

Navigational Cognition: What you do and what you show isn't always all you know

by

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Supervisory Committee

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Abstract

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In the study of navigation, frequently it is assumed that navigation is accomplished using either an allocentric strategy based on a cognitive map, or an egocentric strategy based on stimulus response associations. Further, it is frequently assumed that individual navigators, or even entire genders, are only capable of navigating by one strategy or the other. The present study investigated whether individuals or genders were limited to a particular navigational strategy and whether both strategies might be learned or used at the same time. In the present study, undergraduate students were tested in a virtual Morris water maze that was modified to allow successful and efficient navigation using either an allocentric or an egocentric strategy. Learning trials on which the participants had to learn the location of the platform were alternated with probe trials on which participants would show which strategy they were using. At the end of testing, participants were given a series of tests to determine what knowledge they had acquired and which strategies they were capable of using. Results indicated that: a) most people preferred to navigate egocentrically in this maze, but some preferred to navigate allocentrically, b) people tended to use an egocentrically strategy first, but it was not a necessary step to learning to navigate allocentrically, c) people were better at their preferred strategy, d) people learned information about their non-preferred strategy, and e) those who preferred to navigate egocentrically could nevertheless learn to navigate allocentrically. Surprisingly, all of these results were true for both men and women,

although women tended to prefer egocentric navigation at a higher rate than men, and men outperformed women when forced to navigate allocentrically. These results suggest it may be too simple to think of navigators as being capable of only a single navigational strategy or of learning only one strategy at a time.

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Chapter 1

Introduction

Navigation is the means by which people get from one location to another, and is a key skill in everyday life. From being able to locate your place of work day after day to locating and remembering how to get back to your home after searching for food, navigation has always held a huge importance in humans (and animals) ability to function. Navigation includes cognitive and behavioural components. The cognitive processes include planning and making decisions as to how best reach a particular location, and then monitoring the process as the behavioural component (locomotion or the methods required for moving through space) progresses. In navigation, the ability to locate and remember these locations in space is an integral skill, and a large amount of navigation research has focused on this aspect, in particular on the strategies developed by navigators to reach environmental goals.

Navigation Strategies

Research in navigation, has generally dichotomized strategies into “egocentric” and allocentric”, each with distinct and expected behaviours associated with them (Kolb, Sutherland & Whishaw, 1983). Allocentric navigation, or navigation using a “cognitive map” (Tolman, 1948) involves the encoding of different configurations and the different relationships of spatial cues (normally distal) in order to form a cognitive map of the environment (O’Keefe & Nadel, 1978). This type of strategy has been described as independent of the navigator’s perspective (Nadel & Hardt, 2004). Egocentric navigation, on the other hand, consists of stimulus-response navigation (normally) using a proximal goal-associated cue or cues (Klatzky, 1998). Egocentric navigation has been classified as response-based (based on the memorization of body movements or turns)(e.g., Roof & Stein, 1999) or cue-based (based on the use of individual visual cues)(e.g., O’Keefe & Nadel, 1978; Trullier, Wiener, Berthoz, & Meyer, 1997).

Terminology in Spatial Cognition Research

Allocentric navigation has been referred to as “spatial navigation” (e.g., Morris, 1981; Holscher, 1999), “locale learning” (O’Keefe and Nadel, 1978), “place learning” (Morris, 1983), “wayfinding” (Hartley, Maguire, Spiers, & Burgess, 2003) and even “spatial mapping” (Janus, 2004). Conversely, Egocentric navigation has been referred to as “response learning” (e.g., Packard & McGaugh, 1996), “stimulus-response learning” (e.g., Etchamendy & Bohbot, 2007), and “cue-learning” (Whishaw & Kolb, 1984). Somewhat confusingly, even the term “place learning” has been used ambiguously. It has been used to refer to the cognitive process involved in learning a location that can be found either using stimulus-response associations or using a cognitive map (e.g., White & McDonald, 2002), or it may simply refer to allocentric learning (as in Whishaw & Kolb, 1984). For clarity, in this thesis the terms “allocentric strategy” and “egocentric strategy” will be predominantly used, except for in cases when referring to direct findings from authors.

Neuroanatomy

Research on rats with experimentally induced brain damage suggests a role of the hippocampus (HPC) in allocentric navigation (O’Keefe & Nadel, 1978). The authors of this book proposed that the hippocampus mediates the formation and use of a cognitive map. Following this, the Morris water maze was developed to test the idea that rats would only be impaired on the navigation task when forced to use an allocentric navigation strategy (Morris, 1981). Morris developed his water maze to test rats in a purely allocentric environment, as a test of this theory. The water maze requires rats to locate and remember a hidden platform in a large, murky pool of water from a variety of start locations. Egocentric navigation, on the other hand, is thought to be mediated by the dorsal striatum in the basal ganglia (McDonald & White, 1994). More

specifically, the caudate nucleus has been shown to be involved in egocentric navigation (Packard, Hirsh, & White, 1989; Packard & McGaugh, 1996).

The Morris Water Maze

The Morris water maze (MWM) is a tool that has also been particularly valuable in the study of navigational cognition. It is very commonly used in animals as an example of explicit learning, mediated by hippocampal and cortical systems (e.g., see Squire, 1992 for a review of the role of the hippocampus in explicit memory), and is contrasted with more motoric tasks like the rotorod, or more habit-based (i.e., implicit) tasks such as signalled avoidance tasks (e.g., Mitcham & Thomas, 1972). These latter tasks are often considered to rely on subcortical structures like the amygdala or basal ganglia (e.g., Packard and McGaugh, 1996).

In this maze, the animal must remember a hidden platform in an opaque pool of water. The MWM is frequently used to measure spatial abilities and allocentric navigation through the use of distal visual cues (i.e., outside the arena wall in the distance) that surround the maze (Bradneis, Brandys & Yehuda, 1989). In particular, the MWM has been used in studies attempting to understand the role of the hippocampal formation in navigation and behaviour (e.g., Sutherland & Dyck, 1984; Whishaw, 1985). The MWM is a popular tool because not only has it been shown to be effective for studying allocentric navigation but it has also been effective in studying egocentric navigation on its own (e.g., Whishaw, Mittleman, Bunch, & Dunnett, 1987). In fact, originally two separate versions of the MWM were designed to measure learning during navigation: (1) one was designed to measure spatial “place” learning (i.e., allocentric) with the use of a hidden platform while (2) the other was designed to measure non-spatial “cue” learning (i.e., egocentric) with the use of a visible platform (Morris, 1981). The MWM has also been modified to study both allocentric and egocentric learning together (Whishaw & Mittleman, 1986).

While the vast majority of work with the MWM has been with laboratory animals, several labs have designed virtual versions of the MWM to test navigation in human participants (Jacobs, Laurance, & Thomas, 1997; Astur, Ortiz & Sutherland, 1998; Sandstrom, Kaufman, & Huettel, 1998; Skelton, Bukach, Laurance, Thomas, & Jacobs, 2000). Human navigation in the MWM is virtually identical to laboratory animal navigation (Jacobs et al., 1997; Jacobs, Thomas, Laurance, & Nadel, 1998). In humans, as in lab animals, the MWM can be modified to study egocentric navigation on its own through the addition of a single, proximal cue which consistently predicts the platforms' location (e.g., Livingstone-Lee, Zeman, Gillingham, & Skelton, 2014). As with lab animals, the virtual MWM has also been used to study both allocentric and egocentric navigation at the same time (Livingstone & Skelton, 2007; van Gerven, Schneider, Wuitchik, & Skelton, 2012). Because of the MWM's ability to not only study each type of navigation (and how well each strategy is performed) but also study the learning of both types at once, the MWM will be the primary task used in this thesis. This will include the "classic" allocentric-only maze, and a dual-strategy maze (i.e., one that allows both allocentric and egocentric navigation strategies to be used).

Gender Differences

There are at least four reasons why the study of gender differences in spatial cognition are worthwhile. First, gender differences in spatial cognition, spatial navigation, or navigation in the virtual MWM represent a specific example of cognitive differences between men and women, and this in itself is interesting. In fact, navigational cognition is a large and important component in the study of gender differences (e.g., Lawton, 1994). Frequently it is found that males outperform females on spatial tasks (for a more in-depth discussion of these gender differences in spatial performance that favor males, see Gaulin & Fitzgerald, 1986). Second, gender differences in navigational cognition provides a means of parcelling out different

cognitive aspects of the process (e.g., Cutmore, Hine, Maberly, Langford, & Hawgood, 2000). Third, gender differences in a task are a useful way of assessing the sensitivity of a new task. That is, if a test is sensitive enough to detect differences between two slightly different normal populations, then it should be sensitive enough to detect differences between normal and clinical populations (e.g., Skelton et al., 2000). The fourth reason that gender differences may represent a confounding variable in the study of cognition. (e.g., van Gerven, Ferguson & Skelton, 2016). In this thesis, the primary interest is in understanding navigation, and this includes understanding the differences between genders.

In the MWM (both in lab animals and humans) gender differences have been clearly established. In lab animals, male rats outperform female rats (e.g., Roof, 1993; Perrot-Sinal, Kostenuik, Ossenkopp, & Kavaliers, 1996). In humans in the virtual MWM, men are frequently found to be better navigators than women on a diverse range of measures (such as latency to find the platform, initial heading error and on correct quadrant dwell percent and number of platform crossing on probe trial with platform removed) (e.g., Astur et al., 1998; Sandstrom et al., 1998). The main point is that in any study using the MWM, one should have either the same number of males as females, or at least, a similar number in each group, and should be cognisant of the potential gender differences when using the MWM as an investigative tool.

Interestingly, in the majority of studies of navigation that have found gender differences in performance, the spatial tasks have been solvable only using an allocentric strategy. In one of the first systematic examinations of gender differences in the virtual water maze, participants navigated in an environment in which only allocentric cues are present, and a significant male advantage was observed (Astur et al., 1998). This lack of egocentric cues is a common feature in studies that have found gender differences in performance (e.g., Roof, 1993; Sandstrom, 1998;

Driscoll, Hamilton, Yeo, Brooks, & Sutherland, 2005). These results suggest that gender differences in performance could be due to the exclusive testing of allocentric-only performance, as most studies did not give navigators a choice in what strategy they prefer to use, rather than a significant male advantage over females in the MWM itself (or in navigation overall). Moreover, in an allocentric radial arm maze task (a maze with multiple paths (“arms”) that diverge from a centre area in which navigators are required to find a reward at the end of an arm (see Olton, 1987 for a review)), women performed just as well as men (Levy, Astur, & Frick, 2005). The authors of the study hypothesized this was due to the specific extra-maze cues that women could associate the target location – i.e., they could use them as egocentric-cues rather than having to rely on allocentric cognitive-map based navigation. These findings raise the possibility that men and women have been found to differ in their navigation performance because men are better at navigating allocentrically than women, and that most of the tests are allocentric ones (e.g., the “classic” water maze). In reality, women may be just as good, if not better, than men at navigating egocentrically.

In support of this idea, there is evidence that men and women prefer different navigational strategies, which may underlie the differences in performance that have been observed. There have been several proposals that men navigate using an allocentric strategy, while females navigate using an egocentric strategy (Saucier et al., 2002; Woolley et al., 2010; or see Lawton, 2010 for a review). As well, at least one author has attributed gender differences in spatial navigation performance to gender differences in strategy use (Saucier et al., 2002). In their study, the authors found that men outperform women on both real-world navigation tasks and pen and paper navigation tasks when given Euclidian instructions (i.e., directional (north, south), in other words, allocentric). However, no difference (real-world task), or a difference

favouring women (pen and paper task) was observed when the navigators were given “landmark” instructions (i.e., egocentric). This difference in performance was attributed to differences in strategy use between men and women. In other words, the conclusion was that the genders differed in their ability to use the information given. Further to this point, in one of the few studies that have undertaken a direct comparison, the removal of allocentric cues made men perform worse but did not affect women, while the removal of egocentric cues made women perform worse but did not affect men (Chai & Jacob, 2010). Thus, research seems to suggest that men prefer to navigate allocentrically while females prefer to navigate egocentrically, which may explain why some research has found gender differences in performance while other research has not. However, it is ambiguous if *all* men prefer allocentric navigation and *all* women prefer egocentric navigation, which is implied by the literature.

Other factors in Strategy Selection

Previous analyses of strategy use by individuals have shown that strategy selection can be influenced by a number of other factors, not just gender. For example, a person’s strategy choice has been shown to depend on the type of maze they were tested in (Levy et al., 2005).

Specifically, it was observed that the overall strategy bias of the same group of participants differed between a T-maze (a paradigm that requires navigators to learn a single left or right turn to find a platform) and a water maze. This suggests that some mazes could be “biased” towards one strategy or another. Indeed, pilot work completed in advance of this thesis found that the predominance of allocentric strategies could be shifted by relatively minor changes in the instructions or visibility of the distal environment (Ferguson, van Gerven, & Skelton, 2014), implying that mazes, and not just people, may be biased towards a particular strategy. Further to this point, research investigating the effect of prior experience on strategy selection has found that strategy selection in a dual strategy MWM is influenced by an immediate, prior experience

in a single-strategy maze (Livingstone-Lee et al., 2014). That is, those trained in an allocentric-only or an egocentric-only maze and then tested in a dual-strategy maze tended to select the strategy that was congruent to the maze they were trained in (i.e., 2/3rds (11/17) of those who navigated in the allocentric-only maze first chose an allocentric strategy when given a choice, while 100% (17/17) of those who navigated in an egocentric-only maze first chose an egocentric strategy). Thus, it seems that a number of different factors such as gender and maze design (and interactions between these factors) may determine which strategy is selected by a participant.

Assumption of Single-Strategy Capability

One implicit assumption in many of the previous studies of gender differences in navigation is that some navigators, or even all navigators of a particular gender are only capable of using one strategy. As mentioned, most studies of gender differences in navigation have only examined allocentric navigation (and participants' performance) and have generally shown that males (human and lab animals) are better navigators than females (e.g., Roof, 1993; Astur et al., 1998; Sandstrom et al., 1998; Driscoll et al., 2005). In other words, the assumption becomes that males are more competent at navigating than females. Others have studied which strategies men and women tend to use when both are available (e.g., Saucier et al., 2002) and have generally concluded that men prefer allocentric navigation and women prefer egocentric navigation. These two positions generally assume that navigators are only capable of learning and using only one strategy. This line of research suggests that certain navigators are of a certain type (e.g., women prefer egocentric, men allocentric). This is like saying that with respect to strategy, people are unilingual – they only know 1 strategy and are incapable of using the other. Thus there are allocentric people and egocentric people. A milder form is to assume they have a substantial preference for one over the other. An analogous situation to this substantial preference for one

strategy can be seen in the example of people who know only one language fluently, while having barely any knowledge of a second (so they would be slightly “bilingual” but would probably prefer to use the language they are more comfortable with). It also raises the question of the difference between strategy competence and strategy preference, and the relation between those two. To date, it has been implicitly assumed that these two are the same. In other words, one is best at the strategy one prefers to use, and conversely, one prefers the strategy that one is best at.

If navigators (or certain sub-groups of navigators – e.g., males and females) prefer to use one strategy over the other, does this mean that they completely ignore information relating to the other? To put it simply, in paradigms requiring animals or people to learn the maze (i.e., to find the goal or goals efficiently) they may be required to learn an allocentric or an egocentric strategy. The strategy, once learned, is then used. However, if a paradigm is set up (intentionally or not) such that there is more than one strategy available, the subjects may be acquiring multiple strategies. In these circumstances, the navigator is selecting a strategy to use at a particular point in time, or possibly selecting which strategy is most effective to learn (assuming that strategy selection does not have to be a conscious choice). To use the language analogy, navigators may be learning two different strategies because they are navigationally “bilingual”; they are not restricted to only using one strategy or the other. A navigator may develop a preferred or dominant strategy in a particular context and might even switch strategies between contexts (mazes or environments) or between trials (or trips) or even, within a trial (or trip). Most paradigms tested to date are specifically designed to be strongly biased towards an allocentric or an egocentric strategy (mostly to investigate a topic of interest, such as aging or stress, and its effect on that one strategy – e.g., Thomas, Laurance, Nadel, & Jacobs, 2010), and little testing

has been done to assess what information might have been acquired about the non-preferred (expressed) strategy.

Navigation Learning Terminology

“Strategy use” is the navigation strategy used by a particular navigator in a given context at a particular point in time, and is the aspect that is observed behaviourally. “Strategy acquisition” is the process of acquiring the use of a strategy in a particular context. “Strategy selection” is a cognitive process inferred from the observed use of a particular strategy when it is known that there is more than one strategy available or known to the navigator. This thesis will attempt to avoid the frequently used term “landmark” (except when required when citing the terminology used by an author) because in common usage it can be used to describe a distinctive feature of the environment that might be local or distant, whereas in spatial cognition research it has been used to refer to a distinctive feature or object proximal to a goal (e.g., Biegler & Morris 1993; Doeller & Burgess, 2008).

There is some question as to the proper terminology to be used to describe the learning of a non-preferred strategy, or more strictly, the acquisition of stimulus control (of behaviour) by elements of the environment that are normally associated with the non-preferred strategy. One possibility is to call it “latent learning” because it represents learning that has happened but is not being shown in behaviour. However, in navigation literature, this term has been used to refer to situation in which the animal is exposed to a goal location without reinforcement and is then tested for their knowledge of that goal location (e.g., Keith & McVety, 1988; Chew, Sutherland, & Whishaw, 1989). A second possible term is “occult learning”, defined as hidden or clandestine learning (so un-expressed). Although this definition is appropriate, it is probably a bit arcane, especially compared to the more common use of occult – which implies a supernatural or mystical element. Another possible term is “non-dominant strategy learning”, which suggests an

important concept, i.e., that participants may learn a dominant navigation strategy (that they express through self-report or through observation) but they may also acquire a non-dominant strategy as well, or at least, information that would be useful to them if they chose to use their non-dominant strategy. Ultimately, the best term would seem to be “incidental learning”, defined as a form of indirect or unplanned learning (Church, R.M., 1957), though this term has mostly been applied to an education setting (e.g., Bandura & Huston, 1961). Throughout this thesis, the term incidental learning will be used to refer to the acquisition of a navigation strategy that was learned at the same time as the dominant strategy (or perhaps to the acquisition of stimulus control by environmental elements necessary to the non-preferred strategy).

Nature of Learning during Navigation

Research on navigation in laboratory animals has examined the nature of spatial learning itself; and whether it differs from traditional associative learning. In this latter literature, the difference between strategies has been phrased in terms of differences in “stimulus control” (i.e., which features of the environment are controlling behaviour). This leads to questions regarding what exactly is the relation between strategy and stimulus control. That is, does a navigator select a strategy (egocentric or allocentric) and then attend to the appropriate stimuli (e.g., proximal versus distal) or does a particular set of stimuli acquire control over behaviour and thus lead the navigator to navigate by that strategy? Or, is this essentially two ways of describing the same thing, just from different perspectives (cognition in navigation says that navigators use strategies, while animal learning researchers attribute this to cue usage)? This leads to further questions regarding if the brain can only process cues from one strategy at a time. If this is assumed, then the idea of one navigation strategy being acquired and used at a time makes sense. However, if animals and people can acquire both strategies, then it is possible each type is

acquired simultaneously. If so, then perhaps the strategy used is determined by the set of stimuli present that have the greatest stimuli control.

In the dual-strategy variant of the MWM that allows for both types of strategy learning and has stimuli useful for either strategy, there are two different kinds of learning possible (learning of egocentric and allocentric strategies) and the acquisition of stimulus control becomes open to the effects of overshadowing and blocking, as in traditional associative learning theory (e.g., Rescorla & Wagner, 1972). Blocking occurs if one stimuli has been presented first (prior to the presentation of the second stimuli), and the animal fails to learn anything about a second stimulus after it has been added into the situation (Kamin, 1969). Overshadowing occurs if two stimuli are presented together (coupled) and the animal fails to learn about one of them (Kamin, 1969). In the dual-strategy variant of the MWM (or any environment that allows for multiple strategies) where two types of stimuli are present (e.g., distal and proximal) and two types of strategy are possible (allocentric and egocentric), the question becomes whether one set of cues (or one strategy) overshadows the other.

Latent Learning, Blocking & Overshadowing

Although some navigation research has examined incidental learning (it should be noted mostly of cues rather than strategies), these investigations have mostly attempted to determine if some of the hallmarks of associative learning, blocking and overshadowing, occur during navigation in the MWM. These investigations have, for the most part, been in allocentric-only environments. Mostly this testing of these hallmarks has been done in the context of the debate over whether spatial (allocentric) learning is a different and possibly unique form of learning that allows for many associations to be formed concurrently or whether it follows traditional associative rules in that animals only pay attention to the most predictive stimuli, and acquire associations only to those stimuli. This has led to research on spatial (allocentric) latent learning

and spatial blocking and overshadowing. In spatial latent learning, animals learn about places in which they have not been given reinforcement (e.g., Keith & McVety, 1988; Whishaw, 1991). In spatial blocking and overshadowing, acquisition of some spatial cues can be prevented through prior exposure to other spatial cues (blocking) or by the presence of a more salient cue (overshadowing). To date, human studies have found evidence in support of latent learning (Nadel et al., 1998) and concurrent learning (Hardt, Hupback, & Nadel, 2009) whereas others have provided evidence for blocking & overshadowing (e.g., Hamilton & Sutherland, 1999; Hamilton, Driscoll, & Sutherland, 2002).

However, there have been a few studies which have pitted allocentric learning against egocentric learning, and these studies have examined whether or not learning one strategy overshadows or blocks the ability to learn the other. This research has mostly been conducted in laboratory animals (Redhead, Roberts, Good, & Pearce, 1997; Diez-Chamizo, Sterio, & Mackintosh, 1985), however there have been a number of notable exceptions (e.g., Jacobs et al., 1997; Chamizo et al., 2003; Redhead & Hamilton, 2007). Overall, some research has found no overshadowing of egocentric information over allocentric information (Jacobs et al., 1997) while other research has found that egocentric information can overshadow allocentric (Chamizo et al., 2003; Redhead & Hamilton, 2007). Interestingly, in the second experiment (of three) of Jacobs et al. (1997), navigators who were trained to find a visual platform performed equally well on a probe trial compared to navigators who only received distal, allocentric cues, despite the visible platform being removed for this trial. This finding suggests that navigators (at least egocentric navigators) may in fact learn both egocentric and allocentric information concurrently. This finding highlights the importance of describing the research in overshadowing, as the absence of overshadowing (when examining both egocentric and allocentric navigation) actually implies

incidental learning, as navigators are able to learn information regarding both types of navigation strategy. Thus, while research has examined whether navigators learn two sets of information (and some have even examined egocentric and allocentric learning together), this has mostly been from the perspective of cognitive control (and what type of learning the hippocampus engages in) and few studies have examined if navigators actually learn about both strategies at once (or have even tested for that possibility).

With regard to the issue of whether two strategies can be learned simultaneously, only one study to date has specifically investigated this, and it was in male rats. In the MWM, there is evidence that rats will use both strategies within a trial (Whishaw & Mittleman, 1986). Within trials on an allocentric water maze, rats were found to use not only the surrounding, distal cues (used in the generation of the cognitive map, suggesting an allocentric strategy) but also showed evidence of retracing their path from their starting position (suggesting they acquired an egocentric response strategy). Interestingly, the same was true in the egocentric water maze (rats acquired egocentric information and some allocentric information). The authors took this to suggest that rats use all available stimuli and strategies in order to solve a navigation task.

However, other research in rats has also given indications that navigators may be able to learn both strategies. In one study, rats were tested in a dual-strategy T-maze and, following temporary lesions of the hippocampus and caudate nucleus (through anaesthetic), half the rats who would otherwise navigate allocentrically (and showed no evidence of having acquired anything but an allocentric strategy) could navigate egocentrically, though the necessary statistical comparison was not made (Packard & McGaugh, 1996). As well, in Packard study, it was observed that most rats learned an allocentric strategy initially and switched to an egocentric strategy afterwards (suggesting the learning of the two strategies was sequential), a finding that

has been replicated in laboratory animals in the MWM (Hamilton, Rosenfelt, & Whishaw, 2004; Rice, Wallace, & Hamilton, 2015). This suggests that the two strategies, and their underlying memory systems, may act collaboratively (in fact, this was posited in the Rice et al., 2015 paper).

Virtual navigation research has also found evidence that navigators may be able to learn two strategies when navigating (in environments that allow both strategies to be learned), but this research has emphasized the acquisition of strategies (and if there is an order), rather than if participants are able to acquire two strategies at once. In a radial arm maze, some navigators reported that they switched from an allocentric strategy in the beginning of the task to an egocentric strategy at the conclusion (Iaria, Petrides, Dagher, Pike, & Bohbot, 2003). This was also found in a MWM task, when gaze was analyzed and navigators used allocentric cues in the beginning of the trial and switched to egocentric cues as they approached the target (Hamilton, Johnson, Redhead, & Verney, 2009). However, these findings of allocentric before egocentric have been questioned, as evidence from a Starmaze paradigm (similar to a radial arm maze, but navigators start at the end of arm rather than in the middle) suggests that navigators do not learn one strategy before the other (Igloi, Zaoui, Berthoz, & Rondi-Reig, 2009). In fact, participants in the Starmaze were found to have bi-directional switches in strategy (i.e., some participants switched from egocentric to allocentric while others switched from allocentric to egocentric). These bi-directional strategy switches were also found in a T-maze paradigm (Astur, Purton, Zaniewski, Cimadevilla, & Markus, 2016). Other research that tested participants abilities to use either an allocentric or egocentric strategy found that a third of navigators were able to switch to the most efficient strategy depending on the task (Etchamendy & Bohbot, 2007). Overall, these results suggest that navigational cognition is much more fluid than what is frequently assumed in

the literature. In other words, participants may switch strategies when given the opportunity (though in which direction, and if it always in the same direction, is not entirely clear), which may suggest that some navigators learn information regarding both strategies.

Interestingly, both the Hamilton et al. (2009) and the Igloi et al. (2009) studies found evidence that human navigators do learn information about both strategies. In the Hamilton et al. (2009) study, participants were found to examine the cues of both strategies within a trial (though the authors suggested that use was sequential, i.e., that one strategy/set of cues corresponding to a strategy was always used first; in this case the allocentric cues). In the Igloi et al. (2009) study, some participants used both strategies within a trial (who were called the “mixed” group, and were ~15% (7/50) of participants). The authors even suggested the possibility that the two strategies are acquired in parallel by navigators, though the emphasis was not on the incidental learning of each strategy, but merely that one strategy does not need to be acquired first. However, the Igloi et al. (2009) study was conducted in the Sarmaze (a maze that is not used often in the literature) and the researchers used a unique egocentric strategy. This strategy was known as sequential-egocentric (which required participants learn multiple egocentric relations one after another to find the goal) and the authors hypothesized this strategy had a component of episodic memory. Thus, this strategy required the use of the hippocampus (see Burgess, Maguire & O’Keefe (2002) for more information on the role of the hippocampus in episodic memory), while regular egocentric navigation can occur when the hippocampus is anaesthetized (Packard & McGaugh, 1996). Thus, the sequential egocentric strategy may be distinct from simple stimulus-response egocentric strategies and their findings may not generalize to a MWM (at the very least, the findings require further investigation). Altogether though, these findings from Hamilton et al. (2009) and Igloi et al. (2009) (and the absence of

overshadowing found in the second experiment of Jacobs et al. (1997)) suggest that some human navigators do indeed learn information regarding both strategies, and are capable of using both when the task allows for it. Thus both the animal model finding and virtual environment findings have contributed evidence that suggests, in certain situations, that strategy use is flexible and that multiple navigation strategies may be learned in environments that allow it. In other words, there have been indirect suggestions that navigators in the virtual MWM may engage in incidental learning of both strategies, but there have been no definite demonstrations as of yet. As well, what is not entirely clear is just how great the extent of incidental learning is in navigators (do all navigators engage in it or is it only a small portion?), what the relation is between the learning of a preferred strategy and the learning of a non-preferred strategy (i.e., is one always learned first?), and moreover, what the relation is between demonstrated knowledge that can be observed behaviourally and the latent knowledge that navigators may acquire. In other words, during navigation is the strategy you demonstrate the ability to use always a guarantee of all the information you know? This thesis will be the first experiment to explicitly investigate, in humans, whether or not navigators learn information relating to both strategies in the MWM.

Purpose

The first issue to be addressed in this thesis was to determine whether or not the experimental context (paradigm) would allow both strategies to be used and whether this context encourages the preference of one strategy over the other. This is more of a methodological purpose rather than a theoretical one. Although pilot studies were conducted that found the strategy distribution was not biased towards either an allocentric or an egocentric strategy (Ferguson et al., 2014), it is possible that something unique about the sample population could change the observed bias. Additionally, the pilot studies conducted had a small sample size

($n=10$ for the group that navigated in this maze), and it is possible that simply due to variability, that this thesis may obtain a different distribution of strategies. Given that the pilot study found differences in strategy bias between genders (and due to the research on gender differences in strategy selection (e.g., see Lawton, 2010 for a review), this thesis also investigated whether the observed strategy distribution is the same for men and women.

The second issue to be addressed was whether there is an order in which strategies must be acquired. This was done in order to investigate strategy learning and how navigators acquire their strategy (or strategies). More specifically, do some participants acquire one strategy first, which then leads to use of the other strategy (like Packard & McGaugh, 1996 & Iaria et al., 2003)? Or are both strategies acquired at similar times (like Igloi et al., 2009 & Astur et al., 2016)? In order to fully investigate strategy acquisition, this thesis will also be examining whether or not participants engage in strategy switching, because if one strategy had to be acquired first then then there would be a very high proportion of people switching from that strategy to the other. Despite research into strategy acquisition having not found any gender differences (no gender differences were found in any of the studies mentioned in this paragraph), because it has been suggested that males and females differ in their strategy preference (e.g., see Lawton, 2010 for a review), gender differences in acquisition and switching were investigated (as it is possible that males and females may differ in how easily they acquire each strategy; which could explain some of the observed differences in preference).

The third issue to be addressed was the relation between acquired strategy preference and strategy competence. Previous research has examined gender differences in terms of one or the other. Some have emphasized performance and strategy competence in primarily allocentric-only environments (e.g., Astur et al., 1998; Sandstrom et al., 1998) while others have emphasized

strategy preference in strategy-choice environments (e.g., Saucier et al., 2002; Woolley et al., 2010). Never before have these two been compared directly. Therefore, in this thesis, special single-strategy probes followed strategy-choice testing to determine whether people are more competent at their preferred strategy. The data was examined to determine whether this is true for both men and women.

The fourth issue to be addressed, and the primary concern, was to determine if any incidental learning of a second, non-preferred strategy occurred when people are learning a preferred strategy in a virtual MWM. In other words, to use the language analogy again, are most people bilingual or uni-lingual when it comes to strategy? This thesis hoped to find out if people focus entirely on the information relevant to their preferred strategy or if they also pay attention to the environmental features that relate to an alternate strategy. Given that some studies have found navigators use both egocentric and allocentric strategies within a given trial (rats: Whishaw & Mittleman, 1986; humans: Hamilton et al., 2009), and because evidence suggests that some navigators learn information relating to both strategies when navigating in the Sarmaze (Igloi et al., 2009) and the MWM (Jacobs et al., 1997), it was predicted that people will learn something about both strategies. That is, most people will show incidental learning of their non-preferred strategy. Because men and women may differ in their preferred strategy (Saucier et al., 2002; Woolley et al., 2010) and in their ability to use an allocentric strategy (Astur et al., 1998; Sandstrom et al., 1998), it seemed worthwhile to examine potential gender differences in incidental learning. As well, because incidental learning has only been observed as a by-product during other investigations in the MWM (or in a task not proven to be sensitive to gender differences – the Sarmaze), gender differences have not been fully investigated, and thus were in this thesis.

Finally, the last issue to be addressed by this thesis was the relation between strategy preference and potential strategy competence (i.e., the limits of competence). Following strategy-choice testing, all participants were tested for their ability to learn to navigate allocentrically. It will be interesting to see whether those who preferred to navigate allocentrically find it easier to learn an allocentric task than those who preferred to navigate egocentrically. However, it will also be interesting to see whether those who preferred to navigate egocentrically were capable of learning to navigate allocentrically when required to do so. This has been investigated previously in the Starmaze paradigm, and it was found that both allocentric and egocentric navigators could effectively learn to navigate using the other strategy (Igloi et al., 2009) but it has not been investigated in a MWM task. As before, gender differences in the relation between strategy preference and strategy competence were investigated.

Approach

This thesis tested navigational strategies and abilities using two virtual Morris water mazes. The first water maze was modified to allow participants to use both types of navigation in the environment. This type of maze has been termed as an “ambiguous” (Livingstone & Skelton, 2007) or “Dual-strategy” maze (Ferguson & Skelton, 2015) and has been used in the past to examine gender differences in strategy selection between men and women (van Gerven et al., 2012). This current version of the MWM was designed using a newer game engine, the Unreal Developer’s Kit (and was identical to the final maze used in the pilot study to this thesis – Ferguson et al., 2014). In order to assess navigational cognition, testing consisted of alternating learning trials (which are called Find-It trials) in which participants were required to find a hidden platform and probe trials (which are called Show-Me trials) in which participants were asked to show where they thought the platform was located.

To determine whether the strategy distribution was biased towards one strategy and to measure strategy acquisition, participants strategy choice on Show-Me trials was examined. In order to investigate strategy bias and determine if the Dual-strategy maze allowed participants to acquire either strategy, participants were classified as having a strategy (allocentric or egocentric) by using their predominant strategy choice across all Show-Me trials in the Dual-strategy maze (see Method section for further details). In order to measure acquisition and switching in participants, participants' strategy choice on each individual Show-Me trial was examined (rather than looking at the Show-Me trials as a whole).

In order to determine whether strategy preference was equivalent to acquired strategy competence, and to determine whether or not incidental learning had occurred, participants were given single-strategy probes (forced-strategy probes). There was an allocentric-only probe (the Place probe) and an egocentric-only probe (the Cue probe). In order to investigate strategy preference compared to strategy competence, this thesis examined participants' performance on the forced probe that matched their strategy (i.e., if participants used an allocentric strategy, their performance on the Place probe was examined and vice versa for the egocentric participants). In order to determine whether incidental learning had occurred, this thesis also examined participants' performance on the forced probe opposite to their strategy.

Finally, in order to determine whether (egocentric) participants could learn a second strategy when forced to, all participants had to navigate in a classic, single-strategy allocentric MWM (also known as the "Place Maze"). Participants navigated in the Place maze to determine if allocentric navigators were better at using an allocentric strategy than egocentric navigators, and if egocentric navigators could learn at all (in other words to investigate if participants' strategy preference indicates the limits of their competence).

Just to note, this thesis is based on an experiment originally designed to replicate a previous study showing that low stress affects strategy selection (van Heynigan, Ferguson, van Gerven & Skelton, 2014). However, this effect did not replicate and instead the focus of the thesis has shifted to the examination of incidental learning.

Specific Research Goals

This experiment had 4 goals with respect to increasing our understanding of spatial navigation strategy selection and performance, and the incidental learning of navigation strategies. The preliminary, baseline goal was to determine in the dual strategy maze, whether the strategy distribution was strongly biased towards one of the two strategies (egocentric or allocentric). The other four goals are: (1) investigate strategy acquisition, (2) investigate the relationship between strategy preference and acquired strategy competence, (3) determine the extent of incidental learning of a non-preferred strategy occurring during acquisition of a preferred strategy, and (4) investigate acquisition of and performance using a non-preferred (allocentric) strategy.

The baseline goal was to determine the proportion of individuals who preferred each type of strategy in this Dual-strategy maze. Specifically, how many navigators tended to prefer each strategy over each of the 10 Show-Me trials? Given the pilot work that was completed for this thesis (Ferguson et al., 2014), the strategy distribution was expected to either be unbiased towards either strategy or have a slight allocentric bias. As well, given the gender differences observed in the pilot study (in which men preferred an allocentric strategy, and females preferred an egocentric strategy), the maze was expected to show the same gender difference.

The first goal was to examine how strategies are acquired in the MWM, and if one strategy had to be acquired before the other. To do so, strategy preference was measured from each participant on strategy probe trials (Show-Me trials) that followed each of the 10 learning

(Find-It) trials. Given the inconsistencies of previous findings in the literature (described above), there were no clear expectations as to whether one strategy would be acquired before the other (and if switching would occur). Given that gender differences in strategy acquisition have not been observed previously (discussed above) no gender differences in strategy acquisition were expected.

The second goal was to investigate whether strategy preference is related to strategy competence. That is, does acquired strategy preference on Show-Me trials predict subsequent performance on the forced-strategy probes? In other words, would participants who preferred an allocentric strategy perform better on the Place probe than those who preferred an egocentric strategy, and *vice versa* on the Cue probe? Participants were expected to be more competent on the forced probe (Place or Cue) that matched their preferred strategy on Show-Me trials. Congruence between competence on forced-strategy trials and preference on Show-Me trials would also confirm the assumption that both types of trials were measuring the same thing. The relation between competence and preference was expected to be the same for both genders.

The third goal was to determine whether participants acquire information relating to the other, non-preferred strategy. In other words, did they incidentally learn a second strategy in addition to their preferred strategy? To use the language analogy from above, are participants bilingual or unilingual when they are only required to use a single language? Given the prior indications of incidental learning in the literature (detailed above), and the absence of gender differences in this literature, some degree of incidental learning was expected but no gender differences were expected.

The fourth and final goal was to determine whether navigators who preferred to navigate allocentrically in the Dual-strategy maze would be better at navigation in the Place maze than

those who preferred to navigate egocentrically, and whether people who preferred to navigate egocentrically in the Dual-strategy maze could even learn to navigate allocentrically at all. In other words, does strategy preference indicate the limits of strategy competence?

Accordingly, all participants were tested in the Place maze after completion of testing in the Dual-strategy maze. It was expected that those who preferred to navigate allocentrically would do better in the Place maze than those who preferred to navigate egocentrically, but that those who navigated egocentrically would nevertheless be capable of learning the Place maze.

Although males were expected to be better than females at allocentric navigation, it was not clear what other gender differences might be present.

Method

Participants

Participants were 62 undergraduates (30 females), recruited by gender using the SONA system from the University of Victoria, who received credit towards their final grade in a Psychology course. The average age of students was 21.29 years ($SD = 4.67$), and there was no age difference between males ($M = 21.53$, $SD = 4.48$, 18-42) and females (21.07, $SD = 4.91$, 18-42), $t(61) = 0.39$, $p = 0.69$. Participants were excluded if they reported a history of brain injury, neurological or psychiatric complaints, or had learned English as a second language. Ethics approval was obtained from the Human Research Ethics Committee at the University of Victoria.

Consent form. Immediately before beginning the experiment, participants read and signed the consent form that detailed what could be expected to occur during the experiment and the full benefits and risks of participating in the study. This form was completed to ensure full consent was given.

Background Information Questionnaire. A pre-test demographics questionnaire (see appendix 1) was used to collect information about the participants' age, education, handedness and a history of disorders (including brain injuries, neuropsychological disorders and colour blindness). The purpose was to ensure participants had met the inclusion-exclusion criterion that qualified them to participate and to identify the demographics of the participants.

Post-Test Questionnaire. A post-test questionnaire (see appendix 1) was given to participants to identify any potential confounding variables that could influence participants' navigation performance or strategy selection during the experiment. Participants were asked about their navigation experience and training, childhood influences, video game experience and their perception of the task.

Testing was conducted in a quiet, distraction free room. Two experimenters (one male and one female) were always present in the room. The experiment consisted of two navigation tasks and two different questionnaires: demographics and a post-test.

Materials

Dual-strategy Maze. Navigation strategy was investigated using a modified version of the Dual-strategy virtual Morris water maze (Livingstone & Skelton, 2007) created using the Unreal Developer's Kit (Epic Games). This virtual maze contained environmental features that allowed participants to navigate either egocentrically and allocentrically, and revealed which navigation strategy they preferred. The purpose of the Dual-strategy maze was to determine which strategies participants preferred to use while navigating.

The virtual environment was displayed on a desktop computer, using a 1280x800 screen resolution and was shown from a first-person perspective. Participants used an Xbox 360 game controller for navigation, which allowed only forward travel and left and right turns.

The maze environment consisted of a circular arena appearing to be about 15 m in diameter with a beige tiled floor surrounded by a gray brick wall appearing about 1 m in height. The arena was surrounded by an annular, grassy apron about 5 m deep, ending in a second 1 m high brick wall. In one direction, arbitrarily defined as south, there was a mountainous island (with two peaks) in clear, open water (a big lake, sea or ocean). Beyond the apron in the other three directions was a grassy plain that terminated in a distant mountain range that peaked in the north (See Figure 1). The sky was filled with clouds that did not move and did not provide clues of directionality or location. Preliminary studies revealed that the environment fostered allocentric navigation in too great a proportion of participants and so to reduce this bias, fog was added to partly obscure the surrounding landscape.

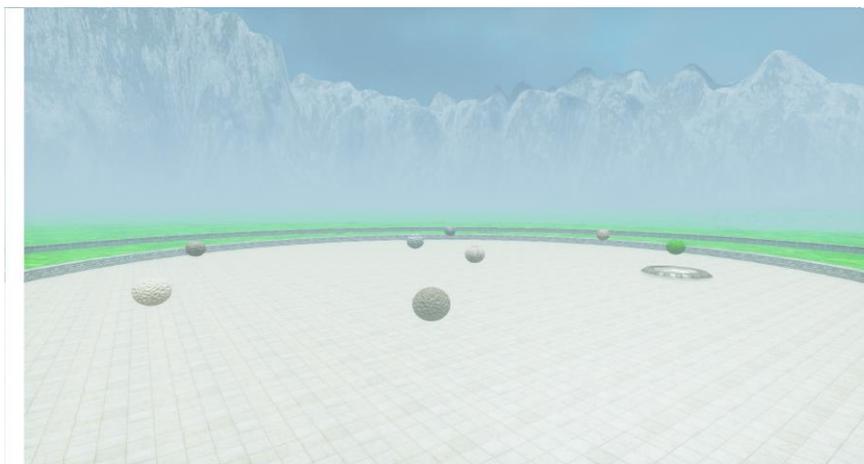


Figure 1. Dual-Strategy Environment with a view to the north-east (with the peak of the mountains, north, visible at the left edge of the image). The view is elevated above that of a participant. Within the arena were floating spheres in fixed locations to provide cues for navigation, The goal was a platform fixed in the center of the southeastern quadrant of the arena that is visible here but was hidden from participant until they stepped on it.

Within the arena, there were 8 spheres floating just above head height in fixed location. Each sphere was given a unique color (white, blue, green, etc.) and a golf-ball like texture was chosen for them. One of the spheres was positioned directly over the platform, located in the center of the southeast quadrant, thereby providing an immediate proximal cue to the goal location. This cue-sphere was green. The field of view was set to 90° and all spheres could be seen from any point around the circumference of the arena. The spheres were laid out in an array that provided no clues to directionality in the arena.

Place Maze. A single-strategy, Place maze was used to test each participant for his or her competence in allocentric navigation competence (i.e. allocentric performance). This maze was the same as the Dual-strategy maze (identical surrounding environment) without the spheres, and with the platform's location shifted to the opposite (northeast) quadrant.

Other Maze Variations. Two additional variations of the mazes were used for specific purposes. The "Visible Platform maze", was used to familiarize participants with the procedures of the task and movement within the virtual space. It was exactly the same dimensions as the

Dual strategy maze but it had visible platforms, no visible landscape and no spheres. In this maze, the platform was visible throughout the trial and was located in different places within the arena on every trial. This maze was designed to prevent development of an allocentric or an egocentric strategy bias in participants because it was solvable by going straight to the visible platform. The “Cue” maze was designed to allow only an egocentric strategy (for the Cue probe). In this maze, the spheres were still present but the fog around the arena was made dense enough to completely obscure the surrounding landscape.

Procedures

Background-Questionnaire. After entering the room and completing the consent form, participants filled out the 14-item background questionnaire.

Virtual Navigation. After signing the consent form and completing the Background questionnaire, participants were trained in virtual navigation procedures, then tested in the Dual-strategy maze and finally the single-strategy maze. There were six different types of trials (See Table 1 for numbers, order and purposes). Briefly, the trials were given as follows. An exploration trial was given to allow the participants to learn the layout of the environment, and how to use the controller. Four visible platform trials were given to help them master the controller and learn the general test procedures and were conducted in the Visible platform maze. A “Guess” trial was used to determine if participants had been biased towards the platforms location by something in the environment or how the maze was set up. Testing consisted of 10 pairs of “Find-It” and “Show-Me” trials. On Find-It trials participants were required to find an invisible platform within the arena. On Show-Me trials participants were asked to show the experimenter where they thought the invisible platform had been hidden on the previous (Find-It) trial. Then, participants completed two forced-strategy probe trials to reveal incidental learning (if any), one solely for egocentric navigation (in the Cue maze) and the other solely for

allocentric navigation (in the Place maze). Participants then completed another 10 pairs of Find-It and Show-Me trials, this time in the Place maze. Finally, they were given one last probe trial, which had no platform present, in order to implicitly measure their knowledge of the platform location.

Table 1
Dual-Strategy Maze Navigation - Trial Order

| Trial | # of Trials | Purpose |
|-------------------------|--------------------|---|
| Exploration Trial | 1 | Allow participants to practice controls and get familiar with the environment |
| Visible Platform Trials | 4 | Allow participants to practice controls and ensure they can follow the task instructions |
| Guess Trial | 1 | Determine if any features of the maze biased participants to the platform's location (before finding the platform) |
| Find-It Trial | 10 | Allow participants to find and remember a hidden platform, determine how easily they found it (performance) |
| Show-Me Trial | 10 | Determine how the participants found the platform (what strategy they used) |
| Cue Probe | 1 | Determine if participants can locate the platform when the allocentric/environmental cues are removed. Used to determine if Incidental learning is present |
| Place Probe | 1 | Determine if participants can locate the platform when the egocentric cues/spheres are removed. Used to determine if Incidental learning is present |

Training: Exploration trial. Participants started this trial in the east of the Dual-strategy maze, outside the arena, and were allowed to explore for as long as they desired (no time-limit). The trial ended when participants indicated they were comfortable with the amount of exploration they had done. They then immediately began the next set of trials.

Training: Visible platform trials. In the Visible platform maze, participants were instructed to move to the visible platform, which was located first in the center of the arena, and then in a far quadrant. These trials started inside the arena. Participants were informed that once they reached the platform, they could move around on it but would be unable to leave it. Trials started just inside the outer wall of the arena. On these visible platform trials, once participants went to the platform, a chime sound was produced by the computer, indicating that the platform was found. This sound was used in all trials in which a platform was present, to ensure the participants knew when they had found the platform. Once they found the platform, they were instructed to look around at the surrounding environment, and were told to rotate a full circle at least once. Once, they had completed looking around, participants immediately began the next trial.

Dual-Strategy Maze. Participants began all trials from one of 6 starting locations; all trials except Show-Me trials began from one of the four cardinal directions (East, West, North, South), while Show-Me trials began on one of two semi-cardinal directions (south-west or north-east).

Guess trial. On the Guess trial, which occurred in the Dual-Strategy maze (although the cue object was not present; another coloured sphere was in its place), participants were instructed that their intuition was being tested and that they should navigate to the location in the arena where they guessed a platform would be hidden. They were told to inform the experimenter once they reached this location.

Following the guess trial, participants' were given instructions regarding the main part of the navigation task. Participants were informed that the goal of the task was for them to find and remember the location of a hidden platform. The participants were told that the hidden platform

would always be in the same location (i.e. the platform did not move), but that they may start from different locations in the maze. Participants were then informed that when the platform was found the same chime noise from the visible platform trials would be played, and invisible barriers would pop up, preventing them from leaving the platform's location (though, as above, they could still move around on the platform if they desired). Participants were told that their ability to find the hidden platform efficiently would be tested on "Find-It" trials, and that their knowledge of the platforms location would be measured on "Show-Me" trials (which were conducted in pairs). Participants were told that a Show-Me trial would always follow right after a Find-It trial and that they would always be informed which type of trial it was.

Find-It Trials. For Find-It trials, participants were instructed to go to the invisible platform as quickly and directly as they could. Participants' performance was assessed by measuring the time (latency) and distance they required to find the platform. On the first trial, participants had no idea where the platform was located, and as such had to explore the arena until they had found the platform. Once they had found the platform on the first trial, participants were instructed to take a moment to remember the location of the platform because it would be in the same place on subsequent trials (and they were informed that they could look around for as long as they liked). These instructions were provided only on the first three Find-It trials. If participants took longer than 180 seconds to reach the platform, then the experimenter stopped timing and guided them to the platform using verbal response-based instructions (i.e., turn right for a few seconds and then go forward). Each Find-It trial ended once participants had found the platform, and immediately after participants were informed the next trial would be a Show-Me trial.

Show-Me trials. For the Show-Me trials, participants were told that no platform would be present and that they were to demonstrate where they believed the platform was located by navigating to that location and indicating when they believed they were in the correct location. No time limit was imposed for these trials as pilot studies showed that participants completed these trials in a timely fashion (i.e., within a minute). Participants' performance was assessed by measuring the difference between where they estimated the platform was located and where the platform actually was located (location error). On the Show-Me trials, in order to differentiate strategy selection, the cue-sphere (the green sphere located above the platform in the south-east) was moved to the opposite quadrant (the north-west quadrant). The logic of the Show-Me trials was that if a participant were navigating to the platform predominantly by the cue-sphere, they would go to the northwest quadrant, but if they were finding the platform by navigating to its location in space (i.e., by the external landscape) then they would go to the southeast quadrant (where the platform was located on all Find-It trials) (See Figure 2). In other words, these trials revealed whether participants were navigating egocentrically (to the cue) or allocentrically (to the place). When the participant informed the experimenter that they were in the estimated location, a black screen was dropped down by the experimenter to prevent viewing of the arena or surrounding landscape.

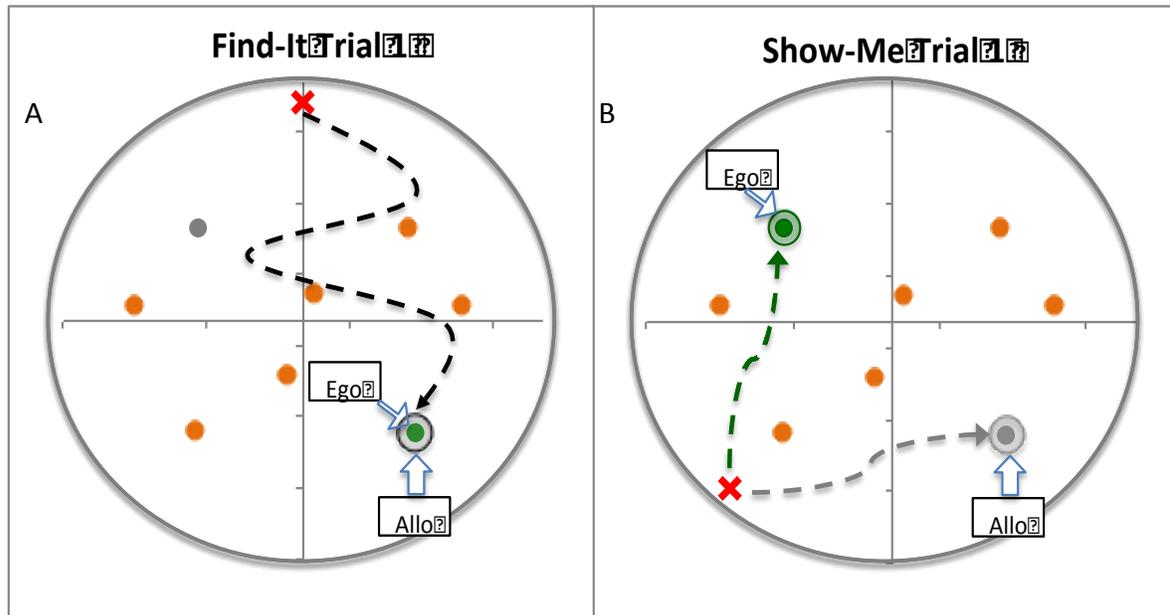


Figure 2. A Find-It and Show-Me trial pair. On the Show-Me trial, the cue-sphere was switched to the opposite quadrant, which allowed for the two strategies to be dissociated (egocentric navigators went to the sphere, allocentric navigators went to the location relative to the surrounding environmental landscape – the landscape remained constant between Find-It and Show-Me trials)

Forced-strategy Probes. At the conclusion of the task two different probe trials were given to participants. These probes were the “Cue” probe (only containing the objects and the arena) and the “Place” probe (the objects are removed and only the surrounding landscape is present). In both trials, no platform was present. Participants’ performance was measured using location error (on both probes) and correct quadrant choice (Place Probe only). The Cue probe was conducted in the Cue maze, while the Place probe was conducted in the Place maze. On these probes, participants were informed that the environment would be slightly modified but that they were simply supposed to navigate to where they believed the platform would have been located (with the location corresponding to the final Find-It trial).

Participants were given the probe that was congruent with their preferred strategy first (i.e, if they used the environment to navigate (i.e., allocentrically) they were given the Place probe first, and vice versa for the Cue probe). If participants did not have a preferred strategy,

they were simply given the probe for the strategy they had used on the final Find-It trial (or the most recent Find-It in which they select a strategy).

Place Maze. After finishing navigation in the Dual-strategy maze, participants completed the single-strategy, Place maze. The purpose of this maze was to measure participant's allocentric navigation competence, or their ability to find the platform when the egocentric cues (the spheres) were removed. There were only three different types of trials (See Table 2 for numbers, order and purposes). Just as in the Dual-strategy protocol, participants were given ten trial pairs, each consisting of a Find-It trial and a Show-Me trial. Participants' performance on the Find-It trials was measured in latency and distance. Participants' performance on Show-Me trials was measured in location error (the difference of their estimate of the platforms' location from the platform itself). This is because in the Place maze Show-Me trials were used to measure participants platform location knowledge rather than the strategy they used. At the conclusion of navigation in the Place maze, participants completed the Implicit probe. Participants were not given any exploration, visible platform trials or forced-strategy probe trials.

Table 2
Place Maze - Trial Order

| Trial Type | # of Trials | Purpose |
|-------------------|--------------------|---|
| Find-It Trial | 10 | Allow participants to find and remember a hidden platform, determine how easily they found it (performance) |
| Show-Me Trial | 10 | Determine how well participants know the platforms locations (performance) |
| Implicit Probe | 1 | Investigate participants search resiliency and pattern |

Implicit probe. In the implicit probe participants were given identical instructions to the Find-It trials (i.e. go find the platform quickly and efficiently), however no platform was present.

After 50 seconds, the chime noise sounded (the same noise that was used to indicate once the platform had been found), the trial ended and the deception (and the reason behind it; to determine participants search pattern) was explained to participants. Participants' performance was measured in quadrant dwell time (percent of time spent searching for the platform in the correct quadrant) on this probe. Participants were then informed that they had completely finished the navigation task, and were to hand over the game controller to the experimenter.

Post Test Questionnaire. At the conclusion of the session, a second questionnaire was completed by participants. Following this, participants were debriefed, thanked and then allowed to leave.

Data Analysis

Behavioural data consisted of participants' latency and distance from each Find-It trial, as well as location estimations (in X and Y coordinates) from each Show-Me trial and forced-strategy probe, plus quadrant dwell times on implicit probes. Data was extracted from both of the mazes using modifications to the UDK Script and with scripts written in MatLab (The MathWorks, Inc.). All data were examined first with genders combined, and then separately for each gender, and all the data is presented this way as well. Although this leads to redundancy in terms of graphical display of data, this format was followed because there were few gender differences found, and therefore the main finding of each analysis was best represented in the gender-combined format. The gender-separate formats were provided simply to visually confirm that the combined results accurately reflected the pattern seen within genders.

Strategy Preference. To examine the distribution of strategies in the Dual-strategy MWM, participants' strategy was determined by using the location they went to on Show-Me trials. If a participant went to the quadrant now containing the cue-sphere, they were considered to have selected an egocentric strategy on this trial. However, if a participant went to the

quadrant containing the original platform location (i.e., relative to the environment), they were considered to have selected an allocentric strategy on this trial. If the participant went to one of the other two quadrants this was considered a “neither” trial. In order to assign overall strategy preferences to participants, they were classified using the Skelton lab’s classification criteria (van Gerven, Ferguson, & Skelton, 2013). According to this criterion, participants were considered to prefer a strategy if they selected one of the two strategies on at least 7 of the 10 Show-Me trials and they picked the same strategy on 60% of the trials on which they picked a strategy. For example, if a participant chose an egocentric strategy on 2 trials and an allocentric strategy on 7 trials (i.e., a strategy on 9 of 10 trials and a preference for allocentric on 7/9 or 78%) they were classified as an allocentric navigator. Participants were categorized as “neithers” and excluded from further analysis if they failed to select a strategy on three or more trials and “switchers” if they selected a strategy on seven or more trials but failed to select the same strategy on 60% of those. The number of participants classified as each navigational strategy was counted and then compared to chance (50%) using a chi square goodness-of-fit test. Participants were also compared using Ego%, which was calculated by using the percentage of trials that each participant chose egocentric navigation out of all trials on which they chose egocentric or allocentric (i.e., excluding trials where they chose neither correct quadrant). In order to assess the degree of bias of all the participants, the average Ego% of all participants was compared to 50% using a one-sample t-test. This test was also conducted separately for males and females. In addition, males and females were compared against each other using an independent samples t-test on Ego% to see if there was a gender difference in strategy preference.

Strategy Acquisition. To see how navigation strategies were acquired, strategy choice rates on individual trials and strategy switching over the course of the 10 trial pairs were

examined. These choice rates for the maze were calculated by using, on each trial, the number of navigators who selected an allocentric strategy, an egocentric strategy, or neither. In order to compare whether there was a bias to use one strategy before the other, strategy choices on the first trial were compared to chance (50%) using a chi square goodness-of-fit test with genders combined and with genders treated separately. In order to determine whether there was a gender difference in first strategy selected, the number of males and females choosing the most popular strategy was compared using a chi square goodness-of-fit test.

Strategy switching was also analyzed to determine whether one strategy had to be acquired before the other. Logically, if one strategy was necessarily acquired first then there would be a very high proportion of people switching from that strategy to the other. Switching was defined simply as any switch from using one strategy (allocentric or egocentric) on one Show-Me trial to the other strategy on the subsequent Show-Me trial. The number of switches from allocentric to egocentric, and from egocentric to allocentric, were recorded individually and compared both absolutely and relatively. To determine whether or not there was an absolute bias to switch in one direction (e.g., from egocentric to allocentric), the number of switches in each direction were compared to what would be expected from chance (50%) using a chi square goodness-of-fit test. The interdependence between preferred (or ultimate) navigational strategy and the number of switches was tested using a chi square test of independence. To determine whether or not there were any within-strategy gender differences in switching rates, the number of switches by allocentric males were compared to the number by allocentric females using a Fisher's exact test (because of the small sample number of males and females allocentric navigators who switched, a chi square test could not be used). Switches by egocentric males and egocentric females were also compared using a Fisher's exact test.

Acquired Strategy Preference versus Competence. In order to determine if strategy selection on Show-Me trials was a good indicator of preferred strategy competence, participant performance on the both the Cue and the Place forced-strategy probes was compared. Participants classified as allocentric navigators and participants classified as egocentric navigators were compared in terms of the magnitude of their location error using independent samples t-tests. As well, differences in performance on each probe (collapsed across navigators' strategy type) were compared using an independent samples t-test to determine if one probe was easier than the other. Due to the sample sizes, independent sample t-tests were performed to determine if there were any gender differences in the relationship between preference and competence.

Incidental Learning. In order to determine if participants learned information relating to their non-preferred strategy, participants' performance on the forced-strategy probes was again compared, but this time using two different measures. The first measure, which was used on the Cue probe, was minimum location error. Minimum location error was calculated by taking the smaller of a) the location error relative to either the cue-sphere that hovered over the platform on Find-It trials or b) the location error relative to the sphere that hovered over the platforms' correct location (relative to the landscape) on Show-Me trials. Allocentric and egocentric navigators were compared using an independent samples t-test. Differences between genders were assessed using independent samples t-tests on minimum location error on the Cue probe.

The second measure of incidental learning, used on the Place probe, was the ability of participants to identify the correct platform location, at least in terms of identifying the correct quadrant (a frequently used measure of competence in allocentric navigation – e.g. Sutherland & Dyck, 1984; Jacobs et al., 1997). Identification of the correct quadrant in the current study was

defined as participants estimating the platform's location within a $\frac{1}{4}$ of a pool diameter from the centre of the platform's location correct location. The proportion of egocentric navigators that successfully completed the probe was then compared to what would be expected from chance (50%) using a chi square goodness-of-fit test. The proportion of male and female egocentric navigators who successfully completed the probe were also compared to chance using a chi square test in order to determine if there were any gender differences.

Limits of Strategy Competence. In order to determine whether those who had demonstrated a preference for egocentric navigation (in the Dual Strategy maze) were capable of learning to navigate allocentrically if required to do so, all participants were tested in the single-strategy, allocentric place maze and then compared to allocentric navigators in terms of latency and distance on Find-It trials 2-10, location error on Show-Me trials 1-10, and quadrant dwell time on the implicit probe. These comparisons were made using independent samples t-tests, across, within and between genders. Note that the reason trial 1 was not included for latency and distance was because on the first trial participants could not know the location of the platform, and thus, these measures of performance would reflect "platform finding" behaviour rather than "return to platform" behaviour and cognition. To identify which egocentric navigators could navigate allocentrically when required to do so, criteria were set for each of the four measures of performance in the Place maze. Egocentric navigators were considered to have achieved criterion if they achieved a level of performance equal to the worst allocentric navigator. These criteria were also used to investigate whether there were any gender differences in the ability of egocentric navigators to learn to navigate allocentrically. Males and females were compared on this criteria using Fisher's exact test.

Results

Strategy Preference: What is the distribution of strategy choices in this maze?

It should be noted that some participants were not included in the analysis due to a failure to learn the dual-strategy maze, or due to data extraction problems. One participant was not included in the analysis because they failed to select a strategy in the dual-strategy maze (i.e., they did not select a strategy on 70% of Show-Me trials and, thus, were classified as a neither). Two participants (an egocentric male and an allocentric male) were not included in the Place maze analysis because their Place maze data was unable to be extracted. Before the participants' ($N = 61$) navigational behaviour could be examined, it was important to understand the context in which this behaviour was observed. That is, before the order in which strategies are acquired could be examined, it was important to examine which strategies were preferred in the Dual-Strategy maze. This provided some indication as to whether the participants had a predisposition to select a particular strategy, or alternatively, whether there was some characteristic of the maze design which led participants to use one navigational strategy more often than the other.

Analysis of strategy selection in the Dual-strategy maze revealed that, contrary to what was expected, the distribution of strategies in this maze was biased towards egocentric navigation (see Figure 3). This bias is evident because many more participants chose to navigate egocentrically ($n=45$) than allocentrically ($n=16$). The chi-squared goodness-of-fit test confirmed that more people preferred to navigate egocentrically than allocentrically, $\chi^2(1) = 13.79$, $p < .0002$. This was also confirmed by calculating the percentage of trials that each participant chose egocentric navigation out of all trials on which they chose egocentric or allocentric (i.e., Ego%), and then using a 1-sample t-test to compare the mean percentage of 69.5% to 50% (i.e., unbiased). This test showed that overall, the bias to egocentric navigation was significant ($t(60) = 3.70$, $p < .0005$).

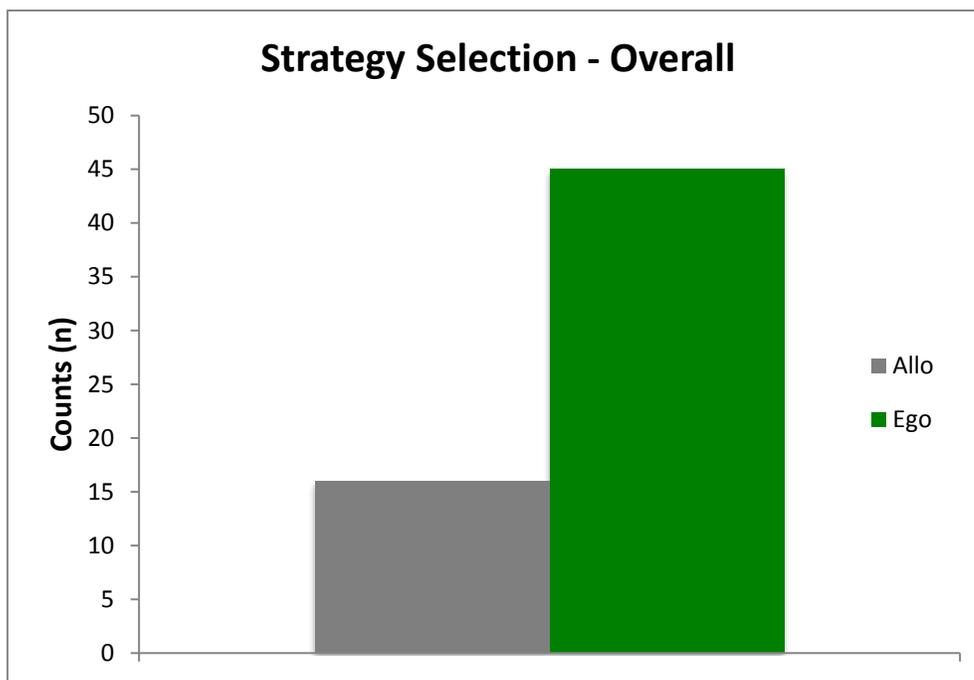


Figure 3. Number of participants selecting an allocentric (“Allo” – grey) or egocentric (“Ego” – green) strategy, on at least 70% of trials overall, with at least 60% of trials being of one type.

This egocentric bias in strategy distribution was present in both males and females, but was stronger, and only significant, in females (see Figure 4). In terms of the number of Show-Me trials on which participants chose one of the two strategies (i.e. Ego%), females chose to navigate egocentrically 82% of the time, which was significantly above 50% ($t(29) = 4.87$, $p < .00005$), whereas males chose to navigate egocentrically only 58% of the time, which was not significantly above 50% ($t(30) = 1.03$, $p = .31$) (see Figure 5). The difference between genders was significant ($t(59) = 2.35$, $p = .03$), indicating that females had a stronger preference for egocentric navigation than males did.

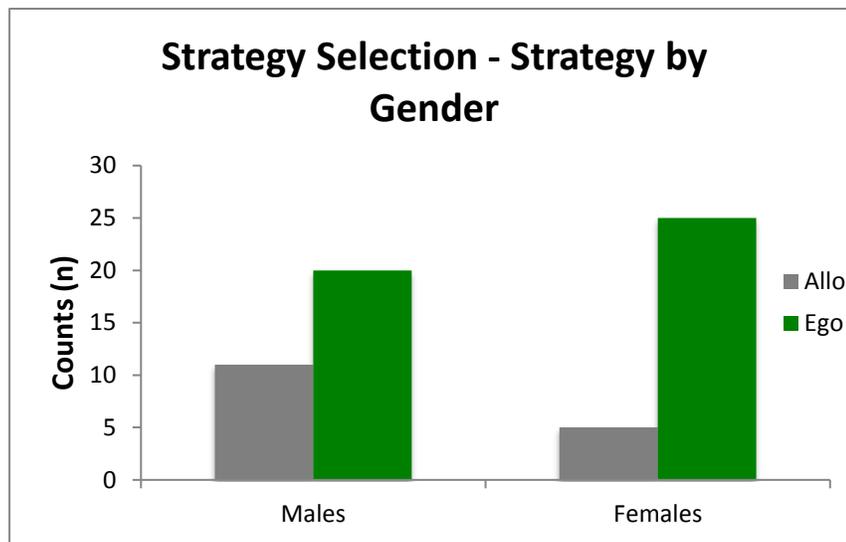


Figure 4. Number of males and females selecting an allocentric (“Allo” – grey) or egocentric (“Ego” – green) strategy on at least 70% of trials overall, with at least 60% of trials being of one type.

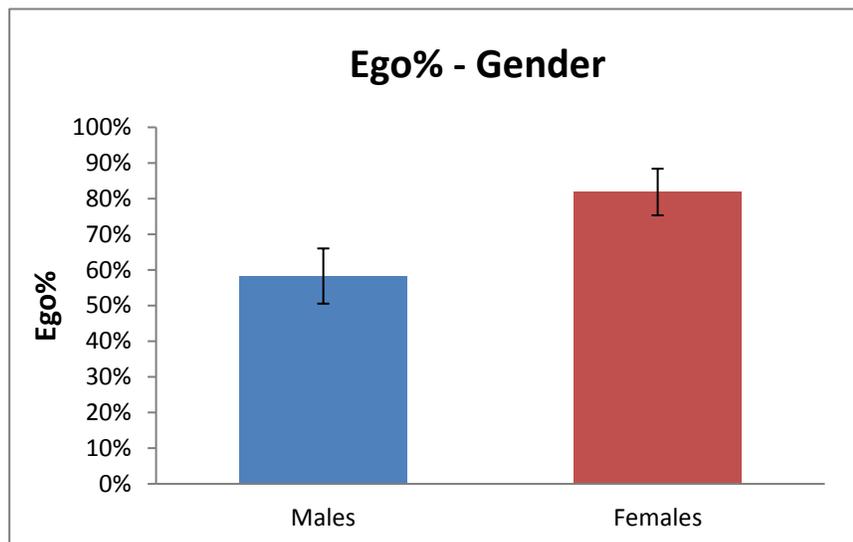


Figure 5. Average Ego% (Average number of Show-Me trials on which participants chose an egocentric strategy divided by the total number of trials in which a strategy was selected) grouped by gender (males and females). Error bars represent the *SEM* (standard error of the mean).

Strategy Acquisition: Do people have to acquire one strategy before the other?

An examination of strategy choice rates indicated that the majority of participants adopted an egocentric strategy early in training (e.g., Trial 1: 47/61, 77%) but that over training, the proportion of participants selecting an allocentric strategy increased (see Figure 6). In fact, on

trial 1, significantly more participants selected an egocentric strategy than would be expected from chance ($X^2(1) = 25.79, p < .00001$).

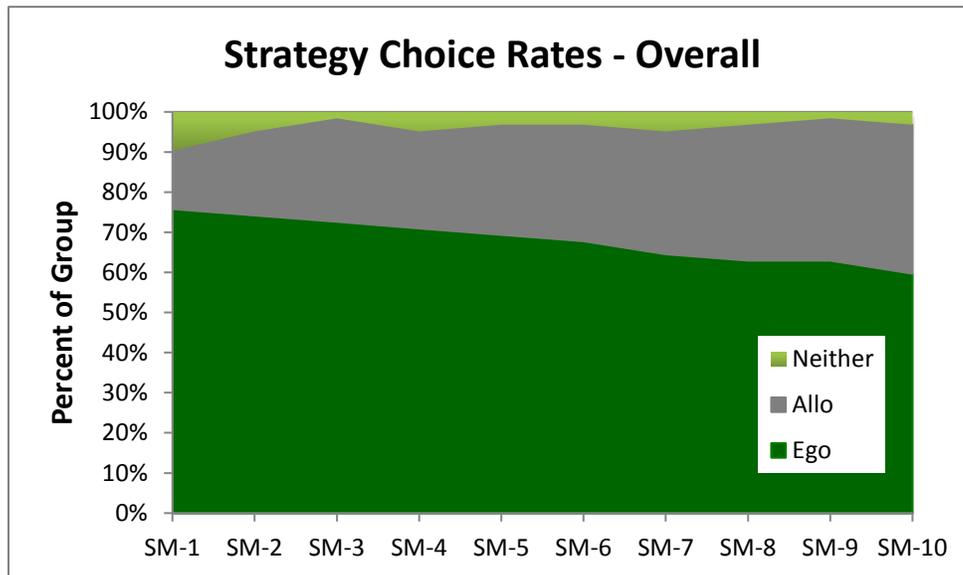


Figure 6. Percent of participants selecting either an allocentric (Allo – grey), an egocentric (Ego – green) or neither (light green) strategy on each of the 10 Show-Me (SM) trials

This tendency for more participants to navigate egocentrically rather than allocentrically early in training was true for both male and female participants (see Figure 7). On trial 1, both males and females were significantly more likely to select an egocentric strategy than what would be expected from chance, Male $X^2(1) = 7.76, p < .005$, Female $X^2(1) = 19.59, p < .0001$. This tendency was stronger in females to the point where on the first trial only 2 females preferred to navigate allocentrically. By treating the female n as observed, and the male n as expected, a chi square goodness-of-fit test revealed that females preferred egocentric navigation significantly more often than males did ($X^2(1) = 4.13, p < .05$). Due sample size difference of participants selecting a strategy on the first trial (males = 29, females = 27), the number of males were adjusted to account for this difference of 2 participants. Thus, because 7 of 29 males

selected allocentric or 24%, the expected value for male allocentric navigators was adjusted to 24% of 27, or 6.5, and the 22 egocentric males were adjusted to 20.5, maintaining the same proportion of males in each category.

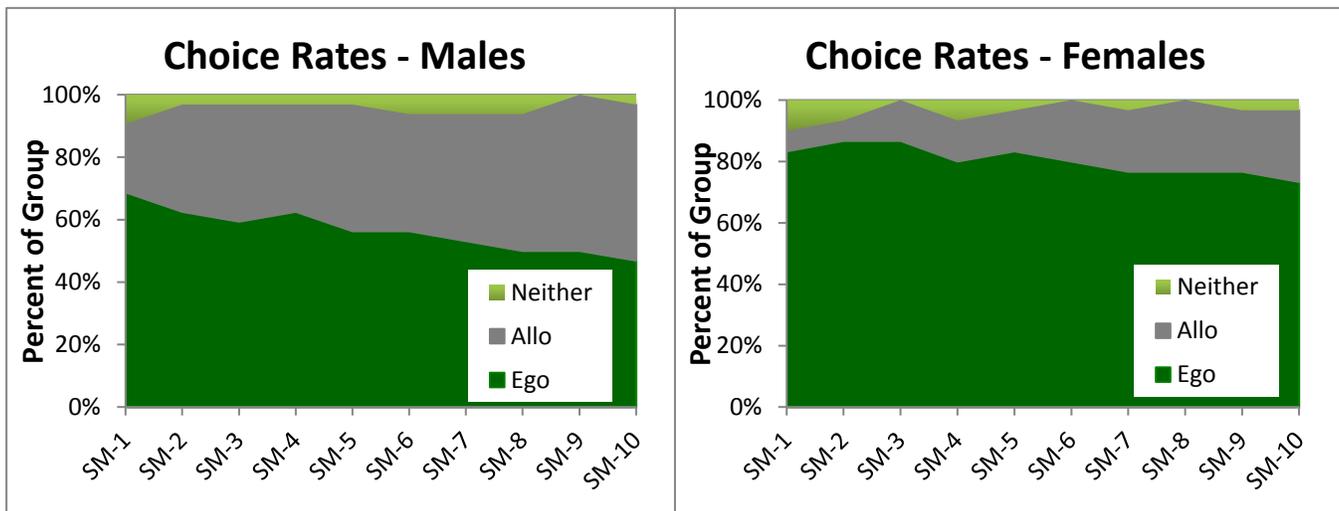


Figure 7. Percent of participants selecting either an allocentric (Allo – grey), an egocentric (Ego – green) or neither (light green) strategy across all 10 Show-Me (SM) trials divided for gender (males depicted on the left side of the figure, females depicted on the right)

However, even though there was a strong preference for egocentric navigation from the outset of testing, this is not strong evidence that it was necessary for participants to learn to navigate egocentrically before learning to navigate allocentrically. Such evidence would be provided by a large number of participants starting with one of the two strategies (i.e., in this case egocentric) and then switching to the other (i.e., allocentric) strategy. Such evidence was not observed (see Figure 8). True, there were more strategy switches from egocentric to allocentric than the reverse, but a) most people never switched strategies, and b) more people started with egocentric than allocentric. Once a participant had selected a strategy for the first time, 44 of the 61 participants (72%) stuck to it for the remaining trials and never tried the other strategy (see Figure 8 – left panel). As expected from the number of people initially preferring to

navigate egocentrically, there were significantly more switches from egocentric to allocentric than what would be expected from chance (i.e., 50-50), $\chi^2 (1) = 5.56$, $p < .02$. When instead analyzing the percentage of the group that engaged in switching, the difference between the directions didn't seem as great (see Figure 8 – right panel). It was observed that 45 of the 61 participants started by navigating egocentrically, but only 11 of those 45 (24%) switched to navigating allocentrically; the remaining majority (76%) navigated egocentrically throughout. Conversely, of the 16 navigators classified as being allocentric navigators, only 6 (38%) started by navigating egocentrically and then switched. The remaining 10 (62%) allocentric navigators navigated allocentrically throughout, starting from the first time they chose a strategy. Thus the 24% of those who started allocentrically and switched to egocentric navigation does not seem all that different from the 38% who started egocentrically and switched to allocentric navigation, indicating that egocentric navigation was not a necessary step to navigating allocentrically (i.e., it was not always acquired first). Conversely, these rates of switching also indicate that allocentric navigation also was not necessarily acquired first. A chi square test of independence between preferred navigational strategy and switching found no significant relation between these two variables, $\chi^2 (1) = 1.00$, $p = .317$.

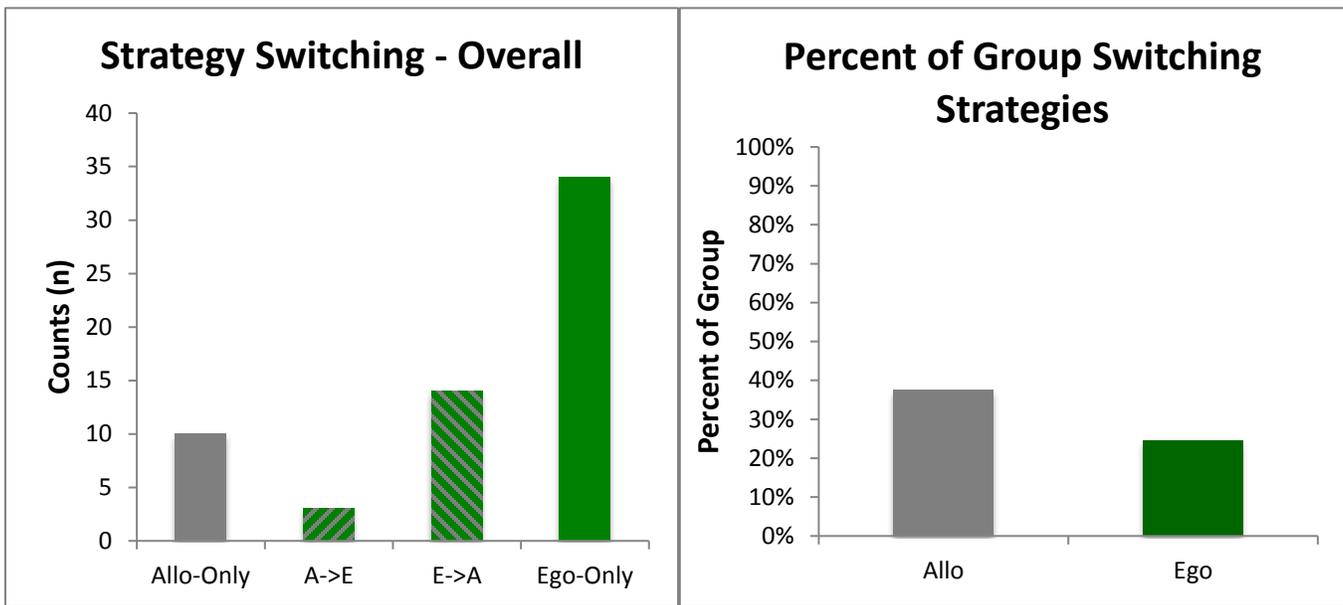


Figure 8. Left panel: Total number of participants either: only using an allocentric (Allo-Only) or egocentric strategy (Ego-Only), switching from an allocentric strategy to an egocentric strategy (A->E), or switching from an egocentric to an allocentric strategy (E->A) at least once. Right Panel: Percent of participants switching strategies (of the total number of navigators classified as that strategy) for both allocentric and egocentric navigators.

With regards to gender, males switched more than females (see Figure 9), though neither gender appeared to have had to acquire one strategy before the other. In terms of within-strategy gender differences, of the 20 males classified as egocentric, only 7 (35%) switched from an egocentric strategy to using an allocentric strategy, while of the 25 females classified as egocentric, only 4 (16%) switched strategies. Analysis using Fisher's exact test revealed that there were no significant differences between males and females in switching from egocentric to allocentric ($p = .131$). Conversely, of the 11 male navigators classified as being allocentric navigators, only 5 (45%) started by navigating egocentrically and then switched, while of the 5 female navigators classified as being allocentric, only 1 (20%) started by navigating egocentrically and then switched. Again, analysis using Fisher's exact test showed no significant differences between males and females ($p = .168$).

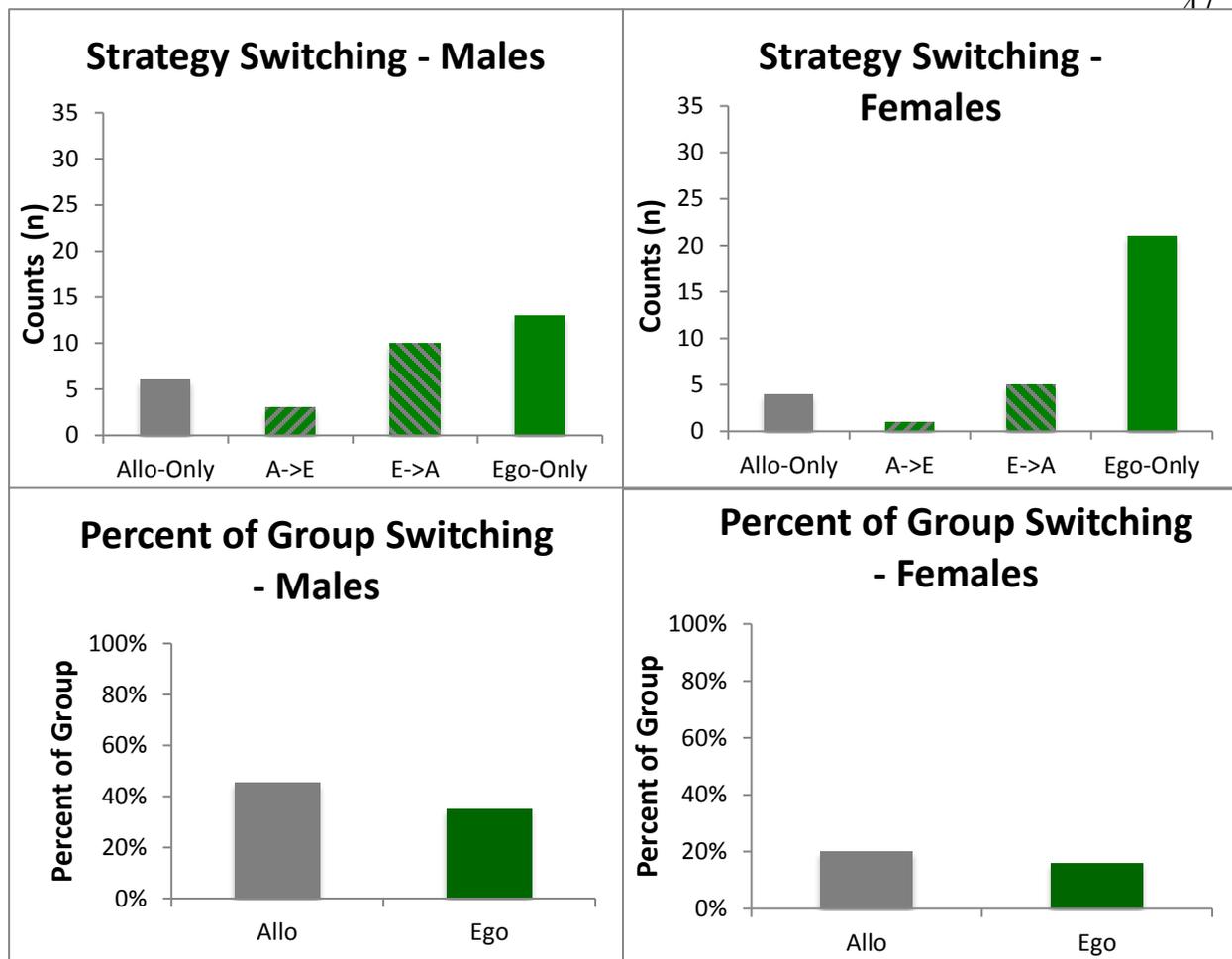


Figure 9. Top Panels: Number of participants either: only using an allocentric (Allo-Only) or egocentric strategy (Ego-Only), switching from an allocentric strategy to an egocentric strategy (A->E), or switching from an egocentric to an allocentric strategy (E->A), grouped by gender (males – left side of the figure, females – right side). Bottom Panels: Percent of participants switching strategies (of the total number of navigators classified as that strategy), for both allocentric and egocentric navigators, divide by males (left side) and females (right side).

Strategy Preference & Strategy Competence: Does acquired strategy preference on Show-Me trials indicate subsequent competence on forced-strategy probes?

Unfortunately, statistical analysis of performance on the forced-strategy probes was difficult due to the unequal distribution of strategy selection by gender (see Table 3). As there were less than 7 participants in one of the groups (female allocentric navigators) it was not appropriate to analyze the results using ANOVA or MANOVA.

Table 3
Number of Each Gender Choosing Each Strategy

| | Allo | Ego |
|---------|-------------|------------|
| Males | 11 | 20 |
| Females | 5 | 25 |

In the Dual-strategy maze, people performed better on the forced-strategy probes when using the strategy they preferred in the Dual-strategy maze (see Figure 10). On the Cue probe, using location error (to the correct cue-sphere), allocentric navigators performed significantly worse than egocentric navigators, $t(59) = 5.23$, $p < .0001$. On the Place probe (this time to the correct location rather than the correct cue, as cues were not present on the Place probe), the reverse was true, allocentric navigators performed significantly better than egocentric navigators, $t(59) = 2.30$, $p < .05$. These two findings (that egocentric navigators are better at the Cue probe and allocentric navigators are better at the Place probe) suggest that strategy preference does, in some way (whether learned or not), lead to greater strategy competence. Overall, performance on the Cue probe ($M = 4.08$, $SEM = 0.70$) was better than performance on the Place probe ($M = 4.91$, $SEM = 0.55$), though this was non-significant, $t(116) = 0.93$, $p = .35$.

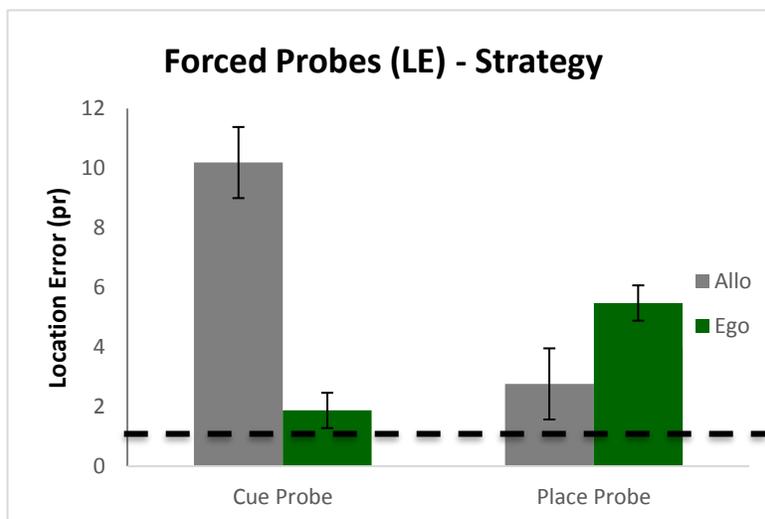


Figure 10. Average location error (in platform radii) of allocentric (Allo – grey bars) and egocentric navigators (Ego –green bars) on the cue (relative to the correct cue-sphere) and place forced-strategy probes (relative to the correct location). Error bars indicate the SEM (standard error of the mean). Black dotted line indicates 1-platform radii, or participants estimating the location directly on the platform (if it had been present).

On both the Cue and Place probes, strategy preference did predict competence for both males and females (see Figure 11). On the Cue probe, the only significant differences observed were that egocentric navigators performed significantly better than allocentric navigators, which was true for both males ($t(29) = 3.37, p < .005$) and females ($t(28) = 14.15, p < .00001$). All other within-gender and within-strategy pairwise comparisons were non-significant (all $p > .09$). On the Place probe all within-gender and within-strategy pairwise comparisons were non-significant (all $p > .08$), though it should be noted that both male and female allocentric navigators did outperform egocentric navigators. That no within-strategy gender differences were significant on either probe and that the only significant within-gender strategy differences (those on the Cue probe) were present in both males and females suggest that males and females did not differ in their relationship between preference and competence.

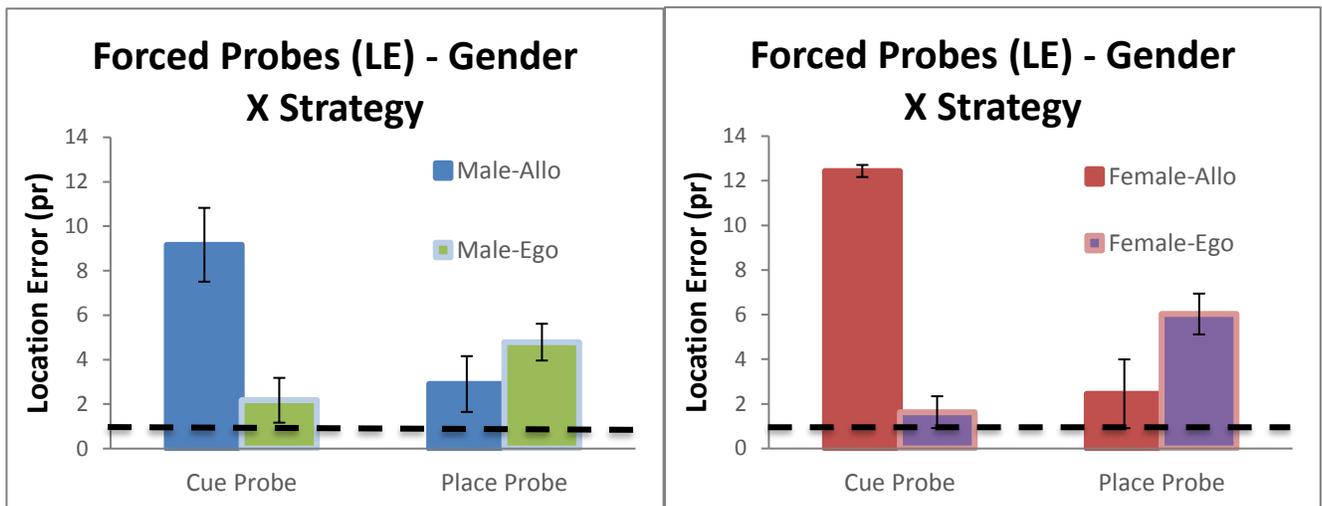


Figure 11. Average location error (in platform radii) of navigators on the cue (relative to the correct cue) and place (relative to the correct location) forced-strategy probes, grouped by gender (left panel = males, right panel = females) by strategy. Error bars indicate the SEM (standard error of the mean). Black dotted line indicates 1-platform radii (i.e., estimates <1 are within the bounds of a platform location). Black dotted line indicates 1-platform radii, or participants estimating the location directly on the platform (if it had been present).

Incidental Learning: Do people acquire information useful to navigating using their non-preferred strategy?

In order to investigate whether any participants had learned information related to their non-preferred strategy, individual estimations of platform position were plotted for both egocentric and allocentric navigators on each of the forced-strategy probes (see Figure 12). On the Cue probe, nearly all the navigators’ responses were clustered around one of two correct positions; the majority of navigators were clustered around the correct cue-sphere, while some (in particular many of the allocentric navigators) were clustered around the sphere hovering above the correct location. Conversely, on the Place probe, a fair number of egocentric navigators were able to identify the correct quadrant that had contained the platform, despite the absence of proximal (egocentric) cues. This suggests that some of the egocentric navigators had “incidentally” learned something about the distal environment.

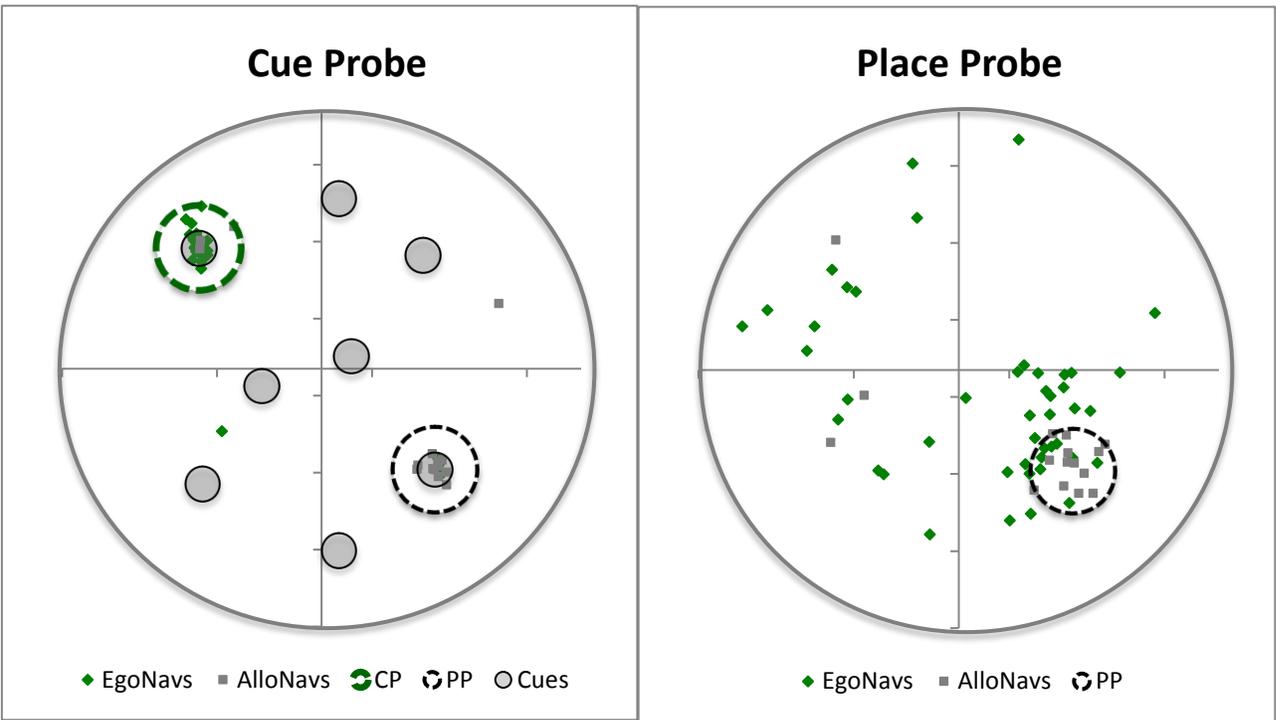


Figure 12. Platform localizations on place and cue probes for individual participants, grouped by their strategy. Participants who preferred an egocentric strategy are indicated by a green circle; participants who preferred an allocentric strategy are indicated by a grey square. Black circles indicate the spheres (only present on the cue probe), the green dotted circle indicates where the egocentric platform would be located if it was present, while the grey dotted circle indicates the allocentric platform's hypothetical location.

Incidental Learning: Allocentric Navigators – Minimum Location Error. It appears that allocentric navigators were able to acquire information relating to their non-preferred strategy. In order to investigate the incidental learning of an egocentric strategy by allocentric navigators in the Cue probe, performance was re-examined by measuring the distance between the platform estimate and either the green cue-sphere or the brown sphere that marked the correct location on Show-Me trials (whichever sphere was closer to the participant's estimate of the platform location). This was termed "minimum location error". After re-plotting the data (see Figure 13 – left panel) allocentric navigators still performed worse than egocentric navigators, though this was now non-significant, $t(59) = 0.81$, $p = .42$, and the difference is much smaller. This effect was also evident when plotting the minimum location error–location error (MLE-LE) difference between the two measures (Figure 13 – right panel), as re-plotting only made a small difference to the performance of egocentric navigators on the Cue probe (LE = 1.87 → MLE =

0.50), but it made a large difference to the performance of the allocentric navigators ($LE = 10.19 \rightarrow MLE = 0.86$). The MLE-LE difference between allocentric and egocentric navigators was significant, $t(59) = 4.91$, $p < .0001$, and shows just how much of the allocentric navigators' poor performance could be attributed to going to the cue hovering over the correct location. It should be mentioned that this incidental learning finding does not negate the fact that preference still indicates competence, as using these measures is more like examining if they had any competence what so-ever. This will be discussed further in the discussion.

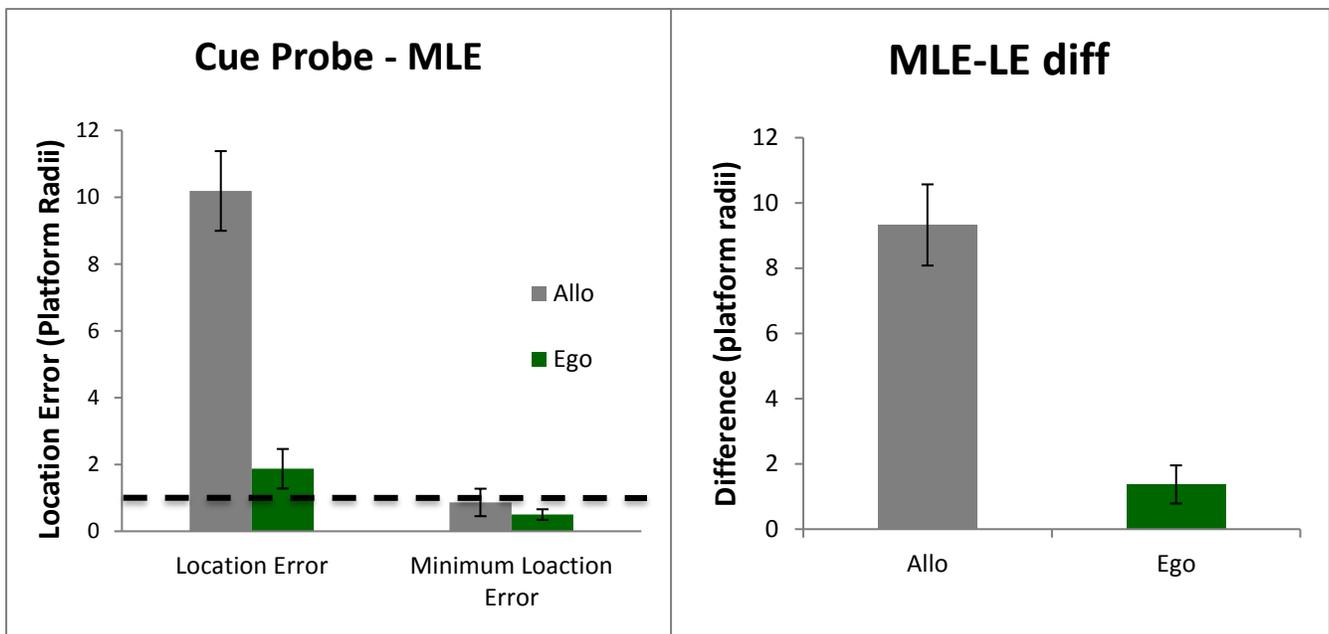


Figure 13. Left panel: Location error on the Cue Probe as plotted in Figure 8 and as Minimum location error (in platform radii) of navigators on the Cue probe (i.e., relative to the correct green cue-sphere or to the reddish-brown sphere that marked the correct location on Show-Me trials, whichever sphere was closer to the participant's estimate of the platform location). The Black dotted line indicates 1-platform radii (i.e., estimates < 1 are within the bounds of a platform location). Right panel: Average minimum location error and location error difference (location error minus minimum location error for each participant; in platform radii) between allocentric and egocentric navigators on the Cue probe. Error bars indicate the SEM (standard error of the mean).

A puzzling feature of the location estimates in the Cue-only probe was that quite a few allocentric navigators (12/16) and even a few egocentric navigators (4/45) estimated the platform location to be close to, or under, the sphere that had been positioned over the location of the

platform during regular Show-Me trials. One explanation for this choice is that the sphere over the allocentric platform location on Show-Me trials was quite distinctive (it looked like a pine cone) and navigators may have associated this cue with the platform location on Show-Me trials, and used it on the Cue-only probe. However, the reasons why they may have done so will be discussed in more detail in the discussion.

When using minimum location error to examine gender differences in non-preferred (egocentric) strategy learning by the allocentric navigators, it is clear that there were almost no gender differences (see Figure 14). When analyzing gender differences (and gender by strategy differences) in the ability of navigators to use information relating to their non-preferred strategy, allocentric navigators from both genders acquired information relating to an egocentric strategy. In terms of minimum-location error, all within-strategy pairwise comparisons (all p 's $> .35$) and all within-gender pairwise comparisons (all p 's $> .40$) were non-significant. In terms of MLE-LE differences, there were no significant within-strategy pairwise comparisons. However, when analyzing within-gender pairwise comparisons, allocentric navigators had significantly greater differences than egocentric navigators, which was true for both males ($t(29) = 3.27, p < .005$) and females ($t(28) = 3.65, p < .001$).

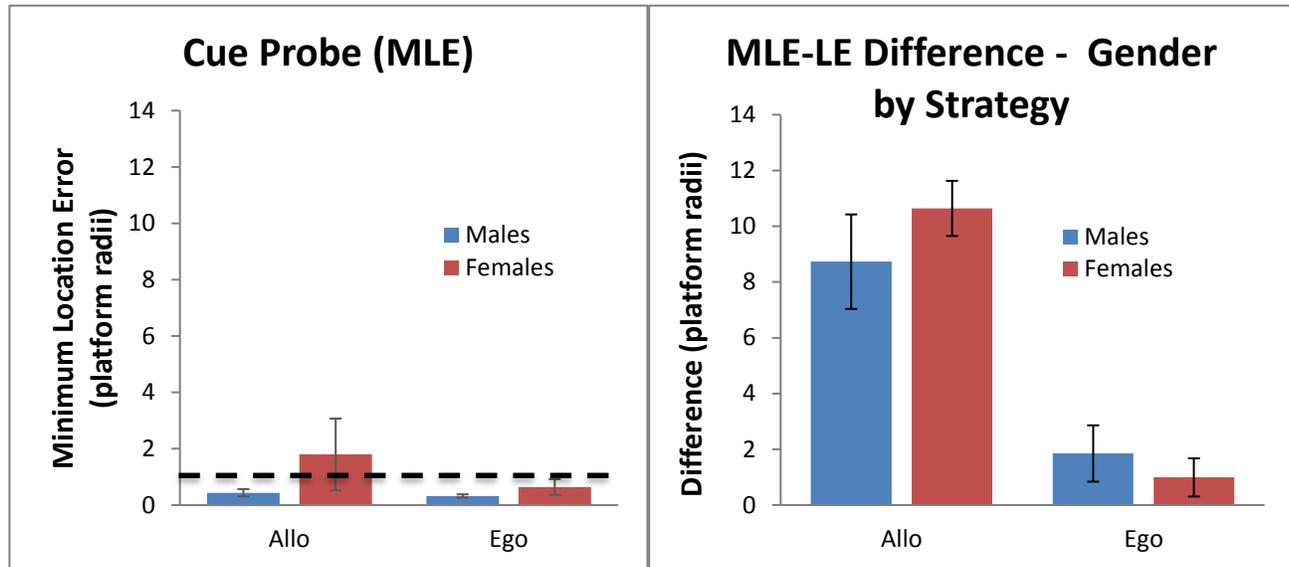


Figure 14. Left Panel: Average minimum location error (platform radii) of navigators on the cue probe (relative to the closer cue; either the correct cue or the cue hovering over the correct place), grouped by gender and strategy. Black dotted line indicates 1-platform radii (i.e., estimates <1 are within the bounds of a platform location). Right Panel: Average minimum location error and location error difference (location error minus minimum location error for each participant; in platform radii) grouped by strategy (allocentric and egocentric) and gender on the cue probe. Error bars indicate the SEM (standard error of the mean).

Incidental Learning: Egocentric Navigators – Identification of Correct Quadrant.

In order to investigate whether egocentric navigators learned any information relating to an allocentric strategy, platform estimates in the Place probe were examined to see how many of each type of navigator estimated the platforms' location within the correct quadrant (see Figure 15). Localization within the correct quadrant is a much-used measure for the MWM in animals (Sutherland & Dyck, 1984) and humans (Jacobs et al., 1997). As expected, over 80% (13/16) of allocentric navigators correctly identified the correct quadrant. Surprisingly, 60% (28/45) of egocentric navigators were also able to identify the correct quadrant location. This proportion was much greater than would be expected by chance ($\chi^2(1) = 29.40, p < .00001$). Thus it is clear that the egocentric navigators learned something about the location of the platform despite choosing to navigate egocentrically most of the time. It is also clear that this level of incidental learning was not at the same level as the intentional learning of allocentric navigators.

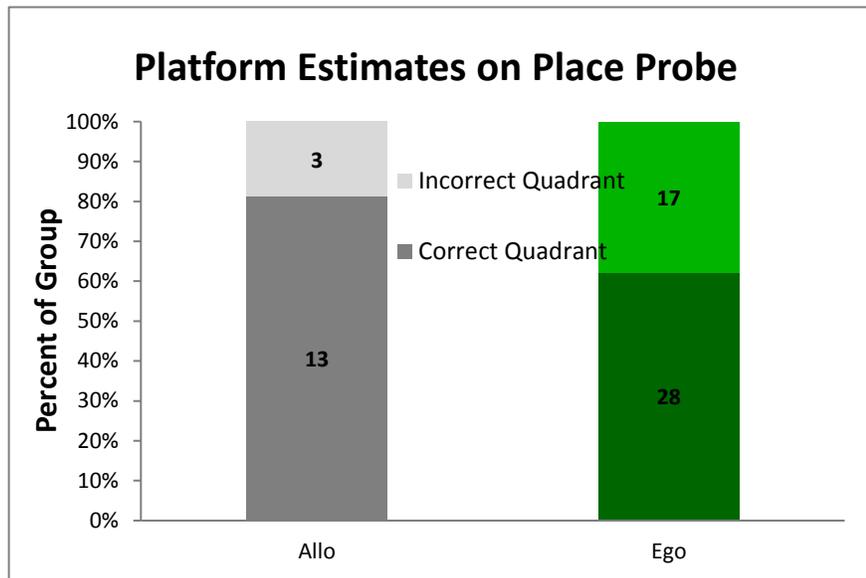


Figure 15. Percentage of navigators either correctly (darker color) or incorrectly (lighter color) estimating the platform's location on the Place probe, grouped by strategy (allocentric or egocentric). The numbers on each section of the bar graph indicate the sample size for that group.

When using correct quadrant choice to examine gender differences in non-preferred (allocentric) strategy learning by the egocentric navigators, there were almost no gender differences (see Figure 16). With regards to gender, 65% (13/20) of male egocentric navigators and 56% (14/25) of female egocentric navigators were able to successfully complete the Place probe. Both the males ($X^2(1) = 17.07, p < .00001$) and females ($X^2(1) = 12.08, p < .0005$) were significantly different from what would be expected from chance. It is also clear that this level of incidental learning was not at the same level as the intentional learning of allocentric navigators for both males and females.

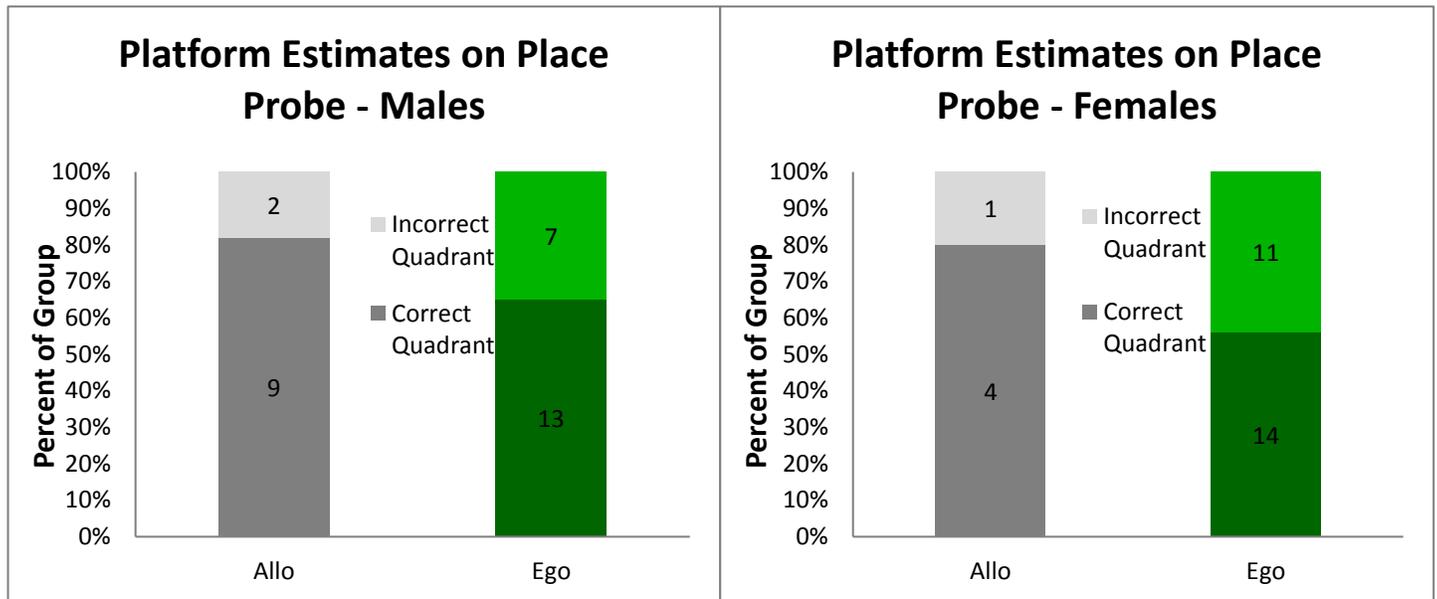


Figure 16. Percentage of navigators either correctly (darker color) or incorrectly (lighter color) estimating the platform's location on the Place probe, grouped by strategy (allocentric or egocentric) by gender (left panel = males, right panel = females). The numbers on each section of the bar graph indicate the sample size for that group.

Limits of Strategy Competence: Does strategy preference indicate the limits of potential strategy performance?

In this phase of the experiment, all participants were required to learn to navigate in a single-strategy allocentric maze (the Place Maze) using only allocentric features. The maze was essentially the same except that the floating spheres marking potential platform locations were removed. This phase of the experiment addressed two related questions: a) could those who preferred to navigate egocentrically learn a maze that required allocentric navigation (the Place maze)? and b) were those who preferred to navigate egocentrically less competent at navigating allocentrically? In other words could egocentric navigators use the other strategy if required and do allocentric navigators prefer the strategy that was best for them? As mentioned above, statistical analysis of performance measures was complicated by the unequal distribution of

strategy selection by gender (see Table 3 above) because of the small sample number of female allocentric navigators (less than 7 participants).

Overall, it appears that people who preferred to navigate allocentrically (in the Dual-strategy maze) performed better than those who preferred to navigate egocentrically (see Figure 17). When comparing participants' performance as an average over Find-It trials 2-10 (distance, latency), Show-Me trials 1-10 (location error), or performance on the implicit probe (correct quadrant dwell time), significant differences are observed on three of the four measures of performance, favouring allocentric navigators (see Table 4). Navigators classified as selecting an allocentric strategy in the dual strategy maze performed significantly better than egocentric navigators on measures of latency, ($t(57) = 3.46$, $p < .001$), distance ($t(57) = 2.93$, $p < .005$), and location error ($t(57) = 3.78$, $p < .0005$). On the implicit probe however, there was no significant difference between allocentric and egocentric navigators in participant's correct quadrant dwell time ($t(57) = 0.96$, $p = .34$), though allocentric navigators did continue to perform better.

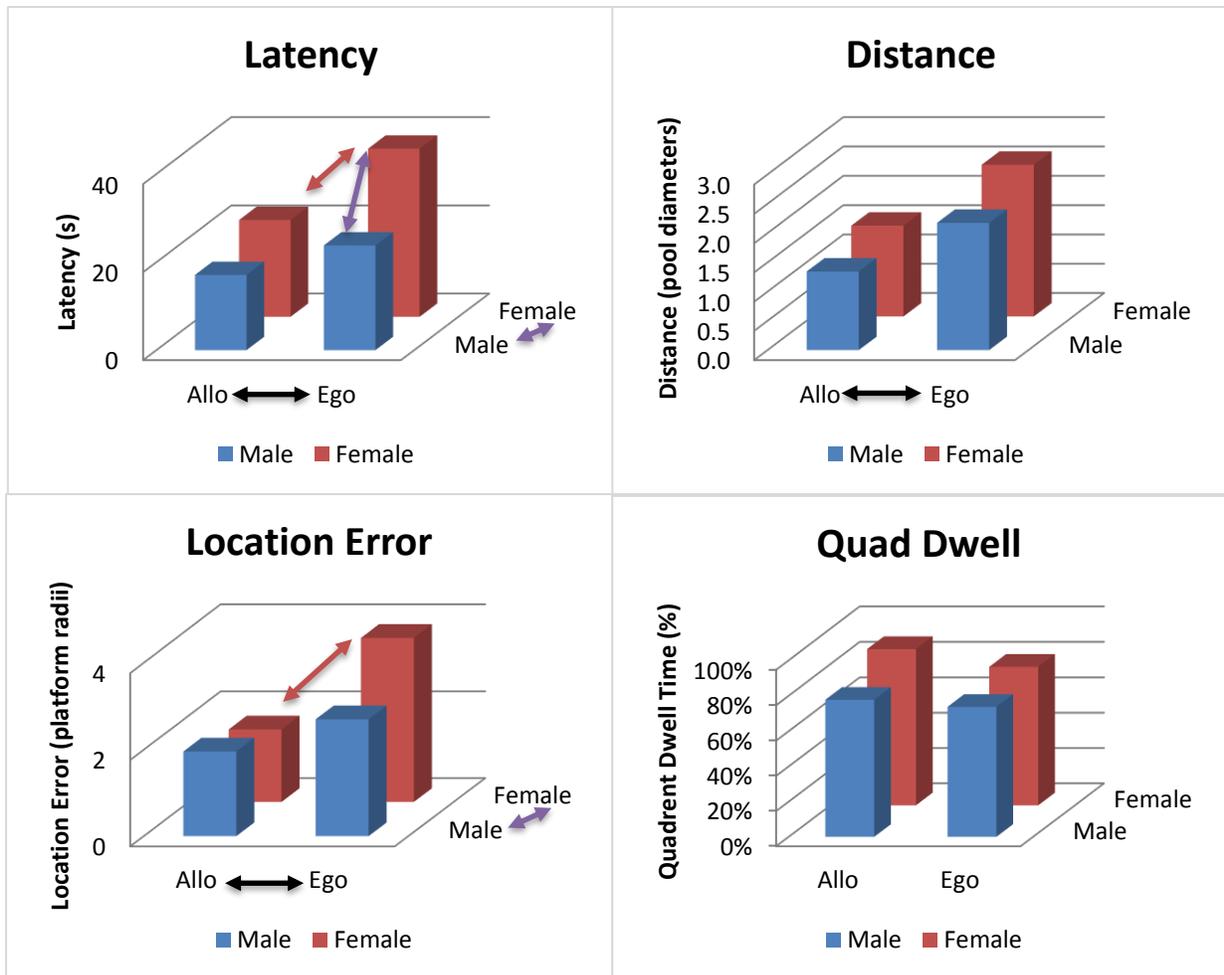


Figure 17. Place Maze performance (Y-axis) on measures of latency (Find-It trials 2-10), distance to the platform (Find-It trials 2-10), location error estimates relative to the platform (Show-Me trials 1-10) and correct quadrant dwell time (Implicit probe), grouped by strategy type by gender (males in blue, females in red). Higher scores indicate poorer performance, except for correct quadrant dwell time. Black arrows indicate significant main effects, purple arrows indicate significant gender, or gender within-strategy effects, and reddish arrows indicate significant differences between strategies within females (independent t-test, $p < .05$).

Table 4

Place Maze Performance and T-Test Results for navigators who preferred allocentric and egocentric in the Dual-strategy maze (indicates a significant difference)*

| | Latency | Distance | Location Error | Quad Dwell Time |
|------------------|----------------|-----------------|-----------------------|------------------------|
| Allo Navs | 18.74 (2.01) | 1.41 (0.18) | 1.87 (0.22) | 81% (3.76%) |
| Ego Navs | 31.96 (3.24) | 2.41 (0.22) | 3.31 (0.30) | 77% (3.21%) |
| P-value (t-test) | .001* | .005* | .0005* | .34 |

When gender differences in allocentric maze performance were examined, males outperformed females on all measures but one (see Figure 17). This difference, favoring males, was significant on latency ($t(57) = 2.92, p < .005$) and location error ($t(57) = 2.06, p < .05$), but not distance ($t(57) = 1.25, p = .22$). In terms of correct quadrant dwell time, males were slightly, and non-significantly worse than females, $t(57) = 0.80, p = .43$ (See Table 5).

Table 5

Place Maze performance and t-test results for males and females (indicates a significant difference)*

| | Latency | Distance | Location Error | Quad Dwell Time |
|------------------|----------------|-----------------|-----------------------|------------------------|
| Males | 21.33 (2.27) | 1.86 (0.30) | 2.45 (0.33) | 76% (3.74%) |
| Females | 35.45 (4.20) | 2.42 (0.33) | 3.43 (0.34) | 80% (3.64%) |
| P-value (t-test) | .005* | .05* | .22 | .43 |

The investigation of gender differences determined that the concordance between allocentric preference and allocentric competence was true for both males and females even though males were generally better than females. Figure 17 show that for both genders, those who preferred to navigate allocentrically were better in the Place maze, but the differences were rarely significant. The arrows in Figure 17 show that only female allocentric navigators were better than female egocentric navigators ($n = 5, 25$) for latency ($t(28) = 2.23, p < .05$) and

location error ($t(28) = 4.25$, $p < .0005$). All other within-strategy pairwise comparisons were not significant (all $p > .05$). When analyzing strategy differences within-gender, at this level of analysis the only significant gender difference was in latency between egocentric navigators with male egocentric navigators having outperformed female egocentric navigators, ($t(42) = 2.44$, $p < 0.02$). All other within-strategy pairwise comparisons were non-significant (all $p > .05$).

Our second key question of interest, related to strategy competence, was if those who preferred to navigate egocentrically could learn a maze that required allocentric navigation. In other words, were egocentric navigators able to learn the Place maze? When looking at the learning curve differences between allocentric and egocentric navigators, it does appear that they can (see Figure 18). Note that there was no learning curve for explicit probe performance as it only occurred at the conclusion of navigation. The proportion of egocentric navigators reaching the criterion of allocentric performance (i.e., reaching the same level of performance as the worst allocentric navigator) was 86% (38/44) for latency, 100% (44/44) for distance, 68% (30/44) for location error, and 89% (40/44) for correct quadrant dwell time. This demonstrates that while egocentric navigators were not as good as allocentric navigators at navigating in the single-strategy maze, the majority of the egocentric navigators are effectively able to learn it by the conclusion of the maze. Only two egocentric navigators (one male and one female) failed to reach criterion on all four of the measures.

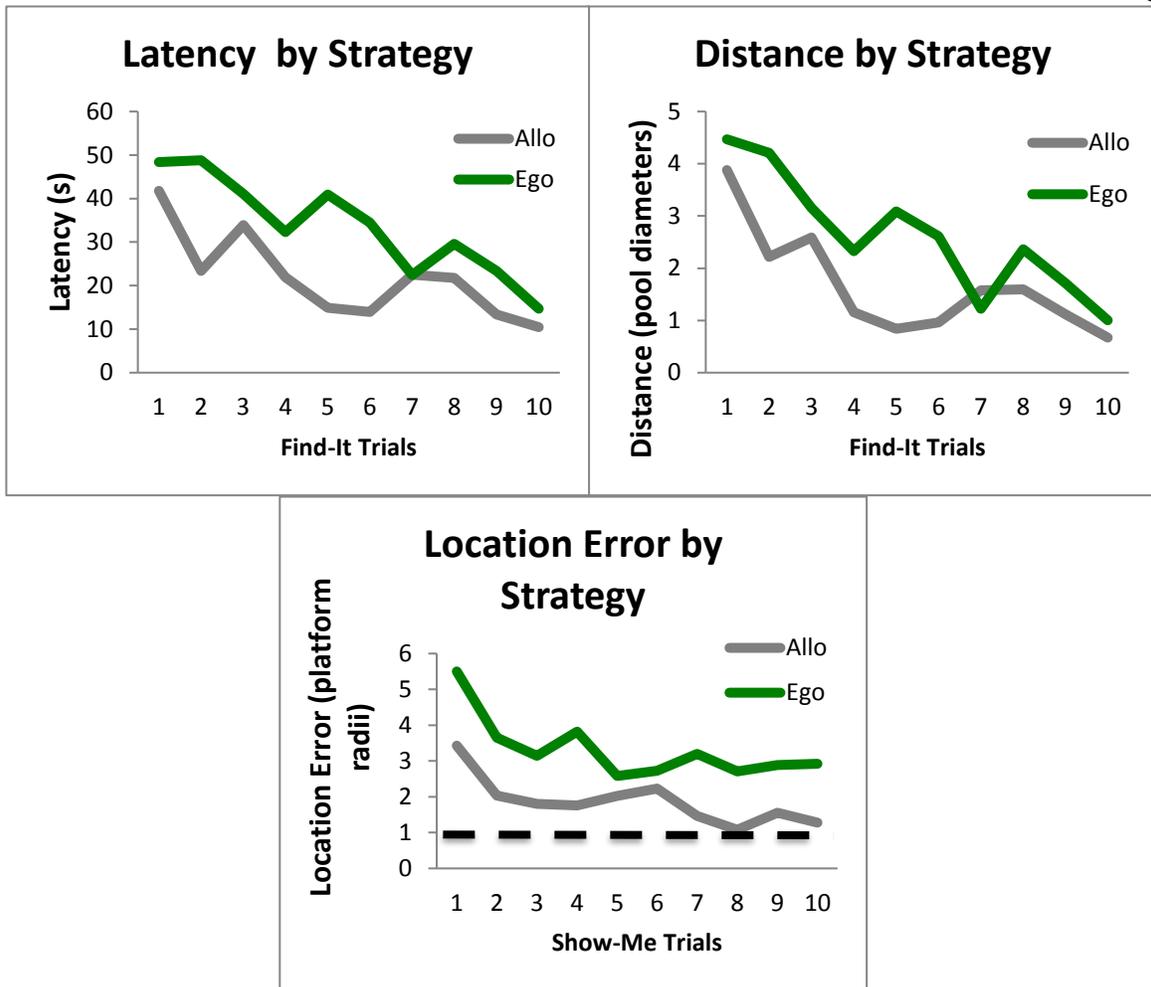


Figure 18. Participants' Place maze performance over ten trial pairs on measures of latency (seconds) and distance (pool diameters) on Find-It trials, and location error (platform radii) on Show-Me trials. (allo = allocentric navigators, ego = egocentric navigators). Black dotted line indicates 1-platform radii (i.e., estimates <1 are within the bounds of a platform location).

There did not appear to be any gender differences in the ability of egocentric navigators to learn to navigate allocentrically. Although a slightly higher proportion of males reached the criterion (i.e., were as good as the worst allocentric navigators) than females (see Table 6) on latency and location error (but not distance or quadrant dwell time) the differences in the numbers reaching criteria were not significant (all Fisher's exact $p > 0.2$).

Table 6

Percentage of successful navigators in the Place Maze (total reaching criterion/ total navigators) grouped by gender (males and females)

| | Latency | Distance | Location Error | Quad Dwell Time |
|--------------------------|----------------|-----------------|-----------------------|------------------------|
| Males | 95% (18/19) | 95% (18/19) | 74% (14/19) | 89% (17/19) |
| Females | 80% (20/25) | 96% (24/25) | 64% (16/25) | 88% (22/25) |
| P-value (Fisher's Exact) | .213 | 1.00 | .534 | 1.00 |

Discussion

The present experiment examined 5 issues: a) the distribution of strategy preferences in a dual-strategy maze, b) the manner in which these strategy preferences are acquired, c) the match between strategy preference and strategy competence, d) the degree to which participants learned information relevant to their non-preferred strategy and e) the navigational competence of participants forced to use their non-preferred strategy. In terms of the distribution of preferences, most navigators appeared to prefer egocentric navigation: females were significantly biased towards egocentric navigation and more so than males, who were also egocentrically biased, but not significantly so. In terms of manner of acquisition, participants tended to start with egocentric navigation, but this was not true for all navigators. Most navigators showed a lasting preference for the strategy they started with and analysis of switch rates showed that the probability of switching from egocentric to allocentric was actually lower than the reverse, once baseline rates of strategy selection were taken into account. In terms of the match between preference and competence, participants tended to be better at their preferred strategy than their non-preferred strategy. In terms of acquisition of information relevant to their non-preferred strategy, most participants showed considerable learning of their non-preferred strategy. Finally, in terms of navigational competence, participants who preferred to navigate egocentrically, were not as good as those who preferred to navigate allocentrically, but most of them proved able to learn to navigate allocentrically when required to do so. There were no meaningful gender differences in any of these areas, although males were found to be more competent at allocentric navigation than females.

Distribution of Strategies (Show-Me trials)

The first, baseline issue of thesis was to determine the distribution of egocentric and allocentric strategy preferences in the Dual-strategy maze. The results showed that participants

were strongly egocentrically biased. With regards to gender, males were somewhat egocentrically biased but not as much as females.

The overall egocentric bias was surprising given previous observations from dual-strategy environments. In the piloting conducted for this thesis, it was found that the strategy distribution was slightly biased towards allocentric navigation (Ferguson et al., 2014). As well, in previous water maze literature from the Skelton lab participants were either slightly allocentrically biased (e.g. van Gerven et al., 2012 in which 61% of navigators were allocentric) or were unbiased (Livingstone & Skelton, 2007 in which 50% of the control group were allocentric). Given the similarities between the design of the current environment and previous iterations, it is surprising that such a strong egocentric bias was obtained in the current experiment, while the previous versions have all either been allocentrically biased or unbiased. Non Skelton lab research using dual-strategy environments have also found varying levels of strategy bias depending on the maze. The observed distribution of allocentric bias has varied from 64% (Astur et al., 2016 – the number using an allocentric strategy on the first probe), 46% (Iaria et al., 2003 –the number using an allocentric strategy at any point), to 25% (Levy et al., 2005) and even 21% (Nowak, Murali, & Driscoll, 2015). In sum, there does not appear to be a consistent distribution of strategies across mazes or even within labs.

With regards to gender, that both males and females were egocentrically biased but females significantly more-so than males was also a surprising finding, at least initially. This was surprising for a few reasons. The first was that during piloting it was found that males preferred to navigate allocentrically while females preferred to navigate egocentrically. The second was because in the literature it has frequently been suggested that males prefer to navigate allocentrically and females prefer to navigate egocentrically (e.g., Saucier et al., 2002; Woolley

et al., 2010; or see Lawton, 2010 for a review). However, it could be that gender may normally control the direction of the bias but not the degree (and perhaps not in all situations). In other words, males may usually prefer to navigate allocentrically and females egocentrically, but it may not always be the case. In fact, depending on the paradigm, both males and females may even prefer the same strategy (Astur et al., 2016; Nowak et al., 2015; the current study). To take this point further, some research has even shown that females may prefer allocentric navigation just as much (Levy et al., 2005) or even more than males (van Gerven et al., 2012). Altogether, the variance in findings in the literature suggest that while males and females may usually differ in strategy preference (with females being more egocentric) it appears that some other factor may determine if the effect of gender is present at all, and to what extent.

The strong egocentric bias in the current study, both overall and between genders, raised a number of questions. That is, why did the current study find strong egocentric bias while previous literature has found allocentrically biased or even unbiased strategy distributions? Why are the findings related to gender in the literature so varied? Specifically, are the different strategy distributions due to the population, the sample or the maze design?

It seems unlikely that the egocentric bias observed here represents an inherent egocentric bias of the entire population. If this was the case, then why has an identical bias not been observed in every study? Does this mean that the present study finally got it right and everyone else is wrong? Or the reverse? Given that different allocentric/egocentric biases have been found in different studies, this questions the assumption that any study of strategy preference reveals the inherent bias with population.

The second possibility is that the egocentric bias observed here is due to the results being drawn from an anomalous sample. However, this also seems unlikely as the present sample is not

much different from previous years. In fact the only real difference from the van Gerven et al., 2012 study was that the current study was conducted several years later. In fact, both studies used undergraduates from the University of Victoria students, were conducted on samples of a similar size and had no significant differences in terms of the age of each gender. As well, when compared to other studies (e.g., Iaria et al., 2003; Nowak et al., 2015; Astur et al., 2016), they also do not appear to have radically different samples; all were conducted on undergraduate students and had a sample size of at least 30 (the majority had at least 60) and were gender balanced (or at least close). The only difference was the locations in which each study was conducted (the current study was in Victoria; Iaria was in Montreal; Nowak was in Wisconsin; Astur was in Connecticut). And yet, differences in strategy distributions were observed. Thus, it seems unlikely that the results were simply due to sampling differences.

The third and most likely possibility is that it was the maze that was biased. Although this current version of the Dual-strategy maze was designed to be similar to previous editions, the strategy distributions are quite different from those observed with previous versions (Livingstone & Skelton, 2007; van Gerven et al., 2012). Two major differences in the current study were that floating spheres were used (in previous versions the intra-maze cues were located on the arena wall), and that the current maze was open-air and allowed a view of the entire surrounding landscape (in previous versions the maze was located within a room with windows that restricted the view of the landscape). In fact, over the course of that pilot study small changes in the script or environment were found to produce dramatic shifts in the observed strategy distribution, further suggesting that strategy distribution depends greatly on the environment (Ferguson et al., 2014). This also matches up with previous suggestions that the type of testing environment determines what level of strategy bias is observed (Levy et al., 2005) and that strategy bias can

be shifted depending on previous experience in navigational environments (Livingstone-Lee et al., 2014).

The fact that the current study obtained different results from the pilot study (Ferguson et al., 2014) is a bit troubling (given identical mazes were used in both studies). However, this is most likely the result of having a small sample size in the pilot study (n of 10).

In sum, the majority of participants preferred to navigate egocentrically in this Dual-strategy maze. This egocentric bias appears to be related to maze design and not to natural predilection. The fact that the egocentric bias was stronger in females than males is consistent with many previous findings at least in this type of virtual, unfamiliar, environment but not all. On one hand, this idea of a maze itself being biased is not new – many mazes are designed to elicit one kind of behaviour over another (e.g., the MWM was designed to be exclusively allocentric – Morris, Garrud, Rawlins, & O’Keefe, 1982). However, what may be new is the idea that many (or all) mazes do not specifically test one form of navigation, but are merely biased one way or the other.

Strategy Acquisition and Switching (Show-Me trials)

The second question of this thesis was to determine how are strategies acquired in the Dual-strategy maze and does one strategy have to be acquired first? With regards to acquisition, some participants acquired an egocentric strategy first but this was not always the case. In fact most navigators were consistent in their strategy from the first trial on which they chose a strategy until the last (10th) trial. Given that both males and females had an early preference for egocentric navigation (females significantly more so – unsurprising, given the stronger preference for egocentric navigation that females had), it was not surprising that the egocentric strategy was the first strategy adopted by most (45/61, 74%) participants and that more than half of these (34/61) stayed with an egocentric strategy for all the remaining trials. Although it is true

that 11 participants began with egocentric navigation and switched to allocentric, almost as many (10) started with allocentric navigation and stayed with it. In other words, egocentric navigation was not a necessary starting point for all participants. In fact, the proportion of participants who started with allocentric navigation and switched to egocentric (0.24) was not all that different from the proportion that started with egocentric navigation and switched to allocentric (0.38). Thus, less than half (38%) of allocentric navigators started by navigating egocentrically, and this data provides no support for the idea that egocentric navigation necessarily precedes allocentric navigation. Male and female participants did not differ in this regard.

This finding that one strategy does not need to be acquired first runs contrary to suggestions that some navigators will acquire an allocentric strategy initially before switching to an egocentric one (rats: Packard & McGaugh, 1996; humans: Iaria et al., 2003) but not vice versa. However, this result does agree other research that has found that neither strategy is acquired first; they can both be acquired in concert (some navigators acquire egocentric first before switching, while others acquire allocentric first before switching)(Igloi et al., 2009; Astur et al., 2016).

It seems clear that in the present study, one strategy did not always need to be acquired before the other strategy. However, that does bring to question the reason for the discrepancies between the current finding and some of the findings in the literature that have found allocentric must be acquired first.

One possible explanation regarding the discrepancies in the literature is that the type of egocentric strategy studied here is different than the egocentric strategies studied previously. Egocentric navigation has been shown to differ between egocentric-response (based on the

memorization of body turns)(e.g., Roof & Stein, 1999) and egocentric-cue (based on the memorization of a cue object directly paired with the goal)(e.g., Trullier et al., 1997). This might explain why in the current study neither strategy had to be acquired before the other (as an egocentric-cue strategy was used) while Packard & McGaugh (1996) along with Iaria et al. (2003) found that an allocentric strategy had to be acquired initially (and they used an egocentric-response strategy). However this doesn't explain the discrepancies with the literature because Astur et al. (2016) used an egocentric-response strategy and observed that neither strategy had to be acquired first.

A better explanation is that the environmental demands and how the environment is set up influences whether one strategy is acquired first (similar to the point made above in the discussion of the strategy distribution bias). This seems likely because differences in environment (specifically cue salience) have been found to affect strategy preference (Ferguson et al., 2014). Other research has also emphasized that strategy use may be determined by cue salience (Wolbers & Hegarty, 2010). The fact that some navigators obtained an allocentric strategy before an egocentric strategy during some navigation tasks may simply indicate that the allocentric cues were easier to use and more salient in those environments. For example, in the Iaria et al., (2003) study, participants were given a continuous view of the landscape that was non-obscured and 46% of navigators adopted an allocentric strategy. In the pilot study for this current experiment more than 75% of navigators adopted an allocentric strategy when the surrounding landscape was not obscured (with an n of 15 in that group)(Ferguson et al., 2014). However, when fog was added to reduce the salience of the surrounding landscape (like in the current study), this dropped to 50% (with an n of 10 in that group). In the current study (which also used the foggy maze), and which had a larger N of 61, this strategy bias decreased all the

way to 26%. Thus, it seems that the ease of use of cues (which is determined by how the environment is set up) may largely determine what behaviour is observed. Conversely, the earlier adoption of an egocentric strategy for some participants in the current study may suggest that the egocentric cues were easier to use (and more salient).

The current study's finding that most navigators (72%) picked a strategy and didn't switch from it is consistent with previous findings by Iaria et al. (2003) (82%), Igloi et al. (2009) (70%), and Astur et al. (2016) (85%). However, this rate does not differentiate strategy consistency due to the environment from strategy consistency due to native preferences.

In sum, it does not appear that one strategy needs to be acquired first in the Dual-strategy maze (in other words there is no order), and that this does not differ for men and women. Specifically, in the Dual-strategy maze this may suggest that the egocentric cues were more salient than the allocentric cues. That navigators can switch strategies in both directions shows that some navigators may not be fixed in their strategy choice and may learn information relating to both strategies. This is the first suggestion in the current study that in the Dual-strategy maze at least some navigators may learn information relating to both strategies. As well, this current result suggests that males and females may not be that different in terms of navigational cognition.

Strategy Competence & Acquired Preference (Show-Me trials versus Forced-Strategy Probes)

The third issue of this thesis was to investigate the relationship between acquired strategy preference and strategy competence. In other words, does acquired preference indicate subsequent strategy competence? In the present study, those who preferred allocentric did better on the Place forced-strategy probe than those who preferred egocentric. Conversely, those who

preferred egocentric performed better on the Cue forced-strategy probe. Interestingly, there were no gender differences in the relationship between preference and competence.

This issue has not been studied systematically before. However, the idea that there may be a relationship has been considered in research on gender differences in strategy preference and competence. In particular, it has been used as a possible explanation for gender differences in strategy competence (specifically, males and females may prefer different strategies, which may explain why males are better at allocentric navigation)(van Gerven et al., 2012; Astur et al., 2016).

While this finding is novel, it was previously assumed that one indicated the other. In other words, most navigation research has assumed that if you measured one (i.e., you measured strategy performance) that it would indicate the other (i.e., that the navigators would be better at that strategy they preferred to use).

The current finding is also a validation of the classification criterion for strategy preference. In the Dual-strategy maze, participants were classified based on the sets of information it was believed they were using (and each set of information corresponded to a strategy; the surrounding landscape to allocentric and the green cue-sphere to egocentric). Until now however, there was no behavioural evidence to confirm that this was the case, it was possible that navigators (in particular the allocentric ones) were using different information than what it was believed they were (e.g., perhaps allocentric navigators were using some combination of spheres to navigate), but this finding suggests that this was not the case.

These results suggest that people prefer the strategy that they are most competent at, and that there are no gender differences in this relationship. On forced-strategy probes, participants proved to be more competent at the strategy they preferred in earlier Show-Me trials, and this

was true for both males and females. This shows a relationship between preference and competence. Thus, in terms of navigational bilingualism, navigators are better at speaking the language they prefer to use. The lack of gender differences suggests that the relationship between preference and competence is the same for each gender, providing one more example of an area of navigational cognition in which males and females do not appear to differ.

Incidental Learning (Show-Me Trials versus Forced-Strategy Probes)

The fourth issue of this thesis was to investigate whether or not participants acquired information related to their non-preferred strategy; in other words do they incidentally learn a second strategy? On the forced-strategy probes, egocentric navigators had some idea as to where the platform was on the Place probe despite not having any access to the spheres, while allocentric navigators tended to go to the “correct place” sphere (that was over the platform on Show-Me trials) on the Cue probe. This was true for both males and females.

This tendency of the egocentric navigators to go the correct location clearly demonstrates incidental learning. However, the tendency of the allocentric navigators is a bit of a puzzle, as the allocentric navigators could have divined the location using subtle clues in the maze (perhaps by peering through the fog or through some clue on the floor or the arena walls) or they could have been reacting to the unique appearance of the cue (the color and texture of that sphere made it look like a pinecone – which was an issue with the Cue probe). Given that the “pinecone” was over the platform on Show-Me trials this means that it would have been observed multiple times in the “correct” location by allocentric navigators which is the same location it was in on the forced-strategy probe. This explanation also holds for the 4 egocentric navigators who, as it turns out, all used an allocentric strategy (i.e., chose this place and cue) on their last Show-Me trial. This latter interpretation (the “pinecone” effect) seems more plausible. Furthermore, a subsequent study with nearly identical procedures but with all the “incorrect” cues an identical

color (off-white) did not observe this same tendency for people to choose the allocentric location (Ferguson, van Gerven, & Skelton, 2015; data currently unpublished). This incidental learning implies that allocentric navigators were learning about the cue properties of the sphere marking the location (on both Find-It and Show-Me trials) and not just the location.

Overall, participants of both strategy type appear able to perform well on the forced-strategy probe opposite to their strategy using a strategy that is normally hidden or unexpressed. In terms of gender, both males and females are able to use information relating to the strategy they did not prefer, so in other words there were no gender differences (although given the low *n* of the female allocentric group, it was difficult to test).

This finding of incidental learning confirms what has been observed previously in rats (chiefly in Whishaw & Mittleman, 1986) and what has been found in humans (Jacobs et al., 1997; Igloi et al., 2009; Hamilton et al., 2009). In fact this current finding directly confirms (in the Dual-strategy MWM) the suggestion that navigators were engaging in parallel information processing of both strategies in the Starmaze (Igloi et al., 2009). However, if strategy learning is incidental then it is curious why some researchers have observed overshadowing of allocentric information by egocentric information (Chamizo et al., 2003; Redhead & Hamilton, 2007). One possible explanation for blocking and overshadowing is that in both mazes a visible platform was used and a visible platform would be very salient for navigators. This may suggest that the salience or ease of use of cues may play a large role in whether or not the cues themselves are learned.

At first glance, the incidental learning shown in participants' non-preferred forced-strategy probes seems to contradict the earlier assertion that navigators are more competent at using the strategy they preferred to navigate with. However, just because a person is more

competent at using the strategy they prefer, it does not follow that they will be incompetent at using their non-preferred strategy. In fact, the present results highlight the pitfall of this logical fallacy.

Thus, in the Dual-strategy MWM, people acquired information related to their non-preferred strategy, or in other words, they incidentally learned information regarding both strategies when navigating. This suggests that navigators aren't solely allocentric or egocentric. In other words navigators are not of one type, the simplistic dichotomy with respect to navigational cognition of individuals is probably false (i.e. seeing individuals as solely one strategy or the other). To use the language analogy again, it seems that people are bilingual with respect to strategy, and learning information in both "languages" all the time, even if not speaking it or showing it (i.e., navigating by it). This means that learning during navigation is not as straight-forward as previously thought. In the right paradigm (using the forced-strategy probes), people learn more than what they show. That this finding was true for both males and females is an indication that both genders learn some information regarding both strategies and that neither gender is only cognitively capable of one strategy. As well, the lack of gender differences in incidental learning suggests that navigators of either gender may not be limited to one strategy or the other.

Strategy Preference & the Limit of Strategy Competence (Show-Me trials versus Place Maze)

The fifth issue to be addressed was whether strategy preference indicates the limits of strategy competence. This was accomplished by forcing all navigators to use an allocentric strategy in the (single-strategy) Place maze. Overall, it was found that allocentric navigators were generally better than egocentric navigators at navigating in the Place maze, but that most of egocentric navigators were able to reach a similar level of performance as the allocentric

navigators by the end of navigation. In fact only one female and one male failed to acquire an allocentric strategy completely (i.e. did not reach an allocentric level of performance on all four measures of performance in the Place maze). Thus, people were better at using an allocentric strategy in the Place maze if they preferred it previously, but those who had not preferred an allocentric strategy were still able to learn to use it. This was generally true for both males and females, though the difference between egocentric and allocentric females was greater than the difference between egocentric and allocentric males. Overall, males performed better than females in the Place maze. As well, the fact that preference predicted competence in the Place maze is further proof that there is a relationship between preference and competence.

The present findings agree with the one other study that examined this question previously. Igloi et al., (2009) similarly found that egocentric navigators were able to learn an allocentric maze when forced to. Given that previous research has found that when navigators who were trained in an egocentric MWM were given the opportunity to navigate in a dual-strategy MWM, all navigators chose an egocentric strategy, it was questionable whether this would occur in the Place maze. However, this finding confirms that, similar to the Starmaze paradigm, egocentric navigators are able to learn to effectively use an allocentric strategy in the MWM. This distinction is important because the MWM is used very frequently with both humans and laboratory animals (e.g., ~9,800 references (papers and citations) in Google Scholar in 2015) whereas the Starmaze seems to be used by only one set of researchers (with 19 references (papers and citations) in Google Scholar in 2015).

In the current experiment, there were not any significant gender differences in the limits of strategy competence. Even though the egocentric females had the poorest performance on the Place maze, and unlike egocentric males, were statistically different from their allocentric

counterparts (of the same gender), males and females were alike in that both genders were poorer performers when forced to use their non-preferred strategy and both genders were capable of learning to use their non-preferred strategy at comparable percentages.

As an aside, that males performed better than females at allocentric navigation in the current study is a consistent finding in the literature (e.g., Astur et al., 1998; Sandstrom et al., 1998). Thus, this finding was not surprising and confirmed that the Place maze used in the current study was sensitive to previously observed gender differences.

One issue with this current finding is that the Place maze was not in a new environment, and consequently, the allocentric navigators were at an advantage over the egocentric navigators, because they had already learned to navigate the maze allocentrically. The use of the same maze for the allocentric learning may thus have exaggerated the difference between the allocentric navigators and the egocentric navigators in their ability to “learn” a Place maze. In other words, the present design confounded specific allocentric learning with general ability to learn to navigate a new maze allocentrically. However, the main point of the present study was not to compare the abilities of allocentric and egocentric navigators, but rather to test the allocentric capabilities of egocentric navigators.

Thus, strategy preference is related to strategy competence but strategy preference did not define its limits. The current findings suggest that while egocentric navigators may learn an allocentric maze slower than their allocentric counterparts, they do learn eventually. This result in turn suggests that people have the capacity for both types of navigation, even if they prefer or show only one type. This further supports the idea of navigational bilingualism, i.e., that navigators are able to use more than one strategy (they are not exclusively one strategy) as they

can learn to use the other strategy when required. Once again, this was true for both males and females.

Summary of Findings & Interpretations

The present experiment has 5 major findings about the capabilities of people with respect to allocentric and egocentric navigation. First, most participants tended to prefer to navigate egocentrically in the Dual-strategy MWM. This egocentric bias does not necessarily represent the strategy bias in the population in the real world and may have been due more to the design of the maze. Second, most navigators chose a strategy and stuck with it, and while egocentric may be adopted first by many, neither strategy had to be adopted first. Some participants adopted an allocentric strategy from the earliest trials. Third, participants were more competent navigators when allowed to use their preferred strategy. However the casual direction of this relationship (i.e., does preference determine competence or vice versa?) is unclear. Fourth, the majority of participants incidentally acquired information about their non-preferred strategy. This suggests that both strategies are concurrently processed by navigators in the Dual-strategy MWM. Finally, all participants, including those who preferred to navigate egocentrically, were found to be capable of learning an allocentric maze, though the egocentric navigators may not have been as quick or competent as allocentric navigators. This finding provides support for the idea that navigators have latent talent, or in other words, have the capacity to learn either strategy. All of these effects were true regardless of gender, so the relationship between environment, strategy selection, strategy competence, and incidental learning was true for both males and females. The observation that males were better at allocentric navigation is consistent with most findings in the literature. However, the present findings suggest that neither gender is limited to one strategy or the other, and that both genders are capable of using either strategy.

Limitations

This present experiment also had a few limitations. One limitation was that the egocentric-bias in strategy distribution complicated some analyses and interpretations, particularly with regards to gender. As 45 of 61 participants preferred egocentric navigation, this meant that the comparison of Place maze performance was between unbalanced groups. Given that there were only 5 females who preferred to navigate allocentrically, it is possible some of the current study's gender findings were due to variability caused by the small allocentric female group. In future, small changes to the environmental cue salience may be needed in order to create a less egocentrically biased strategy distribution. For example, the room restricting the view of the landscape that was used in previous Skelton lab experiments (Livingstone & Skelton, 2007; van Gerven et al., 2012) could be added and the fog removed, or the floating spheres acting as egocentric cues could be shifted to the arena wall (where the egocentric cues have been positioned in the past iterations in the Skelton Lab). The experiment was also limited in the ability to provide a clear interpretation for the incidental learning shown during the cue forced-strategy probe. That is, it was not clear whether navigators were going to the Place location based on its position opposite to the normal Cue probe (i.e., a purely allocentric strategy), or based on the appearance of the sphere that hovered over the platform on previous Show-Me trials (incidental learning of an egocentric characteristic during allocentric navigation). This was an unanticipated result and therefore a difficult-to-foresee design flaw. In future, it would be better to have all non-cue spheres of one colour (and, in fact, this was done in experiments conducted after this current study) or simply switch the sphere hovering over the Place location on Show-Me's on each Show-Me trial. Another limitation of the present study was that it did not examine the ability of allocentric navigators to learn an egocentric maze. However, this would have either required twice as many subjects or a repeated measures design with participants tested in

both place and cue mazes (in balanced order, again requiring more participants). Finally, it is not clear whether, in the Place maze, the egocentric navigators were slower than the allocentric navigators simply because the Place maze was the same as the Dual-strategy maze sans spheres, meaning that the allocentric participants were just re-doing a maze they already knew. In future research, it would be better to use a completely novel Place maze.

Conclusions, Implications & Future Research:

The 5 major findings of the current study have a number of important implications for navigation research and our understanding of navigational cognition. First, the finding that most participants preferred to navigate egocentrically, although primarily methodological, highlights the contribution of maze design to strategy use and preference. This in turn shows the need for caution when interpreting the findings of a given maze. Given that results from different dual-strategy mazes provide different estimates of allocentric strategy preferences (e.g., 64% in Astur et al., 2016; 21% in Nowak et al., 2015 to name a few), or even within a given lab (50% in Livingstone & Skelton, 2007; 61% in van Gerven et al, 2012; 26% in the current study) it is clear that these results are probably not reflecting natural predilections. More generally, it points out the importance of the environment (real or virtual) in determining strategy choice or usage.

Second, the finding that it is not necessary to acquire an egocentric strategy prior to acquiring an allocentric one indicates that strategies do not have to be acquired in a particular order. In other words, neither strategy supersedes the other. In fact, strategy acquisition order may vary from one environment to the other, perhaps depending on relative salience of egocentric and allocentric cues. In fact, cue-salience likely plays a role in determining strategy selected (Wolbers & Hegarty, 2010). The current finding suggests that although egocentric may be initially preferred, it does not necessarily mean that developing egocentric associations is a necessary precursor to allocentric cognition. This earlier adoption of an egocentric strategy by

participants may have been due to the salience of the cues, given that in the current study a large floating sphere directly above the platform was used as an egocentric cue. This reflects the conclusion from the analysis of strategy preference about how important maze design is in what strategies are used. Given that some participants switched from egocentric to allocentric and vice versa, it implies that navigation strategies are not entirely static or rigid and may in fact be quite flexible (as has been concluded in the literature – see Igloi et al., 2009). This also implies that strategy adoption is not final or fixed.

That strategy adoption is flexible highlights the methodological importance of using strategy probes after every trial (or at least after small blocks of trials). It may be that others didn't see changing strategies, and the current study did, because strategy preference was tested after every trial (similar to van Gerven et al., 2016). That many of the other studies that have observed strategy switching (Packard & McGaugh 1996; Igloi et al., 2009; Astur et al., 2016) had probes that were conducted during navigation (or in the case of Iaria et al., 2003 participants were asked to reflect on, and report, their strategy at the beginning and end of the task) is further evidence in favour of this argument. This demonstrates the importance of strategy probes, and even the importance of testing for strategy frequently over the course of navigation (or at least not just at the conclusion of navigation – e.g., Nowak et al., 2015), something not done regularly in the literature. In fact, the Skelton Lab seems to be the only one which tests for strategy after every learning trial.

This finding may also have theoretical implications. For example, it may suggest that egocentric learning occurred immediately (given that navigators preferentially adopted it by the first Show-me trial). In the past, it has been suggested that allocentric learning occurs rapidly (e.g., Whishaw, 1985; Bast, Wilson, Witter, & Morris, 2009) and egocentric learning occurs

much more slowly (White & McDonald, 2002), which the current finding contradicts. This discrepancy could be due to differences in the ease of use for the cues in the current experiment versus those used previously. For example, many of the experiments that suggest that egocentric learning occurs slowly used egocentric-response navigation rather than egocentric-cue (White & McDonald, 2002; Iaria et al., 2003). This requires further investigation.

Third, the finding that strategy preference and strategy competence are related, raises the interesting question of which comes first, or whether they develop concurrently and interactively? Overall, this finding is not surprising. It is only logical that preference would be related to competence. In other words, it is not surprising that navigators would prefer the strategy they are more competent at. However, it is interesting to speculate on is how the relationship between preference and competence is determined. To put it plainly, does preference determine competence or vice versa? It may be due to something innate (or some predilection) that navigators came into the experiment with or may be due to the training navigators received in the Dual-strategy maze (using either strategy successfully). Likely, it is an interaction between both their predilection for a strategy and the practice they received in using this strategy (perhaps both in this unfamiliar virtual environment and other real-world environments). People may initially prefer the strategy they are better at (the one they find it easier to use), but as they get more practice using this strategy they become better at using it. This suggests that navigators may prefer the strategy they are best at (and find easier to use) and may try that strategy first. Perhaps future research could identify factors (demographic or otherwise) that explain how this preference for one strategy over the other develops. For example, it could be that certain life experiences such as living in a rural area or previous experience using a compass and map may bias navigators to choose an allocentric strategy. Thus, it would be interesting to test participants

who have had this experience in allocentric-dominant and egocentric-dominant environments (like downtown in big cities) to determine if they perform better at strategy-appropriate tests than navigators who have not had this experience.

Regardless of the origin of the relationship between preference and competence, this relationship implies that some differences in performance may be due to navigators attempting to use an inappropriate strategy rather than a complete inability to use the other strategy. This is a novel differentiation between the processes underlying navigational performance and those underlying strategy selections. Nevertheless, the inability to identify the most appropriate navigational strategy for a particular context would have a particular effect on studies that have examined navigation and stress (e.g., Duncko, Cornwell, Cui, Merikangas, & Grillon, 2007; Thomas et al., 2010; Klopp, Garcia, Schulman, Ward, & Tartar, 2012). Indeed, stress has been suggested to shift people into different cognitive modes (Metcalf & Jacobs, 1996; Schwabe et al., 2007) and recent research in the Skelton lab has indicated that stress can shift strategy selection (van Gerven et al., 2016). Thus, stress might shift people to an inappropriate strategy, and this may affect navigational performance.

Fourth, the finding that preference does not define the limits of competence suggests that people are quite capable in the use of both egocentric and allocentric strategies. One interesting methodological implication of this finding is that investigating the use of both preferred and non-preferred strategies may be revealing in future research. For example, a particular neural impairment (e.g., from brain injury or Parkinson's) may affect one navigational system more than the other. In such a circumstance, investigating "navigational ability" without referring to strategy preferences or differential strategy competence could under- or over-estimate the degree of cognitive impairment.

Fifth, the finding that information relevant to both strategies was acquired concurrently (seemingly incidentally) once again implies that strategy learning is not simple in dual-strategy environments, and that people may be learning more than they show behaviourally when forced to pick a strategy. This current finding implies that forced-strategy probes can reveal aspects of navigational cognition that may be normally hidden. Although previous studies have used strategy probes to investigate navigation strategies, these have mostly been similar to the current study's Show-Me trials (e.g., they only measured strategy selection like in Igloi et al., 2009 & Astur et al., 2016). Thus, the current study shows that using forced-strategy probes may be an effective way of showing incidental learning, or other hidden aspects of navigational cognition.

There are methodological implications to the presence of concurrent learning of information related to two navigation strategies. For example, in neuroimaging studies, both of the distinct neuroanatomical systems underling egocentric and allocentric navigation may be activated if the participant even thinks that both strategies are viable. This may have implications for understanding fMRI/imaging studies that use the Morris water maze (e.g., Aguirre, Detre, Alsop, & D'Esposito, 1996; Maguire et al., 1998) or in other paradigms (e.g., Iglói, Doeller, Berthoz, Rondi-Reig, & Burgess, 2010, Iaria et al., 2003). Perhaps the most important methodological implication is the most obvious: If you are interested in knowing what navigational strategies participants are learning in a given environment, circumstance or paradigm, then it is worth adding forced-strategy probes to the protocol.

This current experiment's finding of incidental learning of both strategies leads to the question of how common incidental- or dual-strategy learning is. Perhaps the singularity or duality of strategy availability in different environments should be determined empirically, rather

than just assumed. Perhaps it would be good to assess the factors that determine strategy dominance in different dual-strategy environments. Another question relates to strategy use and strategy switching. For example, how common is it for participants to use more than one strategy within a given environment, or even, within a given trial? Finding answers to these questions would deepen our understanding of the cognition underlying everyday navigation.

This finding of incidental learning leads to a number of other potential interesting areas of future research. Given that previous research has found that stress leads to greater adoption of a stimulus-response strategy in a non-MWM navigation tasks (Schwabe et al., 2007), and the suggestion that stress promotes stimulus-response (i.e., egocentric) learning (Schwabe, Oitzl, Richter, & Schächinger, 2009), it would be interesting to investigate whether or not stressed individuals who use an egocentric strategy completely ignore allocentric information in the MWM or whether they engage in some incidental learning of allocentric information at all. In other words, although it has been suggested that stress shifts modes of cognition (Metcalf & Jacobs, 1996; Schwabe et al., 2007) to a caudate nucleus based cognitive mode, does stress also lead to the complete inactivation of the hippocampus? It might also be interesting to investigate the degree to which various clinical populations engage in incidental learning. That is, do people with depression or schizophrenia (two disorders that have been found to hinder navigation performance; depression: Gould et al., 2007, schizophrenia: Hanlon et al., 2006) engage in the same amount of incidental learning as those in the non-clinical population? To take it further, could a lack of incidental learning reveal something about how the brain communicates in people with these disorders? It is difficult to say, but these are interesting topics to speculate on. However, the most important implication is that this finding of incidental learning offers further

proof that people's navigational cognition and abilities may not be as simple as previously thought, and simply classifying navigators as one strategy or the other may not be appropriate.

There are several findings in the current experiment that suggest that males and females may not be all that different when it comes to navigation.

The present findings suggest that it is simplistic or wrong to think that females always prefer egocentric navigation and males always prefer allocentric navigation. In the present study, males preferred egocentric navigation. True, females had an even stronger inclination towards egocentric navigation, but in previous findings in this lab, females on the whole preferred allocentric navigation (van Gerven et al., 2012), and in that case, even more than males. Given that the rates of female preference for egocentric navigation vary from lab to lab (e.g. 28% in van Gerven et al., 2012 compared to 82% in the current study) and study to study (e.g. 44% on the first probe of two in Astur et al., 2016 compared to 89% in Nowak et al., 2015), it seems safe to say that strategy preference depends on the particular environment used for testing.

The present study provides a new source of evidence that males and females did not differ in strategy acquisition suggesting that males and females learn about the environment in very similar ways. Both genders tended to acquire an egocentric strategy first, and the rates of switching to allocentric navigation were about the same, but some members of both genders started with an allocentric strategy, showing that starting with an egocentric strategy was not a necessary step to the development of a strategy preference.

Other findings in the present study suggest that the gender difference in navigational competence may not be as great as previously thought. Both males and females showed a strong relationship between preference and competence, and for both genders, this preference did not define the limits of their competence. That is, both males and females showed considerable

competence in using their non-preferred strategy. The first implication from this is that the idea that men navigate allocentrically and women navigate egocentrically is simplistic and misleading. Both genders seem to have competence in both types of navigation. This is not to deny that men may be better than women at navigating allocentrically. However, in a situation where either allocentric or egocentric navigation can be used, women may navigate as well as men. In contrast, in situations set up to test competence of allocentric navigation, or in situations where allocentric navigation is called “spatial” and egocentric navigation is called “non-spatial” (e.g., Iaria et al., 2003; Harrison, Reiserer, Tomarken, & McDonald, 2006), then women may be found to be less competent than males at “spatial” navigation. However, this may be more a matter of semantics than cognitive capacity.

Another factor may have contributed to previous findings of male superiority in allocentric navigation (e.g., Astur et al., 1998; Sandstrom et al., 1998) other than pure “spatial” competence. This factor may have been to the ability (or lack thereof) to detect or adopt the most appropriate strategy for a given environmental context. Thus in previous studies of allocentric navigation (e.g., Roof, 1993; Astur et al., 1998), females may have attempted to use an egocentric strategy either because they were continuing to use a strategy they had developed a preference for, or because they failed to detect that the test environment was better suited to allocentric rather than egocentric navigation, or some combination of the two.

Finally, the lack of gender differences in incidental learning further suggests that in terms of navigational cognition, both genders may not be that different. Given that both genders were able to complete the probe of their non-preferred strategy effectively it was clear that both males and females were able to learn information relating to either strategy. The information related to their non-preferred strategy was only “incidental” in contexts where the preferred strategy is

being used. It is interesting then, to speculate on why it is that if females do learn information related to allocentric navigation, why they are not as good as males at using this information. One possible explanation is that males and females differ in navigational performance in laboratory situations is because females have greater “spatial anxiety” (Lawton, 1994), which may impair their navigational cognition, perhaps by impairing hippocampal function, similar to the way stress has been known to impair hippocampal function (see Kirschbaum, Wolf, May, Wippich, & Hellhammer, 1996). Or perhaps it is true that females, for any number of reasons (e.g., genetic, hormonal, experiential, societal) are not as good as males at navigating allocentrically. However, this is not the same as saying they are not good navigators. As well, this incidental learning of both strategies suggests that neither gender appears restricted to using, or learning about, one strategy or the other.

All together, the present findings suggest that it is too simple to think that genders or even individuals are limited to thinking about navigation in terms of only egocentric or allocentric. After all, the present research shows that: a) strategy preference may depend on the environment b) no one strategy must be learned first c) people prefer the strategy they are best at, but d) are generally not limited to just using that strategy, and in fact, e) tend to learn about both concurrently. Thus there seems to be no simple dichotomy with respect to navigational cognition. In other words, people aren't normally limited to learning or using one strategy, but rather they will use whatever navigational cues look promising to them.

One way of looking at these findings is to think about the flexibility of the use of navigational strategies as being comparable to bilingualism in language use. That is: a) people prefer to speak a particular language depending on the context b) no language *must* be acquired before the acquisition of another and some people may speak both languages c) people prefer to

speak the language they are more fluent in but d) are not limited to only speaking that language when forced to use the other and e) people learn something about both languages in environments that have both languages present, even if they were only speaking one language at the time. In other words, people can know both languages even if they only show evidence of speaking and using one of them.

Taken together, the present findings also have a number of implications and raise a number of interesting questions for future research. The major implication of this research is that, during navigation, most navigators are bi-strategically competent and learn information relating to both strategies. This is important because it suggests that behaviour during navigation is much more complex than it is given credit for (i.e., navigators are not just one strategy or other, and in fact, may switch strategies). Thus, testing navigators' performance in a single-strategy task or navigators' preference in a dual-strategy task may not show the entire picture. Future research using eye-tracking in the current study's dual-strategy environment might be beneficial, as it would help confirm where navigators are focusing their attention during navigation (similar to Mueller et al., 2008). In other words, how fast do navigators switch, and is it by cue salience? This may have important implications for how strategies develop. For example, participants may examine both sets of cues throughout the entirety of the task, or if as they become more comfortable with using one strategy, then their focus on one set of information shifts to other. Or it is possible that some navigators may consistently switch the information they are using within trials (e.g., similar to what was found in Hamilton et al., 2009 study – which concluded navigators use allocentric cues initially during a trial to orient themselves and switch to egocentric cues later in the trial to locate the platform's specific location). As well, future research should further investigate the interplay between egocentric and allocentric cognitive

processes during navigation (i.e., how the hippocampus and caudate nucleus interact), because this current thesis was only able to investigate the outcome of this interaction and not the process of how this occurs.

Conclusion

This thesis sought to use the Morris water maze to investigate how navigation strategies are learned during navigation, and most importantly, whether navigators learn information relating to both strategies. The present findings indicate that the distribution of egocentric and allocentric navigational competence within the population might not be as simple as previously portrayed, and while there might be a difference between genders, this may not be as great or as simple as previously thought. In fact, the present findings indicate that individuals and genders are not limited to a single navigational strategy, but rather, suggest that nearly every person is likely to be fairly competent at both. The present findings also indicate that strategy selection and acquisition are not static but appear to be very fluid and dependent on the particular spatial environment and may not be specific to the individual. The findings suggest that, unsurprisingly, preference is related to competence, though it is not yet clear how. Nevertheless, while related, preference does not indicate the limits of competence. Finally, the findings indicate that when given information related to both strategies, navigators may develop a preference for one strategy but acquire information about the other one incidentally. In many respects then, people appear to be bilingual with respect to strategy. In other words, they are able to speak in two different languages though they may well be better at one of them (and prefer that one), and may only demonstrate their competence in one language in any given circumstance. Thus, classifying navigators as having only one strategy may be too simple, because what people do and what they show isn't always all they know.

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Appendix A

Questionnaires

Background Questionnaire

1. Sex
(Male, Female)
2. Age:
3. Education (current year standing, i.e., 1st, 2nd...etc):
4. What year did you graduate high school?
5. Handedness
(Left, Right)
6. What is your first language?
7. Do you have any problems with dizziness
(Yes, No)
8. Have you ever sustained a brain injury (i.e., been hospitalized overnight for a head injury)?
(Yes, No)
If yes, please explain:
9. Do you suffer from any neurological disorders (eg. Epilepsy, MS)?
(Yes, No)
If yes, which disorder?
10. Do you suffer from any psychiatric disorders (eg. Depression, schizophrenia)?
(Yes, No)
If yes which disorder?
11. Are you currently taking any medications?
(Yes, No)
If yes, please specify:
12. Is there anything unusual about today that you feel may influence the result of the study?

(lack of sleep/exhausted, consumption of prescription or nonprescription drugs, excessive exercise prior to attending, other", "nothing unusual)

If you chose OTHER, please give a short explanation:

Post-Test Questionnaire:

1. How well do you think you performed on this task?
(Very Poorly, Poorly, Average, Moderately Well, Extremely Well)
2. How often did you play computer or video games as a child/youth?
(Never, Occasionally, Monthly, Weekly, Every few days, Daily)
3. How often have you played 3D games (e.g., Halo, Call of Duty, Skyrim) in the past year?
(Never, Occasionally, Monthly, Weekly, Every few days, Daily)
4. How often have you played 2D computer games (e.g., racing games, angry birds, farmville, street fighter, solitaire) in the past year?
(Never, Occasionally, Monthly, Weekly, Every few days, Daily)
5. How often have you used a controller similar to the one you used in this experiment?
(Never, Occasionally, Monthly, Weekly, Every few days, Daily)
6. Did you ever find your attention wandering during the experiment?
(Yes, No)
7. How do you think high levels of stress, due to increased school work and exams, affects your general memory ability?
(During high stress I remember things better, During high stress, I find it more difficult to remember things)
8. Do you feel you got enough sleep last night?
(Yes, No)
9. What time did you wake up today?
(Before 8 a.m., Between 8 am and 10am, Between 10am and 12pm, After 12pm Did not sleep)
10. Was this normal for you?
(Yes, No)
11. How many caffeinated beverages do you usually consume in a day? (E.g. 6 oz cup of coffee, shot of espresso, cola=1 drink. 12 oz cup of coffee, latte, small energy drink=2 drinks.
Large coffee, large energy drink= 3 drinks.)
(none, non-regularly, 1-2, 2-4, more than 4)

12. How many caffeinated beverages have you consumed in the last 6 hours? (E.g. 6 oz cup of coffee, shot of espresso, cola=1 drink. 12 oz cup of coffee, latte, small energy drink=2 drinks. Large coffee, large energy drink= 3 drinks.)
(none, 1-2, 2-4, more than 4)
13. Did you eat in the 30 minutes prior to the start of this experiment?
(Yes, No)
14. Did you smoke a cigarette in the 30 minutes prior to the start of the experiment?
(Yes, No)
15. In a few words, can you explain how you were able to find the invisible platform in the Arena mazes? (Note: If strategies differed between the two mazes, please describe each strategy and say what maze it corresponded to)