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Direct Measurement of Spontaneous Strategy Selection in a Virtual Morris Water Maze Shows Females Choose an Allocentric Strategy at Least as Often as Males do

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Considerable evidence indicates that males navigate large-scale space better than females, and some have previously attributed this difference to a greater ability of males to select or use an allocentric (cognitive mapping) navigational strategy. We directly tested this proposal by having males and females navigate in an "ambiguous" virtual Morris water maze environment that permitted participants to choose and use either an allocentric or an egocentric strategy. A novel probe trial at the end of training revealed which strategy each participant had been using and showed that the strategy selected by the greatest number of males and females was allocentric, and that this bias was even greater for females. Traditional measures of navigational performance (distance, latency, probe dwell time) indicated that overall, males were more efficient than females. However, this gender difference was not related to strategy choice: males were better than females regardless of strategy, though the difference was significant only in those navigating allocentrically. These data indicate that while males may navigate allocentrically more efficiently than females, this does not account for the male advantage in navigation. The data also indicate that under specific circumstances, females may also prefer and use an allocentric strategy to navigate. These findings have implications for theories regarding the differential use of the hippocampus by men and women.

Keywords: spatial cognition, strategy, virtual MWM, egocentric, allocentric, gender, navigation

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Gender differences in human spatial navigation have been studied for a long time, and males are usually shown to be better navigators in paper-and-pencil tests, real world navigation (Saucier et al., 2002), and 3D virtual tests of spatial navigation (Astur, Ortiz, & Sutherland, 1998; see Coluccia & Louse, 2004; Lawton, 2010, and Voyer, Voyer, & Bryden, 1995, for reviews on gender differences in spatial abilities). Numerous factors have been forwarded (with varying support) to account for this difference, including psychological (Lawton, 1994), experiential (Lawton & Kallai, 2002; see Baenninger & Newcombe, 1989, for a review) and physiological (Williams, Barnett, & Meck, 1990, but see Halari et al., 2005). One factor receiving attention recently is the fluency with which males and females employ appropriate spatial strategies in response to different environments (Iglói, Zaoui, Berthoz, & Rondi-Reig, 2009).

Researchers have identified two distinct strategies that contribute to real-world navigation (O'Keefe & Nadel, 1978; Tolman, 1948), which have come to be known as allocentric and egocentric (Kolb, Sutherland, & Whishaw, 1983). Allocentric navigation employs a cognitive map (O'Keefe & Nadel, 1978), encoding the spatial relationships among (often distal) landmarks in the environment as well as their relationship to a destination. Allocentric navigation is viewer independent because the path to the destination can be deduced from multiple perspectives other than the perspective of the navigator. The strategies associated with this kind of navigation are also referred to as "spatial" strategies (Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; McGregor, Good, & Pearce, 2004). In contrast, egocentric navigation (a.k.a., "route navigation", Hartley, Maguire, Spiers, & Burgess, 2003, or "non-spatial navigation", Iaria et al., 2003) operates from the perspective of the navigator, and relies on the acquisition of simple stimulus–response associations between single (often proximal) landmarks and body-based responses such as "head toward this object" or "turn right at the corner" (O'Keefe & Nadel, 1978). While egocentric strategies are navigational in nature, they are applied to what is known as "simple" (Jeffery, 2003) navigation of space where the navigator either ignores or is ignorant of the spatial relationships among environmental stimuli. These two strategies have also been linked to two quite different neural substrates: the hippocampus for cognitive mapping and the basal ganglia for cue-based egocentric navigation (Iaria et al., 2003; Maguire et al., 1998; McDonald & White, 1993; O'Keefe & Nadel, 1978).

Three lines of evidence from the literature suggest that males and females differ in their capacity to efficiently use allocentric and egocentric strategies. The first line of evidence comes from self-report: males are more likely to report using allocentric strategies after a navigational task, while females are more likely to

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report using egocentric strategies (Lawton, 1994; Lawton, 1996; Schmitz, 1997). The second line of evidence comes from studies in which males and females are required to provide navigational information either by giving instructions or by drawing maps. A number of researchers have shown that males are more likely to give directions or draw maps using allocentric referents, such as cardinal directions or Euclidian distances, while females are more likely to use egocentric referents, such as left–right directions or landmarks (Dabbs, Chang, Strong, & Milun, 1998; Lawton, 2001; Miller & Santoni, 1986). Interestingly, MacFadden, Elias, & Saucier, 2003, with the use of eye tracking, showed that even though males and females tend to give directions differently, they attend to the same information when scanning maps. This suggests the possibility that some of the presumed differences in male and female strategy use are artifacts of expression, not spatial perception. The third line of evidence is the robust performance advantage that males have in allocentric navigational tasks, while performance differences in egocentric tasks are often less pronounced or disappear altogether. This has been most clearly demonstrated in both rodents and humans using variants of the now-classic Morris water maze (MWM; Morris, 1984) design (see Astur et al., 1998; Rizk-Jackson, Acevedo, Inman, Howieson, Benice, & Raber, 2006; Sandstrom, Kaufman, & Huettel, 1998, for examples). These three lines of evidence, taken together, suggest that males are better than females at allocentric processing but not egocentric processing (Saucier et al., 2002).

In summing up this evidence, some authors have proposed that males *prefer* to navigate using an allocentric strategy and females *prefer* to navigate using an egocentric strategy (e.g., Woolley et al., 2009) and that this preference for, and fluency with, allocentric strategies underlies the male advantage in spatial navigation (Coluccia & Louse, 2004). This conclusion may not be justified however, since with one notable exception (Levy, Astur, & Frick, 2005), researchers have not actually tested what strategy males and females prefer to use when given the choice. Furthermore, in this study no gender differences in strategy choice were apparent (Levy et al., 2005).

The present study directly tested the common assumption that males prefer allocentric navigation while females prefer egocentric navigation, and examined the relations between spontaneous strategy choice, gender and performance. We tested male and female participants in a special virtual MWM that allowed both egocentric and allocentric strategies to be used with equal efficiency, and then measured which strategy each participant had selected. It is important to note that the very first spatial test given to the participants was this "Ambiguous" maze. The second spatial test was a standard virtual MWM (the "Place" maze), which could only be solved efficiently using an allocentric strategy. Given the assumptions in the literature, we expected that in the Ambiguous maze, males would be more likely to choose an allocentric than an egocentric strategy and conversely, females would be more likely to choose an egocentric strategy. We also expected that strategy choice would affect performance, and that females, or those who preferred an egocentric strategy, would not perform as well as participants who preferred an allocentric strategy in the Place maze, and possibly even the Ambiguous maze.

Method

Participants

A sample of 38 undergraduate students (19 females and 19 males, with a mean age of 20) participated in the study for course credit. Two male participants were excluded as outliers because their latency or distance was 2 standard deviations greater than the mean (Field, 2009; Grubbs, 1969). Therefore, the analysis included data from 36 participants (19 females and 17 males). Participants were screened for a history of brain injury or neurological disorder, required to speak English as a first language and have normal or corrected to normal vision. Ethics approval was obtained from the University of Victoria, Human Research Ethics Committee.

Apparatus

The virtual environments were designed using the editor supplied by Unreal (Epic Megagames; maze designs and software are available for collaboration). All mazes were displayed on a desktop computer with a 19" LCD monitor set to a resolution of 800 $\times$ 600 and viewed from a distance of approximately 60 cm. Participants experienced the virtual environments from a first-person view, and navigated with a game pad. Virtual motion was restricted to forward, left, or right, analogous to the movements available to a rat in the MWM.

Maze Environment

The maze environment consisted of a square arena room (visually 75 $\times$ 75 m square with 16.5 m high walls) with windows through which an outdoor landscape could be seen. Within the room was a circular arena, 42 m in diameter (i.e., 1 pool diameter $\approx$ 56% of room diameter). The arena was bound by a 1 m high wall that prevented the participant from exiting the arena during trials without blocking their view of the windows and outdoor landscape. The room walls were featureless, except for windows, and were arbitrarily designated as north, south, east, and west. The north and south walls each had large single windows through which distinctive distal landscape features could be seen (mountains to the north, a body of water to the south). The east and west walls each had three smaller windows through which hills that sloped from the mountains to the water could be seen. The target location was a circular, solid green platform, 7 m in diameter (i.e., 1/6th the diameter of the arena; see Figure 1). The platform was positioned in the center of the southeast quadrant, on a diagonal to the cardinal directions, in line with one of the 4 room corners which were indistinguishable because they blocked any view of the outdoor landscape. In other words, there was no single distal feature by which participants could find the platform. (For more detailed descriptions, see Livingstone & Skelton, 2007; Skelton, Ross, Nerad, & Livingstone, 2006.) The key aspect of this environment for the present purposes is that the outdoor landscape was completely stationary, and as such could only provide directional and not positional information. Thus the outdoor landscape could only be used to navigate efficiently if it was used in combination with room cues such as the arena wall.

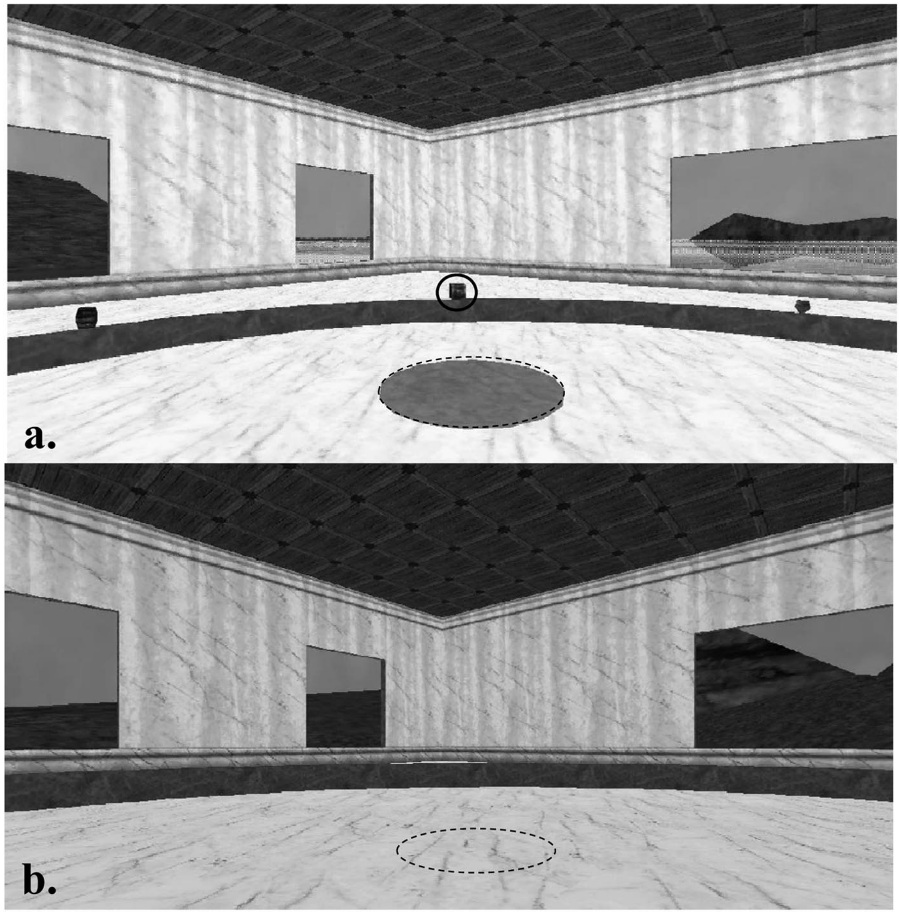

Figure 1. Views of mazes. (a) Ambiguous maze as seen from the northwest from above normal eye level to highlight outside landscape (allocentric features) and square box marking position of platform (egocentric feature). The platform is invisible during test trials. (b) Place maze as seen from southeast at normal eye level. Although the platform position is marked in the figure, it was invisible during testing. A color version of this figure is available in the supplemental materials.

We employed two variants of this maze environment, the Ambiguous maze and the Place maze (a.k.a., the Arena maze). The Ambiguous maze was the same as a standard, allocentrically biased Morris water maze modified by the addition of cue objects, one of which (the "steel box") always indicated the position of the invisible platform (cf., the "landmark maze" of Kolb & Walkey, 1987). The 8 objects were perched on the arena wall, equidistantly and at cardinal points (Figure 1a) and did not move throughout training. Because the platform was in a fixed location and the objects remained in one location throughout, the steel box was a single proximal cue indicating the position of the platform in the arena, thereby allowing the participants to find the platform using an egocentric "taxon" strategy (O'Keefe & Nadel, 1978; Kolb, Sutherland, & Whishaw, 1983). Thus, participants could find the platform by either orienting allocentrically, using the configuration of landmark features outside the windows in combination with features of the room such as the geometric corners or the edges of the windows, or egocentrically, by using a single object close to the platform that independently marked the platform location. Start positions were always located just inside the arena, facing inward, and varied pseudorandomly among the cardinal points (north, east, south, west). Start positions were varied pseudorandomly to discourage the use of (egocentric) response-based strategies based on memorization of body-movement sequences. All four start locations were used in each set of four trials. The second maze, the Place maze simulated the standard MWM task (Morris, 1984), which was designed to test allocentric navigation by requiring rats to find a target location using a constellation of cues both inside and outside the room (Figure 1b). The Place maze required participants to repeatedly navigate to a fixed, hidden goal platform from different start locations.

Participants were tested first in the Ambiguous maze, then in the Place maze. Platform position in the Ambiguous maze was located either in the center of the southeast or the northwest quadrant, and was counterbalanced across participants. The platform in the Place maze was always in the opposite position (northwest or southeast respectively).

Movement of participants in all mazes were converted to conventional dependent variables used to assess learning in both virtual and real MWM environments. Movements were recorded during navigation in Unreal "demo" files. The latency (in seconds) and distance (in arbitrary units with 1 pool diameter = 150 units) to reach the platform, as well as "dwell time" (the percentage of time spent in each quadrant) on probe trials was extracted from the demo files and analyzed using TRAM software (see Skelton et al., 2006).

Procedure

All trials and tasks are described below in the same order as they were given. See Table 1 for the type, order, number of trials and purpose of the tasks. All testing took place in a small, windowless room, free from distractions. The session began with a short background information questionnaire that asked about demographics such as age and education. Detailed descriptions of the instructions given to participants will be provided below, because other research has shown that human behavior in virtual mazes is heavily influenced by the instructions provided (Hardt, Hupback, & Nadel, 2009).

Exploration Trial

The exploration trial was conducted in the Ambiguous maze and was intended to familiarize the participant with the virtual environment. Research in our lab has shown that such exploration improves allocentric navigation (Macdonald, Gillingham, Livingstone, & Skelton, 2009). Upon being introduced into the virtual environment, participants were told they should explore the room until they were comfortable with the environment and game pad controls. The start position for the explore trial was outside the arena, by the east wall, facing inward. Participants were encouraged to look at the objects within the room and out through the windows at the surrounding landscape. The exploration trial ended once a participant indicated that they were familiar with the environment and the controls.

Table 1
Type, Purpose, Number of Trials (in Parentheses), and Order of Tasks

Task	Purpose
Ambiguous Maze	
Explore trial (1)	Familiarizes participants with the virtual environment and with movement using the gamepad.
Visible platform trials (4)	Familiarizes participants with the non-spatial (procedural) requirements of the task.
Practice drop the seed trial (1)	Ensures understanding of the instructions for DTS and dDTS trials.
Invisible platform trials (10)	Tests spatial navigation.
Probe trial (1)	Tests knowledge of the platform location.
dDTS trial (1)	Differentiates strategy selection; measures accuracy of knowledge of the platform location.
Place Maze	
Invisible platform trials (10)	Tests spatial navigation.
Probe trial (1)	Tests knowledge of the platform location.
Drop the seed trial (1)	Measures accuracy of knowledge of the platform location.

Visible Platform Trials

Following the explore trial, participants completed four "visible platform" trials in the Ambiguous maze to ensure they were capable of moving to a destination in the virtual environment. Trials began after instructions were given and participants indicated that they were ready. The circular green platform appeared on the floor of the arena in view of the participants from their start position. Both start positions and platform locations varied for each of the four trials. Participants were asked to walk to the visible platform as quickly and directly as possible. When they reached the platform, a low bell sounded, and they were invited to look around the room visually without moving from the platform.

Practice Drop-the-Seed Trial

In order to familiarize participants with the procedures of the "drop-the-seed" (DTS) probe trials scheduled for later in the session, participants were given a practice DTS trial which required them to drop a virtual "seed" onto a visible platform. Participants simply had to walk over the seeds, go to the platform in the center of the room, and then tell the experimenter when they were standing on it. The experimenter then marked the spot for later analysis by dropping the seeds.

Ambiguous Maze Invisible Platform Trials

Testing in the Ambiguous maze began with 10 invisible platform trials, followed by a standard probe trial. Before starting, participants were informed that the platform would be invisible but would always remain in the same location, and were asked to find it by walking to it as quickly and directly as possible. They were also informed that on one trial (the probe trial), the platform would be small and hard to find, but if they thought that they were in such a trial they should continue to search for it anyway. When participants indicated that they understood the instructions and were ready to begin, the experimenter "teleported" them into the first invisible platform trial. When the participant stepped on the hidden platform, it rose from the ground, became visible, and the low bell sounded. After reaching the platform in the first trial they were encouraged to look around the room visually from that spot until they were satisfied that they could get back to that place. They then notified the experimenter, who started the next trial. For the remaining nine trials, participants were allowed to look around the room as long as they liked from the platform once they had found it, and informed the experimenter when they were ready to begin the next trial.

The 11th trial was a probe trial (a standard MWM trial type) that measured participants' knowledge of the platform location. The probe trial was identical to the previous 10 trials, except that the platform did not appear when stepped on and remained invisible for the 50 s duration of the trial. It then rose from the floor with a bell sound to end the trial.

The final trial of the Ambiguous maze was a "differential Drop-the-Seed" (dDTS) strategy probe trial to assess whether the participants had been using an egocentric or allocentric strategy. Following the procedures from the practice DTS trial, participants were instructed to go to the location of the invisible platform and drop a seed. Unbeknownst to them, the objects on the arena wall had all been moved 180° around the arena wall, so that the predictive cue object (steel box) was located in the diagonally opposite quadrant (see Figure 2). Participants who indicated that the platform was in the original location in the room were considered to have been navigating allocentrically, whereas those who indicated the platform was in a new location, in front of the (newly moved) cue object, were considered to have been navigating egocentrically. Responses were classified as being either allocentric or egocentric, and scores were based on the proximity of the seed placement to either platform using a 7-ring bull's-eye target around each platform location. Scores ranged from 0, for missing the bull's-eye (and quadrant) entirely to 7, for placement directly on the platform (see Figure 2). As described in detail below, participants were later asked whether they had noticed during this trial whether the objects had moved from their usual locations.

Ambiguous Maze Room Reconstruction

After invisible platform trials, participants were asked to "reconstruct" the Ambiguous maze environment to test the quality of the cognitive map that formed while exploring and navigating (see Figure 3). Participants were provided with laminated images that represented landscapes, walls, floor and the platform from the maze environment. They reconstructed the outside environment by choosing 4 from 8 landscape images (representing views at 45°) and placing them into the appropriate areas on the template one at a time. They then placed 4 images of the room walls, an image of the arena floor (containing the arena wall and the 8 proximal objects [enlarged]) and an image of the platform on the template. Participants received 1 point for each landscape image they placed in the correct (relative) spot (max 4), 1 point if all of the walls were placed correctly with respect to each other, 1 point if at least one wall was correctly aligned with a landscape image, 1 point for placing the floor in the correct orientation with respect to the landscape, and 1 point each for placing the platform in the correct hemisphere and quadrant (for a maximum score of 9). Once participants had arranged all of the images, they were asked if they had noticed whether the objects in the room had moved during the "Drop the Seed" trial. This was intended to dissociate participants who had not paid attention to any features of the environment other than the objects ("No they did not move") from those who developed a cognitive map of the room that included the objects, but chose to navigate by the objects.

Place Maze Invisible Platform Trials

Following Ambiguous maze room reconstruction, participants completed another sequence of 10 invisible platform trials and 2 probe trials, in the Place maze. The procedure (i.e., instructions, trial number and order) was identical to that of the Ambiguous maze. Since the Place maze contained no cues that could be used to independently locate the platform, and only one invisible platform, the second probe trial (a DTS) measured only the accuracy of spatial knowledge based on allocentric

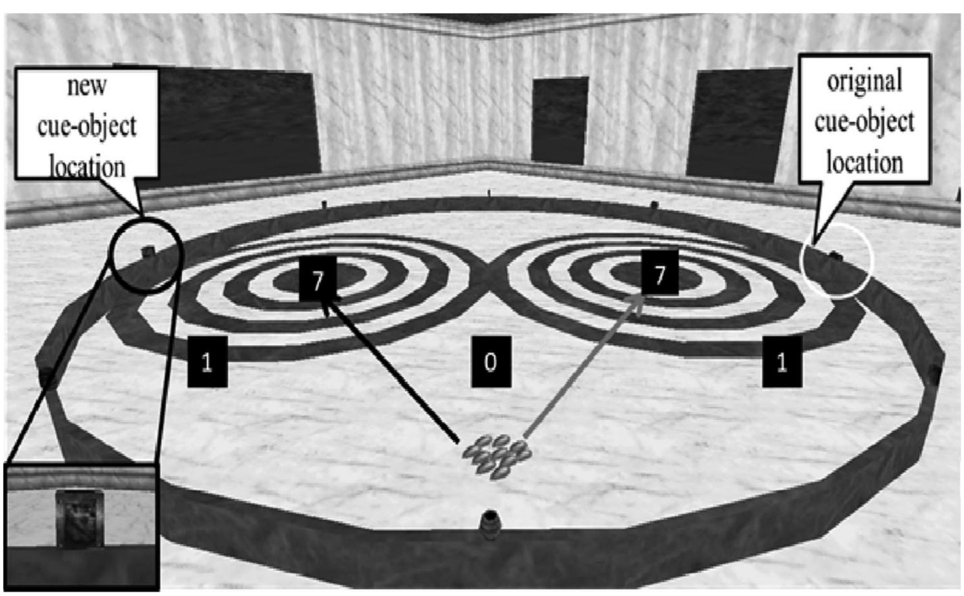

Figure 2. The dDTS trial. Participants collected marker seeds visible from a southwest start position and indicated strategy selection. Participants either indicated an egocentric strategy (black arrow) by marking the location of the platform relative to the predictive proximal cue (steel box, inset), which had been moved 180° away from its original location, or an allocentric strategy by marking the location of the platform relative to distal landscape features visible through the windows (gray arrow). Accuracy of seed dropping was measured using 7-point bull's-eyes. Note that the bull's-eyes were not visible to the participants during testing. Picture is taken from an elevated position outside of the testing arena. A color version of this figure is available in the supplemental materials.

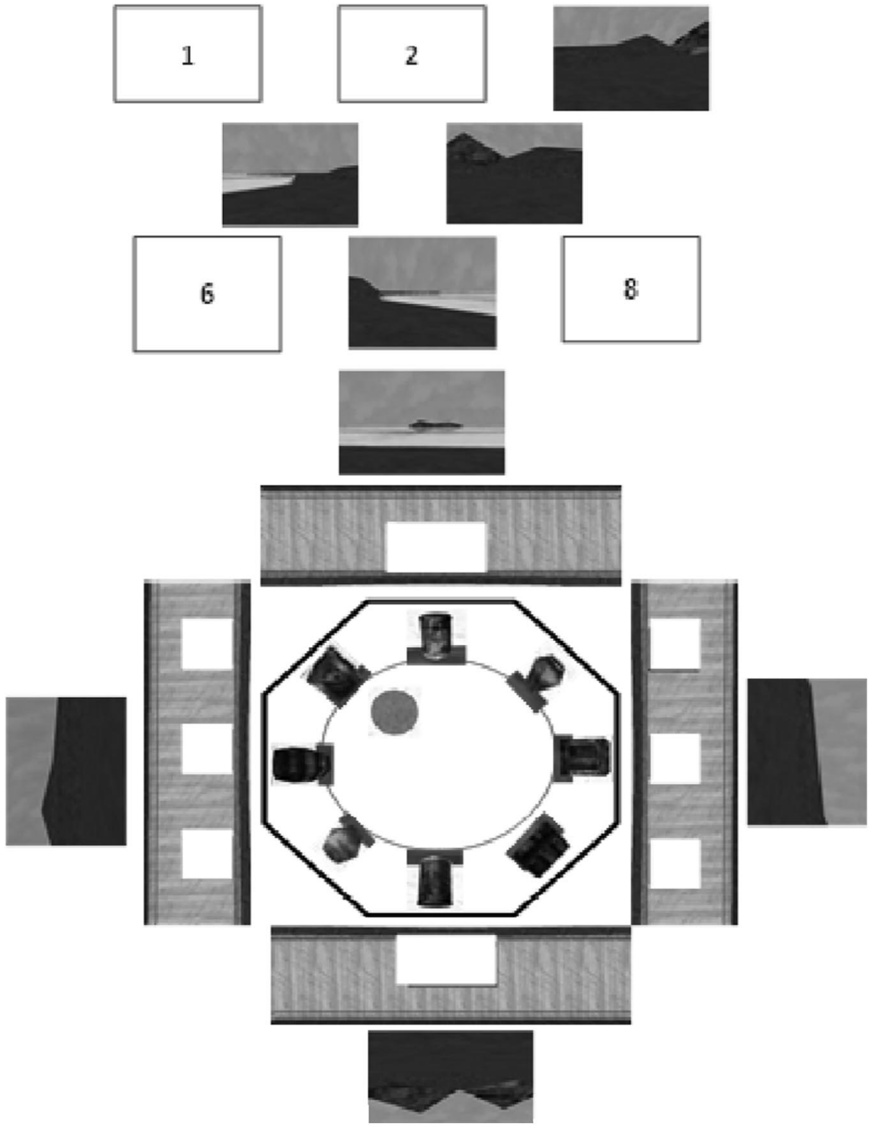

Figure 3. The Ambiguous maze Room Reconstruction task. Participants reconstructed the Ambiguous maze by selecting the most representative laminated images from an available set of 8 images (representing views at 45°), and placing them, one at a time, on a Bristol board template. Participants then positioned the 4 walls, laid the floor with objects oriented to the walls or outside landscape, and lastly placed the platform on the floor. This example depicts a perfect score (9). For scoring details, see Methods. A color version of this figure is available in the supplemental materials.

navigation. As it was for the dDTS, responses were scored 0 to 7 based on the proximity of the dropped seed to the center of the platform location.

Place Maze Room Reconstruction

After the Place maze, participants again reconstructed the virtual environment. Procedures were identical to the Ambiguous maze Room Reconstruction, without an image of the floor and cue objects (since there were none in the maze), and the maximum score was 8.

Where's the Water Test

Participants were asked to indicate the position of a feature of the virtual environment (i.e., the water) while they were facing the opposite direction, to test their degree of immersion (or presence) in the environment and as a second way of assessing their cognitive map. Participants were positioned at the arena wall in the Place maze facing North (i.e., viewing the mountain). They were then asked to indicate the location of the water from their current position by pointing with their hand, without moving or turning. Participants were assigned a score of 0 if they had no idea where the water was (or had not noticed it), 1 if they pointed in the direction of the monitor as if the entire environment was inside the monitor, 2 if they pointed inaccurately somewhere to the left or right of the screen, and 3 if they pointed somewhere behind them (southward) as if the environment wrapped around them in imaginary space.

Questionnaire

Lastly, participants were asked to complete a questionnaire on background information to identify potential confounds, such as dizziness or fatigue. Other relevant questions asked participants to rate their experience with 2D and 3D video games on a 6-point scale. Responses to these 5 questions were later aggregated into a summary "game experience" variable.

Data Analysis

Participants were grouped by 2 factors, gender and strategy choice (according to dDTS in the Ambiguous maze). The relationship between gender, strategy selection and performance was analyzed using a 2 × 2 factorial ANOVA on latency, distance, dwell time and a summary variable, the "spatial score." The spatial score was developed to provide a single summary score of navigational performance in any MWM and does so by equally balancing the influence of the probe trials with the two measures of performance in the invisible platform trials. This formula normalizes scores of distance, latency, and probe dwell time, inverts *z*-scores for distance and latency so that higher scores indicate better performance (like dwell time), and then weights latency and distance equally at 0.25 so their sum is equally weighted with dwell time at 0.50 (Skelton et al., 2006 and Livingstone et al., 2007). These 4 dependent variables were analyzed by first averaging over invisible platform Trials 2 to 10. Data from the first invisible platform trial in both mazes was excluded from the analysis because on this trial the participant is searching for an unknown location, whereas on subsequent trials they are returning to a place they have been and are therefore using different attentional and cognitive processes. Simple main effects of gender and strategy on these same 4 dependent variables were analyzed using standard independent *t* tests in Microsoft Excel. A Pearson's chi-square test (in Excel) was used to compare our observed strategy selection frequencies to those expected from chance and from previous research. Pearson correlations were calculated to determine whether any of the performance measures were related to video game experience or time spent exploring the maze. To investigate the confounding effects of computer experience on any correlated measures an ANCOVA was conducted using Systat 13.

Results

Male and female participants did not differ with respect to age (female $M = 20$ years, male $M = 19.35$ years), $t(35) = 0.49$, $p = .62$, or education (female $M = 13.21$ years, male $M = 12.17$ years), $t(35) = 0.85$, $p = .40$. There were no systematic differences in performance based on the counterbalanced positions of the target platform. There were no differences in the Ambiguous maze: latency: $t(35) = 1.08$, *ns*; distance: $t(35) = 0.63$, *ns*; dwell time: $t(35) = 0.86$, *ns*; spatial score: $t(35) = 1.15$, *ns*, and no differences in the Place maze: latency: $t(35) = 0.01$, *ns*; distance: $t(35) = 1.02$, *ns*; dwell time: $t(35) = 1.37$, *ns*; spatial score: $t(35) = 0.80$, *ns*. Differences in target position will not be considered further.

Both males and females performed well on visible platform trials. On average, males had slightly shorter latencies than females (male = 2.54 ± 0.12 s, female = 3.44 ± 0.18 s). Although this difference was statistically significant, $t(35) = 4.197$, $p < .001$, $d = -1.15$, it may not be meaningful since the mean difference was less than one second, the variances were small due to a floor effect and there were no differences in distances traveled, $t(35) = 1.55$, $p = .13$, $d = -.50$. This performance showed that male and female participants were capable of manipulating the controls and following the instructions required for completing the tasks.

Consistent with previous findings, males had better performance than females in the Ambiguous maze (see Figure 4). In terms of latency, males tended to approach asymptotic performance very quickly, whereas females remained somewhat variable through testing in both Ambiguous and Place mazes. However, in terms of directness of route to the platform (i.e., distance), males and females both reach asymptotic performance quickly in both mazes. To compare these performance differences over the entire testing in each maze, males and females were compared in terms of their average latency and distance in Trials 2 to 10 (i.e., navigational memory trials). In the Ambiguous maze, males took less time to reach the platform, $t(35) = 4.89$, $p < .001$, $d = -1.29$, traveled shorter distances, $t(35) = 2.31$, $p < .05$, $d = -0.72$, and spent more time in the correct quadrant on probe trials, though this latter difference was a medium-sized effect that was not significant, $t(35) = 1.68$, $p = .10$, $d = 0.55$. When these three variables were combined into the summary variable, Spatial Score, males had significantly higher scores $t(35) = 3.57$, $p < .001$, $d = 1.03$. In the standard virtual MWM, the Place maze, which can be optimally solved only by using an allocentric strategy, the expected gender differences were present in all 3 standard measures and the summary spatial score, but were significant only in latency, $t(35) = 3.45$, $p = .001$, $d = -1.01$, and spatial score, $t(35) = 2.02$, $p < .05$, $d = -0.64$; see Figure 5.

The primary purpose of the present study was to determine whether males and females would use different strategies to navigate in an environment that allowed them to navigate equally efficiently using either an allocentric or an egocentric strategy. The dDTS (strategy probe) at the end of the Ambiguous maze revealed that by this point in the experiment, 34 of the 36 participants knew which quadrant the platform was located in, and were clearly using either an allocentric or a cue-based egocentric strategy. On this strategy-test trial, 20 of the 34 participants were identified as using an allocentric strategy to navigate. While males and females were equally accurate in their ability to locate the platform, $t(35) = 0.85$, $p = .40$, $d = 0.29$, surprisingly, the proportion of females navigating allocentrically (13 of 18, 72%) was greater than the proportion of males (9 of 16, 56%). In other words, by the end of 10 trials in the Ambiguous maze, there was a bias for females to be using an allocentric strategy, whereas males were not strongly biased in either direction (see Figure 6). While this difference in frequency was not significant once the apparent allocentric bias of the maze was factored out, $\chi^2(1, N = 34) = 0.95$, $p = .33$, this analysis is based on the expectation that there would be no differ-

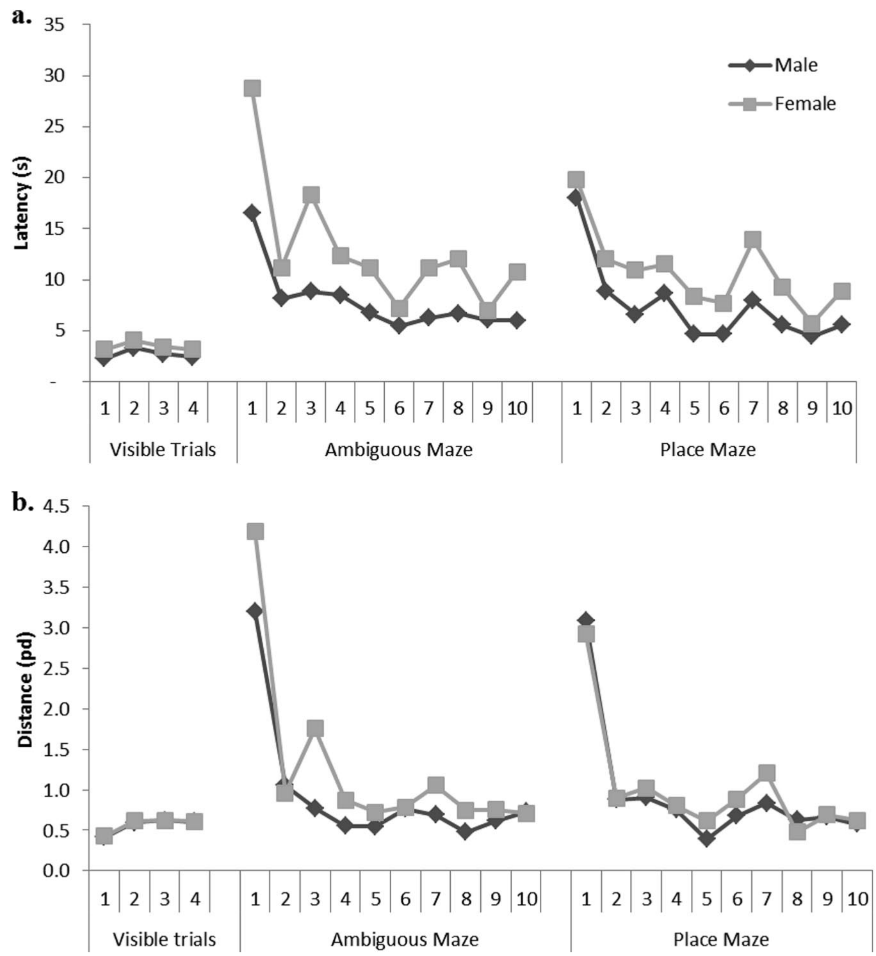

Figure 4. Male and female mean performance on (a) latency (s) and (b) distance (pd) over trials. A color version of this figure is available in the supplemental materials.

ence in the preference for strategies by males and females. However, as described in the introduction, the literature has strongly indicated that most if not all males prefer an allocentric strategy, whereas most if not all females prefer an egocentric strategy (e.g., Woolley et al., 2009; Coluccia & Louse, 2004; Andersen, Dahmani, Konishi, & Bohbot, 2011). In order to test this hypothesis with our data, we adopted the conservative estimate that 60% of males should prefer an allocentric strategy and 60% of females would prefer an egocentric strategy and tested these expected values against the proportion we observed in our study. Pearson chi square analysis for goodness of fit (Zar, 1999) revealed the frequencies of strategy choices in the present study to be significantly different from what one might have predicted based on previous studies, $\chi^2(1, N = 34) = 4.48, p < .05$.

In other words, in our paradigm that allowed free choice of strategy, the expected gender bias in strategy choice did not appear: males were not biased toward using an allocentric strategy and females were not biased toward an egocentric strategy.

Also contrary to what would be expected from the navigation literature, the performance difference between males and females could not be accounted for by strategy selection. Analysis of the relationship between preferred strategy choice and performance in the Ambiguous maze showed that, overall, strategy choice had no significant effect on performance (see Figure 7). No significant differences were found between those using allocentric and egocentric strategies on latency, $F(1, 30) = 0.09$, $p = .76$, $d = -0.30$; distance, $F(1, 30) = 0.002$, $p = .96$, $d = -0.15$; probe trial dwell time, $F(1, 30) = 0.18$, $p = .68$, $d = 0.24$; or spatial score, $F(1, 30) = 0.18$, $p = .68$, $d = 0.30$. Furthermore, there were no significant gender by strategy interactions: latency, $F(1, 30) = 0.47$, $p = .50$; distance, $F(1, 30) = 0.08$, $p = .78$; dwell time, $F(1, 30) = 0.15$, $p = .70$; or spatial score, $F(1, 30) = 0.35$, $p = .56$ (see Figure 7). Males who chose an allocentric strategy tended to perform better than males who chose an egocentric strategy, whereas females who chose an egocentric strategy tended to perform better than females choosing an allocentric strategy, but these tendencies were not supported by gender by strategy interactions ($p > .05$). Nevertheless, it is worth noting that there were significant gender differences among those who chose to use an allocentric strategy in latency, $t(33) = 4.38$, $p < .001$, $d = 1.38$; distance; $t(33) = 2.19$, $p < .05$, $d = 0.83$; and spatial scores, $t(33) = 2.89$, $p < .01$, $d = 1.13$, whereas there were no significant gender difference in any of the 4 measures of navigational

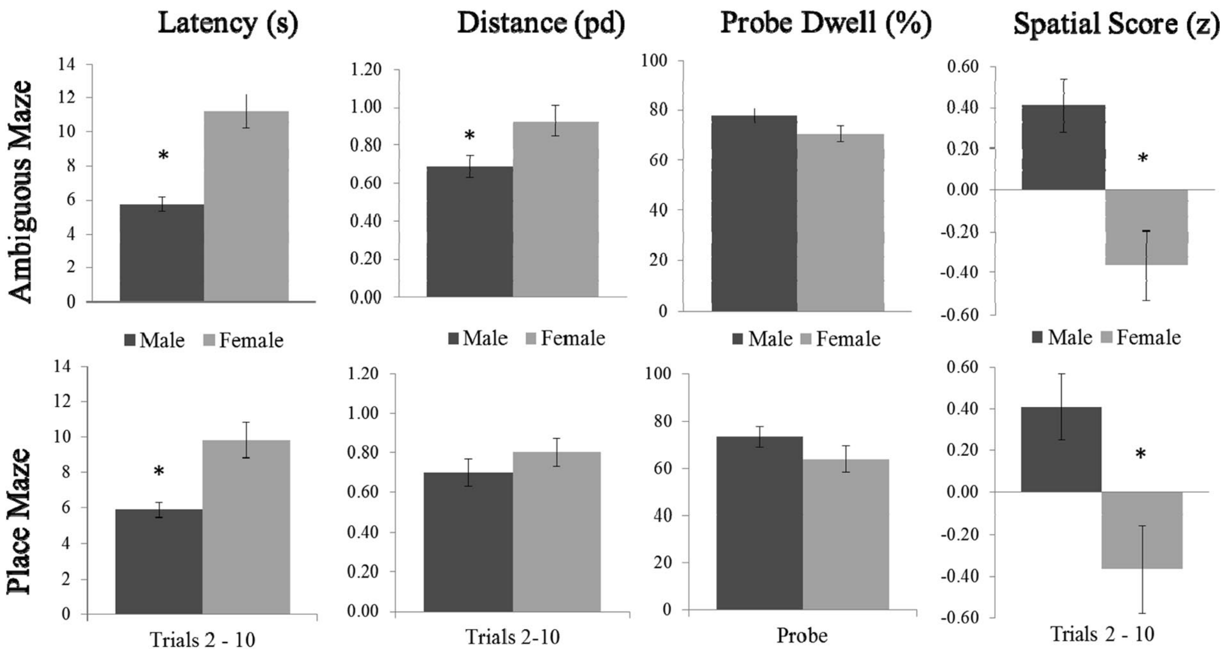

Figure 5. Mean differences of performance results for males and females in the Ambiguous and Place mazes: Latency (s) and distance (pd) to reach the invisible platform are averages of trials 2 to 10; probe dwell time (%) shows the amount of time participants spent in the correct quadrant during probe trials; spatial score (z) is a summary variable that incorporates all three standard measures (see Data Analysis for detailed description). * $p < .05$. Error bars represent the standard error of the mean. Ambiguous maze distance and Place maze latency and spatial score are rendered non-significant after video game experience is factored out. A color version of this figure is available in the supplemental materials.

performance among those who chose to use an egocentric strategy.

The participants' preferred strategy (as shown in the Ambiguous maze) made little or no difference to performance in the Place maze. There were no significant differences in any variable based on preferred strategy: latency: $F(1, 30) = 0.12$, $p = .73$, $d = -0.28$; distance: $F(1, 30) = 0.00$, $p = .98$, $d = -0.08$; probe trial dwell time: $F(1, 30) = 0.33$, $p = .86$, $d = 0.02$; and spatial score: $F(1, 30) = 0.00$, $p = .97$, $d = -0.10$. There also were no gender by preferred strategy interactions: latency: $F(1, 30) = 0.12$, $p = .73$; distance: $F(1, 30) = 0.52$, $p = .48$; dwell time: $F(1, 30) = 0.01$, $p = .93$; and spatial score: $F(1, 30) = 1.07$, $p = .75$.

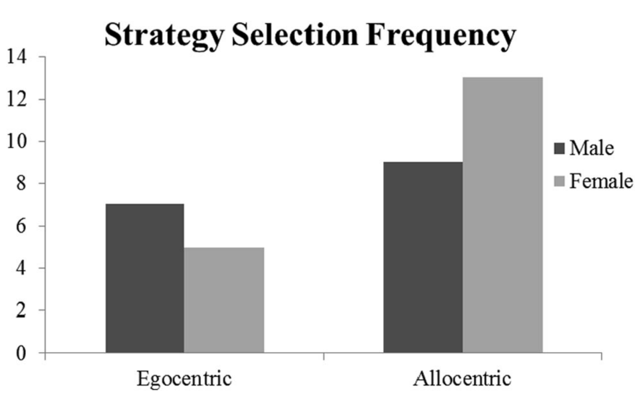

Figure 6. Egocentric and allocentric strategy selection frequencies for males and females based on the dDTS trial. A color version of this figure is available in the supplemental materials.

Figure 7 illustrates the lack of interaction between gender and strategy on performance in the Place maze. While allocentric males reached the platform in significantly less time than allocentric females, $t(33) = 2.74$, $p < .01$, $d = 1.07$, they traveled equivalent distance, $t(33) = 1.58$, $p = .13$, $d = 0.68$, spent the equivalent amount of time in the correct quadrant on probe trials, $t(33) = 1.13$, $p = .27$, $d = -0.52$, and had equivalent spatial scores, $t(33) = 1.73$, $p = .09$, $d = 0.77$. Egocentric males and females did not differ significantly on invisible platform latency, $t(33) = 1.89$, $p = .09$, $d = 0.85$, distance, $t(33) = 0.36$, $p = .73$, $d = 0.15$), probe dwell time, $t(33) = 0.94$, $p = .37$, $d = -0.46$, or spatial score, $t(33) = 1.19$, $p = .24$, $d = 0.53$ (see Table 2).

Although females spent more time learning the environment in the exploration trial, $t(35) = 2.43$, $p < .05$, $d = -0.76$, this difference was not related to any measures of navigational performance or cognitive map quality. Pearson correlations showed that time spent exploring the maze environment did not correlate with any dependent measure of performance or cognitive map usage (Room Reconstruction and Where's the Water scores) in either the Ambiguous maze or the Place maze, nor with video game experience ($p > .05$).

Analysis of Video game experience showed that it explained some but not all of the gender differences in performance in either the Ambiguous maze or the Place maze. Males reported significantly more video game experience than females, $t(35) = 4.62$, $p < .001$, $d = 1.27$, and Pearson correlations revealed that video

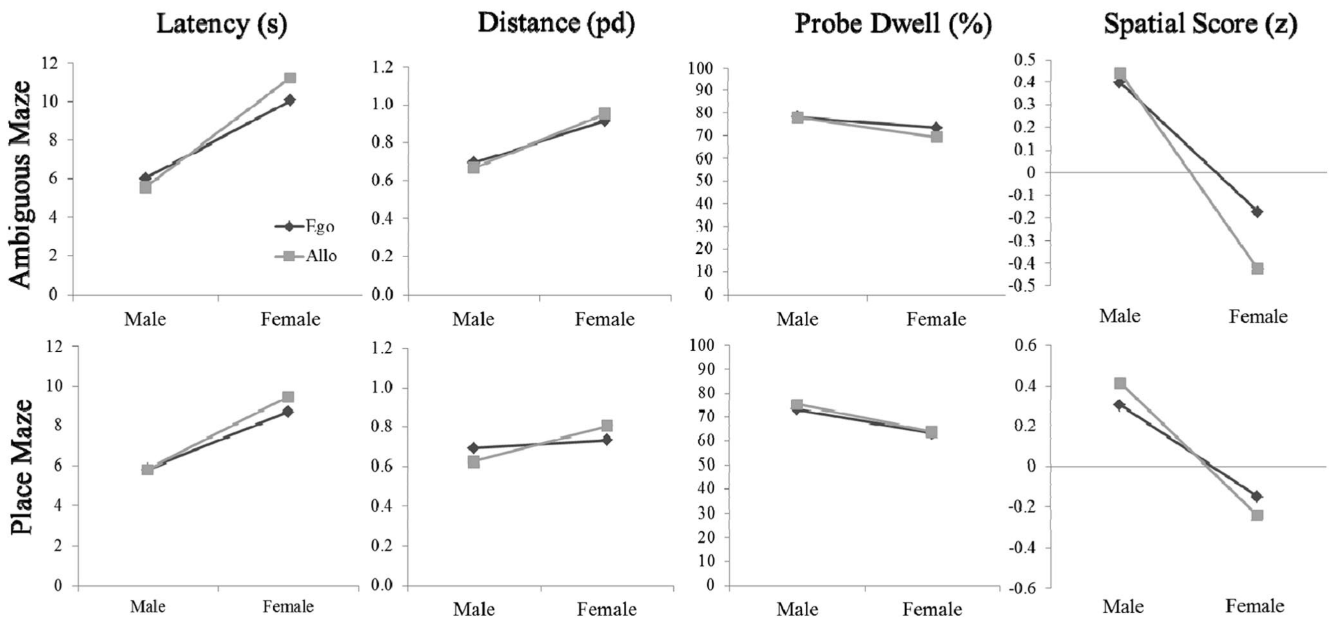

Figure 7. The minimal effect of strategy on gender performance in the Ambiguous and Place mazes: Latency (s) and distance (pd) to reach the invisible platform on trials 2 to 10; dwell time (%), the amount of time participants spent in the correct quadrant during probe trials; spatial score (z), a summary variable that incorporates all three standard measures (see Data Analysis for detailed description). No error bars are shown because no gender differences were significant. A color version of this figure is available in the supplemental materials.

game experience was related to Ambiguous maze latency ($r = -.64$, $p = .001$), distance ($r = -.36$, $p < .05$) and spatial score ($r = .45$, $p < .01$), as well as Place maze latency ($r = -.47$, $p = .01$). An analysis of covariance (ANCOVA) with gender as the independent factor and game experience as the covariate showed that even after partialing out game experience, there remained gender differences in Ambiguous maze latency, $F(1, 33) = 6.71$, $p = .01$, and spatial score, $F(1, 33) = 4.21$, $p < .05$ but not distance, $F(1, 33) = 1.22$, $p > .05$. In the Place maze, once the effect of video game experience was partialed out, there were no significant gender differences in any of the three navigational variables: latency: $F(1, 33) = 3.36$, $p = .08$; distance, $F(1, 33) = .456$, $p > .05$; or spatial scores, $F(1, 33) = 1.63$, $p > .05$.

Although factoring out video game experience did render some gender differences nonsignificant, this does not mean that it was an important contributor to performance. An ANCOVA that factored out both video game experience and strategy revealed that for Ambiguous maze latency, the variable which showed the greatest gender differences, the effect size for gender was 1.67, the effect size for video game experience was 0.25 and the effect size for strategy was 0.005. In other words, video game experience had very little effect and strategy almost none at all.

Neither measure of cognitive map usage revealed any difference between males and females (see Table 3). Results from the Ambiguous maze Room Reconstruction test revealed no significant differences between gender or strategy groups in the ability to

Table 2
Mean Scores (± SEM) by Gender and Strategy

Measures	Allocentric		Egocentric	
	Male	Female	Male	Female
Ambiguous maze trials 2–10				
Latency (s)	5.56 ± 0.51	11.23 ± 1.12	6.01 ± 0.81	10.04 ± 2.07
Distance (pd)	0.67 ± 0.08	0.95 ± 0.10	0.70 ± 0.12	0.91 ± 0.17
Probe (%)	78.00 ± 3.86	69.23 ± 4.46	78.14 ± 6.03	73.40 ± 3.61
Spatial Score (z)	0.44 ± 0.17	−0.43 ± 0.23	0.40 ± 0.23	−0.17 ± 0.27
Place maze trials 2–10				
Latency (s)	5.89 ± 0.41	9.81 ± 1.01	5.80 ± 0.57	8.68 ± 1.26
Distance (units)	105.19 ± 9.98	120.40 ± 10.69	103.71 ± 12.66	109.71 ± 11.10
Probe (%)	73.24 ± 4.55	63.89 ± 5.36	73.14 ± 6.16	63.00 ± 8.57
Spatial Score (z)	0.41 ± 0.22	−0.24 ± 0.30	0.30 ± 0.24	−0.15 ± 0.27

Table 3
Mean Scores and Significance of Differences for Cognitive Map Measures

Test	Male (Mean ± *SEM*)	Female (Mean ± *SEM*)	$t(35)$	$p <$	Cohen's d
Room Reconstruction after Ambiguous maze	4.12 ± 0.40	3.79 ± 0.27	0.68	.50	0.23
Room Reconstruction after Place maze	6.59 ± 0.36	4.79 ± 0.46	3.07	.01	0.91
Where's the Water after Place maze	2.71 ± 0.11	2.63 ± 0.11	0.46	0.65	0.16

capture the spatial relations between environmental elements. Males scored slightly higher than females, but this difference failed to reach significance, $t(35) = 0.68$, $p = .50$, $d = 0.23$, as did the overall difference between allocentric and egocentric choosers, $t(33) = 0.08$, $p = .94$, $d = 0.03$. There were also no significant differences based on gender and preferred strategy selection, with allocentric males and females, $t(33) = 0.19$, $p = .85$, $d = 0.08$ and egocentric males and females, $t(33) = 1.39$, $p = .19$, $d = -0.95$ performing equivalently. There were no significant correlations between Ambiguous maze Room Reconstruction scores and the navigational performance on any measure of navigational performance in the Ambiguous maze ($p > .05$). After the Place maze, males scored significantly better than females in Room Reconstruction, $t(35) = 3.07$, $p < .01$, $p = .91$. However, strategy selection in the Ambiguous maze (as per the dDTS trial) was not related to Place maze Room Reconstruction score, $t(33) = 0.16$, $p = .87$, $d = 0.06$, and there was no difference between egocentric males and females, $t(33) = 1.19$, $p = .26$, $d = -0.74$. Allocentric males were significantly better than allocentric females in the Place maze Room Reconstruction, $t(33) = 2.79$, $p = .01$, $d = -1.03$, but once again, Room Reconstruction scores were unrelated to navigational performance scores in either the Place or the Ambiguous maze ($p > .05$).

When asked whether the objects had moved on the dDTS trial, only 5 (2 female, 3 male) out of the 34 participants with a clear strategy reported noticing that it had moved, none of whom had been classified as "egocentric."

The results of the Where's the Water test revealed neither gender nor spatial strategy made a difference in the ability to apply a cognitive map in an environment. Males scored slightly higher on average than females but this was not significantly different, $t(35) = 0.46$, $p = .65$, $d = 0.16$. The scores from Where's the Water did not differ overall with respect to spatial strategy used in the dDTS trial, with allocentric navigators performing only slightly better than egocentric navigators, $t(33) = 1.52$, $p = .14$, $d = -0.57$. Lastly, there were no significant differences based on gender and strategy use on Where's the Water scores. Males and females who selected an allocentric strategy in the dDTS were equivalent, $t(33) = 1.13$, $p = .27$, $d = 0.41$, as were males and females who selected an egocentric strategy, $t(33) = 0.54$, $p = .60$, $d = -0.36$.

Discussion

The present study directly tested the proposition that males and females prefer to use different spatial strategies—specifically, that males prefer allocentric strategies, while females prefer egocentric strategies, and that this explains why the gender differences in performance are larger under allocentric conditions than egocentric conditions (Astur et al., 1998; Sandstrom et al., 1998; Saucier et al., 2002). The present results showed that when healthy male and female participants are given the opportunity to spontaneously select a spatial strategy in a situation in which both allocentric and egocentric strategies lead to efficient navigation, males do not prefer allocentric navigation more than females do, and navigational performance does not depend on their strategy choice. In a probe trial at the end of training in our Ambiguous maze, which could be solved equally well using egocentric or allocentric strategies, females showed that they had been using an allocentric strategy with a frequency as great as, if not greater, than males. Although females performed well in both mazes, their performance was not quite as efficient at finding the platform as males were (i.e., they had longer latencies and better spatial scores), but it is important to note that strategy choice did not account for the difference in performance. Males and females performed equally well on reconstructions of the environment after the Ambiguous maze, and individual differences in the ability to form cognitive maps did not account for differences in navigation performance.

In this study we employed a novel method of differentiating navigational strategy choice, based on the combination of a specially constructed virtual environment (the Ambiguous maze) and a novel test, the "dDTS" trial. The Ambiguous maze permits egocentric navigation because a single cue maintains a simple, stable relationship with the stationary goal platform. That is, one cue is all the participant needs to make the appropriate body turns to get to the target (if the cue is to the person's left, then simply turn left). At the same time, the Ambiguous maze permits allocentric navigation through the use of a configuration of primarily distal cues. No distal feature is directly in line with the platform location because the platform is on the diagonal and room corners block all diagonal views of the environment. Therefore, participants must use the unvarying features of the landscape, in combination with the window configurations to determine their position and directionality to move until they are in the correct quadrant at the right distance from the arena wall. In this, the Ambiguous maze is like the standard MWM, the "gold standard" of allocentric navigation.

The environmental features of the Ambiguous maze allowed participants to choose to navigate using an allocentric or egocentric strategy. A novel probe trial was used to discern which strategy each participant had selected. On this dDTS trial, the predictive cue object that supported egocentric navigation was placed in competition with the configurational landscape and room features that supported allocentric navigation. Others have used a similar procedure to identify accuracy of platform knowledge in a virtual MWM (Hardt et al., 2009) or to dissociate allocentric from response-based egocentric strategies in a star maze (Iglói et al., 2009). Iaria et al. (2003) dissociated allocentric and cue-based egocentric strategies in a virtual radial arm maze (RAM) based on a combination of self-report and performance decrements on removal of environmental cues.

In the present study, navigational choice on the strategy probe trial at the end of testing was used to indicate the preferred strategy each participant had been using throughout training. Although this trial only provides direct data on the spatial strategy in use during the dDTS itself, and not on preceding trials, it is reasonable to suppose that once a participant has selected a strategy, that that strategy predominates through the remainder of testing. It is worth noting that not only did the participants choose to navigate according to one or the other strategies, not a single participant in the egocentric navigation group even noticed that the objects moved against the background. This indicates that those who had selected an egocentric strategy had been using this strategy throughout. Ongoing research in our laboratory on the course of spatial strategy acquisition has indicated that in our paradigm at least, once participants select a particular strategy, they do not switch (Yim, Murchison, & Skelton, NOWCAM 2011). In other words, the strategy used on the strategy probe trial closely reflects the strategy participants had been using on previous trials.

Although gender bias in strategy selection has been studied previously, we believe that the present results provide a better estimate of "spontaneous" strategy selection, and therefore a better indication of the presence or absence of gender differences. In a previous study, Levy, Astur, and Frick (2005) tested whether participants went to a platform that had the same visual appearance, or the same spatial location, as the platform used in training. In this study, they found that approximately 65% of females and 60% of males went to the visually similar platform (i.e., following egocentric navigation). However, this preference for the egocentric navigational strategy may have been influenced by the salience of the platform color, or by the virtual navigation tasks which preceded the virtual MWM task. In the immediately proceeding task, a T-Maze, almost 90% of males and over 60% of females navigated egocentrically. Performance in this task could have been influenced by immediately preceding training in a virtual RAM. Although the authors did not measure strategy choice in this, the participants' first maze, others have found the virtual RAM to be 72% egocentrically biased by the end of training (Iaria et al., 2003). The idea is that participants would adopt and continue to use a navigational strategy for which they had been recently rewarded. In fact, we have found this to be true (Livingstone, Zeman, Gandhi, Stewart, & Skelton, 2009, manuscript in preparation). A key feature of the present study is that we tested strategy selection in an ambiguous maze before training in any other maze.[1]

One of the most important findings of this study was that the strategy selection frequencies that we found were different from what we would expect from the literature. Previous studies of gender differences in navigation strategies seem to indicate that males prefer navigating allocentrically and females prefer to navigate egocentrically, and that this difference is large and reliable. For example, when participants are asked to verbally report or draw how they navigate generally (Lawton, 1994) or how they navigated recently experienced prescribed indoor environments (Lawton, 1996; Pazzaglia & De Beni, 2001), and their descriptions are classified by the experimenters as relying on egocentric or allocentric environmental features, then men are more likely to report using an allocentric (orienting) strategy whereas women are more likely to report using an egocentric (route) strategy. Similarly, when experimenters have asked participants to give directions based on recently learned maps (Dabbs et al., 1998), or have classified participants' navigation ability based on self-report surveys, males more frequently use allocentric referents (e.g., cardinal directions, Euclidian distances) while females more frequently use egocentric referents (Lawton & Kallai, 2002; Pazzaglia & De Beni, 2001). When navigating virtual MWMs, males perform better than females under allocentric conditions, while under egocentric conditions gender performance is equivalent (Astur et al., 1998; Sandstrom et al., 1998; Saucier et al., 2002). Unfortunately, most researchers studying gender differences do not measure or report what proportion of men and women rely on each form of navigational strategy.

When the frequencies of strategy preference are measured directly, neither males nor females seem to have a consistent, dominant strategy. Pazzaglia and De Beni (2001) had participants navigate an indoor environment and then classified their self-reported strategies. They found that males were slightly more likely (56%, 10 of 18 participants) to describe their navigation as being oriented to local landmarks (i.e., egocentrically) than by overview of the spatial layout (i.e., allocentrically), whereas an equal number of women (13 of 26) used either frame of reference. Levy et al. (2005) reported that in their virtual MWM, an egocentric strategy was selected by 65% of females (17 of 26) and 57% of males (12 of 21). Our findings trended in the opposite direction, with an allocentric strategy being selected by 72% of females (13 of 18) and 56% of males (9 of 16). To our mind, these findings together indicate that there is no consistent gender bias in strategy selection. This idea is supported Iaria et al.'s (2003) finding that people can and do switch strategies rapidly in response to environmental demands.

Previous authors have suggested that gender differences in navigational performance in allocentric and egocentric environments is due to females not being able to choose or properly use an allocentric strategy. The present results repudiate the idea that navigational performance is due to differences in strategy selection, but provide some support for the idea that females may not be as adept as males at using an allocentric strategy. In previous research (Astur et al., 1998; Sandstrom et al., 1998; Saucier et al., 2002), males performed better than females, and appeared to perform slightly better when they were navigating allocentrically and females when they were navigating egocentrically. These observations were replicated in the present study. The summary variable, spatial score, shows that males performed best when they were navigating allocentrically, and females performed best when they were navigating egocentrically (see Figure 8). This suggests that females perform worse in navigational tasks not because they cannot or do not choose an allocentric strategy, but rather because they are not as good as males at using an allocentric strategy, and not as good at using it as they are an egocentric strategy.

[1] Although it could be argued that our "visible platform" training reinforced egocentric navigation, this seems unlikely because there was strong visual difference between the mazes (i.e., visible versus invisible platform) and because overall, both males and females predominantly selected an allocentric strategy.

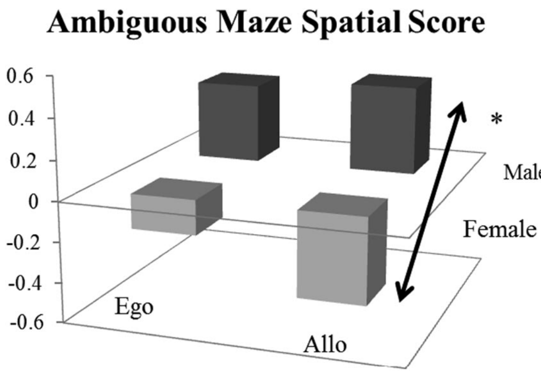

Figure 8. Mean strategy by gender group spatial scores on the Ambiguous maze for trials 2 to 10. Star represents significant difference. $^{*} p < .05$. A color version of this figure is available in the supplemental materials.

It is not clear that navigational performance is related to an individual's or a gender's ability to construct cognitive maps. In a situation where it was not essential to construct a cognitive map of the environment, males and females seemed to build comparable maps, as shown by the Room Reconstruction and "Where's the Water" scores. This is despite superior performance by males. However, when in a situation where knowledge of the whole environment was critical (i.e., in the Place maze), males constructed a demonstrably better cognitive map (as shown by the Place maze Room reconstruction). Although males were also better than females at navigating the Place maze, there was no evidence that this was related to a superior cognitive map.

One might expect that the gender difference in navigational performance should have been larger in the allocentric Place maze than in the strategy-equivalent Ambiguous maze. However, the performance of males in the Ambiguous maze was close to asymptotic, and there was little room from improvement through practice. In their metastudy, Baenninger and Newcombe (1989) concluded that males and females are equally sensitive to practice effects in spatial tasks. Because females were not at asymptotic performance by the end of the Ambiguous maze, there was room for practice effects to improve their performance in the Place maze, and thereby shrink the observed gender effect.

Although our strategy selection results contradict the idea that genders have different preferred strategies, on the face of it, our performance results are consistent with the idea that individuals have preferred strategies, and do not navigate as well if forced to use an alternate strategy. This idea has received support from several previous studies (Etchamendy & Bohbot, 2007; Iaria et al., 2003; Iglói et al., 2009). However, even in these studies, there was evidence that some individuals "switched" strategies during training. We believe that strategy selection is not an immutable trait of an individual, but rather, is a cognitive skill available to a larger portion of the male and female population. In future studies we plan to investigate the process and determinants of strategy selection, by a variety of means, including tracking gaze position to determine what strategy an individual is using at any given time (Livingstone et al., 2009; Livingstone-Lee et al., 2011).

In conclusion, the results of this study reveal similarities, not differences, in patterns of male and female spontaneous spatial strategy selection. While performance data replicated previous research and showed a general male advantage in navigation, especially under allocentric conditions, there was no evidence for a systematic pattern of strategy preference or any effect of spatial strategy selection on navigational performance. In other words, when strategy selection was measured directly in a situation where either strategy was efficient, females preferred an allocentric strategy at least as often as males did. These results highlight the importance of measuring strategy selection directly, rather than indirectly inferring strategy preference from verbal reports or performance data alone. Our results indicate that males and females may not maintain a dominant strategy consistently within gender or across time or circumstance. Rather, it seems that other factors, such as immediate environment and recent experience, influence strategy selection over and above gender. This has important implications for the design and approach of experiments that seek to explain gender differences in navigational performance and for our understanding of apparent gender differences in navigation. It also has implications for the idea that the different genders may be differentially biased toward the use of different neural systems for navigation. Our findings indicate that males are not dominated by their hippocampus and females by their basal ganglia, but that both genders use these systems in concert, to a degree required by the environment and their knowledge of it.

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