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Navigational strategy may be more a matter of environment and experience than gender

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ABSTRACT

In the study of wayfinding there is considerable controversy about what factors determine when and how strategies are selected. Allocentric strategies rely on the presence of distal, relational stimuli whereas egocentric strategies rely on the presence of proximal or simple guidance stimuli. Strategy use has often been explained by studies of internal factors like gender but little weight has been given to the study of how strategies are selected. The present study examined the effects of recent experience on strategy selection in three specially designed versions of a virtual Morris water maze (vMWM). Thirty-seven participants were trained either in an allocentrically biased "Place" maze or an egocentrically biased "Cue" maze, and then tested in a "Dual-strategy" maze, in which both allocentric and egocentric strategies were equally efficient. All participants trained with the Cue maze selected an egocentric strategy whereas two thirds of participants trained in the Place maze chose an allocentric strategy. A verbal probe revealed that allocentric strategists were more aware of features in the virtual environment than were egocentric strategists. No evidence of gender differences in strategy selection or navigation performance was found.

Navigational strategy may be more a matter of environment and experience than gender.

Wayfinding is the means by which people navigate from one place to another in familiar and unfamiliar large-scale space, and as such, is a critical ability for everyday life. However, the cognitive mechanisms underlying navigation are not completely understood. Although a number of different categorizations of navigational strategy have been proposed (O'Keefe & Nadel, 1978; Sutherland & Dyck, 1984; Trullier, Wiener, Berthoz, & Meyer, 1997), perhaps the most accepted is the dichotomy into egocentric and allocentric strategies (Klatzky, Loomis, Beall, Chance, & Golledge, 1998; Kolb, Sutherland, & Whishaw, 1983). Egocentric strategies rely on perceptions of the environment from the perspective of the navigator and may be either response-based (e.g., navigation by a series of left/right turns) or cue-based (navigation to a landmark or sequence of them) or a combination of the two (Trullier et al., 1997). In contrast, allocentric strategies rely on a cognitive map, an internal representation of the environment that is independent of the navigator's current perspective (Nadel & Hardt, 2004; O'Keefe & Nadel, 1978). Converging evidence from behavioral and brain imaging studies suggests that each strategy is mediated by a different cognitive-neural system (for review see, Burgess, 2008).

A third navigational strategy has been proposed which, depending on definition and circumstances, overlaps with egocentric and allocentric strategies. This type of navigation has been called path integration, inertial navigation, dead reckoning and ideothetic navigation (for review, see Etienne & Jeffery, 2004). When studied in an open featureless environment where

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direct paths can be taken between any two points, especially when the navigator is deprived of sight or visual cues, navigation can be accomplished by the navigator keeping track of internal cues. These cues are generated by the navigator's own (egocentric) responses (movements and actions) in order to compute distances and directions traveled. This information can be used to compute the most direct route back to the origin; under these circumstances this form of navigation would be considered egocentric. However, in more common circumstances where there are paths and obstacles which limit travel, and environmental features which define locations and choice points for routes, such inertial navigation might well act as an additional source of information to help select egocentric responses to environmental stimuli or to locate the navigator within a cognitive map of the environment. In their extensive review of research on the role of self-generated movements (i.e., path integration or ideothetic navigation), by insects, birds, rodents and humans, Cheng, Shettleworth, Huttenlocher, and Reiser (2007) conclude that this system serves largely as a reference and back-up to resolve ambiguity among navigational cues and plays no significant role when navigational stimuli are clear and unambiguous. Accordingly, the present study addressed only the dichotomy between egocentric and allocentric navigation.

The study of egocentric and allocentric strategy use is a relatively new field and much of the research seems to be based on the assumption that strategy use is determined mainly by innate factors such as stimulus salience (e.g., Wolbers & Hegarty, 2010), gender (e.g., Chai & Jacobs, 2010; Saucier et al., 2002) or age (e.g., Moffat & Resnick, 2002). Far fewer investigations have considered that strategy use may also be affected by external factors such as the availability of useful stimuli or the opportunity for experience with these stimuli (Wolbers & Hegarty, 2010). This is partly because many navigation tasks are designed in such a way that only one strategy type is likely to be elicited. For example, studies may exclusively investigate either route learning (e.g., Nemmi et al., 2011) or place learning (e.g., Woolley et al., 2010). Indeed, the most common type of navigation study appears to employ place-based tasks to study internal factors (e.g., gender, aging) that might influence the ability to form a cognitive map (and use allocentric strategies) (e.g., Kallai, Makani, Karodi, & Jacobs, 2005; Moffat & Resnick, 2002; Woolley et al., 2010). To date, attention has been paid mostly to the identification of strategies and to their use rather than to the availability and selection of these strategies. Thus there is a need to investigate the factors affecting strategy choice.

Although several studies have demonstrated that strategy choice and use is determined by gender (for review see, Lawton, 2010), others suggest that several factors may contribute. In virtual environments that offer the opportunity to navigate using either an egocentric or an allocentric strategy, male and female participants spontaneously selected one or the other in relatively equal proportions (Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Schmitzer-Torbert, 2007; Van Gerven, Schneider, Wuitchik, & Skelton, 2012). Furthermore, in some studies, participants were able to switch strategies (Etchamendy & Bohbot, 2007; Iaria et al., 2003; Igloi, Zaoui, Berthoz, & Rondi-Reig, 2009) suggesting that many (and perhaps most) people have both egocentric and allocentric strategies at their disposal. Together these studies raise the important issue of what factors might influence the choice of one strategy over another.

The factor most commonly assumed to control which strategy is used at a given time is familiarity with the environment or route (e.g., Golledge, 1999; Maguire et al., 1998). Familiarity is crucial to strategy selection because the ability to select a given strategy may depend on both the availability of useful environmental information and the degree of prior exposure to this type information (Burgess, 2006). In other words, for a strategy to be selected, relevant stimuli have to be present and the person has to be sufficiently experienced (or familiar) with these stimuli (or similar ones). For example, Jacobs and Schenk (2003) proposed that if the navigating animal has not gained experience with particular types of stimuli then the system that utilizes those stimuli will not be activated. However, the effects of experience presumably extend beyond just a familiarity with the visual features of the environment. That is, experience consists also of reinforced behavior and successful navigation resulting from the use of a particular navigational strategy. Therefore, experience should have an effect on strategy selection.

Although there has been considerable research on the effects of experience per se on subsequent navigational learning, most of this work has been conducted in the context of testing the cognitive map theory versus the associative learning theory and many of the studies have compared simple cues to configurations of cues (see Chamizo, Aznar-Casanova, & Artigas, 2003; Cheng et al., 2007). Cheng et al. (2007) cite one study showing that in rats in a Morris water maze (MWM), training with a proximal cue that stays the same between trials and between training and testing can lead to overshadowing of room cues (Roberts & Pearce, 1999). Although they never test the reverse, these authors do cite two rat studies showing that (a) distal extra-maze cues can overshadow intramaze cues proximal to the goal, only if the proximal cues are made unreliable (Redhead, Roberts, Good, & Pearce, 1997) and (b) in a radial maze, extra-maze visual cues can overshadow or block intra-maze tactile cues (Diez-Chamizo, Sterio, & Mackintosh, 1985). Although there have also been human studies investigating the possibility of overshadowing and blocking of distal cues by proximal cues (Bodily, Eastman, & Sturz, 2011; Ratliff & Newcombe, 2008), these studies have examined only orientation (i.e., pointing to a goal from a fixed location) and not navigation (which involves movement and multiple decisions). The difference may seem trivial until one remembers the importance of relative spatial locations (of environmental features to each other) to allocentric navigation (O'Keefe & Nadel, 1978) and how, in many cases, this is not apparent from a fixed location at the start of navigation. Furthermore, using eye-tracking, we have recently found that the environmental cues used during orientation are not necessarily the ones used later during navigation (Yim & Skelton, 2013). This finding is consistent with that of a study (Hamilton, Rosenfelt, & Whishaw, 2004) showing that rats in a MWM with a visible platform orient using allocentric cues but use egocentric cues to navigate to the platform.

Miller and Shettleworth (2007) review several studies showing that in humans, the geometry of an enclosed room (e.g., locations relative to the long axis of a rectangular room) might or might not block or overshadow proximal cues depending

on cue size and proximity to the goal. However, in these studies, no cues were distal and the allocentricity of room geometry has not been established. We have not been able to find any studies that have examined the possibility that distal visual (allocentric) cues might block proximal visual cues used for navigation.

There have been a few human studies that have examined strategy selection in environments that allow both allocentric and egocentric navigation (Etchamendy & Bohbot, 2007; Iaria et al., 2003; Igloi et al., 2009; Schmitzer-Torbert, 2007). However, none of these studies examined the effects of training in one strategy on subsequent strategy selection.

Our experiment addressed the question of whether antecedent experience of successful navigation using either an egocentric or an allocentric strategy (i.e., navigating by proximal or distal cues respectively) would have a measurable effect on later strategy selection. We used a virtual environment in which both allocentric and egocentric strategies could be used successfully, and we developed a new means of measuring strategy selection. The environment was based on the MWM, the gold standard for testing allocentric navigation in laboratory animals (Brandeis, Brandys, & Yehuda, 1989; D'Hooge & De Deyn, 2001). This paradigm has already been used to differentiate place-based (allocentric) from cue-based (egocentric) strategies (Morris, 1981; Pearce, Roberts, & Good, 1998) and to show that individual rats may learn and use both strategies within a single session or even a single trial (Hamilton et al., 2004; McGregor, Good, & Pearce, 2004).

The present experiment employed two virtual adaptations of the water maze task. The Place maze was a human analog of the MWM and the absence of reliable cues proximal to the fixed-location platform meant that it was biased toward the use of allocentric strategies. The Cue maze was the same as the Place maze except that there were objects situated on the arena wall with one being proximal to the platform; the position of the platform and proximal cue varied from trial to trial, making this maze egocentrically biased. In both mazes the platform was in the center of the quadrant, i.e., equidistant between the arena wall and the center of the arena. Classification of the two mazes as allocentric and egocentric was also justified by neuroanatomical evidence. Previous work in our laboratory has shown that people with damage to the hippocampus from traumatic brain injury or anoxia cannot solve the Place maze unless landmark cues (objects on the arena walls) are available (Goodrich-Hunsaker, Livingstone, Skelton, & Hopkins, 2010; Livingstone & Skelton, 2007). In addition, an eye tracking study using these environments has shown that, for allocentric navigation, participants orient toward the landscapes outside the windows (Livingstone-Lee et al., 2011).

In the present study, participants were trained to use an allocentric strategy in the Place maze, or an egocentric strategy in the Cue maze. They were then tested in a third environment, the Dual-strategy maze that allowed them to adopt either an egocentric or an allocentric strategy. In this maze, the platform was always in the center of the same quadrant, allowing allocentric navigation, but, in addition, there were eight objects on the arena wall, one of which indicated the platform position, thereby allowing egocentric navigation. At the end of testing in this Dual-strategy maze, participants were tested in a specially designed strategy probe trial to determine which strategy type (allocentric or egocentric) they had selected. We also asked participants whether they had noticed the objects being in different locations on the strategy probe trials.

We expected that in the Dual strategy maze, participants would continue to use the strategy with which they had had previous experience and success. That is, we expected that in the Dual strategy maze, those trained in the Cue maze would use an egocentric strategy whereas those trained in the Place maze would use an allocentric strategy.

Methods and materials

Participants

Participants ($n = 37$; male = 16, female = 21) were recruited from two source populations, first year Psychology students ($n = 23$; male = 11, female = 12; mean age 22 years) and volunteers from the local Victoria community ($n = 14$; male = 5, female = 9; mean age 33 years). Participants were excluded from the study if they had a history of psychiatric or neurological disorders or a brain injury, operationally defined as an injury to the head requiring an overnight stay in the hospital. All participants gave informed consent, and the study was approved by the Human Research Ethics Board at the University of Victoria.

Navigation training apparatus

The apparatus consisted mainly of a single virtual environment, the "Arena Maze" (Skelton, Bukach, Laurance, Thomas, & Jacobs, 2000; Skelton, Ross, Nerad, & Livingstone, 2006), designed to be an analog of the MWM. Training employed three versions of this virtual MWM task: the "Place maze", the "Cue maze", and the "Visible platform maze". Testing took place in a fourth version of the task, the "Dual-strategy maze". The landscape outside the room and all features of the room (i.e., the dimensions and textures of the walls, windows, ceiling, floor and arena wall) remained constant throughout testing (i.e., they were identical in all mazes). These desktop virtual environments were created using the commercially available video game editor, Unreal® (Epic Megagames), and were displayed on a 19 in. LCD monitor at a resolution of 800×600 and thus, a 4:3 aspect ratio. The screen refresh rate was .30 fps and the rate of rotation was 360° in 5 s. Participants navigated through the trials using a typical gaming joystick that was stable on the desk in front of them and which allowed participants to turn left and right, and move forward but not backward.

The Place maze was an adaptation of the Arena maze (Skelton et al., 2000, 2006) and consisted of a large circular arena bordered by a low wall and situated in a large square room. Specifically, the arena appeared to be 42 m in diameter, bounded

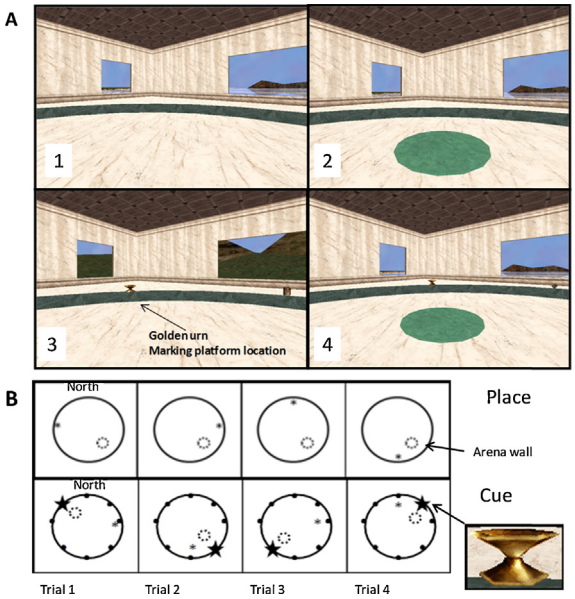

Fig. 1. (A) First-person views of the virtual environments used for training. (1) The Place maze during an invisible platform trial. (2) The Place maze after the participant has stepped on the platform. (3) The Cue maze, showing 2 of the 8 objects spaced equidistantly, one of which (the golden urn) marked the platform location. (4) The Cue maze after the participant stepped on the platform, on a trial where the platform was (coincidentally) in the southeast quadrant. (B) Overhead view of Place and Cue mazes on the first 4 (of 10) trials showing the relative positions of the arena wall, start positions (*), goal/platform locations (dotted circle), objects on the arena wall (dots) and cue object (star). Note the fixed location of the goal/platform in the Place maze and the varying location of goal/platform and cue object in the Cue maze.

by a wall 1 m high, and set within a room with dimensions 75 m × 75 m × 17 m. The room had large windows in all four walls, arbitrarily designated as north, south, east and west. The north and south walls each had one large window whereas the east and west walls had three smaller windows, though all the sills were the same height and all provided panoramic views of an outdoor landscape (Fig. 1). The north window showed mountains; the east and west windows showed hills sloping down to the large body of water (and island) visible through the south window. Directionality could not be determined from features within the room (as it was quadrilaterally symmetrical). Rather, participants had to rely on the distinctive views through the windows. The outdoor landscape did not change as the participant moved (i.e., perceptual distance equivalent to the moon), so that when participants did move, the view in the (more proximal) windows shifted due to parallax. This environment design meant that distal features provided directional but not positional information. The goal location was a round platform 7 m in diameter; i.e., 1/6th of the arena diameter and 1/36th (i.e., 2.7% of the surface area) hidden under the floor until the participant stepped on it. Because it was always hidden in a fixed, unmarked location within the room (viz., the center of the southeast quadrant) (Fig. 1), participants had to use a configuration of distal and proximal features (e.g., landscapes and the arena wall) in order to identify its position within the arena. Due to its design features, the Place maze was strongly biased toward the use of an allocentric strategy. That is, participants had to find the platform allocentrically (using the outdoor landscape features) because there were no cues sufficiently proximal to the goal location to support an egocentric (cue-based) guidance strategy, and because simple egocentric (response-based) navigation was obviated by varying start positions from trial to trial.

In contrast, the Cue maze was strongly biased toward the use of a cue-based egocentric strategy. The virtual environment was identical in appearance to the Place maze except that there were eight objects in fixed locations at four cardinal points and 4 inter-cardinal points and perched on the low wall bounding the arena (Fig. 1) to support cue-based egocentric navigation strategies. In addition, the goal (platform) location changed from trial to trial to impede the use of both an allocentric strategy and a response-based egocentric strategy. The goal was always in the center of a quadrant and the quadrant was always marked by a ninth, single, highly salient cue object (a golden urn) on the arena wall. Fig. 1 illustrates the difference between the Place maze and the Cue maze and shows how the relation between the cue object, platform and environment changed with each trial, thereby rendering the room and landscape features (i.e., allocentric cues) irrelevant for finding the platform. Because this proximal object provided the only reliable navigational feature identifying the goal location, and because the start positions changed from trial to trial and were balanced to be to the left and right of the goal location, allocentric strategies, and response-based egocentric strategies were much less efficient than a cue-based egocentric strategy.

The Visible platform maze utilized the same virtual environment as the Place maze. Start positions varied from trial to trial, and the platform was always visible on the floor of the arena but its location changed on each trial.

For strategy testing, the Dual-strategy maze (Fig. 2) combined features of both the Place and Cue mazes. It was identical in appearance to the Place maze except that the same eight objects used as cues in the Cue maze were evenly spaced around the

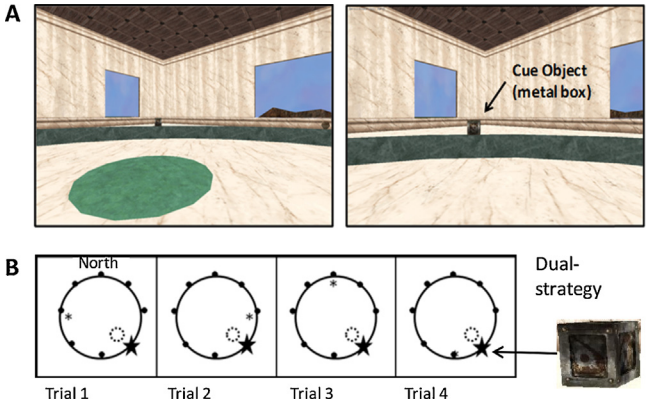

Fig. 2. (A) First-person views of the Dual-strategy testing maze showing (left) the cue object (gray box) marking the location of the goal/platform in the center of the southeast quadrant and (right) the platform and cue after the participant had stepped on it. (B) Overhead view of the first 4 (of 10) trials in the Dual strategy maze showing the relative positions of the arena wall, start positions (*), and the fixed relation between goal/platform locations (dotted circle), objects on the arena wall (dots) and cue object (star).

arena wall at the same cardinal and intercardinal points (see Fig. 2). As per the Cue maze, the platform was always situated in front of the same cue object (though now it was a metal box rather than a golden urn) which could serve as a proximal cue that the participant could use to navigate to a hidden platform. However, unlike the Cue maze (and like the Place maze), the hidden platform was always in the same location thereby allowing the participant to find the platform using an allocentric strategy. In designing the Dual-strategy maze, we chose to use distal environments and proximal cues identical to those used in the Place and Cue mazes (Fig. 2). This approach enhanced the contribution of familiarity to performance in the Dual-strategy maze and in addition enhanced the value of experience acquired in the Place and Cue mazes. As per both Place and Cue mazes, start positions in the Dual-strategy maze varied from trial to trial, obviating the use of a response-based egocentric strategy. Thus, in this maze, participants were free to solve the task by using either landscape features or proximal cue objects, i.e., by using either an allocentric or an egocentric (cue-based) strategy.

Experimental design

All participants completed the Visible platform maze and then half ($n = 20$) were trained in the Place maze (place-trained) and half ($n = 17$) in the Cue maze (cue-trained). Participants were then tested in the Dual-strategy maze. Males and females were randomly assigned to the two training conditions. All participants completed a strategy probe trial at the end of testing in the Dual-strategy maze. Note that this experiment formed part of a collaborative study that involved collecting electroencephalography (EEG) data and tracking eye movements (gaze position analyses reported in dissertation; Lee, 2012). Although there were steps necessary to prepare the person and fit them with an electrode cap, and also to calibrate the eye-tracker, and these steps required interaction and sometimes instructions to the participant, no additional instructions were given regarding the behavioral task. Although participants were somewhat restricted in their head movements because their chin was on a chin rest this did not appear to influence their behavior. Behavior in the Place and Cue mazes was the same as we have observed previously (Livingstone-Lee et al., 2011; Van Gerven et al., 2012). Eye tracking data are not included here because gaze fixation was not found to be a reliable indicator of navigational strategy.

Procedures

For training, the order of presentation of trials was as follows: 1 exploration trial (in the virtual room but outside the arena), 4 visible platform trials, 1 arena exploration trial (either place or cue), 10 invisible platform trials (either Place maze or Cue maze), 1 standard probe trial, and 1 explicit Drop-the-Seed (DTS) trial. For testing the effects of experience, trials in the Dual strategy maze were presented in the following order: 1 arena exploration trial (Dual-strategy), 10 invisible platform trials (Dual-strategy), 1 standard probe trial, and 1 Strategy probe trial.

Room exploration trial

The purpose of this one trial was to familiarize the participants with movement using the joystick and to allow them to view the outdoor landscape and develop a cognitive map (Livingstone-Lee, MacDonald, Gillingham, & Skelton, 2013). Participants could explore the room and view the landscape for as long as they liked, and the trial ended only when they indicated comfort with locomotion using the joystick and satisfaction with their exploration of the virtual environment.

Visible platform trials

The purpose of these four trials was to confirm that participants were able to navigate to a single visible target in the environment, that is, a large, green, circular platform which was visible on the floor of the arena in the center of a different quadrant for each trial. The start position for each trial was different, with all start positions being just inside the arena wall and at a cardinal point. When the participant "stepped" on the platform, it made a sound like a bell. Participants were informed that they should "stay on the platform" until they were ready to proceed to the next trial, which began when they indicated they were ready.

Place or Cue arena exploration trial

The purpose of this trial was to allow participants to become familiar with the environment (room features and landscapes) from the perspective of the arena and, if present, the cue objects on the arena wall. Participants explored the arena for as long as they liked but could not pass beyond the arena wall. The trial ended when the participant indicated satisfaction with his/her exploration. Preliminary studies have shown that omission of this trial results in long latencies on the first Cue maze trials because many participants spend time examining the objects before trying to find the platform.

Place or Cue maze invisible platform training trials

The purpose of these 10 trials was to train participants to navigate to a location in the environment using either a configuration of room features and landscapes outside the windows (in the Place maze) or by using a single cue object on the arena wall that moved with the platform to mark its location (i.e., in the Cue maze). In the Place maze, the invisible platform was in a fixed location in the center of the southeast quadrant of the arena. Participants were informed that "the platform will always be in the same place" and that they should "go to the platform as quickly and directly as possible". In the Cue maze, the invisible platform was always in the center of one of the quadrants, with the quadrant changing from trial to trial, but with its position marked by the cue object (a distinctive golden urn). Participants were told that the platform "will not always be in the same place" but that "there will always be a clue to its location". Start positions were always just inside the arena wall, at one of the four cardinal points and varied in a fixed, pseudo-random order. Start positions were also balanced according to whether the participant should make a left or right turn and according to the distance from the start position to the target location. The platform remained invisible until the participant stepped on it, at which point it rose up making a sound like a bell. While on the platform, participants were able to look around the room for as long as they liked. When they informed the experimenter that they were ready, the experimenter initiated the next trial by pressing a key on a keyboard linked to the presentation screen.

Standard probe trial

The purpose of this one trial was to implicitly test how well participants learned the platform location. Prior to testing, participants were informed that on one trial (the probe) the platform "will be very difficult to find" but that they "should continue to search for it anyway". This trial followed the 10 invisible platform trials without notification to the participants that it was in any way different from the preceding 10 trials. Participants were not informed how many invisible platform trials there would be. During this probe trial, the platform remained hidden for 50 s and the end of the trial was indicated by the bell sound associated with finding the platform.

Explicit "Drop-the-Seed" (DTS) trial

The purpose was to explicitly test how well participants learned the platform location (Van Gerven et al., 2012). Participants were instructed to "go to the spot where you think the platform was (based on the trials you were just completing)" and once there the experimenter dropped a virtual seed to mark the location. On a monitor not visible to the participant, the location of the seed and therefore the participant's explicit estimate of the platform location was scored on a 0–7 scale, using a ringed "bull's eye" target. The center of the target matched the platform in size and location and a placement here was scored as 7. The center was surrounded by six equal width rings, with the outermost ring reaching the boundaries of the quadrant. Placements in one of these rings were scored from 6 for the innermost ring to 1 for the outermost ring. Placements outside the rings (and hence not in the correct quadrant) were scored 0.

Dual-strategy arena exploration trial

This trial started inside the arena for both place- and cue-trained participants. Its purpose was to allow place-trained participants to examine the objects that were added to the arena wall.

Dual-strategy maze invisible platform testing trials

The purpose of these ten trials was to determine which strategy participants would use to navigate to a location in the room that could be found either by using an allocentric strategy based on a configuration of the distal features (arena wall and landscapes) or by using an egocentric strategy based on a cue object proximal to the platform. The platform was always in the same location (in the southeast quadrant of the arena) and was always located in front of the same cue object (a metal box) (Fig. 2). All cue objects remained in fixed locations throughout testing. Invisible platform testing in the Dual-strategy maze followed the same procedures as for the training maze trials described above. However, participants were not given

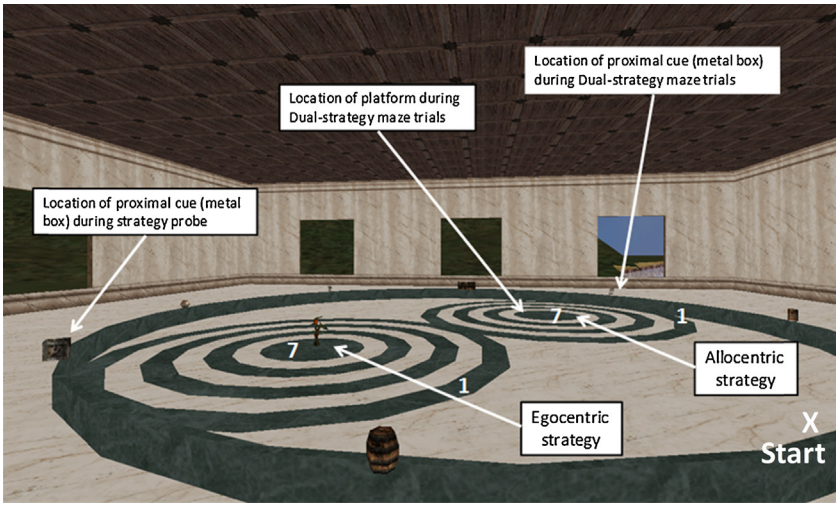

Fig. 3. Strategy probe trial. Note: (a) start position in southwest, (b) previously correct platform position in southeast, and c) proximal cue object now marking the northwest quadrant. Participants were instructed to go to where they thought the platform was located. Their location estimate was marked for later analysis. Platform location estimates were scored as indicating an egocentric strategy (near cue object) or an allocentric strategy (in "place" quadrant) and for accuracy on a 0–7 scale. The little tree marking a platform location estimate would be scored as "egocentric 7". No part of the bull's-eye targets was ever visible to the participant.

any instructions with regard to the platform location. That is, unlike the instructions prior to the training trials, they were not informed that the platform would always be in the same place nor that there would be any clues to its location.

Standard probe trial

This 50 s probe trial was as described for the training mazes.

Strategy probe trial

The purpose of this trial was to reveal whether participants were using an egocentric or allocentric strategy to locate the platform. Instructions for the strategy probe trial were the same as for the DTS trial described above. That is, participants were instructed to indicate their estimate of the platform location by going to where they thought it was located. For this trial, the proximal cue object was moved to the opposite side of the arena from its location on the previous 10 test trials in order to reveal which participants were navigating primarily by the cue object (i.e., those who went to this quadrant opposite the original one) as opposed to participants navigating by distal features (landscapes) who would go to the previously correct quadrant. The start position was near the arena wall, midway between the previously correct quadrant and the one now marked by the cue object (Fig. 3). Once the participant reached his/her estimated target location, the experimenter marked the spot for later analysis. Platform location estimates were scored as to whether the estimate indicated an egocentric strategy (i.e., positioned relative to the cue object) or an allocentric strategy (i.e., positioned relative to the landscape). In order to assess platform position accuracy, placements were also scored on a 0–7 scale by how close they were to the center of one of the platform locations (one of two bull's eyes in Fig. 3). Participants who indicated the platform was in an incorrect quadrant (i.e., received a score of zero) were excluded from the analysis of strategy preference.

Verbal report question

Immediately after the strategy probe, participants were asked if they noticed that the cue object had changed location for the strategy probe trial.

Computer game experience and demographic variables

After the end of all testing, participants were asked whether they play or have played two and/or three dimensional video games, how often they played (now and as children) and whether they were experienced with game controllers and joysticks. Participants responded to each of the five questions on a 6-point Likert-type scale: "never", "occasionally", "monthly", "weekly", "every few days", or "daily". Participants were also asked about their age, gender and education level to check for confounds with the navigational variables.

Analysis

The data were summarized using Excel® and inferential statistics were computed using SPSS® (Statistical Package for the Social Sciences). Maze navigation data collected in Unreal® were converted and analyzed using TRAM©, a locally developed

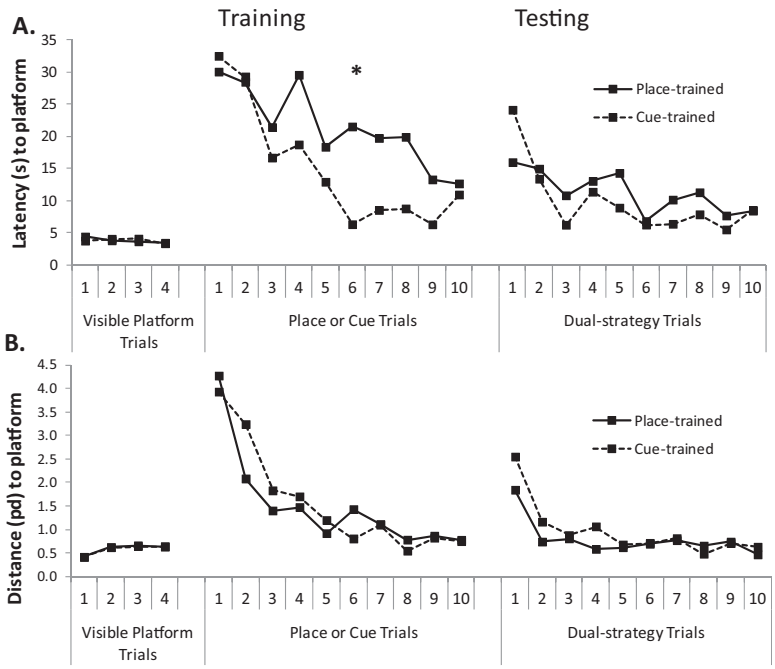

Fig. 4. Acquisition curves for (A) latency and (B) distance (in pool diameters: pd) to the platform in training and testing mazes for the place-trained and cue-trained groups. Latency to the platform was greater (*$p < .05$) during training in the Place maze than in the Cue maze, but distance was not. Performance of place and cue-trained groups was similar in the Dual strategy maze.

software program. The data were analyzed using three conventional dependent measures of performance: (1) latency (time in seconds) to reach the platform, (2) distance (in pool diameters) traveled to the platform, and (3) dwell time or percentage of time spent searching in the correct quadrant of the arena on standard probe trials. Latency and distance variables were analyzed for trials 2–10, excluding the first trial because it a search trial.

In order to test whether place or cue training (i.e., experience) affected performance in the Dual-strategy maze, a 2 × 2 repeated measures mixed ANOVA was conducted for each of three behavioral variables (latency, distance, and probe dwell time). To further determine the effect of experience on strategy selection and environmental awareness, three frequency analyses (chi square type) were performed: (1) experience (place or cue training) × strategy (by room or by object), (2) strategy × environmental awareness (notice/not notice object relocation), and (3) experience × environmental awareness. Additional frequency analyses were also performed to determine whether there were gender differences in strategy selection or environmental awareness: (1) gender (M/F) × environmental awareness, and (2) gender × strategy selection. Because of the relatively small sample size, the Likelihood Ratio statistic ($L\chi^2$) was reported (rather than χ^2), as recommended by Field (2005). The sample size did not permit any 3- or 4-way analyses.

Secondary analyses (using *t*-tests) were conducted to examine potential group differences (by training) in mastery of the basic procedural aspects of virtual navigation (indicated by visible platform trials) or in the accuracy of participants' explicit knowledge of the platform location at the end of training (indicated by DTS scores). Correlations (using Pearson's *r*) were conducted to examine relationships between behavioral variables and both demographic and computer game experience variables.

Results

Navigation training

As expected, performance on the visible platform trials showed that all participants were able to follow task instructions and master the use of the joystick (Fig. 4). Prior to training, there were no detectable differences based on which condition participants were assigned to: place-training (Latency, $M = 3.8$ s, $SEM = .22$; Distance, $M = .6$ pd, $SEM = .004$), cue-training (Latency, $M = 3.7$ s, $SEM = .29$; Distance, $M = .57$ pd, SEM = .003). Performance on training trials in Place and Cue mazes was consistent with previous research using similar mazes (e.g., Livingstone & Skelton, 2007; Van Gerven et al., 2012), and there were essentially no differences between the two conditions (Fig. 4) though latency to the platform was significantly shorter in the Cue maze ($M = 10.7$ s, $SEM = 1.08$) than in the Place maze ($M = 16.8$ s, $SEM = 2.7$), $t(36) = 2.42$, $p < .02$, $d = .49$. There was no significant difference in the distance traveled in the Place ($M = 1.08$ pd, $SEM = .10$) and Cue ($M = .96$ pd, $SEM = .10$) mazes, $t(36) = .91$, $p = .37$, $d = .20$.

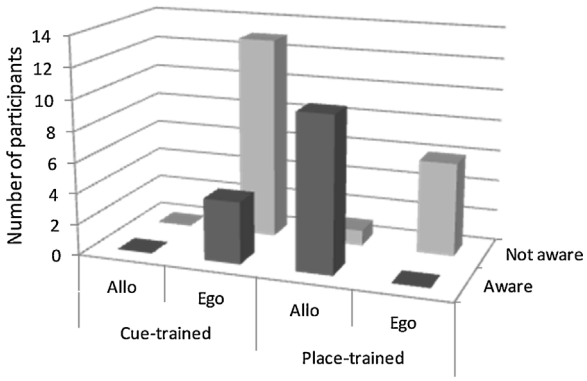

Fig. 5. The relation between training, environmental awareness and strategy selection by participants. All cue trained participants navigated egocentrically regardless of awareness. All place-trained participants who were environmentally aware navigated allocentrically. All but one of the remainder navigated egocentrically.

Performance on the standard and the explicit probe (DTS) trials at the end of training confirmed that participants in both Place and Cue mazes had developed fluency with the strategy required by their training maze. Dwell times in the correct quadrant on the standard probe were well above chance (25%) for both mazes and there was no significant difference between the groups (Place, $M = 57\%$, $SEM = 5\%$; Cue, $M = 58\%$, $SEM = 6\%$). Accuracy of platform knowledge was also good for both groups on the explicit probe trials, though it was slightly but not significantly greater in the Cue maze ($M = 5.3$, $SEM = .55$) than in the Place maze ($M = 5.0$, $SEM = .56$). "Good" scores (6 or 7 of 7) were achieved by 60% of participants after Cue maze training and by 55% of participants after Place maze training. In both mazes, 90% of participants correctly identified the correct quadrant of the arena.

Navigation testing

As expected, experience in the training mazes improved navigational performance and platform knowledge in the Dual-strategy maze regardless of the type of training (place or cue) (Fig. 4). A repeated-measure mixed ANOVA showed no overall effect of training type (place or cue) on latency or distance to the platform and no interaction between training type and phase. In other words, the effect of training on navigational performance in the Dual-strategy maze was about the same for both place and cue training. The effect of training/experience was evident as shorter latencies $F(1,35) = 17.44$, $p < .001$, $r = .58$ and shorter distances $F(1,35) = 27.48$, $p < .001$, $r = .66$, and slightly better probes in the Dual-strategy maze than the training mazes, $F(1,35) = 4.5$, $p < .05$, $r = .34$.

Experience in the training phase (either place or cue) improved but did not eliminate the need for learning in the testing phase. Trial by trial acquisition curves show that latency and distance were greater on Trial 1 of testing than on the last two trials of training (Fig. 4), indicating that participants required at least one trial to learn the platform location. Type of training made little difference. Acquisition was similar for the place and cue-trained groups in both latency and distance. By the end of testing (Trials 9 and 10), latency to the platform was less than 10 s and distance less than .75 pool diameters for both groups, indicating that participants were traveling to the platform quickly and directly.

Strategy selection

At the end of testing in the Dual-strategy maze nearly all participants demonstrated a clear choice of strategy on the strategy probe. The majority (35 of 37 participants) demonstrated a preference to navigate by either the cue object or the room features and landscape. Data from the two participants who failed to identify either of the two correct quadrants were dropped from further analysis, leaving 17 cue-trained and 18 place-trained participants. Data from an additional place-trained participant were dropped because this participant failed to answer the verbal report question. Therefore subsequent analyses were for a sample of 34 participants ($n = 17$ cue-trained, $n = 17$ place-trained). It is important to note that there were no differences in strategy selection based on whether participants were students or community based participants.

The participants' selection of strategies was strongly related to experience during training. All 17 participants trained in the Cue maze subsequently navigated using an egocentric strategy in the Dual strategy maze. In contrast, 11 of 17 participants trained in the Place maze subsequently chose an allocentric strategy (Fig. 5). This association between the type of training (place or cue) and the choice of strategy (allocentric or egocentric) was significant, $L\chi^2(1) = 22.09$, $p < .001$, phi = .70. In essence there were three groups of participants based on training and strategy selection: "cue-trained-egocentric" ($n = 17$), "place-trained-egocentric" ($n = 6$), and "place-trained-allocentric" ($n = 11$).

The verbal probe for strategy and environmental awareness given at the end of testing revealed a relationship between the strategy participants selected and their awareness of the environment. Specifically, 10 of 11 participants (91%) who

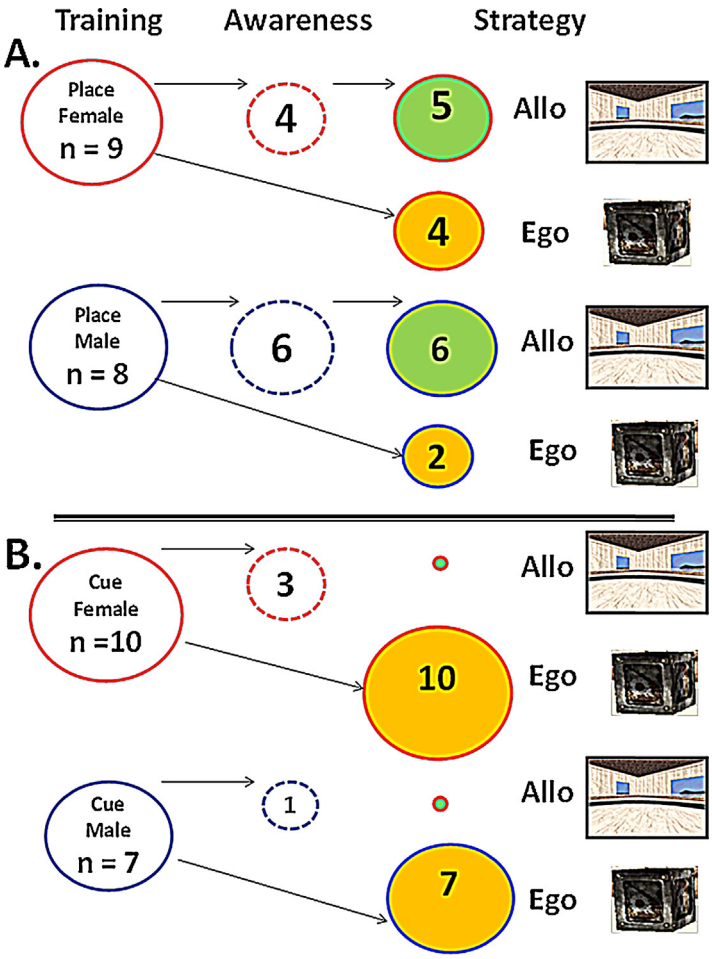

Fig. 6. Proposed effect of training (experience) and environmental awareness on strategy selection based on observed frequencies (numbers in circles). Arrows indicate a potential path from training to allocentric strategy via environmental awareness for place-trained participants (A) but not cue-trained participants (B). There appears to be little or no effect of gender (M = male, F = female) on strategy selection. Both males and females were divided in their selection of an allocentric or an egocentric strategy after place training (A) and all participants (male or female) selected an egocentric strategy after cue training. However, after place training males (6:2) were slightly more likely to choose an allocentric strategy than were females (5:4).

navigated by room features on the strategy probe noticed that the cue object had moved whereas 19 of 23 participants (83%) who navigated by the cue object did not, $L\chi^2(1) = 14.29$, $p < .001$ (Fig. 5). Based on the odds ratio, participants who navigated by room features were 52 times more likely to notice that the object had moved than those who navigated by the cue object. In other words, participants who navigated allocentrically coded the location of the cue object in relation to the rest of the environment, whereas participants who navigated egocentrically using the cue object tended not to notice a substantial change in the relation between the object and the environment.

Analysis of the verbal reports about the strategy probe revealed a relationship between pre-training, environmental awareness, and strategy selection in the Dual-strategy maze. Place-trained participants were 4.73 times more likely to notice that the object had moved than were cue-trained participants, $L\chi^2(1) = 4.49$, $p < .05$, phi = .36 (Fig. 5). Furthermore, most place-trained participants (10/17 or 59%) noticed that the object changed location whereas most cue-trained participants (13/17 or 76%) did not, $L\chi^2(1) = 16.26$, $p < .001$, phi = .69.

Although the small sample size precluded further analyses, the pattern of the data suggests a pathway from training (experience) to strategy mediated by environmental awareness (Fig. 6). Cue maze training appeared to lead to egocentric navigation in the Dual strategy maze, regardless of environmental awareness (i.e., as evidenced by awareness of the relocation of the cue object). In contrast, Place maze training appeared to lead to allocentric navigation when participants were aware of the environment and to egocentric navigation when they were not. In other words, experience (and success) with egocentric navigation (in the Cue maze) encouraged subsequent egocentric navigation regardless, but experience (and success) with allocentric navigation encouraged subsequent allocentric navigation only when the early training enhanced awareness of the environment.

Gender effects

In contrast to the effects of environment (place or cue) and experience (maze training), gender was not a major contributor to environmental awareness or strategy selection. Overall, there were no gender differences in strategy selection. $L\chi^2 = .715$, $p = .40$, phi = .15. There were also no overall differences in environmental awareness (i.e., noticing the cue object relocation), $L\chi^2 = .334$, $p = .56$, phi = .10. Unfortunately, there were insufficient numbers to directly test three-way gender effects (e.g., gender × training × strategy). However, the proportions of males and females choosing an allocentric strategy after place-training were very similar: 75% (6/8) of males versus 56% (5/9) of females (Fig. 6). All males and females chose egocentric navigation after cue training. There was also no gender difference in navigational performance related to strategy choice (data not shown).

Computer game experience

Computer gaming experience correlated only with latency in the Place and Cue mazes (Place maze, $r = -.43$, $p = .01$; Cue maze, $r = -.39$, $p = .02$), suggesting an association between more gaming experience and faster navigation, but because other navigational performance variables did not correlate, and because these were just two of many correlations in the matrix, gaming experience has limited explanatory power for the other effects in this study.

Discussion

As expected, navigation performance was good in both training and testing conditions. Participants traveled to the platform quickly and directly on visible platform trials, on invisible platform trials in place and cue training conditions, and on dual-strategy testing trials. Navigation performance (latency, distance, probe) was slightly better during testing in the Dual-strategy maze than in training but did not differ according to training type (place or cue). Knowledge of the platform location on the probe trials at the end of training and testing was good for all participants. By all measures, the performance of males and females was roughly equivalent.

The main finding of the present study was that a participant's choice of whether to use an allocentric or an egocentric strategy in a given environment was affected by his/her previous experience with navigational strategies. In the present study, 65% of participants trained in allocentric navigation chose to navigate allocentrically while the remaining 35% switched to egocentric navigation. In contrast, all participants trained in egocentric navigation chose to navigate egocentrically in an environment that accorded them the opportunity to navigate allocentrically as well. These results indicate that the choice of navigational strategy is affected by prior experience and that the effect is dependent on the type of experience.

A striking aspect of the present results is that all participants who were trained in the Cue maze continued to utilize an egocentric strategy throughout Dual-strategy maze testing trials. One explanation for this finding is that proximal cues, when present, bias participants toward using them when navigating. Another (not mutually exclusive) explanation is that pre-training with both proximal and distal cues present, but with only the proximal cues reliably indicating the platform location, led to the distal cues being overshadowed by the proximal cues. In his review of spatial cognition, Burgess (2008) notes that one cue may overshadow another if it is a better predictor of the target location. The importance of prior experience with cue reliability was clearly shown by humans in a virtual environment (Doeller & Burgess, 2008), though in this study, "Learning to the boundary [distal cue] blocks learning to the landmark [proximal cue], but not vice versa" (Burgess, 2008). In other words, this finding was the opposite of ours.

Our results are more consistent with a rat study cited in Chamizo et al. (2003). Roberts and Pearce (1999) showed that in the MWM, prior cue learning can block learning of surrounding landmarks. However, they did not test the effect of prior place learning on subsequent cue learning. One earlier rat study showed that, in a MWM, distal extra-maze cues can overshadow proximal intramaze cues, but only if the proximal cues are made unreliable (Redhead et al., 1997). An even earlier rat study found that in a radial maze, extra-maze cues just beyond the end of individual arms could overshadow or block intra-maze tactile cues consisting of two different floor surfaces (Diez-Chamizo et al., 1985).

As mentioned in "Introduction" section, a number of "prior-experience" studies (reviewed by Miller & Shettleworth, 2007) have used real or virtual rooms (enclosures) to compare the ability of room geometry versus proximal cues to overshadow or block each other in humans, though in these studies (e.g., Bodily et al., 2011; Ratliff & Newcombe, 2008), stimulus control was assessed only on tests of orientation, not navigation. Participants were asked merely to point to where they thought the goal object was in the room, from a fixed start location, and it is unclear whether such a task requires a cognitive map or the hippocampus in the way the MWM is known to.

The effects of allocentric training are a little more difficult to interpret. As mentioned earlier, two rat studies have examined whether training with distal cues could block learning of proximal cues, and one found that cues at the end of arms could overshadow tactile floor cues (Diez-Chamizo et al., 1985), whereas the other found that blocking only occurred if the proximal cues were made unreliable (Redhead et al., 1997). It is not clear how much one can generalize from these studies to the present study. In our previous study of spontaneous strategy selection in the Dual-strategy maze (Van Gerven et al., 2012), albeit with smaller (and therefore less salient) cue objects, the proportion of (untrained) participants choosing an allocentric strategy in the Dual strategy maze was 59% (20 of 34) compared to the 65% (11 of 17) of place trained participants in the present study. Given that these two proportions are very similar (i.e., 59% = 10 of 17, a difference of just one

participant), it seems that that the effect of prior training was not so much to foster allocentric strategy use but rather to permit spontaneous selection of an allocentric strategy in the presence of proximal cues.

We propose that the influence of place training on subsequent strategy selection was mediated by cognitive map formation, as manifest in our measure of environmental awareness. Every place-trained participant who noticed the objects had moved on the strategy probe chose an allocentric strategy to find the platform on that probe trial. Every participant who chose an egocentric strategy reported not noticing whether the object had moved. The only exception to this double dissociation was one participant who navigated allocentrically on the strategy probe trial but did not notice the objects move. In order to notice whether the objects had moved in the room, the participant would have had to learn the spatial relationship between the objects and the environment outside the windows. In other words, they would have had to have formed a cognitive map that included the spatial relationship of proximal objects and distal landscapes.

In contrast to the place-trained participants, most cue-trained participants (76%) did not even notice that the cues were in a different location on the probe trial. Clearly, even if they had developed a cognitive map of the room, they were not using it while navigating. This indicates that together, navigational experience and environmental awareness affect strategy selection and adds to previous findings that task demand and immediate environment determine whether a navigator will adopt an egocentric or allocentric reference frame (Doeller, King, & Burgess, 2008; Etchamendy & Bohbot, 2007).

A limitation of the present study was that the strategy training took place in exactly the same room with almost exactly the same cues as the strategy testing. However, this is the same procedure used in every other previous study of the effects of prior experience (or stimulus exposure) on navigation. It is also worth noting that the cue object in the cue-training was not the same as the cue object in the Dual strategy maze, so it could not have been carry-over of a simple stimulus association. In future, it would be interesting to test whether pre-training in one environment would influence strategy choice in another. However, the main point we are making is that prior experience with navigational strategy influences subsequent strategy choice. If this is true, then each participant's prior experience throughout his/her life would affect his/her strategy choice when tested in a Dual-strategy maze. If the pre-training environment were like the Dual strategy maze, then it could be argued that this was just a carry-over from the training environment. If the pre-training environment were very different, then strategy choice might depend more on the participant's accumulated prior experience than the pre-training. In other words, the greater the observed effect, the more it could be argued that the effect was artificial and non-generalizable. Our goal was merely to demonstrate that the effect exists.

Differences in strategy selection did not appear to be the result of non-navigational factors such as computer gaming experience or task difficulty. Computer gaming experience was comparable for all three strategy groups (cue-trained, egocentric; place-trained, egocentric; place-trained, allocentric). Task difficulty may seem lower for the Cue maze than the Place maze both intuitively and because trial latencies were shorter. However, analysis of the other two standard navigational measures (distance and probe dwell times) revealed no differences in difficulty between the mazes.

Surprisingly, differences in strategy selection also did not appear to be related to gender. At the end of testing in the Dual strategy maze, the number of males and females using each strategy was nearly equal in both training groups. In the literature, authors generally conclude that males prefer allocentric strategies and females prefer egocentric strategies (for reviews see, Gluck & Fitting, 2003; Lawton, 2010). However, this effect is not always found (Andersen, Dahmani, Konishi, & Bohbot, 2012; Iaria et al., 2003) and is rarely tested directly. Our finding here is consistent with our recent report showing that gender has no effect on spontaneous strategy selection when tested behaviorally (as opposed to verbally) (Van Gerven et al., 2012). This is consistent with the suggestion that reliable gender differences in navigational ability may be small (Gluck & Fitting, 2003) and like other gender differences in spatial ability may be influenced by cognitive styles that could be changed or eliminated with training (Bosco, Longoni, & Vecchi, 2004).

One finding that was related to gender was our verbal probe of environmental awareness. More males than females were aware that the cue object was moved and therefore may have been more aware of the distal room features than were females. This is consistent with the proposition that males may be better than females at processing information from the distal environment (Woolley et al., 2010) and therefore may prefer to navigate using distal, directional information, whereas females may prefer to navigate by positional cues (Chai & Jacobs, 2010).

The finding that experience with strategies, especially egocentric ones, strongly affects subsequent strategy selection has important implications for the interpretation of studies utilizing more than one navigation task, especially if one or more of the tasks is biased toward an egocentric strategy. For example, in Levy, Astur, and Frick (2005), a study of gender differences in navigation, three tasks were presented in sequence: a virtual radial arm maze, a virtual T-maze and a virtual MWM. Although each task was designed to be solvable using either an egocentric or an allocentric strategy, the authors noted that the environmental stimuli in the radial arm maze may have promoted the utilization of an egocentric strategy. By the end of testing in the virtual MWM, all participants selected an egocentric strategy on the strategy probe. The authors were surprised by this outcome, having expected some participants to utilize an allocentric strategy in the dual-strategy MWM. In light of the present results it seems possible that prior experience with an egocentric strategy in the radial arm maze could have influenced navigation in later maze tasks and that this effect could have overshadowed any gender-specific strategy preference.

The present results support the proposition that individuals are not limited to, or even dominated by a single navigational strategy controlled by genetic or hormonal factors. By looking at how individuals navigated, rather than just groups, we observed that all participants were capable of navigating either egocentrically or allocentrically depending on the demands

of the virtual environments, and many demonstrated the ability to switch from one strategy to the other. We saw no differences in either performance or strategy selection based on gender. In other words, neither individuals nor genders were inherently egocentric or allocentric navigators. Rather, the present findings agree with proposals that each person has two navigation systems and two available strategy types from which he/she can select based on a combination of environmental features, past experiences and possibly fluency or competency with particular strategies (Becic, Boot, & Kramer, 2008; Blanch, Brennan, Condon, Santosh, & Hadley, 2004).

In conclusion, the present results indicate that strategies people select for navigating are associated with the nature of antecedent experience with environments containing different types and combinations of environment stimuli. They also indicate that strategy use is not determined solely by innate factors such as gender. Combining behavioral analysis with verbal reports indicated that selection of an allocentric strategy depends on the acquisition of a cognitive map of the immediate environment. Understanding the factors contributing to strategy selection may improve our understanding of the learning processes involved and the stimuli controlling behavior. This in turn should lead to improved design of virtual environments and navigational tasks used in the analysis of the neuroanatomy of navigation as well as the neural pathology underlying navigational deficits known to occur in aging (Moffat & Resnick, 2002), Alzheimer's disease (Pai & Jacobs, 2004), brain injury (Skelton et al., 2000, 2006), stroke (Van Asselen et al., 2006), schizophrenia (Hanlon et al., 2006) and other brain-based disorders.

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