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Men and Women Differ in Object Memory but Not Performance of a Virtual Radial Maze

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The present study examined sex differences in object memory by using 2-dimensional object arrays and in spatial memory by using a computerized virtual 12-arm radial maze. Virtual T-maze and water maze tasks were also used to examine sex differences in the use of spatial and nonspatial strategies during navigation. Women significantly outperformed men in recalling the locations and identities of objects. However, the sexes did not differ in the commission of working memory and reference memory errors in the radial maze or in the use of particular navigational strategies. Because arms in the radial maze may become associated with specific extramaze cues, the superior object memory demonstrated by women may have eliminated the typical male advantage found in spatial navigation tasks.

Keywords: sex differences, spatial memory, radial-arm maze, spatial strategy, human

Numerous studies have shown that men outperform women in a variety of cognitive tasks (Astur, Tropp, Sava, Constable, & Markus, 2004; Moffat, Hampson, & Hatzipantelis, 1998; Postma, Izendoorn, & De Haan, 1998). Among these cognitive paradigms, perhaps the most studied behaviors are spatial memory and navigational abilities (Astur, Ortiz, & Sutherland, 1998; Groen, Wunderlich, Spitzer, Tomczak, & Riepe, 2000; Sandstrom, Kaufman, & Huettel, 1998; Saucier et al., 2002). In rodents, one of the most commonly used tasks to test spatial memory is the radial-arm maze. This maze consists of a circular arena, from which multiple arms radiate outward, placed in a room with various extramaze cues. In the standard version of the task, animals learn to navigate around the maze by using extramaze cues and to visit each arm only once to retrieve rewards placed at the ends of the arms (Olton & Samuelson, 1976). Because rodents naturally enter arms in a different sequence from trial to trial, memory for arms visited in a given session is trial dependent. Thus, this version of the radial-arm maze tests spatial working memory, a type of memory that is dependent on the integrity of the hippocampus (Olton & Pappas, 1979). Although male rodents typically learn the standard radial-arm maze task faster than do females (Einon, 1980; Roof, 1993), other studies report no sex differences in radial maze performance (Juraska, Henderson, & Muller, 1984; Williams & Meck, 1991), likely because nonmnemonic strategies (such as entering adjacent arms) can be used to locate the rewards (Williams, Barnett, & Meck, 1990; Williams & Meck, 1991).

An alternative version of the radial-arm maze reduces the effectiveness of nonspatial strategies. This version tests both spatial working memory and spatial reference memory by leaving half of the arms unbaited (Olton & Pappas, 1979). These unbaited arms are interspersed among the baited arms, thereby reducing the effectiveness of a nonspatial adjacent arm strategy. The location of the unbaited arms remains constant throughout all trials, and thus, memory for visits to these arms is trial independent. As such, the unbaited arms test spatial reference memory, which in this task is more dependent on the neocortex than on the hippocampus (Olton & Pappas, 1979; Porter & Mair, 1997). Sex differences in this version of the task are reliably observed in both rats (Williams et al., 1990; Williams & Meck, 1991) and mice (Gresack & Frick, 2003; LaBuda, Mellgren, & Hale, 2002; Mishima, Higashitani, Teraoka, & Yoshioka, 1986), such that males exhibit better working and reference memory than do females, particularly during task acquisition. Compelling evidence suggests that the male advantage in radial-arm maze learning is due to organizational effects of sex steroid hormones, primarily estradiol (Roof, 1993; Williams et al., 1990; Williams & Meck, 1991).

Increasingly sophisticated three-dimensional computer graphics have led to the development of virtual maze tasks based on those used in rodents. Virtual versions of many rodent spatial memory tasks have been developed, including the radial-arm maze, the Morris water maze, and the T-maze. Men typically perform better than women in virtual Morris water mazes (Astur et al., 1998), miniature two-dimensional mazes (Moffat et al., 1998), and virtual mazes with no extramaze cues (Groen et al., 2000; Moffat et al., 1998). However, Sandstrom et al. (1998) tested subjects on three different versions of the Morris water maze and found that men

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performed better than women when landmark information did not predict the target platform location, whereas sex differences in task performance were not observed when extramaze cues were available and reliable. It is interesting to note that Astur et al. (2004) recently reported no sex differences in performance of an 8-arm radial maze testing both spatial working and reference memory. This finding is curious because these same men and women differed in performance of a virtual spatial Morris water maze task (Astur et al., 2004) and given the predominance of data showing that men outperform women in spatial navigation tasks. Astur et al. speculated that the association of specific landmark cues with each arm in the radial maze may have facilitated performance in women, or perhaps the different strategies that men and women use are equally effective at helping them solve the task. Alternatively, it is possible that the task was too easy to tap into sex differences in spatial memory, and, therefore, sex differences might emerge in a more challenging version of the task. Thus, one goal of the present study was to explore further the performance of men and women in the radial-arm maze by using a more difficult 12-arm maze. The increased number of arms may reduce the association of individual landmarks with specific arms and reduce the effectiveness of the nonmnemonic strategies that women may use. Thus, we hypothesized that men would outperform women on the 12-arm version of the task.

Sex differences have also been noted in the navigational strategies that males and females use to solve spatial tasks. For example, in both rats and humans, males have been shown to primarily use euclidean (geometric) information to navigate (Sandstrom et al., 1998; Saucier et al., 2002; Williams et al., 1990; Williams & Meck, 1991), whereas females use both landmarks and euclidean information (Sandstrom et al., 1998; Williams et al., 1990; Williams & Meck, 1991). It is interesting to note that females navigate poorly when only euclidean information is available (Saucier et al., 2002), which suggests that they rely heavily on landmark cues to navigate properly. When landmark and euclidean strategy use has been systematically varied in two-dimensional and real world environments, men are most adept at using euclidean strategies, whereas women perform best using landmarks (Moffat et al., 1998; Saucier et al., 2002). In rats, strategy choice has been examined by using a modified T-maze task (Packard & McGaugh, 1996). Rats were first presented with a T-shaped maze and were consistently rewarded for entering the same arm (e.g., left) and finding a reward at the end. After the rats received considerable training, the T-maze was rotated 180° so that a left turn now led to the previously unrewarded arm. Use of a euclidean (or place) strategy was demonstrated if the rat entered the arm that was formerly baited (now requiring a right turn), which suggests the use of extramaze spatial cues to locate the rewarded arm. Use of a nonspatial response strategy was indicated if the rat simply made a left, which suggests the use of egocentric left–right turn responses to locate the reward. Previous work with lesioned rats run in this task suggests that the hippocampus facilitates the use of the place strategy, whereas the striatum promotes the use of the response strategy (Packard & McGaugh, 1996). Although sex differences in this task have not previously been examined in rodents or humans, exogenous estrogen and high levels of endogenous estrogen facilitate the use of a place strategy in female rats (Korol & Kolo, 2002; Korol, Malin, Borden, Busby, & Couper-Leo, 2004). To examine sex differences in strategy use in humans, we developed a virtual T-maze strategy task, as well as a virtual Morris water maze strategy task, for use in this study. In the water maze task, many trials were run in which a platform was found in the same location; for the final trial, the platform was moved to a new location and a new visible platform that differed in color and texture was substituted in its place. A response to the original platform was deemed a cue strategy because it was based on local features of the platform. In contrast, a response to the new platform (located in the original place) was deemed a place strategy because it was based on extramaze spatial cues. The hippocampus should mediate the place strategy in this task, given the reliance of this strategy on extramaze cues. On the other hand, the cue strategy is likely mediated by a region of the perirhinal cortex that is involved in object memory (Winters & Bussey, 2005), given the processing of local cues inherent to the cue strategy. Although this task is somewhat similar to the virtual T-maze in nature, it may be more susceptible to sex differences in strategy use given the robust male advantage in virtual Morris water maze tasks (Astur et al., 1998). Because estrogen promotes the use of a place strategy in female rats (Korol & Kolo, 2002; Korol et al., 2004), we hypothesized that women might use place strategies more than men would in both the T-maze and water maze tasks. This is the first study to examine sex differences by using these tasks.

The fact that women navigate by primarily using landmark cues may indicate that women encode more information about objects and object locations than do men. Indeed, several studies have shown that women are better than men at noticing object substitutions and displacements in two-dimensional object arrays when familiar objects are moved to previously occupied positions or when new objects are added to an object array (Eals & Silverman, 1994; McBurney, Gaulin, Devineni, & Adams, 1997; Silverman & Eals, 1992). However, this female advantage reportedly disappears when objects are displaced to previously unoccupied locations (James & Kimura, 1997) or when objects simply exchange positions (Duff & Hampson, 2001). Because these manipulations (exchanging object positions, moving objects to new positions, introducing new objects) have not been tested in the same subjects, it is not clear if these disparate findings are due to subtleties in the nature of sex differences in object memory or to methodological differences among studies. To address this issue, we tested men and women in the present study in three variations of an original two-dimensional object array.

The present study was designed to examine sex differences in spatial memory, spatial strategy utilization, and object memory in men and women. Spatial working and reference memory were tested with a virtual 12-arm radial maze. Strategy utilization was examined by using virtual T-maze and virtual water maze tasks. Object memory was examined by using pen-and-paper object arrays similar to those used by Silverman and Eals (1992). Elucidating differential sex differences in various cognitive domains in healthy subjects may ultimately lead to a better understanding of sex differences in the incidence of psychiatric illnesses and in the neural basis of sex differences in cognition. Furthermore, identifying sex differences in spatial strategy use may lead to the development of methods to teach more effective spatial skills that minimize sex differences in spatial navigation.

Method

Subjects

Graduate and undergraduate students at Yale University, ages 18–30 (24 women; 31 men; average age = 20.18 years), were recruited to participate in this study. Of these subjects, 35 were recruited from the subject pool of an introductory psychology class, 10 responded to an Internet advertisement and received $10 cash, and 10 were uncompensated volunteers. Approval for this study was obtained from the Yale University Institutional Review Board.

Apparatus

An IBM-compatible computer with a color monitor was used for the three virtual tasks. Each task was run with custom-written software. Participants navigated through the mazes by manipulating a joystick. The virtual mazes gave a first-person view so that if subjects pushed the joystick to the left, the view on the screen would pan to the left, and so on with other joystick movements. Each of the virtual rooms contained salient landmarks, such as wall hangings and bookshelves present around the room (see Figure 1).

Procedure

After providing informed consent, participants answered a personal information questionnaire requesting information about age, sex, race, SAT scores, handedness, and computer game experience. Specifically, participants marked on a 5-point scale the frequency with which they played general computer or video games (1 = *never,* 2 = *several times a year,* 3 = *several times a month,* 4 = *several times a week,* 5 = *everyday*). Using the same scale, they also rated how often they played computer or video games that require navigation through a simulated three-dimensional environment. Once subjects finished filling out the questionnaire, they received both verbal and written instructions about how each task would proceed. All participants were tested on the first two parts of the object array task, followed by three computer mazes and then the last part of the object array task. The duration of the entire experiment was approximately 60 min.

Object Array Task

Subjects were presented with an array of black and white line drawings of 31 recognizable objects (Microsoft Office OSX) on an 8 1/2 × 11 piece of paper (Figure 2A) and were asked to study the objects for 1 min. They were then shown a second array in which seven pairs of objects exchanged positions (object-exchange condition, Figure 2B). The distance of the exchange varied such that exchanged objects could be immediately adjacent to each other or from opposite sides of the array. Subjects were given 1 min to circle any objects that moved from their positions in the original array. They were then presented with a third array in which 14 of the objects moved to positions that were not occupied in the original array (object-shift condition, Figure 2C) and were given 1 min to circle the moved objects.

After participants completed the three virtual maze tasks, they were asked to picture the original object array that was presented before computer testing. They were then shown a new object array containing 17 original objects in their original positions and 14 new objects in the same positions as the old objects (novel object condition, Figure 2D). Subjects were given 1 min to circle the new objects. For all three object test arrays, scores were calculated as the number of objects correctly circled minus the number of objects incorrectly circled. Because only 14 objects were altered in each array, the maximum possible score for each array was 14.

Radial-Arm Maze

Participants were told that they would find themselves in a virtual maze that had 12 arms extending out from a round central arena (Figure 1A and 1B). They were further instructed that at the end of each arm was an area that may or may not contain a reward. Six of the arms always contained a reward, and the other 6 never contained a reward. Subjects were informed that their goal was to retrieve all six rewards without reentering an arm in which they had already retrieved a reward. Upon discovering a reward, the text message “Reward!” appeared on the screen. Once participants found all six rewards, another message appeared on the screen: “Congratulations. You have found all the rewards.” The screen then turned black for an intertrial interval of 2 s, and a new trial began in which the subjects had to locate the six rewards again. Rewards were located in the same arms as in Trial 1. The six unrewarded arms tested reference memory, because this trial-independent information remained the same throughout testing (Olton & Pappas, 1979). The six rewarded arms measured working memory because information about which rewards had been previously retrieved varied from trial to trial (Olton & Pappas, 1979). Ten trials were administered in which the subjects were required to find all six rewards. The sequence of rewarded arms was varied among subjects to reduce the likelihood that a single reward pattern would unintentionally favor one sex. Three different reward sequences were used, and these were equally distributed between the sexes (Sequence A: 10 men, 8 women; Sequence B: 10 men, 8 women; Sequence C: 11 men, 8 women). These sequences differed only in which arms contained the six rewards. A reference memory error was scored as the first entry into an arm that was never rewarded. A working memory error was scored every time a participant reentered an arm that he or she had already visited during that trial, regardless of whether that arm was rewarded.

Strategy Tasks

T-maze. The purpose of this task was to determine whether subjects find rewards by using a place strategy (i.e., navigating by using extramaze cues) or a response strategy (i.e., navigating by using egocentric left–right movements). Participants were informed that they would find themselves in a T-shaped maze that had two arms extending in opposite directions from a middle start arm (Figure 1C and 1D). Like the radial-arm maze, the end of each arm contained an area that may or may not have a reward. Subjects were told that one of the arms always contained a reward, that the other arm was never rewarded, and that their goal was to retrieve the reward. When they found the reward, a text message displayed “Reward.” The maze was then reset, and the subjects were instructed to find the reward again. For the first five trials, the reward was always located on the right-hand side of the T.

On the 6th trial, the maze was rotated 180° and both arms were baited with rewards. If subjects chose the arm to their right, then they were recorded as using a response strategy. If the subjects chose the arm to their left, then they were recorded as using a place strategy. For Trials 7–11, the T-maze returned to its original position in the room. For the 12th trial, the T-maze was again rotated 180° and both arms were baited with rewards. Subjects were allowed to correct themselves in the T-maze, and a trial did not end until subjects found a reward.

Water maze. This task also addressed whether subjects used a spatial or nonspatial strategy to find rewards. Instructions for this task informed subjects that they would find themselves in a virtual round water maze in which they would be “swimming” at the surface of the water (Figure 1E and 1F). In order to escape from the water, they were told to swim to a visible circular escape platform and to climb onto it. The visible escape platform protruded from the water and was black with a smooth surface. Participants knew when they found a platform because the word “Congratulations!” appeared on the screen. Once the platform was found, the maze was reset and participants were required to find the platform again. Participants started from each of four

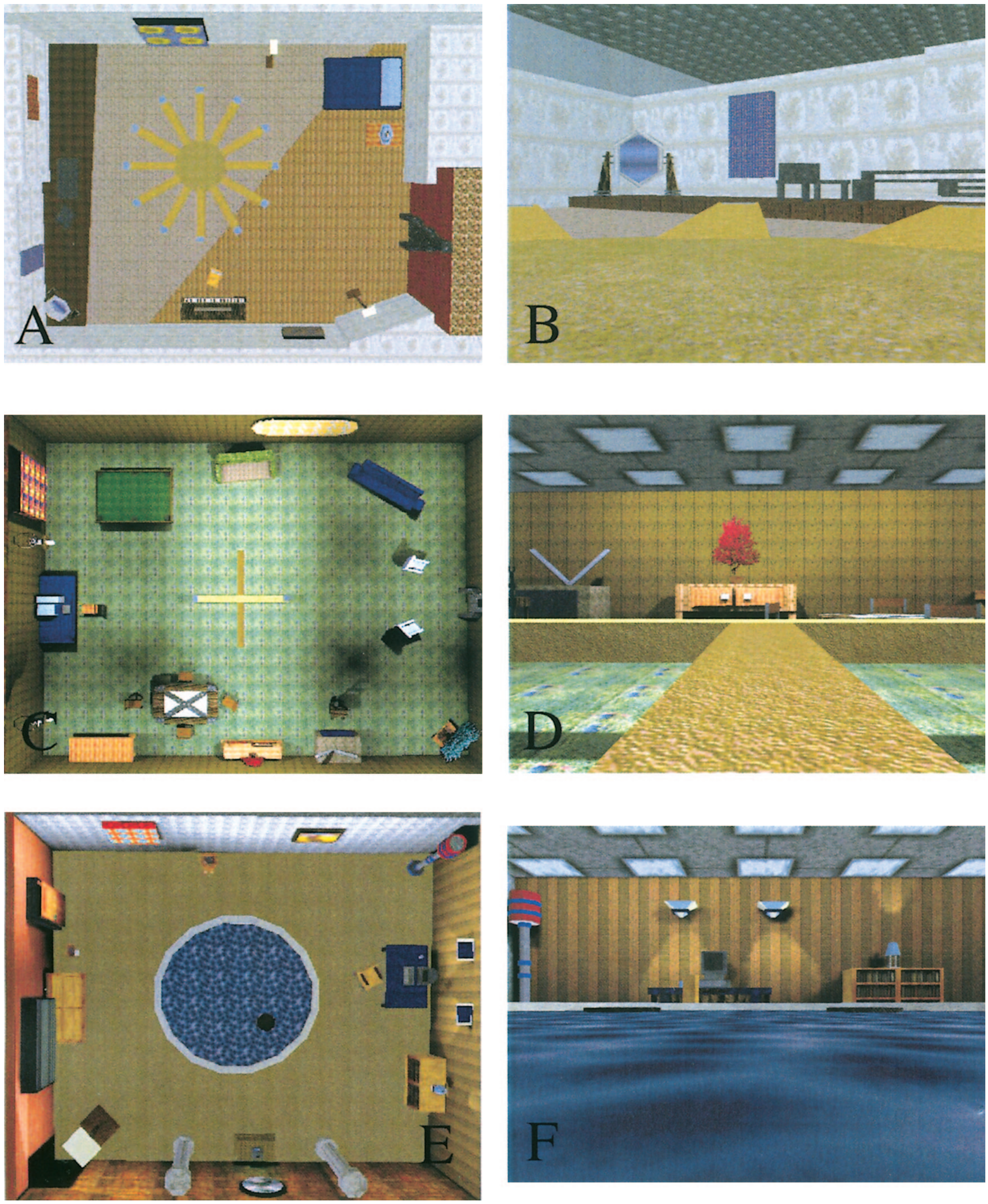

Figure 1. Extramaze and intramaze views of the 12-arm radial-arm maze (A and B), T-maze (C and D), and water maze (E and F). The radial-arm maze is shown from overhead (A) and from the perspective of the subject at the start position (B). The T-maze and water maze strategy tasks are also shown from the overhead perspective (C and E) and the start position perspective (D and F). Figure 1E illustrates the water maze during a training trial (only one platform is available), and Figure 1F illustrates the two available platforms in the water maze probe trial.

different locations (north, south, east, and west) five times each for a total of 20 trials with a 2-s intertrial interval.

On the 20th trial, two visible platforms were made available. The black platform from the previous trials was moved to a new location in the pool, and a new circular platform occupied its former position. The new platform also protruded from the water but was gray with a raised checkerboard texture. Both platforms were visible from the start position. Participants were rewarded for choosing either platform. Those choosing the old platform were categorized as using a cue strategy because they responded on the basis of the physical appearance of the familiar platform. In contrast,

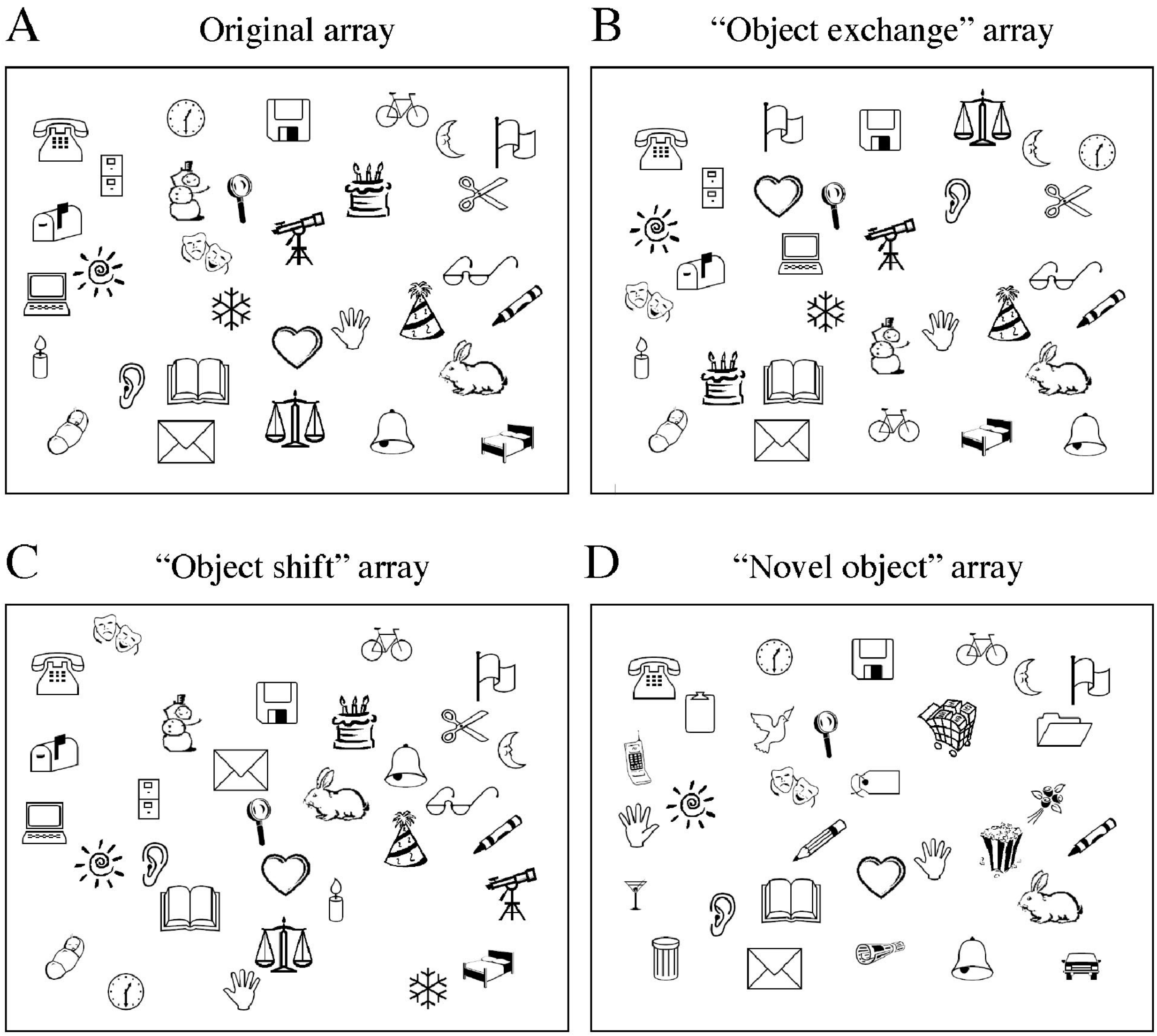

Figure 2. Subjects were given 1 min to study the original object array (A). They were then allowed 1 min for each of the following arrays to circle objects exchanged (B), switched (C), or new to the array (D).

those choosing the new platform (old location) were categorized as using a place strategy because they responded on the basis of the location of the platform (i.e., they swam to the previously rewarded location) rather than the visual cues on the platforms.

Results

Subjects

Fifty-five subjects (31 men and 24 women) completed the object array task, and 47 subjects completed all three virtual maze tasks (26 men and 21 women). There were 2 men and 3 women who did not finish the radial-arm maze because of nausea, 1 man did not finish the virtual T-maze and water maze strategy task because of nausea, and another 2 men were excluded from virtual maze task analyses because of a computer error resulting in missing data. Data analyses for the virtual maze tasks included only those subjects who completed all three tasks in order to ensure that variations in the subjects from task to task did not affect the observance of sex differences.

A one-way analysis of variance (ANOVA) demonstrated no sex difference in video game experience. The personal information questionnaire asked subjects to rate their video game experience, and responses reflected no main effect of sex on video game experience for general games or for three-dimensional navigational video games, $Fs(1, 45) = 0.04$ and 0.90, respectively, $ps >$

.05. There was also no main effect of sex on SAT scores, $F(1, 44) = 0.60$, $p > .05$.

Object Arrays

Women performed significantly better than did men in all object array tasks, as demonstrated by an ANOVA with object manipulation as the repeated measure, $F(1, 53) = 9.74$, $p < .01$ (see Figure 3). There was also a significant main effect of object manipulation, $F(2, 106) = 74.91$, $p < .0001$, but no significant Sex × Object Manipulation interaction, $F(2, 106) = 0.24$, $p > .05$. Independent *t* tests conducted for each array showed that women performed better than did men in each condition: object exchange, $t(53) = -2.01$, $p = .05$; object shift, $t(53) = -3.23$, $p < .05$; and novel object, $t(53) = -2.13$, $p < .05$. There were no significant sex differences in the total number of objects circled, as demonstrated by a repeated measures ANOVA, $F(1, 53) = 2.67$, $p > .05$, which suggests that sex differences in performance of the three arrays were the result of women making more correct and fewer incorrect choices than did men.

Radial-Arm Maze

The performance of women and men did not significantly differ on any radial-arm maze measure. ANOVAs with trial as the repeated measure were conducted for working memory errors, reference memory errors, and time to complete each trial. The main effect of sex was not significant for working memory or reference memory errors, $Fs(1, 45) = 0.32$ and 0.04, respectively, $ps > .05$ (Figures 4A and 4B). The significant main effects of trial for working and reference memory errors, $Fs(9, 405) = 7.11$ and 52.01, respectively, $ps < .001$, suggest that both sexes made fewer errors during the course of training. The Sex × Trial interaction was not significant for either error type: $Fs(9, 405) = 0.83$ and 0.30, for working and reference memory errors, respectively, $ps > 0.05$. For time to complete each trial, the main effect of trial was significant (Figure 4C), indicating that the time to complete a trial decreased with testing, $F(9, 405) = 16.09$, $p < .001$. However, time to complete a trial was not affected by sex, as suggested by a nonsignificant main effect of sex, $F(1, 45) = 1.11$, $p > .05$, and Sex × Trial interaction, $F(9, 405) = 1.38$, $p > .05$.

To examine the effects of SAT scores and video game experience on radial-arm maze performance, we conducted a correlation

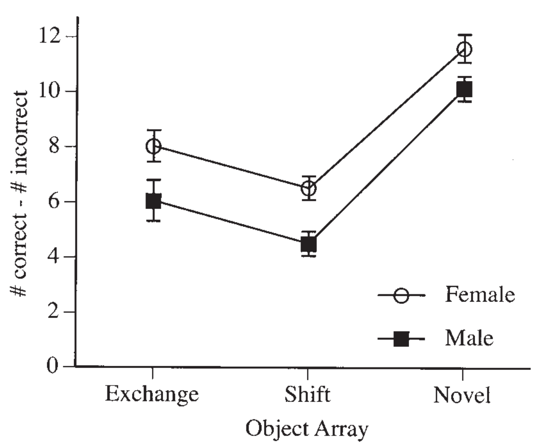

Figure 3. Women were better than men at correctly identifying objects that had changed locations or were replaced with novel objects in the array ($p < .05$ for each condition). Each symbol represents the mean (± *SEM*) number of objects correctly circled minus the number of objects incorrectly circled.

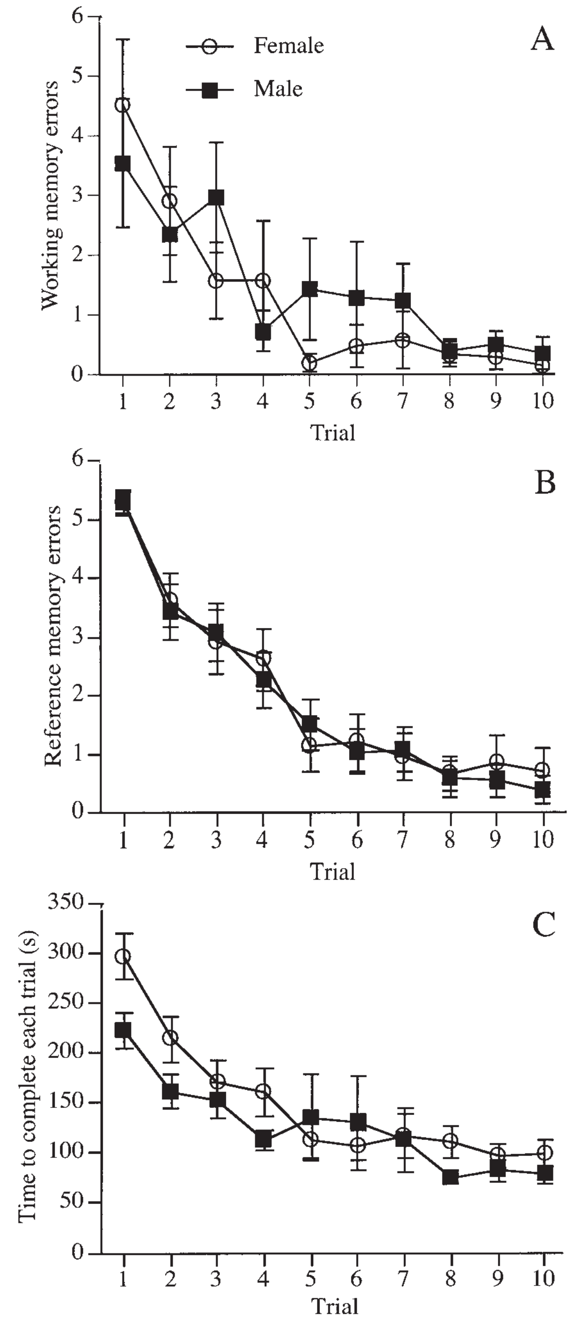

Figure 4. Performance in the 12-arm radial-arm maze, as illustrated by working memory errors (A), reference memory errors (B), and time to complete the task (C). Each symbol represents the mean (± *SEM*) of each group for one trial. Men and women performed similarly on all measures of task performance ($p > .05$).

analysis with subject personal information data and radial-arm maze measures. Pearson *r* values are listed in Table 1. General video game experience included categorical data for the frequency of computer or video game playing. Navigational video game experience included categorical data for how often subjects played computer or video games that required navigation through a simulated three-dimensional environment. SAT scores, general video game experience, and navigational video game experience were not significantly correlated with working memory errors, reference memory errors, or time to complete a trial. General and navigational video game experience correlated significantly ($r = .79$, $p < .0001$), as did reference memory and working memory errors ($r = .47$, $p < .01$). Radial-arm maze time was significantly correlated with both working and reference memory errors (*r*s = .57 and .33, respectively, *p*s < .05).

T-Maze

During the first training trial, 12 men and 9 women selected the incorrect arm. In subsequent training trials, no subject made more than three errors in any trial. In the trials immediately before the probe trials, only 2 subjects made errors in Trial 5 and only 1 subject made an error in Trial 11. Men and women did not differ in terms of strategy selection during the T-maze probe trials. Most subjects used a response strategy in both probe trials (Figure 5A). For the first probe trial, a Pearson chi-square analysis revealed a sex difference in the likelihood of using a place or response strategy to find the rewarded arm, $\chi^2(1, N = 47) = 4.57$, $p < .05$, such that men used a response strategy more than did women. However, the majority of both men and women used a response strategy. No sex differences in strategy selection were evident during the second probe trial, $\chi^2(1, N = 47) = 3.15$, $p > .05$. Only 3 subjects switched their responses between the two probe trials: 1 man and 1 woman used a response strategy on the first probe trial and a place strategy on the second, whereas another woman switched from place to response strategies from the first to the second trial. Women completed the trials slower than men (Figure 5B), as indicated by a repeated measures ANOVA for time to complete the maze: main effect of sex, $F(1, 45) = 4.71$, $p < .05$; trial, $F(11, 495) = 27.61$, $p < .001$; Sex × Trial interaction, $F(11, 495) = 0.426$, $p > .05$. This may suggest that women were more thoughtful while navigating through the maze, despite the lack of sex differences in strategy use.

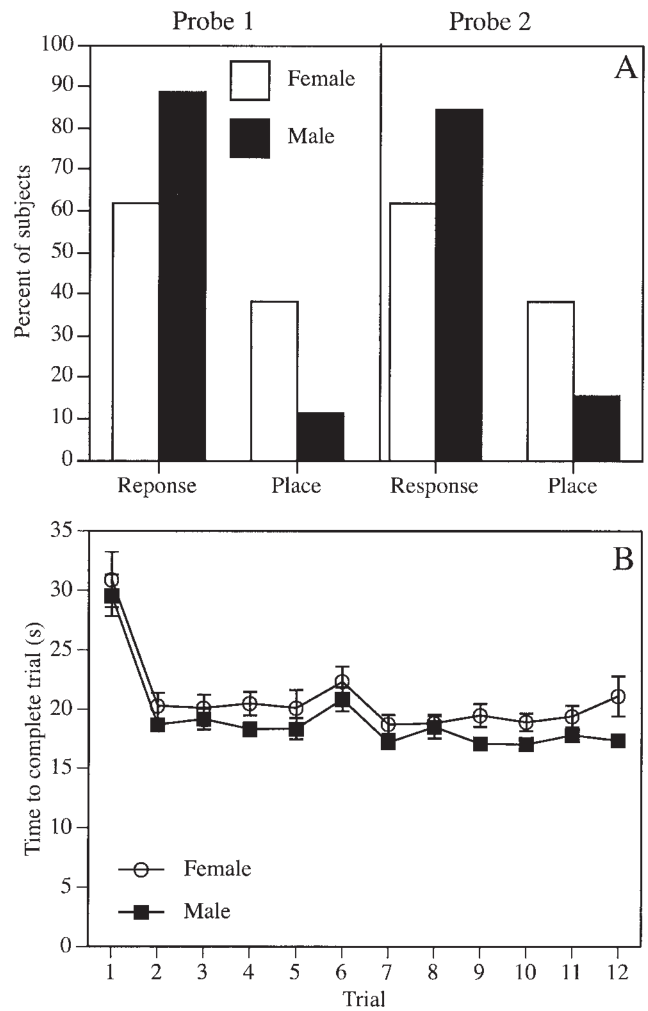

Figure 5. Men and women responded similarly in the T-maze probe trials, as illustrated by the percentage of subjects in each group making response and place choices (A). Both groups also spent equivalent amounts of time (in seconds) navigating through the maze during the training trials (1–5 and 7–11) and the probe trials (6 and 12) (B). Each symbol represents the mean (± *SEM*) time to complete each trial.

Table 1
Correlations Among Radial-Arm Maze Measures, SAT Scores, and Video Game Experience

	Correlations (*r* value)					
Measure	SAT score	Video game	Navig. game	WM errors	RM errors	RAM time
SAT score	—					
Video game	.07	—				
Navig. game	.03	.80*	—			
WM errors	.14	.10	.01	—		
RM errors	.08	.24	.22	.47*	—	
RAM time	−.003	−.13	−.24	.57*	.32*	—

Note. Navig. = navigational; WM = working memory; RM = reference memory; RAM = radial-arm maze.
* $p < .05$.

Water Maze Strategy Task

There was no significant sex difference in platform choice during the probe trial; the majority of both sexes used a nonspatial (cue) strategy. Pearson chi-square tests revealed no sex difference in the number of men and women selecting the old platform in the new location (cue) or the new platform in the old location (place), $\chi^2(1, N = 47) = 0.40, p > .05$ (see Figure 6).

Discussion

The results of the present study indicate that women are superior to men in remembering the location and identity of objects in a two-dimensional array. However, no sex differences were observed in the 12-arm radial-arm maze or in either strategy task, which suggests that men and women do not differ in navigating a complex radial-arm maze, and they did not use different strategies when navigating through the virtual mazes.

In the object array task, women were significantly more accurate than men were at identifying new objects and objects that exchanged and shifted locations. With respect to object novelty, these data are somewhat inconsistent with the findings of Eals and Silverman (1994), who used two-dimensional object arrays consisting of nonsense objects (uncommon objects without verbal labels) to examine object memory. They found a tendency for women to perform better than men when 11 objects were added to the original array, but this difference was not statistically significant. In contrast, the present data indicate that women significantly outperform men when novel objects are substituted for familiar objects (rather than being added to the familiar objects). We think it likely that the substitution of the novel objects, rather than their addition, made it more difficult for men to detect a change in the array. If men encode less information about specific visual features of the objects, then they would be less able to detect novel objects in familiar locations. On the other hand, the addition of novel objects in new locations as in the Eals and Silverman (1994) study also disrupts the spatial configuration of the array, thereby tapping into the superior male knowledge of spatial relationships and minimizing sex differences in performance.

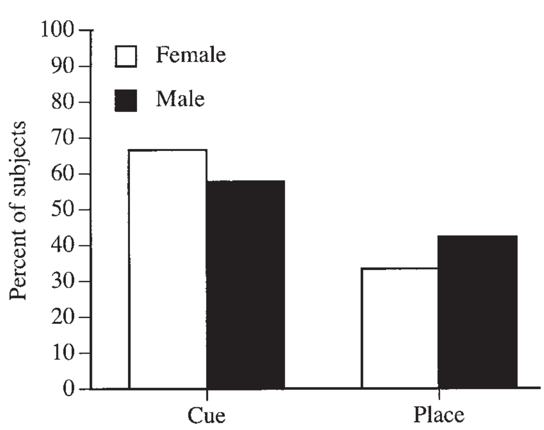

Figure 6. Responses in the water maze strategy task were similar for men and women. Each bar represents the percentage of subjects in each group who made place or cue choices during the probe trial.

With regard to object location, our object-exchange data are entirely consistent with previous reports that women are superior to men at recognizing changes in object location when pairs of objects exchange places (Eals & Silverman, 1994; James & Kimura, 1997; Silverman & Eals, 1992). Our object-shift data are also consistent with those of Eals and Silverman (1994), who shifted objects to both previously occupied and new locations in the array. However, James and Kimura (1997) used an object-shift condition identical to that of the present experiment and found no sex differences in performance. Unlike in the object-exchange condition, where object identity is the only cue that can be used to recognize change, alterations in the object-shift condition can be recalled by using both object identity and object location (because the objects move to novel locations). Thus, James and Kimura interpreted the lack of a sex difference in object shift, in conjunction with a female advantage in object exchange, as suggesting that women outperform men when only object identity can be used to recognize change. However, our data suggest that women have a more global advantage in these tasks regardless of whether the objects can be remembered by using only object identity or by both identity and location information.

The reasons for the discrepancy between our results and those of James and Kimura (1997) are unclear, as the array used in this study was similar to that of James and Kimura. Subtle differences in the arrays may have made a difference. For example, our arrays contained more objects, although it is unclear how this would have disadvantaged men. Alternatively, our inclusion of some objects drawn with heavier black lines may have made those objects more salient, and thus easier to remember, for women. Also, the fact that subjects in our study viewed all test arrays, whereas subjects in the James and Kimura study viewed only one test array, may have contributed to the discrepancy by introducing some type of proactive interference that may differ between the sexes. Interference is unlikely to account for the sex difference in the object-exchange array because this was presented immediately after the original test array. However, it is possible that information from the second array interfered with performance on the third array, as suggested by the reduced accuracy in both sexes in the shift condition compared with the object-exchange condition. Nevertheless, it does not appear that any interference differentially affected the sexes because the magnitude of the sex difference is the same in both the exchange and shift conditions. It is also somewhat unlikely that interference from the virtual tasks affected performance in the novel object array, because accuracy in this task was significantly higher for this array than for the other arrays.

Sex differences have been demonstrated consistently by using real world and virtual maze navigation tasks (Astur et al., 1998; Groen et al., 2000; Moffat et al., 1998; Sandstrom et al., 1998; Saucier et al., 2002), where men have been shown to navigate by using predominantly euclidean information and women have been shown to navigate by primarily using landmark cues. One study by Sandstrom et al. (1998) used three versions of a virtual Morris water maze to demonstrate that men perform better than women do when landmark information does not predict the target platform location (such as in rooms with geometric cues only or in rooms where landmark cues were inconsistent). However, sex differences do not emerge in environments with stable landmarks cues (Sandstrom et al., 1998). Astur et al. (2004) recently reported a robust sex difference favoring men in a virtual Morris maze task and no sex difference in the same subjects tested in an 8-arm version of the radial-arm maze task. Contrary to our expectations, the lack of a sex difference in the radial-arm maze was replicated in the present study with a 12-arm version of the task, suggesting that increasing the number of rewards to be remembered had no bearing on the presence of a sex difference in radial-arm mazes.

One reason for the discrepancy between the virtual water maze (Astur et al., 1998) and radial-arm maze tasks (Astur et al., 2004) may be that the more restricted nature of movement in the radial-arm maze compared with the water maze leads to the perception of more stable landmark cues in the radial maze task. This increase in perceived stability may render the radial-arm maze task, regardless of the number of arms, easier for women. Alternatively, the radial-arm maze has arms that guide the subject to the reward, whereas the water maze has no such guides, which may improve women's performance. Indeed, each arm could easily be associated with a single landmark cue, rather than having to associate multiple landmarks as in the water maze, so the use of a landmark-based strategy may work just as well in women as a spatial strategy. Given that increasing the number of arms does not appear to elicit a sex difference in learning the radial-arm maze, future work should focus on manipulating extramaze landmarks in this task to determine how women learn to solve this task. Last, perhaps men and women are equally capable of using both spatial and nonspatial strategies to navigate, but the varying requirements of each task elicit the sex differences. For example, the use of a nonspatial strategy by women in the virtual water maze resulted in a delay of about 6 s to find the platform compared with men who used a spatial strategy (Astur et al., 1998). However, the use of a nonspatial strategy in the radial-arm maze resulted in a minimum 20-s delay in finding the reward (10 s to travel to the end of the arm, 10 s to travel back to the central arena), which could add several minutes to the time to complete a trial. Factors such as these may be important considerations when interpreting sex differences in these tasks.

This study is the first to examine sex differences in spatial memory strategies by using virtual T-maze and water maze tasks. In both of these mazes, subjects can find rewards by using either a nonspatial strategy (response for the T-maze, cue for the water maze) or a spatial strategy (always going to the same place for reward). We failed to find a consistent sex difference in strategy selection, despite the fact that estradiol can modulate place response learning in female rats (Korol & Kolo, 2002; Korol et al., 2004). Because spatial abilities reportedly fluctuate during the menstrual cycle (Hampson, 1990), sex differences in this study may have been obscured by variations in strategy preferences among subgroups of cycling women. Such a determination would require correlating virtual maze performance with serum estradiol levels. Alternatively, the fact that both sexes tended to use a nonspatial strategy more often than a place strategy may suggest that the probe trials occurred too late in training. Previous studies have shown that male rats initially use a place strategy in the T-maze task but then adopt the response strategy later in training (Packard & McGaugh, 1996). Given that our subjects favored response over place in the T-maze, the placement of probe trials earlier in training in future studies may reveal whether sex differences in strategy selection exist in humans. Furthermore, other components of the environment, such as cue density, room configuration, or object size, could lead to a bias toward a response strategy (Restle, 1957). In addition, the task may be too easy to engage both spatial and nonspatial strategies. Indeed, Figure 4 suggests one-trial learning in the T-maze. Unlike rats (Packard & McGaugh, 1996), our subjects were told the rules of the task, which may have made it impossible to tap into both strategies. Finally, the relevance of these two tasks to the radial-arm maze data could be questioned, given that these tasks used mazes of different shapes in rooms with different visual landmarks. Nevertheless, the fact that both strategy tasks produced the same results (no sex difference and a predominance of nonspatial strategy use) would suggest that the data from these tasks could be generalized to strategy use in the radial-arm maze.

Because brain activity was not measured in this study, the neurobiological bases of our observed sex differences are unclear. In the object array, women were better than men at identifying new objects and objects that exchanged or shifted locations. The perirhinal cortex is involved in object memory in rats, humans, and monkeys (Winters & Bussey, 2005), and therefore, sexual dimorphisms in this brain region may underlie the female advantage observed in this study. Although there is no sex difference in the volume of the perirhinal cortex (Insausti et al., 1998; Pruessner et al., 2002), one study reported that men have more gray matter than do women (Good et al., 2001). The impact of this increase is unclear, as gray matter volume in the perirhinal cortex has yet to be correlated with object memory performance. Furthermore, no animal studies have examined sex differences in the perirhinal cortex, so it is unknown what morphological or functional sex differences may underlie the object memory findings reported in the present study. Also, the fact that the cue strategy, which is nonspatial and also presumably perirhinal dependent (Mumby, 2001), did not differ between the sexes may indicate that any dimorphism in the perirhinal cortex influences memory but not strategy selection. It is interesting to note that despite the fact that sex differences in presynaptic dopamine synthesis have been reported in the human striatum (Laakso et al., 2002), we did not find a sex difference in response strategy selection in the T-maze. In rats, this brain region has been implicated in response strategy selection in the T-maze (Packard & McGaugh, 1996). However, it is possible that the virtual environment did not engage the striatum in the same way as a real world maze. Last, morphological and functional sex differences in the hippocampus have also been observed in rodents (Madeira, Sousa, & Paula-Barbosa, 1991; Smith, Jones, & Wilson, 2002) and in humans (Filipek, Richelme, Kennedy, & Caviness, 1994), and therefore, it is surprising that we did not see a sex difference in the 12-arm radial-arm maze. Possible reasons for this have already been discussed. These issues can be more specifically addressed in future work by recording brain activity during testing.

In conclusion, the present study indicates for the first time that women are better than men at recalling the identity and locations of objects on a two-dimensional array but that the sexes do not differ in the performance of a 12-arm radial-arm maze task or in the use of spatial or nonspatial strategies. The fact that the same subjects were tested in multiple object arrays helps to resolve the inconsistencies among previous studies that tested different manipulations in different subjects. Furthermore, the 12-arm maze expands on our previous findings by demonstrating that increasing the number of rewards to be remembered does not influence the likelihood of observing a sex difference. The object memory data are consistent with previous findings that women remember landmark cues better than men, and the radial maze data suggest that landmark information may be used successfully to solve this task.

However, the female superiority in the object array tasks may suggest that men and women process landmark information differently while exploring the environment.

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