEASURE_1							
Source	test	quad	Type III Sum of Squares	df	Mean Square	F	Sig.
quad		Level 1 vs. Later	41039.252	1	41039.252	122.346	.000
Error(quad)		Level 1 vs. Later	6708.720	20	335.436		
test * quad	Level 1 vs. Later	Level 1 vs. Later	165.384	1	165.384	.205	.655
	Level 2 vs. Level 3	Level 1 vs. Later	1402.969	1	1402.969	2.215	.152

Error(test*quad)	Level 1 vs. Later	Level 1 vs. Later	16105.713	20	805.286		
	Level 2 vs. Level 3	Level 1 vs. Later	12667.926	20	633.396		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
56.667	.959	54.667	58.667

2. test

Measure: MEASURE_1

test	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	57.810	2.221	53.177	62.443
2	57.673	1.528	54.485	60.861
3	54.517	1.031	52.367	56.668

3. quad

Measure: MEASURE_1

quad	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	23.512	2.569	18.152	28.871
2	61.644	2.202	57.050	66.237
3	81.992	2.678	76.406	87.578
4	59.520	2.135	55.067	63.973

4. test * quad

Measure: MEASURE_1

test	quad	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
1	1	26.058	3.361	19.048	33.069
	2	64.277	3.462	57.056	71.499
	3	81.643	5.224	70.745	92.540
	4	59.263	3.413	52.143	66.383
2	1	20.751	2.795	14.921	26.581
	2	64.668	3.219	57.953	71.382
	3	85.220	3.651	77.604	92.835
	4	60.053	2.452	54.938	65.168
3	1	23.726	3.790	15.819	31.632
	2	55.986	3.784	48.094	63.879
	3	79.113	2.809	73.254	84.973
	4	59.244	4.060	50.774	67.714

Appendix 1.2.3: Egocentric test 3 x 4 Within Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
test1_targ	57.3433	33.56404	21
test1_NW	61.7187	30.61617	21
test1_NE	64.7620	27.74645	21
test1_SE	62.4810	30.33827	21
test2_targ	51.2409	33.17380	21
test2_NW	52.1783	16.94416	21
test2_NE	68.8881	33.71750	21
test2_SE	77.3668	23.37556	21
test3_targ	27.4871	25.82779	21
test3_NW	55.0716	16.13332	21
test3_NE	85.7127	18.69781	21
test3_SE	70.9808	22.78043	21

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	296.980	2	148.490	.406	.669
	Greenhouse-Geisser	296.980	1.926	154.218	.406	.662
	Huynh-Feldt	296.980	2.000	148.490	.406	.669
	Lower-bound	296.980	1.000	296.980	.406	.531
Error(test)	Sphericity Assumed	14639.917	40	365.998		
	Greenhouse-Geisser	14639.917	38.514	380.115		
	Huynh-Feldt	14639.917	40.000	365.998		
	Lower-bound	14639.917	20.000	731.996		
quad	Sphericity Assumed	31452.722	3	10484.241	8.509	.000
	Greenhouse-Geisser	31452.722	1.829	17192.187	8.509	.001
	Huynh-Feldt	31452.722	2.004	15692.685	8.509	.001
	Lower-bound	31452.722	1.000	31452.722	8.509	.009
Error(quad)	Sphericity Assumed	73925.051	60	1232.084		
	Greenhouse-Geisser	73925.051	36.590	2020.387		
	Huynh-Feldt	73925.051	40.086	1844.169		
	Lower-bound	73925.051	20.000	3696.253		
test * quad	Sphericity Assumed	18673.608	6	3112.268	4.966	.000
	Greenhouse-Geisser	18673.608	3.068	6085.975	4.966	.004
	Huynh-Feldt	18673.608	3.687	5064.134	4.966	.002
	Lower-bound	18673.608	1.000	18673.608	4.966	.037
Error(test*quad)	Sphericity Assumed	75198.839	120	626.657		
	Greenhouse-Geisser	75198.839	61.366	1225.415		
	Huynh-Feldt	75198.839	73.748	1019.666		
	Lower-bound	75198.839	20.000	3759.942		

Appendix 1.2.4: Egocentric test planned contrasts

Tests of Within-Subjects Contrasts							
Measure: MEASURE_1							
Source	test	quad	Type III Sum of Squares	df	Mean Square	F	Sig.
quad		Level 1 vs. Later	9452.697	1	9452.697	11.015	.003
Error(quad)		Level 1 vs. Later	17162.548	20	858.127		
test * quad	Level 1 vs. Later	Level 1 vs. Later	11457.907	1	11457.907	7.913	.011
	Level 2 vs. Level 3	Level 1 vs. Later	16697.379	1	16697.379	9.627	.006
Error(test*quad)	Level 1 vs. Later	Level 1 vs. Later	28960.564	20	1448.028		
	Level 2 vs. Level 3	Level 1 vs. Later	34689.532	20	1734.477		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
61.269	1.310	58.536	64.003

2. test

Measure: MEASURE_1

test	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	61.576	2.136	57.121	66.032
2	62.419	2.131	57.974	66.863
3	59.813	2.183	55.260	64.366

3. quad

Measure: MEASURE_1

quad	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	45.357	5.381	34.133	56.581
2	56.323	2.947	50.175	62.471
3	73.121	3.863	65.062	81.180
4	70.276	3.602	62.763	77.790

4. test * quad

Measure: MEASURE_1

test	quad	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
1	1	57.343	7.324	42.065	72.621
	2	61.719	6.681	47.782	75.655
	3	64.762	6.055	52.132	77.392
	4	62.481	6.620	48.671	76.291
2	1	51.241	7.239	36.140	66.341
	2	52.178	3.698	44.465	59.891
	3	68.888	7.358	53.540	84.236
	4	77.367	5.101	66.726	88.007
3	1	27.487	5.636	15.730	39.244
	2	55.072	3.521	47.728	62.415
	3	85.713	4.080	77.202	94.224
	4	70.981	4.971	60.611	81.350

Appendix 1.2.5: Allocentric test One Way Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
test1_targ	26.0583	15.40180	21
test2_targ	20.7510	12.80754	21
test3_targ	23.7258	17.36909	21

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	297.209	2	148.605	1.035	.364
	Greenhouse-Geisser	297.209	1.936	153.515	1.035	.363
	Huynh-Feldt	297.209	2.000	148.605	1.035	.364
	Lower-bound	297.209	1.000	297.209	1.035	.321
Error(test)	Sphericity Assumed	5741.913	40	143.548		
	Greenhouse-Geisser	5741.913	38.721	148.291		
	Huynh-Feldt	5741.913	40.000	143.548		
	Lower-bound	5741.913	20.000	287.096		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
23.512	2.569	18.152	28.871

2. test

Measure: MEASURE_1

test	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	26.058	3.361	19.048	33.069
2	20.751	2.795	14.921	26.581
3	23.726	3.790	15.819	31.632

Appendix 1.2.6: Egocentric Test One Way Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
test1_targ	57.3433	33.56404	21
test2_targ	51.2409	33.17380	21
test3_targ	27.4871	25.82779	21

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	10450.069	2	5225.035	9.766	.000
	Greenhouse-Geisser	10450.069	1.496	6986.975	9.766	.001
	Huynh-Feldt	10450.069	1.589	6575.335	9.766	.001
	Lower-bound	10450.069	1.000	10450.069	9.766	.005
Error(test)	Sphericity Assumed	21400.275	40	535.007		
	Greenhouse-Geisser	21400.275	29.913	715.417		
	Huynh-Feldt	21400.275	31.786	673.268		
	Lower-bound	21400.275	20.000	1070.014		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
45.357	5.381	34.133	56.581

2. test

Measure: MEASURE_1

test	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	57.343	7.324	42.065	72.621
2	51.241	7.239	36.140	66.341
3	27.487	5.636	15.730	39.244

Appendix 1.3.1: Paired samples t-test comparing bin 0 frequency

T-Test

	Mean	N	Std. Deviation	Std. Error Mean
Pair 1 block1_bin0	71.7619	21	12.58930	2.74721
block3_bin0	116.2381	21	23.47319	5.12227

	Paired Differences					t	df	Sig. (2-tailed)
	Mean	Std. Deviation	Std. Error Mean	95% Confidence Interval of the Difference				
				Lower	Upper			
Pair 1 block1_bin0 - block3_bin0	-44.47619	25.91065	5.65417	-56.27058	-32.68180	-7.866	20	.000

Appendix 1.3.2: Bin percentage 2 x 5 Within-Subjects ANOVA

General Linear Model

	Mean	Std. Deviation	N
block1_pbin1	71.1766	7.82209	21
block1_pbin2	18.4790	8.36266	21
block1_pbin3	7.6276	4.41562	21
block1_pbin4	2.1744	2.71527	21
block1_pbin5	.5425	1.58158	21
block3_pbin1	36.4230	22.71708	21
block3_pbin2	16.8558	14.42572	21
block3_pbin3	10.8982	11.68272	21
block3_pbin4	9.4463	11.66878	21
block3_pbin5	26.3767	37.86867	21

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
block	Sphericity Assumed	.000	1	.000	.	.
	Greenhouse-Geisser	.000
	Huynh-Feldt	.000
	Lower-bound	.000	1.000	.000	.	.
Error(block)	Sphericity Assumed	.000	20	.000		
	Greenhouse-Geisser	.000	.	.		
	Huynh-Feldt	.000	.	.		
	Lower-bound	.000	20.000	.000		
bin	Sphericity Assumed	63305.724	4	15826.431	46.979	.000
	Greenhouse-Geisser	63305.724	1.776	35655.036	46.979	.000
	Huynh-Feldt	63305.724	1.936	32696.456	46.979	.000
	Lower-bound	63305.724	1.000	63305.724	46.979	.000
Error(bin)	Sphericity Assumed	26950.617	80	336.883		
	Greenhouse-Geisser	26950.617	35.510	758.956		
	Huynh-Feldt	26950.617	38.723	695.979		
	Lower-bound	26950.617	20.000	1347.531		
block * bin	Sphericity Assumed	20385.072	4	5096.268	16.389	.000
	Greenhouse-Geisser	20385.072	1.518	13431.042	16.389	.000
	Huynh-Feldt	20385.072	1.616	12612.153	16.389	.000
	Lower-bound	20385.072	1.000	20385.072	16.389	.001
Error(block*bin)	Sphericity Assumed	24876.197	80	310.952		
	Greenhouse-Geisser	24876.197	30.355	819.505		
	Huynh-Feldt	24876.197	32.326	769.540		
	Lower-bound	24876.197	20.000	1243.810		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
20.000	.000	20.000	20.000

3. bin

Measure: MEASURE_1

bin	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	53.800	2.823	47.912	59.688
2	17.667	1.994	13.507	21.828
3	9.263	1.375	6.395	12.131
4	5.810	1.216	3.275	8.346
5	13.460	4.095	4.917	22.002

4. block * bin

Measure: MEASURE_1

block	bin	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
1	1	71.177	1.707	67.616	74.737
	2	18.479	1.825	14.672	22.286
	3	7.628	.964	5.618	9.638
	4	2.174	.593	.938	3.410
	5	.542	.345	-.177	1.262
2	1	36.423	4.957	26.082	46.764
	2	16.856	3.148	10.289	23.422
	3	10.898	2.549	5.580	16.216
	4	9.446	2.546	4.135	14.758
	5	26.377	8.264	9.139	43.614

Appendix 2

SPSS Data Output – Experiment 2

Appendix 2.1.1: Distance travelled One Way Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
trial	Sphericity Assumed	830325.147	14	59308.939	4.215	.000
	Greenhouse-Geisser	830325.147	6.295	131909.262	4.215	.001
	Huynh-Feldt	830325.147	12.844	64645.355	4.215	.000
	Lower-bound	830325.147	1.000	830325.147	4.215	.061
Error(trial)	Sphericity Assumed	2560973.420	182	14071.283		
	Greenhouse-Geisser	2560973.420	81.831	31295.999		
	Huynh-Feldt	2560973.420	166.976	15337.369		
	Lower-bound	2560973.420	13.000	196997.955		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
324.098	13.664	294.578	353.619

2. trial

Measure: MEASURE_1

trial	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	472.579	20.154	429.040	516.119
2	404.556	25.483	349.504	459.609
3	376.228	31.265	308.684	443.772
4	371.811	27.813	311.724	431.898
5	369.235	35.112	293.379	445.091
6	296.319	29.177	233.286	359.352
7	351.741	36.548	272.785	430.698
8	285.502	33.093	214.009	356.995
9	245.139	30.982	178.207	312.071

10	280.610	42.293	189.241	371.979
11	294.515	40.105	207.874	381.156
12	305.947	37.141	225.708	386.186
13	288.516	38.824	204.641	372.391
14	289.057	39.307	204.139	373.974
15	229.719	27.596	170.102	289.336

Appendix 2.1.2: Latency to target One Way Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
trial	Sphericity Assumed	71.364	14	5.097	5.284	.000
	Greenhouse-Geisser	71.364	6.103	11.694	5.284	.000
	Huynh-Feldt	71.364	12.097	5.899	5.284	.000
	Lower-bound	71.364	1.000	71.364	5.284	.039
Error(trial)	Sphericity Assumed	175.588	182	.965		
	Greenhouse-Geisser	175.588	79.336	2.213		
	Huynh-Feldt	175.588	157.266	1.117		
	Lower-bound	175.588	13.000	13.507		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
2.861	.131	2.578	3.145

2. trial

Measure: MEASURE_1

trial	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	3.791	.158	3.449	4.132
2	3.769	.158	3.428	4.110
3	3.606	.268	3.026	4.185
4	3.495	.237	2.984	4.006
5	3.313	.280	2.709	3.917
6	2.780	.294	2.144	3.415
7	3.096	.287	2.477	3.715
8	2.572	.302	1.920	3.224
9	2.152	.276	1.556	2.749
10	2.393	.363	1.609	3.177
11	2.510	.340	1.776	3.245
12	2.601	.309	1.934	3.268
13	2.466	.330	1.752	3.180
14	2.442	.337	1.715	3.169
15	1.934	.257	1.380	2.489

Appendix 2.2.1: Allocentric-n test 2 x 4 Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
test1_targ	25.2883	13.62127	14
test1_NW	68.6751	14.21056	14
test1_NE	88.4604	20.84184	14
test1_SE	61.3708	19.96757	14
test2_targ	22.7194	10.46145	14
test2_NW	71.5954	16.40477	14
test2_NE	97.5564	19.42674	14
test2_SE	69.6622	16.63221	14

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	550.676	1	550.676	.799	.388
	Greenhouse-Geisser	550.676	1.000	550.676	.799	.388
	Huynh-Feldt	550.676	1.000	550.676	.799	.388
	Lower-bound	550.676	1.000	550.676	.799	.388
Error(test)	Sphericity Assumed	8956.943	13	688.996		
	Greenhouse-Geisser	8956.943	13.000	688.996		
	Huynh-Feldt	8956.943	13.000	688.996		
	Lower-bound	8956.943	13.000	688.996		
quad	Sphericity Assumed	69393.491	3	23131.164	104.022	.000
	Greenhouse-Geisser	69393.491	1.659	41828.119	104.022	.000
	Huynh-Feldt	69393.491	1.872	37076.347	104.022	.000
	Lower-bound	69393.491	1.000	69393.491	104.022	.000
Error(quad)	Sphericity Assumed	8672.391	39	222.369		
	Greenhouse-Geisser	8672.391	21.567	402.110		
	Huynh-Feldt	8672.391	24.331	356.430		
	Lower-bound	8672.391	13.000	667.107		
test * quad	Sphericity Assumed	615.617	3	205.206	1.549	.217
	Greenhouse-Geisser	615.617	1.393	441.836	1.549	.237
	Huynh-Feldt	615.617	1.508	408.152	1.549	.236
	Lower-bound	615.617	1.000	615.617	1.549	.235
Error(test*quad)	Sphericity Assumed	5165.470	39	132.448		
	Greenhouse-Geisser	5165.470	18.113	285.179		
	Huynh-Feldt	5165.470	19.608	263.438		
	Lower-bound	5165.470	13.000	397.344		

Appendix 2.2.2: Allocentric-n planned contrasts

Tests of Within-Subjects Contrasts							
Measure: MEASURE_1							
Source	test	quad	Type III Sum of Squares	df	Mean Square	F	Sig.
quad		Level 1 vs. Later	38171.450	1	38171.450	212.627	.000
Error(quad)		Level 1 vs. Later	2333.794	13	179.523		
test * quad	Level 1 vs. Level 2	Level 1 vs. Later	1220.802	1	1220.802	1.724	.212
Error(test*quad)	Level 1 vs. Level 2	Level 1 vs. Later	9204.501	13	708.039		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
63.166	2.112	58.603	67.729

2. test

Measure: MEASURE_1

test	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	60.949	2.854	54.783	67.114
2	65.383	3.617	57.569	73.197

3. quad

Measure: MEASURE_1

quad	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	24.004	2.964	17.600	30.408
2	70.135	3.222	63.175	77.095
3	93.008	3.155	86.191	99.825
4	65.516	3.543	57.863	73.170

4. test * quad

Measure: MEASURE_1

test	quad	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
1	1	25.288	3.640	17.424	33.153
	2	68.675	3.798	60.470	76.880
	3	88.460	5.570	76.427	100.494
	4	61.371	5.337	49.842	72.900
2	1	22.719	2.796	16.679	28.760
	2	71.595	4.384	62.124	81.067
	3	97.556	5.192	86.340	108.773
	4	69.662	4.445	60.059	79.265

Appendix 2.2.3: Allocentric-r test 2 x 4 Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
test1_targ	60.4516	27.07287	14
test1_NW	65.9498	24.46107	14
test1_NE	65.2813	34.84299	14
test1_SE	59.7125	36.73969	14
test2_targ	75.0855	45.44000	14
test2_NW	93.0454	32.55254	14
test2_NE	86.9881	31.34515	14
test2_SE	71.9953	36.09305	14

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	10033.411	1	10033.411	30.781	.000
	Greenhouse-Geisser	10033.411	1.000	10033.411	30.781	.000
	Huynh-Feldt	10033.411	1.000	10033.411	30.781	.000
	Lower-bound	10033.411	1.000	10033.411	30.781	.000
Error(test)	Sphericity Assumed	4237.509	13	325.962		
	Greenhouse-Geisser	4237.509	13.000	325.962		
	Huynh-Feldt	4237.509	13.000	325.962		
	Lower-bound	4237.509	13.000	325.962		
quad	Sphericity Assumed	3600.698	3	1200.233	1.114	.355
	Greenhouse-Geisser	3600.698	1.715	2099.720	1.114	.338
	Huynh-Feldt	3600.698	1.950	1846.360	1.114	.343
	Lower-bound	3600.698	1.000	3600.698	1.114	.311
Error(quad)	Sphericity Assumed	42035.689	39	1077.838		
	Greenhouse-Geisser	42035.689	22.293	1885.600		
	Huynh-Feldt	42035.689	25.352	1658.077		
	Lower-bound	42035.689	13.000	3233.515		
test * quad	Sphericity Assumed	959.201	3	319.734	.288	.834
	Greenhouse-Geisser	959.201	1.520	631.205	.288	.693
	Huynh-Feldt	959.201	1.679	571.312	.288	.715
	Lower-bound	959.201	1.000	959.201	.288	.601
Error(test*quad)	Sphericity Assumed	43355.323	39	1111.675		
	Greenhouse-Geisser	43355.323	19.755	2194.624		
	Huynh-Feldt	43355.323	21.826	1986.385		
	Lower-bound	43355.323	13.000	3335.025		

Appendix 2.2.4: Allocentric-r planned contrasts (target vs. rest)

Tests of Within-Subjects Contrasts							
Measure: MEASURE_1							
Source	test	quad	Type III Sum of Squares	df	Mean Square	F	Sig.
quad		Level 1 vs. Later	514.163	1	514.163	.562	.467
Error(quad)		Level 1 vs. Later	11885.983	13	914.306		
test * quad	Level 1 vs. Level 2	Level 1 vs. Later	459.315	1	459.315	.139	.715
Error(test*quad)	Level 1 vs. Level 2	Level 1 vs. Later	42961.844	13	3304.757		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
72.314	4.639	62.292	82.336

2. test

Measure: MEASURE_1

test	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	62.849	3.839	54.555	71.143
2	81.779	5.841	69.159	94.398

3. quad

Measure: MEASURE_1

quad	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	67.769	7.857	50.794	84.743
2	79.498	5.549	67.510	91.485
3	76.135	7.200	60.580	91.689
4	65.854	7.563	49.516	82.192

4. test * quad

Measure: MEASURE_1

test	quad	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
1	1	60.452	7.236	44.820	76.083
	2	65.950	6.537	51.826	80.073
	3	65.281	9.312	45.164	85.399
	4	59.712	9.819	38.500	80.925
2	1	75.085	12.144	48.849	101.322
	2	93.045	8.700	74.250	111.841
	3	86.988	8.377	68.890	105.086
	4	71.995	9.646	51.156	92.835

Appendix 2.2.5: Allocentric-r test planned contrast: SE vs. rest

Tests of Within-Subjects Contrasts							
Measure: MEASURE_1							
Source	test	quad	Type III Sum of Squares	df	Mean Square	F	Sig.
quad		Level 1 vs. Later	1038.589	1	1038.589	1.769	.206
Error(quad)		Level 1 vs. Later	7631.162	13	587.012		
test * quad	Level 1 vs. Level 2	Level 1 vs. Later	1099.633	1	1099.633	.327	.577
Error(test*quad)	Level 1 vs. Level 2	Level 1 vs. Later	43721.954	13	3363.227		

Appendix 2.2.6: Allocentric-n test One Way Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects						
Measure: MEASURE_1						
Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	46.192	1	46.192	.943	.349
	Greenhouse-Geisser	46.192	1.000	46.192	.943	.349
	Huynh-Feldt	46.192	1.000	46.192	.943	.349
	Lower-bound	46.192	1.000	46.192	.943	.349
Error(test)	Sphericity Assumed	636.485	13	48.960		
	Greenhouse-Geisser	636.485	13.000	48.960		
	Huynh-Feldt	636.485	13.000	48.960		
	Lower-bound	636.485	13.000	48.960		

Appendix 2.2.7: Allocentric-r One Way Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	1499.054	1	1499.054	1.402	.258
	Greenhouse-Geisser	1499.054	1.000	1499.054	1.402	.258
	Huynh-Feldt	1499.054	1.000	1499.054	1.402	.258
	Lower-bound	1499.054	1.000	1499.054	1.402	.258
Error(test)	Sphericity Assumed	13897.461	13	1069.035		
	Greenhouse-Geisser	13897.461	13.000	1069.035		
	Huynh-Feldt	13897.461	13.000	1069.035		
	Lower-bound	13897.461	13.000	1069.035		

Appendix 2.2.8: Allocentric-n vs. Allocentric-r 2 x 2 Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	26814.877	1	26814.877	32.822	.000
	Greenhouse-Geisser	26814.877	1.000	26814.877	32.822	.000
	Huynh-Feldt	26814.877	1.000	26814.877	32.822	.000
	Lower-bound	26814.877	1.000	26814.877	32.822	.000
Error(test)	Sphericity Assumed	10620.783	13	816.983		
	Greenhouse-Geisser	10620.783	13.000	816.983		
	Huynh-Feldt	10620.783	13.000	816.983		
	Lower-bound	10620.783	13.000	816.983		
time	Sphericity Assumed	509.479	1	509.479	.967	.343
	Greenhouse-Geisser	509.479	1.000	509.479	.967	.343
	Huynh-Feldt	509.479	1.000	509.479	.967	.343
	Lower-bound	509.479	1.000	509.479	.967	.343
Error(time)	Sphericity Assumed	6848.602	13	526.816		
	Greenhouse-Geisser	6848.602	13.000	526.816		
	Huynh-Feldt	6848.602	13.000	526.816		
	Lower-bound	6848.602	13.000	526.816		
test * time	Sphericity Assumed	1035.766	1	1035.766	1.752	.208
	Greenhouse-Geisser	1035.766	1.000	1035.766	1.752	.208
	Huynh-Feldt	1035.766	1.000	1035.766	1.752	.208
	Lower-bound	1035.766	1.000	1035.766	1.752	.208
Error(test*time)	Sphericity Assumed	7685.344	13	591.180		
	Greenhouse-Geisser	7685.344	13.000	591.180		
	Huynh-Feldt	7685.344	13.000	591.180		
	Lower-bound	7685.344	13.000	591.180		

Appendix 2.3.1: Egocentric-p test 2 x 2 Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
tloc_time1	94.4090	73.40311	14
tloc_time2	74.9976	24.25174	14
ploc_time1	152.4058	87.42194	14
ploc_time2	120.2400	44.82236	14

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
loc	Sphericity Assumed	37304.221	1	37304.221	37.544	.000
	Greenhouse-Geisser	37304.221	1.000	37304.221	37.544	.000
	Huynh-Feldt	37304.221	1.000	37304.221	37.544	.000
	Lower-bound	37304.221	1.000	37304.221	37.544	.000
Error(loc)	Sphericity Assumed	12917.027	13	993.617		
	Greenhouse-Geisser	12917.027	13.000	993.617		
	Huynh-Feldt	12917.027	13.000	993.617		
	Lower-bound	12917.027	13.000	993.617		
time	Sphericity Assumed	9310.725	1	9310.725	1.683	.217
	Greenhouse-Geisser	9310.725	1.000	9310.725	1.683	.217
	Huynh-Feldt	9310.725	1.000	9310.725	1.683	.217
	Lower-bound	9310.725	1.000	9310.725	1.683	.217
Error(time)	Sphericity Assumed	71914.018	13	5531.848		
	Greenhouse-Geisser	71914.018	13.000	5531.848		
	Huynh-Feldt	71914.018	13.000	5531.848		
	Lower-bound	71914.018	13.000	5531.848		
loc * time	Sphericity Assumed	569.367	1	569.367	.661	.431
	Greenhouse-Geisser	569.367	1.000	569.367	.661	.431
	Huynh-Feldt	569.367	1.000	569.367	.661	.431
	Lower-bound	569.367	1.000	569.367	.661	.431
Error(loc*time)	Sphericity Assumed	11198.768	13	861.444		
	Greenhouse-Geisser	11198.768	13.000	861.444		
	Huynh-Feldt	11198.768	13.000	861.444		

Lower-bound	11198.768	13.000	861.444		
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Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
110.513	12.131	84.306	136.720

2. time

Measure: MEASURE_1

time	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	123.407	20.912	78.231	168.584
2	97.619	7.389	81.657	113.581

Appendix 2.3.2: Egocentric-np test 2 x 4 Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
test1_targ	83.9745	45.17150	14
test1_NW	60.1412	32.39268	14
test1_NE	95.4191	32.20588	14
test1_SE	115.4601	34.29331	14
test2_targ	62.4386	36.63008	14
test2_NW	64.6432	25.01153	14
test2_NE	89.0900	41.30964	14
test2_SE	93.4828	35.45775	14

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	3597.545	1	3597.545	1.151	.303
	Greenhouse-Geisser	3597.545	1.000	3597.545	1.151	.303
	Huynh-Feldt	3597.545	1.000	3597.545	1.151	.303
	Lower-bound	3597.545	1.000	3597.545	1.151	.303
Error(test)	Sphericity Assumed	40619.315	13	3124.563		
	Greenhouse-Geisser	40619.315	13.000	3124.563		
	Huynh-Feldt	40619.315	13.000	3124.563		
	Lower-bound	40619.315	13.000	3124.563		
quad	Sphericity Assumed	29882.618	3	9960.873	9.807	.000
	Greenhouse-Geisser	29882.618	1.557	19197.462	9.807	.002
	Huynh-Feldt	29882.618	1.730	17277.384	9.807	.001
	Lower-bound	29882.618	1.000	29882.618	9.807	.008
Error(quad)	Sphericity Assumed	39610.989	39	1015.666		
	Greenhouse-Geisser	39610.989	20.236	1957.481		
	Huynh-Feldt	39610.989	22.485	1761.699		
	Lower-bound	39610.989	13.000	3046.999		
test * quad	Sphericity Assumed	3452.335	3	1150.778	1.613	.202
	Greenhouse-Geisser	3452.335	1.858	1858.089	1.613	.221
	Huynh-Feldt	3452.335	2.155	1601.942	1.613	.216
	Lower-bound	3452.335	1.000	3452.335	1.613	.226
Error(test*quad)	Sphericity Assumed	27819.491	39	713.320		
	Greenhouse-Geisser	27819.491	24.154	1151.753		
	Huynh-Feldt	27819.491	28.016	992.978		
	Lower-bound	27819.491	13.000	2139.961		

Appendix 2.3.3: Egocentric-np test planned contrasts

Tests of Within-Subjects Contrasts							
Measure: MEASURE_1							
Source	test	quad	Type III Sum of Squares	df	Mean Square	F	Sig.
quad		Level 1 vs. Later	2426.876	1	2426.876	2.197	.162
Error(quad)		Level 1 vs. Later	14359.678	13	1104.591		
test * quad	Level 1 vs. Level 2	Level 1 vs. Later	2589.899	1	2589.899	1.202	.293
Error(test*quad)	Level 1 vs. Level 2	Level 1 vs. Later	28012.575	13	2154.813		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
83.081	4.143	74.130	92.032

2. test

Measure: MEASURE_1

test	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	88.749	7.481	72.586	104.911
2	77.414	5.844	64.788	90.040

3. quad

Measure: MEASURE_1

quad	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	73.207	8.968	53.833	92.580
2	62.392	6.518	48.311	76.473
3	92.255	5.763	79.805	104.704
4	104.471	4.623	94.484	114.459

4. test * quad

Measure: MEASURE_1

test	quad	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
1	1	83.975	12.073	57.893	110.056
	2	60.141	8.657	41.438	78.844
	3	95.419	8.607	76.824	114.014
	4	115.460	9.165	95.660	135.260
2	1	62.439	9.790	41.289	83.588
	2	64.643	6.685	50.202	79.084
	3	89.090	11.040	65.239	112.942
	4	93.483	9.476	73.010	113.956

Appendix 2.3.4: Egocentric-np test One Way Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	3246.587	1	3246.587	2.872	.114
	Greenhouse-Geisser	3246.587	1.000	3246.587	2.872	.114
	Huynh-Feldt	3246.587	1.000	3246.587	2.872	.114

	Lower-bound	3246.587	1.000	3246.587	2.872	.114
Error(test)	Sphericity Assumed	14695.101	13	1130.392		
	Greenhouse-Geisser	14695.101	13.000	1130.392		
	Huynh-Feldt	14695.101	13.000	1130.392		
	Lower-bound	14695.101	13.000	1130.392		

Appendix 2.3.5: Egocentric-p vs. Egocentric-np 2 x 2 Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	1850.439	1	1850.439	.608	.450
	Greenhouse-Geisser	1850.439	1.000	1850.439	.608	.450
	Huynh-Feldt	1850.439	1.000	1850.439	.608	.450
	Lower-bound	1850.439	1.000	1850.439	.608	.450
Error(test)	Sphericity Assumed	39572.724	13	3044.056		
	Greenhouse-Geisser	39572.724	13.000	3044.056		
	Huynh-Feldt	39572.724	13.000	3044.056		
	Lower-bound	39572.724	13.000	3044.056		
time	Sphericity Assumed	5868.396	1	5868.396	4.339	.058
	Greenhouse-Geisser	5868.396	1.000	5868.396	4.339	.058
	Huynh-Feldt	5868.396	1.000	5868.396	4.339	.058
	Lower-bound	5868.396	1.000	5868.396	4.339	.058
Error(time)	Sphericity Assumed	17581.022	13	1352.386		
	Greenhouse-Geisser	17581.022	13.000	1352.386		
	Huynh-Feldt	17581.022	13.000	1352.386		
	Lower-bound	17581.022	13.000	1352.386		
test * time	Sphericity Assumed	15.799	1	15.799	.009	.928
	Greenhouse-Geisser	15.799	1.000	15.799	.009	.928
	Huynh-Feldt	15.799	1.000	15.799	.009	.928
	Lower-bound	15.799	1.000	15.799	.009	.928
Error(test*time)	Sphericity Assumed	23867.115	13	1835.932		
	Greenhouse-Geisser	23867.115	13.000	1835.932		
	Huynh-Feldt	23867.115	13.000	1835.932		
	Lower-bound	23867.115	13.000	1835.932		

Appendix 2.4.1: Paired samples t-test comparing bin 0 frequency

T-Test

	Mean	N	Std. Deviation	Std. Error Mean
Pair 1 block1_bin0	64.5000	14	17.02826	4.55099
block3_bin0	105.7143	14	19.26507	5.14881

	Paired Differences					t	df	Sig. (2-tailed)
	Mean	Std. Deviation	Std. Error Mean	95% Confidence Interval of the Difference				
				Lower	Upper			
Pair 1 block1_bin0 - block3_bin0	-41.21429	20.08129	5.36695	-52.80888	-29.61969	-7.679	13	.000

Appendix 2.4.2: Bin percentage 2 x 5 Within-Subjects ANOVA

General Linear Model

	Mean	Std. Deviation	N
block1_pbin1	58.5571	12.73348	14
block1_pbin2	27.1428	10.56792	14
block1_pbin3	10.1702	8.15485	14
block1_pbin4	2.2101	3.60438	14
block1_pbin5	1.9198	1.13965	14
block3_pbin1	38.7720	17.40314	14
block3_pbin2	22.9684	18.58581	14
block3_pbin3	13.4414	10.74321	14
block3_pbin4	8.4041	10.33227	14
block3_pbin5	16.4142	27.28757	14

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
block	Sphericity Assumed	.000	1	.000	.	.
	Greenhouse-Geisser	.000
	Huynh-Feldt	.000
	Lower-bound	.000	1.000	.000	.	.
Error(block)	Sphericity Assumed	.000	13	.000		
	Greenhouse-Geisser	.000	.	.		
	Huynh-Feldt	.000	.	.		
	Lower-bound	.000	13.000	.000		
bin	Sphericity Assumed	34932.625	4	8733.156	36.212	.000
	Greenhouse-Geisser	34932.625	2.236	15623.668	36.212	.000
	Huynh-Feldt	34932.625	2.722	12832.405	36.212	.000
	Lower-bound	34932.625	1.000	34932.625	36.212	.000
Error(bin)	Sphericity Assumed	12540.740	52	241.168		
	Greenhouse-Geisser	12540.740	29.066	431.451		
	Huynh-Feldt	12540.740	35.389	354.370		
	Lower-bound	12540.740	13.000	964.672		
block * bin	Sphericity Assumed	4676.211	4	1169.053	4.653	.003
	Greenhouse-Geisser	4676.211	2.536	1844.111	4.653	.011
	Huynh-Feldt	4676.211	3.201	1460.663	4.653	.006
	Lower-bound	4676.211	1.000	4676.211	4.653	.050
Error(block*bin)	Sphericity Assumed	13065.356	52	251.257		
	Greenhouse-Geisser	13065.356	32.965	396.343		
	Huynh-Feldt	13065.356	41.619	313.931		
	Lower-bound	13065.356	13.000	1005.027		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
20.000	.000	20.000	20.000

2. block

Measure: MEASURE_1

block	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	20.000	.000	20.000	20.000
2	20.000	.000	20.000	20.000

3. bin

Measure: MEASURE_1

bin	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	48.665	2.887	42.427	54.902
2	25.056	2.683	19.259	30.852
3	11.806	1.663	8.214	15.397
4	5.307	1.436	2.204	8.410
5	9.167	3.754	1.057	17.277

4. block * bin

Measure: MEASURE_1

block	bin	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
1	1	58.557	3.403	51.205	65.909
	2	27.143	2.824	21.041	33.245
	3	10.170	2.179	5.462	14.879
	4	2.210	.963	.129	4.291
	5	1.920	.305	1.262	2.578
2	1	38.772	4.651	28.724	48.820
	2	22.968	4.967	12.237	33.699
	3	13.441	2.871	7.238	19.644
	4	8.404	2.761	2.438	14.370
	5	16.414	7.293	.659	32.170

Appendix 3

SPSS Data Output – Experiment 3

Appendix 3.1.1: Distance travelled One Way Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
trial	Sphericity Assumed	1115845.460	14	79703.247	4.573	.000
	Greenhouse-Geisser	1115845.460	6.361	175424.476	4.573	.000
	Huynh-Feldt	1115845.460	14.000	79703.247	4.573	.000
	Lower-bound	1115845.460	1.000	1115845.460	4.573	.054
Error(trial)	Sphericity Assumed	2927846.728	168	17427.659		
	Greenhouse-Geisser	2927846.728	76.330	38357.759		
	Huynh-Feldt	2927846.728	168.000	17427.659		
	Lower-bound	2927846.728	12.000	243987.227		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
263.189	17.234	225.639	300.738

2. trial

Measure: MEASURE_1

trial	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	439.289	38.621	355.141	523.437
2	347.987	46.056	247.641	448.333
3	312.620	43.267	218.349	406.891
4	334.582	34.030	260.436	408.728
5	315.353	34.945	239.213	391.492
6	282.569	42.957	188.973	376.164
7	289.118	45.814	189.298	388.938
8	257.422	42.380	165.085	349.760
9	199.785	35.964	121.425	278.144

10	218.930	42.252	126.870	310.990
11	170.472	32.498	99.664	241.280
12	154.053	28.415	92.142	215.964
13	203.851	39.042	118.785	288.917
14	190.722	34.436	115.693	265.752
15	231.076	44.347	134.453	327.699

Appendix 3.1.2: Latency to target One Way Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
trial	Sphericity Assumed	85.591	14	6.114	4.615	.000
	Greenhouse-Geisser	85.591	6.562	13.044	4.615	.000
	Huynh-Feldt	85.591	14.000	6.114	4.615	.000
	Lower-bound	85.591	1.000	85.591	4.615	.053
Error(trial)	Sphericity Assumed	222.543	168	1.325		
	Greenhouse-Geisser	222.543	78.743	2.826		
	Huynh-Feldt	222.543	168.000	1.325		
	Lower-bound	222.543	12.000	18.545		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
2.432	.161	2.082	2.782

2. trial

Measure: MEASURE_1

trial	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	3.580	.275	2.981	4.179
2	3.162	.368	2.360	3.965
3	3.002	.381	2.173	3.831
4	3.266	.338	2.530	4.001
5	3.087	.329	2.371	3.803
6	2.703	.369	1.900	3.506
7	2.701	.384	1.864	3.537
8	2.381	.370	1.575	3.187
9	1.911	.360	1.126	2.696
10	2.050	.362	1.261	2.839
11	1.658	.332	.936	2.381
12	1.382	.266	.803	1.961
13	1.846	.350	1.083	2.609
14	1.708	.302	1.050	2.366
15	2.045	.400	1.174	2.917

Appendix 3.2.1: Allocentric-n test 2 x 4 Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
test1_targ	29.6720	20.19950	13
test1_NW	62.5799	29.88680	13
test1_NE	92.4644	28.20773	13
test1_SE	73.4964	20.78322	13
test2_targ	35.7918	20.98129	13
test2_NW	72.6568	24.92168	13
test2_NE	94.4634	29.83483	13
test2_SE	70.6598	25.22283	13

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	383.346	1	383.346	.351	.565
	Greenhouse-Geisser	383.346	1.000	383.346	.351	.565
	Huynh-Feldt	383.346	1.000	383.346	.351	.565
	Lower-bound	383.346	1.000	383.346	.351	.565
Error(test)	Sphericity Assumed	13122.930	12	1093.577		
	Greenhouse-Geisser	13122.930	12.000	1093.577		
	Huynh-Feldt	13122.930	12.000	1093.577		
	Lower-bound	13122.930	12.000	1093.577		
quad	Sphericity Assumed	49392.266	3	16464.089	36.918	.000
	Greenhouse-Geisser	49392.266	1.943	25425.872	36.918	.000
	Huynh-Feldt	49392.266	2.312	21362.453	36.918	.000
	Lower-bound	49392.266	1.000	49392.266	36.918	.000
Error(quad)	Sphericity Assumed	16054.892	36	445.969		
	Greenhouse-Geisser	16054.892	23.311	688.721		
	Huynh-Feldt	16054.892	27.745	578.653		
	Lower-bound	16054.892	12.000	1337.908		
test * quad	Sphericity Assumed	598.413	3	199.471	.530	.665
	Greenhouse-Geisser	598.413	1.441	415.154	.530	.541
	Huynh-Feldt	598.413	1.585	377.476	.530	.556
	Lower-bound	598.413	1.000	598.413	.530	.481
Error(test*quad)	Sphericity Assumed	13558.480	36	376.624		
	Greenhouse-Geisser	13558.480	17.297	783.859		
	Huynh-Feldt	13558.480	19.024	712.719		
	Lower-bound	13558.480	12.000	1129.873		

Appendix 3.2.2: Allocentric-n planned contrasts

Tests of Within-Subjects Contrasts							
Measure: MEASURE_1							
Source	test	quad	Type III Sum of Squares	df	Mean Square	F	Sig.
quad		Level 1 vs. Later	26311.261	1	26311.261	83.877	.000
Error(quad)		Level 1 vs. Later	3764.276	12	313.690		
test * quad	Level 1 vs. Level 2	Level 1 vs. Later	120.144	1	120.144	.061	.809
Error(test*quad)	Level 1 vs. Level 2	Level 1 vs. Later	23602.748	12	1966.896		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
66.473	3.867	58.048	74.898

2. test

Measure: MEASURE_1

test	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	64.553	5.431	52.720	76.386
2	68.393	4.631	58.304	78.482

3. quad

Measure: MEASURE_1

quad	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	32.732	4.075	23.854	41.610
2	67.618	6.742	52.929	82.308
3	93.464	5.504	81.472	105.456
4	72.078	4.349	62.602	81.554

4. test * quad

Measure: MEASURE_1

test	quad	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
1	1	29.672	5.602	17.466	41.878
	2	62.580	8.289	44.519	80.640
	3	92.464	7.823	75.419	109.510
	4	73.496	5.764	60.937	86.056
2	1	35.792	5.819	23.113	48.471
	2	72.657	6.912	57.597	87.717
	3	94.463	8.275	76.434	112.492
	4	70.660	6.996	55.418	85.902

Appendix 3.2.3: Allocentric-n One Way Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	243.440	1	243.440	.584	.459
	Greenhouse-Geisser	243.440	1.000	243.440	.584	.459
	Huynh-Feldt	243.440	1.000	243.440	.584	.459
	Lower-bound	243.440	1.000	243.440	.584	.459
Error(test)	Sphericity Assumed	4998.269	12	416.522		
	Greenhouse-Geisser	4998.269	12.000	416.522		
	Huynh-Feldt	4998.269	12.000	416.522		
	Lower-bound	4998.269	12.000	416.522		

Appendix 3.2.4: Allocentric-r 2 x 4 Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
test1_targ	54.4490	29.45902	13
test1_NW	50.3134	25.79142	13
test1_NE	60.0606	17.45600	13
test1_SE	61.4029	28.28582	13
test2_targ	76.6517	36.02591	13
test2_NW	90.7023	29.62231	13
test2_NE	58.6137	22.76419	13
test2_SE	40.4271	18.50749	13

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	2622.005	1	2622.005	2.688	.127
	Greenhouse-Geisser	2622.005	1.000	2622.005	2.688	.127
	Huynh-Feldt	2622.005	1.000	2622.005	2.688	.127
	Lower-bound	2622.005	1.000	2622.005	2.688	.127
Error(test)	Sphericity Assumed	11705.046	12	975.421		
	Greenhouse-Geisser	11705.046	12.000	975.421		
	Huynh-Feldt	11705.046	12.000	975.421		
	Lower-bound	11705.046	12.000	975.421		
quad	Sphericity Assumed	5570.348	3	1856.783	3.418	.027
	Greenhouse-Geisser	5570.348	1.645	3386.674	3.418	.061
	Huynh-Feldt	5570.348	1.872	2976.039	3.418	.053
	Lower-bound	5570.348	1.000	5570.348	3.418	.089
Error(quad)	Sphericity Assumed	19559.364	36	543.316		
	Greenhouse-Geisser	19559.364	19.737	990.979		
	Huynh-Feldt	19559.364	22.461	870.823		
	Lower-bound	19559.364	12.000	1629.947		
test * quad	Sphericity Assumed	14058.937	3	4686.312	7.681	.000
	Greenhouse-Geisser	14058.937	1.818	7732.008	7.681	.004
	Huynh-Feldt	14058.937	2.125	6615.527	7.681	.002
	Lower-bound	14058.937	1.000	14058.937	7.681	.017

Error(test*quad)	Sphericity Assumed	21964.466	36	610.124		
	Greenhouse-Geisser	21964.466	21.819	1006.652		
	Huynh-Feldt	21964.466	25.502	861.294		
	Lower-bound	21964.466	12.000	1830.372		

Appendix 3.2.5: Allocentric-r planned contrasts (target vs. rest)

Tests of Within-Subjects Contrasts							
Measure: MEASURE_1							
Source	test	quad	Type III Sum of Squares	df	Mean Square	F	Sig.
quad		Level 1 vs. Later	364.762	1	364.762	.699	.420
Error(quad)		Level 1 vs. Later	6266.486	12	522.207		
test * quad	Level 1 vs. Level 2	Level 1 vs. Later	3417.573	1	3417.573	2.551	.136
Error(test*quad)	Level 1 vs. Level 2	Level 1 vs. Later	16074.974	12	1339.581		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
61.578	3.450	54.060	69.095

2. test

Measure: MEASURE_1

test	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	56.556	4.006	47.828	65.285
2	66.599	5.150	55.378	77.819

3. quad

Measure: MEASURE_1

quad	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	65.550	7.195	49.874	81.227
2	70.508	4.744	60.171	80.845
3	59.337	4.178	50.235	68.440
4	50.915	4.311	41.522	60.308

4. test * quad

Measure: MEASURE_1

test	quad	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
1	1	54.449	8.170	36.647	72.251
	2	50.313	7.153	34.728	65.899
	3	60.061	4.841	49.512	70.609
	4	61.403	7.845	44.310	78.496
2	1	76.652	9.992	54.881	98.422
	2	90.702	8.216	72.802	108.603
	3	58.614	6.314	44.857	72.370
	4	40.427	5.133	29.243	51.611

Appendix 3.2.6: Allocentric-r planned contrasts (SE vs. rest)

Tests of Within-Subjects Contrasts							
Measure: MEASURE_1							
Source	test	quad	Type III Sum of Squares	df	Mean Square	F	Sig.
quad		Level 1 vs. Later	2627.536	1	2627.536	13.450	.003
		Error(quad)	Level 1 vs. Later	2344.202	12	195.350	
test * quad	Level 1 vs. Level 2	Level 1 vs. Later	22235.583	1	22235.583	10.955	.006

Error(test*quad	Level 1 vs. Level 2	Level 1 vs. Later	24356.159	12	2029.680		
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Appendix 3.2.7: Allocentric-r One Way Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	3204.224	1	3204.224	3.909	.071
	Greenhouse-Geisser	3204.224	1.000	3204.224	3.909	.071
	Huynh-Feldt	3204.224	1.000	3204.224	3.909	.071
	Lower-bound	3204.224	1.000	3204.224	3.909	.071
Error(test)	Sphericity Assumed	9837.430	12	819.786		
	Greenhouse-Geisser	9837.430	12.000	819.786		
	Huynh-Feldt	9837.430	12.000	819.786		
	Lower-bound	9837.430	12.000	819.786		

Appendix 3.2.8: Allocentric-n vs. Allocentric-r 2 x 2 Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	14001.690	1	14001.690	20.201	.001
	Greenhouse-Geisser	14001.690	1.000	14001.690	20.201	.001
	Huynh-Feldt	14001.690	1.000	14001.690	20.201	.001
	Lower-bound	14001.690	1.000	14001.690	20.201	.001
Error(test)	Sphericity Assumed	8317.291	12	693.108		
	Greenhouse-Geisser	8317.291	12.000	693.108		
	Huynh-Feldt	8317.291	12.000	693.108		
	Lower-bound	8317.291	12.000	693.108		

time	Sphericity Assumed	2607.028	1	2607.028	3.299	.094
	Greenhouse-Geisser	2607.028	1.000	2607.028	3.299	.094
	Huynh-Feldt	2607.028	1.000	2607.028	3.299	.094
	Lower-bound	2607.028	1.000	2607.028	3.299	.094
Error(time)	Sphericity Assumed	9481.629	12	790.136		
	Greenhouse-Geisser	9481.629	12.000	790.136		
	Huynh-Feldt	9481.629	12.000	790.136		
	Lower-bound	9481.629	12.000	790.136		
test * time	Sphericity Assumed	840.635	1	840.635	1.884	.195
	Greenhouse-Geisser	840.635	1.000	840.635	1.884	.195
	Huynh-Feldt	840.635	1.000	840.635	1.884	.195
	Lower-bound	840.635	1.000	840.635	1.884	.195
Error(test*time)	Sphericity Assumed	5354.070	12	446.172		
	Greenhouse-Geisser	5354.070	12.000	446.172		
	Huynh-Feldt	5354.070	12.000	446.172		
	Lower-bound	5354.070	12.000	446.172		

Appendix 3.3.1: Egocentric-p test 2 x 4 Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
test1_targ	88.9533	40.64157	13
test1_NW	65.2518	30.26210	13
test1_NE	88.8245	46.56153	13
test1_SE	112.0086	46.01753	13
test2_targ	47.0434	42.82571	13
test2_NW	64.1134	25.68021	13
test2_NE	101.6828	39.35333	13
test2_SE	94.0766	47.75717	13

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	3763.049	1	3763.049	.814	.385
	Greenhouse-Geisser	3763.049	1.000	3763.049	.814	.385
	Huynh-Feldt	3763.049	1.000	3763.049	.814	.385
	Lower-bound	3763.049	1.000	3763.049	.814	.385
Error(test)	Sphericity Assumed	55461.456	12	4621.788		
	Greenhouse-Geisser	55461.456	12.000	4621.788		
	Huynh-Feldt	55461.456	12.000	4621.788		
	Lower-bound	55461.456	12.000	4621.788		
quad	Sphericity Assumed	28916.513	3	9638.838	16.244	.000
	Greenhouse-Geisser	28916.513	2.026	14269.212	16.244	.000
	Huynh-Feldt	28916.513	2.441	11846.595	16.244	.000
	Lower-bound	28916.513	1.000	28916.513	16.244	.002
Error(quad)	Sphericity Assumed	21361.093	36	593.364		
	Greenhouse-Geisser	21361.093	24.318	878.408		
	Huynh-Feldt	21361.093	29.291	729.273		
	Lower-bound	21361.093	12.000	1780.091		
test * quad	Sphericity Assumed	10827.059	3	3609.020	4.045	.014
	Greenhouse-Geisser	10827.059	1.969	5497.533	4.045	.031
	Huynh-Feldt	10827.059	2.353	4601.228	4.045	.023
	Lower-bound	10827.059	1.000	10827.059	4.045	.067
Error(test*quad)	Sphericity Assumed	32123.281	36	892.313		
	Greenhouse-Geisser	32123.281	23.633	1359.240		
	Huynh-Feldt	32123.281	28.237	1137.632		
	Lower-bound	32123.281	12.000	2676.940		

Appendix 3.3.2: Egocentric-p test planned contrasts

Tests of Within-Subjects Contrasts							
Measure: MEASURE_1							
Source	test	quad	Type III Sum of Squares	df	Mean Square	F	Sig.
quad		Level 1 vs. Later	5025.344	1	5025.344	12.290	.004
Error(quad)		Level 1 vs. Later	4906.962	12	408.913		
test * quad	Level 1 vs. Level 2	Level 1 vs. Later	20633.168	1	20633.168	7.881	.016
Error(test*quad)	Level 1 vs. Level 2	Level 1 vs. Later	31416.183	12	2618.015		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
82.744	6.277	69.069	96.420

2. test

Measure: MEASURE_1

test	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	88.760	8.870	69.434	108.085
2	76.729	9.434	56.174	97.284

3. quad

Measure: MEASURE_1

quad	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	67.998	7.922	50.738	85.259
2	64.683	6.771	49.931	79.435
3	95.254	7.190	79.588	110.920
4	103.043	8.109	85.375	120.711

4. test * quad

Measure: MEASURE_1

test	quad	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
1	1	88.953	11.272	64.394	113.513
	2	65.252	8.393	46.965	83.539
	3	88.824	12.914	60.688	116.961
	4	112.009	12.763	84.201	139.817
2	1	47.043	11.878	21.164	72.923
	2	64.113	7.122	48.595	79.632
	3	101.683	10.915	77.902	125.464
	4	94.077	13.245	65.217	122.936

Appendix 3.3.3: Egocentric-p test One Way Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	11416.877	1	11416.877	6.158	.029
	Greenhouse-Geisser	11416.877	1.000	11416.877	6.158	.029
	Huynh-Feldt	11416.877	1.000	11416.877	6.158	.029
	Lower-bound	11416.877	1.000	11416.877	6.158	.029

Error(test)	Sphericity Assumed	22249.636	12	1854.136		
	Greenhouse-Geisser	22249.636	12.000	1854.136		
	Huynh-Feldt	22249.636	12.000	1854.136		
	Lower-bound	22249.636	12.000	1854.136		

Appendix 3.3.4: Egocentric-np test 2 x 4 Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
test1_targ	73.1265	45.37617	13
test1_NW	55.3574	34.52964	13
test1_NE	102.9203	40.12555	13
test1_SE	114.4308	47.32598	13
test2_targ	42.7403	18.92424	13
test2_NW	53.6470	28.28886	13
test2_NE	92.0213	28.41332	13
test2_SE	84.6312	25.30972	13

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	8611.125	1	8611.125	4.366	.059
	Greenhouse-Geisser	8611.125	1.000	8611.125	4.366	.059
	Huynh-Feldt	8611.125	1.000	8611.125	4.366	.059
	Lower-bound	8611.125	1.000	8611.125	4.366	.059
Error(test)	Sphericity Assumed	23668.519	12	1972.377		
	Greenhouse-Geisser	23668.519	12.000	1972.377		
	Huynh-Feldt	23668.519	12.000	1972.377		
	Lower-bound	23668.519	12.000	1972.377		
quad	Sphericity Assumed	46692.562	3	15564.187	23.750	.000
	Greenhouse-Geisser	46692.562	1.639	28495.890	23.750	.000
	Huynh-Feldt	46692.562	1.863	25065.580	23.750	.000
	Lower-bound	46692.562	1.000	46692.562	23.750	.000

Error(quad)	Sphericity Assumed	23592.118	36	655.337		
	Greenhouse-Geisser	23592.118	19.663	1199.831		
	Huynh-Feldt	23592.118	22.354	1055.397		
	Lower-bound	23592.118	12.000	1966.010		
test * quad	Sphericity Assumed	3953.721	3	1317.907	4.189	.012
	Greenhouse-Geisser	3953.721	1.867	2118.089	4.189	.031
	Huynh-Feldt	3953.721	2.197	1799.324	4.189	.023
	Lower-bound	3953.721	1.000	3953.721	4.189	.063
Error(test*quad)	Sphericity Assumed	11326.333	36	314.620		
	Greenhouse-Geisser	11326.333	22.400	505.646		
	Huynh-Feldt	11326.333	26.368	429.548		
	Lower-bound	11326.333	12.000	943.861		

Appendix 3.3.5: Egocentric-np test planned contrasts

Tests of Within-Subjects Contrasts							
Measure: MEASURE_1							
Source	test	quad	Type III Sum of Squares	df	Mean Square	F	Sig.
quad		Level 1 vs. Later	8721.360	1	8721.360	15.471	.002
Error(quad)		Level 1 vs. Later	6764.668	12	563.722		
test * quad	Level 1 vs. Level 2	Level 1 vs. Later	3432.746	1	3432.746	3.848	.073
Error(test*quad)	Level 1 vs. Level 2	Level 1 vs. Later	10704.710	12	892.059		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
77.359	6.811	62.519	92.200

2. test

Measure: MEASURE_1

test	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	86.459	10.474	63.638	109.280
2	68.260	4.584	58.272	78.248

3. quad

Measure: MEASURE_1

quad	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	57.933	7.945	40.623	75.244
2	54.502	7.263	38.677	70.327
3	97.471	8.393	79.184	115.758
4	99.531	8.653	80.677	118.385

4. test * quad

Measure: MEASURE_1

test	quad	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
1	1	73.127	12.585	45.706	100.547
	2	55.357	9.577	34.491	76.223
	3	102.920	11.129	78.673	127.168
	4	114.431	13.126	85.832	143.030
2	1	42.740	5.249	31.305	54.176
	2	53.647	7.846	36.552	70.742
	3	92.021	7.880	74.851	109.191
	4	84.631	7.020	69.337	99.926

Appendix 3.3.6: Egocentric-np One Way Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	6001.589	1	6001.589	7.734	.017
	Greenhouse-Geisser	6001.589	1.000	6001.589	7.734	.017
	Huynh-Feldt	6001.589	1.000	6001.589	7.734	.017
	Lower-bound	6001.589	1.000	6001.589	7.734	.017
Error(test)	Sphericity Assumed	9311.520	12	775.960		
	Greenhouse-Geisser	9311.520	12.000	775.960		
	Huynh-Feldt	9311.520	12.000	775.960		
	Lower-bound	9311.520	12.000	775.960		

Appendix 3.3.7: Egocentric-p vs. Egocentric-np 2 x 2 Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	1316.943	1	1316.943	2.018	.181
	Greenhouse-Geisser	1316.943	1.000	1316.943	2.018	.181
	Huynh-Feldt	1316.943	1.000	1316.943	2.018	.181
	Lower-bound	1316.943	1.000	1316.943	2.018	.181
Error(test)	Sphericity Assumed	7831.130	12	652.594		
	Greenhouse-Geisser	7831.130	12.000	652.594		
	Huynh-Feldt	7831.130	12.000	652.594		
	Lower-bound	7831.130	12.000	652.594		
time	Sphericity Assumed	16986.878	1	16986.878	17.503	.001
	Greenhouse-Geisser	16986.878	1.000	16986.878	17.503	.001
	Huynh-Feldt	16986.878	1.000	16986.878	17.503	.001
	Lower-bound	16986.878	1.000	16986.878	17.503	.001
Error(time)	Sphericity Assumed	11645.905	12	970.492		
	Greenhouse-Geisser	11645.905	12.000	970.492		
	Huynh-Feldt	11645.905	12.000	970.492		
	Lower-bound	11645.905	12.000	970.492		

test * time	Sphericity Assumed	431.588	1	431.588	.260	.619
	Greenhouse-Geisser	431.588	1.000	431.588	.260	.619
	Huynh-Feldt	431.588	1.000	431.588	.260	.619
	Lower-bound	431.588	1.000	431.588	.260	.619
Error(test*time)	Sphericity Assumed	19915.251	12	1659.604		
	Greenhouse-Geisser	19915.251	12.000	1659.604		
	Huynh-Feldt	19915.251	12.000	1659.604		
	Lower-bound	19915.251	12.000	1659.604		

Appendix 3.4.1: Paired samples t-test comparing bin 0 frequency

T-Test

Paired Samples Statistics

	Mean	N	Std. Deviation	Std. Error Mean
Pair 1 block1_bin0	73.8462	13	20.61491	5.71755
block3_bin0	119.6923	13	13.21858	3.66617

Paired Samples Test

	Paired Differences					t	df	Sig. (2-tailed)
	Mean	Std. Deviation	Std. Error Mean	95% Confidence Interval of the Difference				
				Lower	Upper			
Pair 1 block1_bin0 - block3_bin0	-45.84615	25.20531	6.99070	-61.07757	-30.61474	-6.558	12	.000

Appendix 3.4.2: Bin percentage 2 x 5 Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
block1_pbin1	63.4327	9.39107	13
block1_pbin2	22.3570	10.53980	13
block1_pbin3	8.3918	4.50909	13
block1_pbin4	3.6662	4.36002	13
block1_pbin5	2.1523	2.30110	13
block3_pbin1	30.7164	20.32310	13
block3_pbin2	17.2990	14.81364	13
block3_pbin3	12.1978	11.99932	13
block3_pbin4	9.7415	8.79216	13
block3_pbin5	30.0452	35.30852	13

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
block	Sphericity Assumed	.000	1	.000	.	.
	Greenhouse-Geisser	.000
	Huynh-Feldt	.000
	Lower-bound	.000	1.000	.000	.	.
Error(block)	Sphericity Assumed	.000	12	.000		
	Greenhouse-Geisser	.000	.	.		
	Huynh-Feldt	.000	.	.		
	Lower-bound	.000	12.000	.000		
bin	Sphericity Assumed	26500.770	4	6625.193	25.254	.000
	Greenhouse-Geisser	26500.770	1.605	16514.997	25.254	.000
	Huynh-Feldt	26500.770	1.814	14606.493	25.254	.000
	Lower-bound	26500.770	1.000	26500.770	25.254	.000
Error(bin)	Sphericity Assumed	12592.580	48	262.345		
	Greenhouse-Geisser	12592.580	19.256	653.963		
	Huynh-Feldt	12592.580	21.772	578.390		
	Lower-bound	12592.580	12.000	1049.382		
block * bin	Sphericity Assumed	12514.764	4	3128.691	9.664	.000
	Greenhouse-Geisser	12514.764	1.874	6678.065	9.664	.001
	Huynh-Feldt	12514.764	2.208	5666.917	9.664	.001
	Lower-bound	12514.764	1.000	12514.764	9.664	.009
Error(block*bin)	Sphericity Assumed	15539.813	48	323.746		
	Greenhouse-Geisser	15539.813	22.488	691.023		
	Huynh-Feldt	15539.813	26.501	586.393		
	Lower-bound	15539.813	12.000	1294.984		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
20.000	.000	20.000	20.000

2. block

Measure: MEASURE_1

block	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	20.000	.000	20.000	20.000
2	20.000	.000	20.000	20.000

3. bin

Measure: MEASURE_1

bin	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	47.075	2.474	41.684	52.465
2	19.828	2.456	14.477	25.179
3	10.295	1.666	6.665	13.925
4	6.704	1.382	3.694	9.714
5	16.099	4.850	5.531	26.666

4. block * bin

Measure: MEASURE_1

block	bin	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
1	1	63.433	2.605	57.758	69.108
	2	22.357	2.923	15.988	28.726
	3	8.392	1.251	5.667	11.117
	4	3.666	1.209	1.031	6.301
	5	2.152	.638	.762	3.543
2	1	30.716	5.637	18.435	42.998
	2	17.299	4.109	8.347	26.251
	3	12.198	3.328	4.947	19.449
	4	9.742	2.439	4.428	15.055
	5	30.045	9.793	8.708	51.382

Appendix 4

SPSS Data Output – Experiment 4

Appendix 4.1.1: Distance travelled One Way Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
dist_trial1	431.0346	84.08468	19
dist_trial2	359.7877	93.30491	19
dist_trial3	317.9739	119.32190	19
dist_trial4	310.2958	118.29132	19
dist_trial5	228.7161	103.20946	19
dist_trial6	301.6083	103.77610	19
dist_trial7	231.6008	136.44379	19
dist_trial8	268.6776	122.11605	19
dist_trial9	293.6671	111.90805	19
dist_trial10	296.9845	132.17122	19
dist_trial11	247.7753	115.37776	19
dist_trial12	239.5488	123.58074	19
dist_trial13	193.4977	116.01957	19
dist_trial14	209.5032	120.35750	19
dist_trial15	222.5283	139.83297	19

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
trial	Sphericity Assumed	1061423.881	14	75815.991	6.357	.000
	Greenhouse-Geisser	1061423.881	6.551	162034.599	6.357	.000
	Huynh-Feldt	1061423.881	10.696	99236.706	6.357	.000
	Lower-bound	1061423.881	1.000	1061423.881	6.357	.021
Error(trial)	Sphericity Assumed	3005669.304	252	11927.259		
	Greenhouse-Geisser	3005669.304	117.911	25491.042		
	Huynh-Feldt	3005669.304	192.526	15611.771		
	Lower-bound	3005669.304	18.000	166981.628		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
276.880	11.555	252.604	301.156

**Appendix 4.1.2: Latency to target One Way Within-Subjects ANOVA
General Linear Model**

Descriptive Statistics

	Mean	Std. Deviation	N
time_trial1	3.8251	.58270	19
time_trial2	3.7678	.68272	19
time_trial3	3.4422	.99003	19
time_trial4	3.4010	1.10840	19
time_trial5	2.5749	1.14611	19
time_trial6	3.2607	1.03605	19
time_trial7	2.4512	1.29283	19
time_trial8	2.8739	1.38566	19
time_trial9	3.2650	1.10909	19
time_trial10	3.0785	1.16417	19
time_trial11	2.6541	1.32294	19
time_trial12	2.5053	1.32233	19
time_trial13	1.9493	1.26055	19
time_trial14	2.2291	1.43233	19
time_trial15	2.2313	1.37481	19

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
trial	Sphericity Assumed	90.710	14	6.479	5.374	.000
	Greenhouse-Geisser	90.710	6.298	14.403	5.374	.000
	Huynh-Feldt	90.710	10.055	9.021	5.374	.000
	Lower-bound	90.710	1.000	90.710	5.374	.032
Error(trial)	Sphericity Assumed	303.819	252	1.206		
	Greenhouse-Geisser	303.819	113.366	2.680		
	Huynh-Feldt	303.819	180.993	1.679		
	Lower-bound	303.819	18.000	16.879		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
2.901	.114	2.660	3.141

Appendix 4.2.1: Allocentric test 2 x 4 Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
test1_targ	27.5070	13.48939	19
test1_NW	69.3972	14.34474	19
test1_NE	100.1237	23.16445	19
test1_SE	76.3389	25.65561	19
test2_targ	21.0890	10.93510	19
test2_NW	70.4416	14.09516	19
test2_NE	97.7797	18.16509	19
test2_SE	70.6320	17.56789	19

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	428.017	1	428.017	.788	.387
	Greenhouse-Geisser	428.017	1.000	428.017	.788	.387
	Huynh-Feldt	428.017	1.000	428.017	.788	.387
	Lower-bound	428.017	1.000	428.017	.788	.387
Error(test)	Sphericity Assumed	9781.122	18	543.396		
	Greenhouse-Geisser	9781.122	18.000	543.396		
	Huynh-Feldt	9781.122	18.000	543.396		
	Lower-bound	9781.122	18.000	543.396		

quad	Sphericity Assumed	109991.001	3	36663.667	237.403	.000
	Greenhouse-Geisser	109991.001	1.689	65121.677	237.403	.000
	Huynh-Feldt	109991.001	1.845	59620.946	237.403	.000
	Lower-bound	109991.001	1.000	109991.001	237.403	.000
Error(quad)	Sphericity Assumed	8339.562	54	154.436		
	Greenhouse-Geisser	8339.562	30.402	274.308		
	Huynh-Feldt	8339.562	33.207	251.138		
	Lower-bound	8339.562	18.000	463.309		
test * quad	Sphericity Assumed	335.261	3	111.754	.718	.545
	Greenhouse-Geisser	335.261	1.743	192.384	.718	.477
	Huynh-Feldt	335.261	1.914	175.196	.718	.489
	Lower-bound	335.261	1.000	335.261	.718	.408
Error(test*quad)	Sphericity Assumed	8402.938	54	155.610		
	Greenhouse-Geisser	8402.938	31.368	267.883		
	Huynh-Feldt	8402.938	34.445	243.950		
	Lower-bound	8402.938	18.000	466.830		

Appendix 4.2.2: Allocentric test planned contrasts

Tests of Within-Subjects Contrasts							
Measure: MEASURE_1							
Source	test	quad	Type III Sum of Squares	df	Mean Square	F	Sig.
quad		Level 1 vs. Later	60625.910	1	60625.910	374.273	.000
Error(quad)		Level 1 vs. Later	2915.696	18	161.983		
test * quad	Level 1 vs. Level 2	Level 1 vs. Later	316.666	1	316.666	.764	.394
Error(test*quad)	Level 1 vs. Level 2	Level 1 vs. Later	7461.229	18	414.513		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
66.664	2.648	61.100	72.227

2. test

Measure: MEASURE_1

test	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	68.342	3.518	60.951	75.732
2	64.986	2.966	58.754	71.218

3. quad

Measure: MEASURE_1

quad	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	24.298	2.049	19.992	28.604
2	69.919	2.449	64.775	75.064
3	98.952	3.902	90.753	107.150
4	73.485	3.849	65.398	81.573

4. test * quad

Measure: MEASURE_1

test	quad	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
1	1	27.507	3.095	21.005	34.009
	2	69.397	3.291	62.483	76.311
	3	100.124	5.314	88.959	111.289
	4	76.339	5.886	63.973	88.705
2	1	21.089	2.509	15.818	26.360
	2	70.442	3.234	63.648	77.235
	3	97.780	4.167	89.024	106.535
	4	70.632	4.030	62.165	79.099

Appendix 4.2.3: Allocentric test One Way Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	391.310	1	391.310	2.757	.114
	Greenhouse-Geisser	391.310	1.000	391.310	2.757	.114
	Huynh-Feldt	391.310	1.000	391.310	2.757	.114
	Lower-bound	391.310	1.000	391.310	2.757	.114
Error(test)	Sphericity Assumed	2554.633	18	141.924		
	Greenhouse-Geisser	2554.633	18.000	141.924		
	Huynh-Feldt	2554.633	18.000	141.924		
	Lower-bound	2554.633	18.000	141.924		

Appendix 4.3.1: Egocentric-p 2 x 4 Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
test1_targ	80.1641	32.80158	19
test1_NW	58.4810	30.50798	19
test1_NE	104.0700	35.92176	19
test1_SE	116.0231	33.70593	19
test2_targ	52.8711	34.10542	19
test2_NW	61.9877	28.63745	19
test2_NE	95.6519	33.63043	19
test2_SE	89.3357	39.43363	19

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	8237.123	1	8237.123	5.085	.037
	Greenhouse-Geisser	8237.123	1.000	8237.123	5.085	.037
	Huynh-Feldt	8237.123	1.000	8237.123	5.085	.037
	Lower-bound	8237.123	1.000	8237.123	5.085	.037
Error(test)	Sphericity Assumed	29156.991	18	1619.833		
	Greenhouse-Geisser	29156.991	18.000	1619.833		
	Huynh-Feldt	29156.991	18.000	1619.833		
	Lower-bound	29156.991	18.000	1619.833		
quad	Sphericity Assumed	55467.846	3	18489.282	29.474	.000
	Greenhouse-Geisser	55467.846	1.984	27955.261	29.474	.000
	Huynh-Feldt	55467.846	2.229	24884.748	29.474	.000
	Lower-bound	55467.846	1.000	55467.846	29.474	.000
Error(quad)	Sphericity Assumed	33875.106	54	627.317		
	Greenhouse-Geisser	33875.106	35.715	948.485		
	Huynh-Feldt	33875.106	40.122	844.306		
	Lower-bound	33875.106	18.000	1881.950		
test * quad	Sphericity Assumed	6395.654	3	2131.885	3.783	.015
	Greenhouse-Geisser	6395.654	1.977	3235.673	3.783	.033
	Huynh-Feldt	6395.654	2.219	2882.254	3.783	.027
	Lower-bound	6395.654	1.000	6395.654	3.783	.068
Error(test*quad)	Sphericity Assumed	30431.257	54	563.542		
	Greenhouse-Geisser	30431.257	35.579	855.317		
	Huynh-Feldt	30431.257	39.942	761.894		
	Lower-bound	30431.257	18.000	1690.625		

Appendix 4.3.2: Egocentric-p planned contrasts

Tests of Within-Subjects Contrasts							
Measure: MEASURE_1							
Source	test	quad	Type III Sum of Squares	df	Mean Square	F	Sig.
quad		Level 1 vs. Later	8438.142	1	8438.142	13.654	.002
Error(quad)		Level 1 vs. Later	11123.939	18	617.997		
test * quad	Level 1 vs. Level 2	Level 1 vs. Later	5337.111	1	5337.111	3.762	.068
Error(test*quad)	Level 1 vs. Level 2	Level 1 vs. Later	25537.548	18	1418.753		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
82.323	5.072	71.667	92.979

2. test

Measure: MEASURE_1

test	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	89.685	6.172	76.718	102.651
2	74.962	5.888	62.591	87.332

3. quad

Measure: MEASURE_1

quad	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	66.518	5.890	54.143	78.892
2	60.234	4.938	49.860	70.609
3	99.861	6.773	85.632	114.090
4	102.679	6.890	88.204	117.155

4. test * quad

Measure: MEASURE_1

test	quad	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
1	1	80.164	7.525	64.354	95.974
	2	58.481	6.999	43.777	73.185
	3	104.070	8.241	86.756	121.384
	4	116.023	7.733	99.777	132.269
2	1	52.871	7.824	36.433	69.309
	2	61.988	6.570	48.185	75.791
	3	95.652	7.715	79.443	111.861
	4	89.336	9.047	70.329	108.342

Appendix 4.3.3: Egocentric-p test One Way Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	7076.653	1	7076.653	7.685	.013
	Greenhouse-Geisser	7076.653	1.000	7076.653	7.685	.013
	Huynh-Feldt	7076.653	1.000	7076.653	7.685	.013
	Lower-bound	7076.653	1.000	7076.653	7.685	.013

Error(test)	Sphericity Assumed	16575.784	18	920.877	
	Greenhouse-Geisser	16575.784	18.000	920.877	
	Huynh-Feldt	16575.784	18.000	920.877	
	Lower-bound	16575.784	18.000	920.877	

Appendix 4.3.4: Egocentric-np 2 x 4 Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
test1_targ	70.6267	40.06090	19
test1_NW	64.4300	58.71975	19
test1_NE	93.3310	52.18860	19
test1_SE	112.2388	49.36120	19
test2_targ	45.8779	23.02274	19
test2_NW	49.4772	29.11654	19
test2_NE	84.4317	27.31684	19
test2_SE	79.6932	29.78455	19

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	15638.767	1	15638.767	5.979	.025
	Greenhouse-Geisser	15638.767	1.000	15638.767	5.979	.025
	Huynh-Feldt	15638.767	1.000	15638.767	5.979	.025
	Lower-bound	15638.767	1.000	15638.767	5.979	.025
Error(test)	Sphericity Assumed	47083.326	18	2615.740		
	Greenhouse-Geisser	47083.326	18.000	2615.740		
	Huynh-Feldt	47083.326	18.000	2615.740		
	Lower-bound	47083.326	18.000	2615.740		
quad	Sphericity Assumed	47060.137	3	15686.712	15.957	.000
	Greenhouse-Geisser	47060.137	2.528	18612.477	15.957	.000
	Huynh-Feldt	47060.137	2.976	15814.410	15.957	.000
	Lower-bound	47060.137	1.000	47060.137	15.957	.001
Error(quad)	Sphericity Assumed	53083.767	54	983.033		
	Greenhouse-Geisser	53083.767	45.512	1166.380		
	Huynh-Feldt	53083.767	53.564	991.035		
	Lower-bound	53083.767	18.000	2949.098		

test * quad	Sphericity Assumed	3118.976	3	1039.659	1.914	.138
	Greenhouse-Geisser	3118.976	2.713	1149.824	1.914	.145
	Huynh-Feldt	3118.976	3.000	1039.659	1.914	.138
	Lower-bound	3118.976	1.000	3118.976	1.914	.183
Error(test*quad)	Sphericity Assumed	29330.657	54	543.160		
	Greenhouse-Geisser	29330.657	48.826	600.715		
	Huynh-Feldt	29330.657	54.000	543.160		
	Lower-bound	29330.657	18.000	1629.481		

Appendix 4.3.5: Egocentric-np planned contrasts

Tests of Within-Subjects Contrasts							
Measure: MEASURE_1							
Source	test	quad	Type III Sum of Squares	df	Mean Square	F	Sig.
quad		Level 1 vs. Later	9489.253	1	9489.253	10.495	.005
Error(quad)		Level 1 vs. Later	16274.691	18	904.150		
test * quad	Level 1 vs. Level 2	Level 1 vs. Later	672.533	1	672.533	.441	.515
Error(test*quad)	Level 1 vs. Level 2	Level 1 vs. Later	27464.132	18	1525.785		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
75.013	6.298	61.781	88.246

2. test

Measure: MEASURE_1

test	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	85.157	9.849	64.465	105.848
2	64.870	4.094	56.268	73.472

3. quad

Measure: MEASURE_1

quad	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	58.252	5.684	46.312	70.193
2	56.954	9.079	37.878	76.029
3	88.881	8.331	71.379	106.384
4	95.966	7.221	80.795	111.137

4. test * quad

Measure: MEASURE_1

test	quad	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
1	1	70.627	9.191	51.318	89.935
	2	64.430	13.471	36.128	92.732
	3	93.331	11.973	68.177	118.485
	4	112.239	11.324	88.447	136.030
2	1	45.878	5.282	34.781	56.975
	2	49.477	6.680	35.443	63.511
	3	84.432	6.267	71.265	97.598
	4	79.693	6.833	65.338	94.049

**Appendix 4.3.6: Egocentric-np One Way Within-Subjects ANOVA
General Linear Model**

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	5818.747	1	5818.747	6.412	.021
	Greenhouse-Geisser	5818.747	1.000	5818.747	6.412	.021
	Huynh-Feldt	5818.747	1.000	5818.747	6.412	.021
	Lower-bound	5818.747	1.000	5818.747	6.412	.021
Error(test)	Sphericity Assumed	16333.488	18	907.416		
	Greenhouse-Geisser	16333.488	18.000	907.416		
	Huynh-Feldt	16333.488	18.000	907.416		
	Lower-bound	16333.488	18.000	907.416		

Appendix 4.3.7: Egocentric-p vs. Egocentric-np 2 x 2 Within-Subjects ANOVA

General Linear Model

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	1297.989	1	1297.989	.785	.387
	Greenhouse-Geisser	1297.989	1.000	1297.989	.785	.387
	Huynh-Feldt	1297.989	1.000	1297.989	.785	.387
	Lower-bound	1297.989	1.000	1297.989	.785	.387
Error(test)	Sphericity Assumed	29773.709	18	1654.095		
	Greenhouse-Geisser	29773.709	18.000	1654.095		
	Huynh-Feldt	29773.709	18.000	1654.095		
	Lower-bound	29773.709	18.000	1654.095		
time	Sphericity Assumed	12864.650	1	12864.650	15.598	.001
	Greenhouse-Geisser	12864.650	1.000	12864.650	15.598	.001
	Huynh-Feldt	12864.650	1.000	12864.650	15.598	.001
	Lower-bound	12864.650	1.000	12864.650	15.598	.001
Error(time)	Sphericity Assumed	14846.095	18	824.783		
	Greenhouse-Geisser	14846.095	18.000	824.783		
	Huynh-Feldt	14846.095	18.000	824.783		
	Lower-bound	14846.095	18.000	824.783		

test * time	Sphericity Assumed	30.750	1	30.750	.031	.863
	Greenhouse-Geisser	30.750	1.000	30.750	.031	.863
	Huynh-Feldt	30.750	1.000	30.750	.031	.863
	Lower-bound	30.750	1.000	30.750	.031	.863
Error(test*time)	Sphericity Assumed	18063.177	18	1003.510		
	Greenhouse-Geisser	18063.177	18.000	1003.510		
	Huynh-Feldt	18063.177	18.000	1003.510		
	Lower-bound	18063.177	18.000	1003.510		

Appendix 4.4.1: Binomial test of choice frequency

NPar Tests

Binomial Test

		Category	N	Observed Prop.	Test Prop.	Exact Sig. (2-tailed)
conf_choice	Group 1	allo	19	1.00	.50	.000
	Total		19	1.00		

Appendix 4.4.2: Conflict test search time Paired samples t-test

T-Test

Paired Samples Statistics

		Mean	N	Std. Deviation	Std. Error Mean
Pair 1	allo_choice	.7691	19	.14416	.03307
	ego_choice	.0000	19	.00000	.00000

Paired Samples Test

	Paired Differences					t	df	Sig. (2-tailed)	
	Mean	Std. Deviation	Std. Error	95% Confidence Interval of the Difference					
				Lower	Upper				
Pair 1	allo_choice - ego_choice	.76914	.14416	.03307	.69966	.83863	23.256	18	.000

Appendix 4.5.1: Paired samples t-test comparing bin 0 frequency

T-Test

Paired Samples Statistics

	Mean	N	Std. Deviation	Std. Error Mean
Pair 1 block1_bin0	78.3684	19	16.74717	3.84207
block3_bin0	110.8947	19	14.11026	3.23712

Paired Samples Test

	Paired Differences					t	df	Sig. (2-tailed)
	Mean	Std. Deviation	Std. Error Mean	95% Confidence Interval of the Difference				
				Lower	Upper			
Pair 1 block1_bin0 - block3_bin0	-32.52632	22.51263	5.16475	-43.37706	-21.67557	-6.298	18	.000

Appendix 4.5.2: Bin percentage 2 x 5 Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
block1_pbin1	64.9157	10.18693	19
block1_pbin2	21.2103	7.72164	19
block1_pbin3	9.3707	7.97527	19
block1_pbin4	3.7599	4.87868	19
block1_pbin5	.7434	1.36234	19
block3_pbin1	46.4762	13.43620	19
block3_pbin2	23.2834	10.98662	19
block3_pbin3	14.8967	8.98383	19
block3_pbin4	8.4965	10.05166	19
block3_pbin5	6.8472	8.00306	19

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
block	Sphericity Assumed	.000	1	.000	.	.
	Greenhouse-Geisser	.000
	Huynh-Feldt	.000
	Lower-bound	.000	1.000	.000	.	.
Error(block)	Sphericity Assumed	.000	18	.000		
	Greenhouse-Geisser	.000	.	.		
	Huynh-Feldt	.000	.	.		
	Lower-bound	.000	18.000	.000		
bin	Sphericity Assumed	68253.534	4	17063.383	158.549	.000
	Greenhouse-Geisser	68253.534	2.453	27821.044	158.549	.000
	Huynh-Feldt	68253.534	2.870	23785.023	158.549	.000
	Lower-bound	68253.534	1.000	68253.534	158.549	.000
Error(bin)	Sphericity Assumed	7748.791	72	107.622		
	Greenhouse-Geisser	7748.791	44.160	175.473		
	Huynh-Feldt	7748.791	51.653	150.017		
	Lower-bound	7748.791	18.000	430.488		
block * bin	Sphericity Assumed	4128.139	4	1032.035	11.181	.000
	Greenhouse-Geisser	4128.139	2.460	1678.109	11.181	.000
	Huynh-Feldt	4128.139	2.879	1433.872	11.181	.000
	Lower-bound	4128.139	1.000	4128.139	11.181	.004
Error(block*bin)	Sphericity Assumed	6645.646	72	92.301		
	Greenhouse-Geisser	6645.646	44.280	150.083		
	Huynh-Feldt	6645.646	51.822	128.239		
	Lower-bound	6645.646	18.000	369.203		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
20.000	.000	20.000	20.000

2. block

Measure: MEASURE_1

block	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	20.000	.000	20.000	20.000
2	20.000	.000	20.000	20.000

3. bin

Measure: MEASURE_1

bin	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	55.696	2.132	51.216	60.175
2	22.247	1.491	19.115	25.379
3	12.134	1.440	9.109	15.158
4	6.128	1.272	3.455	8.801
5	3.795	.932	1.837	5.754

4. block * bin

Measure: MEASURE_1

block	bin	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
1	1	64.916	2.337	60.006	69.826
	2	21.210	1.771	17.489	24.932
	3	9.371	1.830	5.527	13.215
	4	3.760	1.119	1.408	6.111
	5	.743	.313	.087	1.400
2	1	46.476	3.082	40.000	52.952
	2	23.283	2.521	17.988	28.579
	3	14.897	2.061	10.567	19.227
	4	8.496	2.306	3.652	13.341
	5	6.847	1.836	2.990	10.705

Appendix 5

SPSS Data Output – Experiment 5

Appendix 5.1.1: Distance travelled One Way Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
dist_trial1	437.6108	59.42357	18
dist_trial2	442.9519	63.31236	18
dist_trial3	383.2908	77.05155	18
dist_trial4	379.8233	93.49714	18
dist_trial5	343.9539	82.59060	18
dist_trial6	355.8634	97.26806	18
dist_trial7	320.8459	95.68783	18
dist_trial8	318.3997	102.98199	18
dist_trial9	292.3267	54.73534	18
dist_trial10	301.0863	80.77946	18
dist_trial11	294.8067	68.27650	18
dist_trial12	266.9773	43.48880	18
dist_trial13	271.9488	60.24933	18
dist_trial14	272.9341	59.81468	18
dist_trial15	251.8264	24.74052	18

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
trial	Sphericity Assumed	916740.733	14	65481.481	17.680	.000
	Greenhouse-Geisser	916740.733	4.043	226734.822	17.680	.000
	Huynh-Feldt	916740.733	5.463	167820.234	17.680	.000
	Lower-bound	916740.733	1.000	916740.733	17.680	.001
Error(trial)	Sphericity Assumed	881477.617	238	3703.687		
	Greenhouse-Geisser	881477.617	68.735	12824.312		
	Huynh-Feldt	881477.617	92.865	9492.053		
	Lower-bound	881477.617	17.000	51851.625		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
328.976	10.594	306.624	351.328

Appendix 5.1.2: Latency to target One Way Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
time_trial1	3.8437	.39657	18
time_trial2	3.8440	.39342	18
time_trial3	3.3837	.68400	18
time_trial4	3.2143	.83567	18
time_trial5	2.9464	.73574	18
time_trial6	2.9074	.88041	18
time_trial7	2.6309	.82889	18
time_trial8	2.6305	.86339	18
time_trial9	2.3110	.52400	18
time_trial10	2.4050	.67724	18
time_trial11	2.4014	.68346	18
time_trial12	2.1047	.41527	18
time_trial13	2.1204	.52730	18
time_trial14	2.1603	.53492	18
time_trial15	1.9504	.27214	18

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
trial	Sphericity Assumed	95.848	14	6.846	27.302	.000
	Greenhouse-Geisser	95.848	4.052	23.655	27.302	.000
	Huynh-Feldt	95.848	5.478	17.495	27.302	.000
	Lower-bound	95.848	1.000	95.848	27.302	.000
Error(trial)	Sphericity Assumed	59.681	238	.251		
	Greenhouse-Geisser	59.681	68.883	.866		
	Huynh-Feldt	59.681	93.133	.641		
	Lower-bound	59.681	17.000	3.511		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
2.724	.101	2.512	2.936

Appendix 5.2.1: Allocentric test One Way Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
test1_targ	33.7927	14.81304	18
test1_NW	72.9820	22.11970	18
test1_SW	110.7468	24.58236	18
test1_SE	87.6567	27.45927	18

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
quad	Sphericity Assumed	56401.951	3	18800.650	52.987	.000
	Greenhouse-Geisser	56401.951	1.851	30463.429	52.987	.000
	Huynh-Feldt	56401.951	2.068	27274.380	52.987	.000
	Lower-bound	56401.951	1.000	56401.951	52.987	.000
Error(quad)	Sphericity Assumed	18095.495	51	354.814		
	Greenhouse-Geisser	18095.495	31.475	574.918		
	Huynh-Feldt	18095.495	35.155	514.733		
	Lower-bound	18095.495	17.000	1064.441		

Appendix 5.2.2: Allocentric test planned contrasts

Tests of Within-Subjects Contrasts						
Measure: MEASURE_1						
Source	quad	Type III Sum of Squares	df	Mean Square	F	Sig.
quad	Level 1 vs. Later	57805.124	1	57805.124	134.336	.000
Error(quad)	Level 1 vs. Later	7315.163	17	430.304		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
76.295	3.732	68.422	84.167

2. quad

Measure: MEASURE_1

quad	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	33.793	3.491	26.426	41.159
2	72.982	5.214	61.982	83.982
3	110.747	5.794	98.522	122.971
4	87.657	6.472	74.002	101.312

Appendix 5.3.1: Egocentric-p test One Way Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
test1_targ	73.6192	41.14250	18
test1_NW	63.8310	35.54887	18
test1_SW	78.7398	39.06506	18
test1_SE	91.9866	31.22465	18

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
quad	Sphericity Assumed	7424.446	3	2474.815	1.997	.126
	Greenhouse-Geisser	7424.446	1.709	4343.286	1.997	.159
	Huynh-Feldt	7424.446	1.882	3946.013	1.997	.155
	Lower-bound	7424.446	1.000	7424.446	1.997	.176
Error(quad)	Sphericity Assumed	63204.637	51	1239.307		
	Greenhouse-Geisser	63204.637	29.060	2174.976		
	Huynh-Feldt	63204.637	31.986	1976.034		
	Lower-bound	63204.637	17.000	3717.920		

Appendix 5.3.2: Egocentric-p test planned contrasts

Tests of Within-Subjects Contrasts						
Measure: MEASURE_1						
Source	quad	Type III Sum of Squares	df	Mean Square	F	Sig.
quad	Level 1 vs. Later	375.374	1	375.374	.177	.680
Error(quad)	Level 1 vs. Later	36125.636	17	2125.037		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
77.044	4.915	66.674	87.415

2. quad

Measure: MEASURE_1

quad	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	73.619	9.697	53.159	94.079
2	63.831	8.379	46.153	81.509
3	78.740	9.208	59.313	98.166
4	91.987	7.360	76.459	107.514

Appendix 5.3.3: Egocentric-np One Way Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
test1_targ	76.9087	48.81714	18
test1_NW	66.5097	40.84278	18
test1_SW	114.9575	35.25702	18
test1_SE	123.2030	38.04324	18

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
quad	Sphericity Assumed	41977.381	3	13992.460	14.211	.000
	Greenhouse-Geisser	41977.381	1.627	25797.993	14.211	.000
	Huynh-Feldt	41977.381	1.775	23647.473	14.211	.000
	Lower-bound	41977.381	1.000	41977.381	14.211	.002
Error(quad)	Sphericity Assumed	50217.269	51	984.652		
	Greenhouse-Geisser	50217.269	27.662	1815.410		
	Huynh-Feldt	50217.269	30.177	1664.078		
	Lower-bound	50217.269	17.000	2953.957		

Appendix 5.3.4: Egocentric-np test planned contrasts

Tests of Within-Subjects Contrasts						
Measure: MEASURE_1						
Source	quad	Type III Sum of Squares	df	Mean Square	F	Sig.
quad	Level 1 vs. Later	10935.436	1	10935.436	5.494	.031
Error(quad)	Level 1 vs. Later	33840.063	17	1990.592		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
95.395	7.253	80.092	110.697

2. quad

Measure: MEASURE_1

quad	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	76.909	11.506	52.633	101.185
2	66.510	9.627	46.199	86.820
3	114.957	8.310	97.425	132.490
4	123.203	8.967	104.285	142.121

Appendix 5.3.5: Egocentric-p vs. Egocentric-np One Way Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
type1_time1	73.6192	41.14250	18
type2_time1	76.9087	48.81714	18

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
test	Sphericity Assumed	97.390	1	97.390	.058	.813
	Greenhouse-Geisser	97.390	1.000	97.390	.058	.813
	Huynh-Feldt	97.390	1.000	97.390	.058	.813
	Lower-bound	97.390	1.000	97.390	.058	.813
Error(test)	Sphericity Assumed	28573.019	17	1680.766		
	Greenhouse-Geisser	28573.019	17.000	1680.766		
	Huynh-Feldt	28573.019	17.000	1680.766		
	Lower-bound	28573.019	17.000	1680.766		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
75.264	8.157	58.055	92.473

2. test

Measure: MEASURE_1

test	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	73.619	9.697	53.159	94.079
2	76.909	11.506	52.633	101.185

Appendix 5.4.1: Conflict test Chi-Square test

NPar Tests

Chi-Square Test

Frequencies

conf_choice

	Observed N	Expected N	Residual
ego	5	9.0	-4.0
allo	13	9.0	4.0
Total	18		

Test Statistics

	conf_choice
Chi-Square	3.556 ^a
df	1
Asymp. Sig.	.059

a. 0 cells (.0%) have expected frequencies less than 5. The minimum expected cell frequency is 9.0.

Appendix 5.4.2: Distance travelled on conflict test Independent samples t-test

T-Test

Group Statistics

	conf_choice	N	Mean	Std. Deviation	Std. Error Mean
conflict_dist	ego	5	265.2268	35.66802	15.95122
	allo	13	387.8831	97.19574	26.95725

Independent Samples Test

	Levene's Test for Equality of Variances		t-test for Equality of Means						
	F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	95% Confidence Interval of the Difference	
								Lower	Upper
conflict_dist	5.079	.039	-2.709	16	.015	-122.65627	45.27855	-218.64251	-26.67002
			-3.916	15.993	.001	-122.65627	31.32307	-189.06072	-56.25181

Appendix 5.5.1: Paired samples t-test comparing bin 0 frequency

T-Test

Paired Samples Statistics

	Mean	N	Std. Deviation	Std. Error Mean
Pair 1 block1_bin0	6.3333	18	4.47214	1.05409
block3_bin0	15.2222	18	4.46629	1.05271

Paired Samples Test

	Paired Differences					t	df	Sig. (2-tailed)
	Mean	Std. Deviation	Std. Error Mean	95% Confidence Interval of the Difference				
				Lower	Upper			
Pair 1 block1_bin0 - block3_bin0	-8.88889	5.64529	1.33061	-11.69622	-6.08155	-6.680	17	.000

Appendix 5.5.2: Bin percentage 2 x 5 Within-Subjects ANOVA

General Linear Model

Descriptive Statistics

	Mean	Std. Deviation	N
block1_pbin1	19.2054	12.58442	18
block1_pbin2	15.5537	11.49526	18
block1_pbin3	12.7427	6.69136	18
block1_pbin4	12.5889	12.49342	18
block1_pbin5	39.9093	16.64381	18
block3_pbin1	8.9296	11.03103	18
block3_pbin2	4.6741	4.43066	18
block3_pbin3	4.7512	6.82468	18
block3_pbin4	4.1261	3.83897	18
block3_pbin5	77.5189	13.51774	18

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
block	Sphericity Assumed	.000	1	.000	.	.
	Greenhouse-Geisser	.000
	Huynh-Feldt	.000
	Lower-bound	.000	1.000	.000	.	.
Error(block)	Sphericity Assumed	.000	17	.000		
	Greenhouse-Geisser	.000	.	.		
	Huynh-Feldt	.000	.	.		
	Lower-bound	.000	17.000	.000		
bin	Sphericity Assumed	68180.091	4	17045.023	84.042	.000
	Greenhouse-Geisser	68180.091	2.207	30891.933	84.042	.000
	Huynh-Feldt	68180.091	2.550	26733.810	84.042	.000
	Lower-bound	68180.091	1.000	68180.091	84.042	.000
Error(bin)	Sphericity Assumed	13791.502	68	202.816		
	Greenhouse-Geisser	13791.502	37.520	367.579		
	Huynh-Feldt	13791.502	43.356	318.102		
	Lower-bound	13791.502	17.000	811.265		
block * bin	Sphericity Assumed	15965.330	4	3991.333	46.617	.000
	Greenhouse-Geisser	15965.330	2.933	5443.809	46.617	.000
	Huynh-Feldt	15965.330	3.610	4421.943	46.617	.000
	Lower-bound	15965.330	1.000	15965.330	46.617	.000
Error(block*bin)	Sphericity Assumed	5822.123	68	85.619		
	Greenhouse-Geisser	5822.123	49.857	116.777		
	Huynh-Feldt	5822.123	61.378	94.857		
	Lower-bound	5822.123	17.000	342.478		

Estimated Marginal Means

1. Grand Mean

Measure: MEASURE_1

Mean	Std. Error	95% Confidence Interval	
		Lower Bound	Upper Bound
20.000	.000	20.000	20.000

2. block

Measure: MEASURE_1

block	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	20.000	.000	20.000	20.000
2	20.000	.000	20.000	20.000

3. bin

Measure: MEASURE_1

bin	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	14.068	2.440	8.919	19.216
2	10.114	1.470	7.012	13.215
3	8.747	1.361	5.875	11.619
4	8.358	1.825	4.507	12.208
5	58.714	3.039	52.302	65.126

4. block * bin

Measure: MEASURE_1

block	bin	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
1	1	19.205	2.966	12.947	25.463
	2	15.554	2.709	9.837	21.270
	3	12.743	1.577	9.415	16.070
	4	12.589	2.945	6.376	18.802
	5	39.909	3.923	31.633	48.186
2	1	8.930	2.600	3.444	14.415
	2	4.674	1.044	2.471	6.877
	3	4.751	1.609	1.357	8.145
	4	4.126	.905	2.217	6.035
	5	77.519	3.186	70.797	84.241

Appendix F

HREC Approval Letter

Research Integrity

Human Research Ethics Committee

Friday, 22 May 2015

Dr Ian Johnston
Psychology; Faculty of Science
Email: i.johnston@sydney.edu.au

Dear Ian

I am pleased to inform you that the University of Sydney Human Research Ethics Committee (HREC) has approved your project entitled "**Neuropsychological applications of virtual reality**".

Details of the approval are as follows:

Project No.: 2015/347

Approval Date: 22 May 2015

First Annual Report Due: 22 May 2016

Authorised Personnel: Johnston Ian; Segula Blake; Verstraten Frans (Franciscus);

Documents Approved:

<u>Date</u>	<u>Type</u>	<u>Document</u>
18/05/2015	Participant Info Statement	Participant information sheet v.2
18/05/2015	Other Type	Debrief sheet
17/04/2015	Participant Consent Form	Participant consent form
17/04/2015	Study Protocol	Procedural instructions and script

HREC approval is valid for four (4) years from the approval date stated in this letter and is granted pending the following conditions being met:

Condition/s of Approval

- Continuing compliance with the National Statement on Ethical Conduct in Research Involving Humans.
- Provision of an annual report on this research to the Human Research Ethics Committee from the approval date and at the completion of the study. Failure to submit reports will result in withdrawal of ethics approval for the project.
- All serious and unexpected adverse events should be reported to the HREC within 72 hours.
- All unforeseen events that might affect continued ethical acceptability of the project should be reported to the HREC as soon as possible.



- Any changes to the project including changes to research personnel must be approved by the HREC before the research project can proceed.
- Note that for student research projects, a copy of this letter must be included in the candidate's thesis.

Chief Investigator / Supervisor's responsibilities:

1. You must retain copies of all signed Consent Forms (if applicable) and provide these to the HREC on request.
2. It is your responsibility to provide a copy of this letter to any internal/external granting agencies if requested.

Please do not hesitate to contact Research Integrity (Human Ethics) should you require further information or clarification.

Yours sincerely

**Associate Professor Rita Shackel
Chair
Human Research Ethics Committee**

This HREC is constituted and operates in accordance with the National Health and Medical Research Council's (NHMRC) National Statement on Ethical Conduct in Human Research (2007), NHMRC and Universities Australia Australian Code for the Responsible Conduct of Research (2007) and the CPMP/ICH Note for Guidance on Good Clinical Practice.