



Research report

Effects of cue types on sex differences in human spatial memory

Xiaoqian J. Chai^{a,b,*}, Lucia F. Jacobs^a^a Department of Psychology, University of California, Berkeley, CA 94720, USA^b Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology, Cambridge, MA 02139, USA

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ABSTRACT

We examined the effects of cue types on human spatial memory in 3D virtual environments adapted from classical animal and human tasks. Two classes of cues of different functions were investigated: those that provide directional information, and those that provide positional information. Adding a directional cue (geographical slant) to the spatial delayed-match-to-sample task improved performance in males but not in females. When the slant directional cue was removed in a hidden-target location task, male performance was impaired but female performance was unaffected. The removal of positional cues, on the other hand, impaired female performance but not male performance. These results are consistent with results from laboratory rodents and thus support the hypothesis that sex differences in spatial memory arise from the dissociation between a preferential reliance on directional cues in males and on positional cues in females.

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1. Introduction

A consistent pattern of sex differences in spatial cognition and hippocampal structure and function has emerged from studies in birds and mammals [34]. Male polygamous meadow voles outperform females in spatial mazes and also have relatively larger hippocampi than females [12,34]. There is increasing evidence that such sex differences in spatial memory are dependent on the types of cues in the environment. In laboratory rodents, males outperformed females on the water maze task where the environment contained mostly distant cues [27,33], while females outperformed males in detecting local objects whose locations had been switched [33]. When local landmarks were removed or randomized, performance of female kangaroo rats [4] and laboratory rats [39] was significantly impaired, while male performance was unaltered. When the geometry of the space was altered, performance was impaired in males but not in females [39].

The nature of cue use in humans [6,31,35] follows a pattern that is similar to that in polygamous rodents. Females are often more sensitive to the switching of object location, when objects are located in peri-personal space (i.e., close to the participant) [32]. Males, in contrast, are less sensitive to the identity and location of objects, although this result is highly sensitive to task [32,38].

Instead, males are most sensitive to the presence of more distant or distributed cues, such as distant objects or the geometry of the space and gradient cues. When only geometric room cues were available, males were faster at learning the location of a hidden target than females [31]. In a recent virtual navigation study, we examined navigation accuracy in virtual environments that contained only one type of cue: either gradient cues, such as geographical slant, and distant cues, or only intra-maze discrete object cues. Participants learned a target location under a single cue type and then, after a short delay, navigated back to the target location from a novel starting point. Male advantage in navigation accuracy was greater in the gradient and distant cue condition [6].

Although distant cues, geometry of the space, and gradient cues appear to be quite different types of cues, they can be used to polarize the environment and thereby extract compass direction. The parallel map model of the cognitive map classifies cues not by location (e.g., proximate vs. distal) but by function [14]. Thus all of the above are classified as “directional cues”, i.e., cues that are primarily used as a compass for providing direction. Distal landmarks, for example, are too far away to provide accurate positional information but can nevertheless provide directions. Similarly, gradient cues (i.e., a field of cues of graded intensity) such as odor, light, and terrain slant primarily provide directional information. In contrast, unique and proximate pinpoint objects provide relatively precise positional information within a local cue array. These cues belong to the second class, that of “positional cues. The parallel map model proposes that the cognitive map is formed by integrating information from directional and positional cues, and that

* Corresponding author at: 43 Vassar St, 46-5081, Cambridge, MA 02139, USA. Tel.: +1 617 324 5120; fax: +1 617 324 5311.

E-mail address: xiaoqian@mit.edu (X.J. Chai).

sex differences in spatial memory emerge as a natural dissociation of the two mapping systems based on directional and positional cues, respectively. The model predicts a male advantage in environments that are rich in directional cues and female advantage in environments that are rich in positional cues. Consistent with these predictions, a recent study on sex differences in cue perception found that females were slower to identify previously seen photographs when proximal positional cue were erased from the photos, but were unaffected when directional cues were removed [3]. However, manipulations of these functional cue classes have not been performed in 3D-virtual orientation tasks.

The goal of the present study was to examine sex-specific responses to directional and positional cue classes, as predicted by the parallel map model. We used three virtual environment tasks adapted from classical animal and human spatial memory tasks. Virtual environments offer the flexibility to manipulate and dissociate different cue types. We adapted tasks from a variety of sources, both studies of rodent and studies of human, which have shown a strong sex difference in performance, or directly test either one of the two cue classes. Task A was adapted from a 2D paper-and-pencil version of the multiple object location memory task which showed female advantage, and contained only positional cues [35]. Task B was adapted from a spatial memory task for the laboratory rat (spatial delayed-match-to-sample), which contained only directional cues [10]. Task C was modified from the task structure of the Morris water maze for laboratory rats [25]. Virtual versions of the water maze task result in a performance advantage for men [1]. Task C required participants to search for a hidden target in a naturalistic landscape where both directional and positional cues were present. This allowed us to assay sex differences in the presence of both cue functional classes, and to examine the interaction of sex and cue class when either cue class has been removed, since prior studies [1,6,31] had included only one cue class. In addition, we also added the gradient cue of terrain slant to the roster of directional cues. A distinct slant of the terrain provides strong directional information by polarizing an otherwise homogenous environment. A growing body of evidence from multiple species now suggests that it is indeed an important cue for orientation (pigeons [26]; rats [23]; humans [6,30]). Terrain slant also supplies orientation input to the hippocampus in laboratory rats, as their hippocampal place fields remained oriented in the presence of a terrain slant [16]. Finally, our recent results suggested that in virtual orientation tasks, men used terrain slant more effectively than did women [6]. One goal, therefore, of the present study was to measure the effect of the addition and removal of slant information on sex differences in orientation in different spatial tasks.

2. General materials and methods

2.1. Participants

Fifty-one students (25 females, 18–33 years of age, mean age = 20.7, SD = 2.95; 26 males, 18–27 years of age, mean age = 20.4, SD = 1.96) participated in all three parts of this study. Due to computer failure, three males did not complete Task C and two of these males also did not complete Task B. One additional male did not complete task C due to dizziness. All participants were right-handed undergraduate students at the University of California, Berkeley, enrolled in psychology courses and received course credit for their participation.

2.2. Apparatus

We constructed computerized 3D virtual environments using a commercially available video game engine (Unreal Engine 2 by Epic Games, Raleigh, NC). These environments were presented on a 21-in. computer monitor with participants sitting approximately 55 cm in front of the monitor. Horizontal field of view was approximately 39° and vertical field of view was approximately 30°. Participants used a joystick (Cyborg Evo by Saitek, Bristol, UK) with forward, backward, left-turn and right-turn options to move in the environment. Coordinates of the movement were recorded into a log file every 0.2 s.

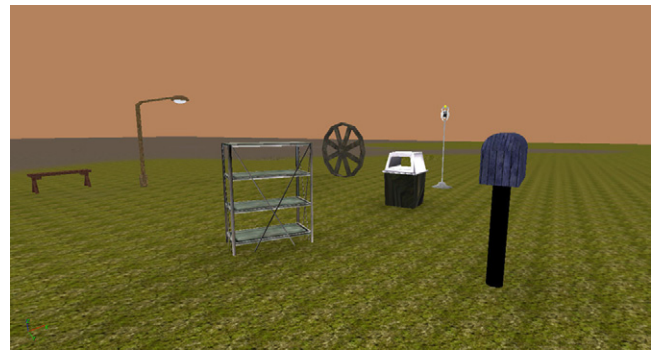


Fig. 1. Screenshot of one of the virtual environments used in part A.

2.3. Procedure

All participants were tested in Task A (positional cue location memory) and Task B (directional cue task) and finally in a task that integrated both cue classes (Task C). We fixed the order of the three tasks to decrease data loss. Task C was considerably longer than Tasks A and B, and in pilot tests had caused significant fatigue and occasionally nausea. Participants faced this task last, therefore, to minimize data loss from fatigue, although it would have been more ideal to counterbalance the order.

Practice trials were administered before each task to familiarize the participant with the virtual environment interface and task. The practice environment was situated in a virtual landscape that was similar to the task environment but contained no objects (Task A) or targets (Tasks B and C). Participants were instructed to practice moving around in the environment using the joystick. Each trial was 30 s. A second trial was given if the participant was still not comfortable moving around the environment with the joystick. Two females and one male asked for the second practice trial during Task A. All participants reported they were comfortable with the virtual environment interface by the end of the practice.

After the virtual environment tasks, participants completed a questionnaire which measured computer and video gaming experience. A 7-point scale was used to assess the frequency of 2D video game and 3D virtual environment video game experience, joystick use, and general computer use (1 = never, 2 = once, 3 = less than once a year, 4 = less than once a month, 5 = less than once a week, 6 = several times per week, 7 = every day).

2.4. Task A: multiple object location memory

2.4.1. Rationale

The female advantage in object location memory is highly sensitive to test conditions [38] but the strongest effect is seen when the task demands the participant to recognize which objects in an array have been switched [35]. In the original study, participants viewed 2D drawings of an array of common objects and were presented with the same object array with some of the object positions switched after a short delay. Subsequent studies of the effect have generally used 2D arrays of objects or 3D tabletop displays [21,29,32]. In our study, we constructed a 3D virtual version of an object-switching task that closely resembles a real-world environment, to assay possible sex differences in positional cue memory.

2.4.2. Apparatus and procedure

We constructed three virtual environments: open fields with configurations of either 8, 16, or 32 common and gender-neutral objects such as a chair, rock, street lamp or bench (Fig. 1). Each object configuration was tested once. Each trial started with a 45 s learning phase where participants were instructed to memorize the objects and their locations in the environment. After a 10 s interval where a small white cross was displayed on a black screen, participants were given a fixed-length probe phase (45 s) to study the test environment. In the probe phase, two objects that differed by semantic category and were not adjacent, were switched in location. Participants were instructed to find these two switched objects. Their starting location in the probe phase was different from that of the learning phase. Immediately after the probe phase, a screen was presented with images (screen shots) of the objects. Participants then used the mouse button to choose the two objects that they thought had been switched in location in the probe phase compared to the learning phase. The images of the objects were arranged in rows of 4 objects, in random order. The order of the three conditions (8, 16 or 32 objects) was counterbalanced across participants.

2.4.3. Video game experience results

Males reported higher scores than did females in 2D gaming ($t(49)=2.06$; $p=.044$), 3D gaming ($t(49)=2.3$; $p=.025$) and joystick use ($t(49)=2.64$; $p=.01$) (Fig. S1). General computer use experience did not differ between the groups ($p=.48$).

Table 1
Results of Task A (no sex differences).

Number of objects	Number of participants who found both switched objects		Number of participants who found one switched object	
	Female (N = 25)	Male (N = 26)	Female (N = 25)	Male (N = 26)
8	10	14	25	25
16	4	6	18	21
32	1	2	16	14

The number of participants who found one or both of the switched objects in the 8-, 16-, and 32-object conditions.

2.4.4. Results

There was no sex difference in the number of individuals who successfully identified switched objects in any of the conditions, for either one or both of the objects (Fisher's exact test, p 's > .2 for all conditions; Table 1).

For each participant, the total distance traveled in the environment (path length) was calculated for each trial. On average, males traveled longer distances in the 32-object condition than did females during the learning phase ($t(49) = -2.37, p = .02$), but not during the probe phase ($t(49) = -1.67, p = .10$). There was no sex difference in path length in the 8-object condition (learning phase: $p = .45$; probe phase: $p = .13$) or in the 16-object condition (learning phase: $p = .28$; probe phase: $p = .73$). To test if path length is associated with the success of finding the switched objects, we compared the path lengths between participants who successfully identified both switched objects and participants who failed to identify either switched object. There were no significant differences in any of the 8-, 16- and 32-object conditions (p 's > .2). We repeated the same analysis to compare participants who identified one switched object versus those who identified neither object and found no significant difference in path length (p 's > .4). Therefore, path length did not predict the success in finding the switched objects.

To measure the possible effect of video game experience on task performance, for each condition, we used the Mann–Whitney test to compare video gaming scores in participants who found both switched objects to those who did not. The performance groups did not differ in 3D gaming (p 's > .3), joystick use (p 's > .3), or 2D gaming (p 's > .2), in any of the 3 conditions. These data suggest that video game experience did not predict the success of finding the switched objects.

2.5. Task B: spatial delayed-match-to-sample

2.5.1. Rationale

The goal of this task was to test humans in a virtual version of a laboratory rat task that appears to rely on directional cues and to depend on the function of the dentate gyrus of the laboratory rat hippocampus [10]. Lesions of this subfield in laboratory rats produce a specific impairment on a spatial delayed-match-to-sample task. In this task, rats learned to return to a location that was cued by a single object on a round 'cheese-board' maze. After a delay, a decoy object is added to the maze and the rat must now return to the original object's location for a reward, ignoring the location of the decoy object [10]. Rats with dentate gyrus lesions showed progressively poorer performance as the distance decreased between the target and the decoy objects.

Because rats must use distant objects to disambiguate the target and decoy, this result is consistent with the assignment of distant cue encoding to the dentate gyrus in the parallel map model [17]. The original study by Gilbert et al. used only male laboratory rats, yet we predicted that a virtual version of this task should result in a male performance advantage in humans. We therefore replicated the rodent design in virtual space. The arena contained no positional cue (local objects) in or around the test arena, which forces the participants to rely completely on distant, i.e., directional, cues, which were present in all trials. We varied task difficulty by having four different target-decoy distances. At the most difficult (i.e., shortest) target-decoy distance, we introduced two additional manipulations: (1) the addition of a directional gradient cue (geographical slant), and (2) the addition of two positional cues (trees). These additions were designed to assess a sex-specific sensitivity to slant and to positional cues. We predicted that adding positional cues, thereby increasing

Table 2
Results of Task B.

Target-decoy distance (virtual meters)	Additional cues	Number of participants who found the target	
		Female (N = 25)	Male (N = 24)
15 m	None	22	22
10 m	None	21	20
5 m	None	19	18
2.5 m	None	15	11
2.5 m	Trees	17	16
2.5 m	Slant*	12	19

The number of participants who successfully identified the target under the different target-decoy distances. The 2.5 m target-decoy distance had two additional conditions: additional positional cues (trees) and an additional directional cue (geographic slant).

* Significant sex difference ($p = .02$).

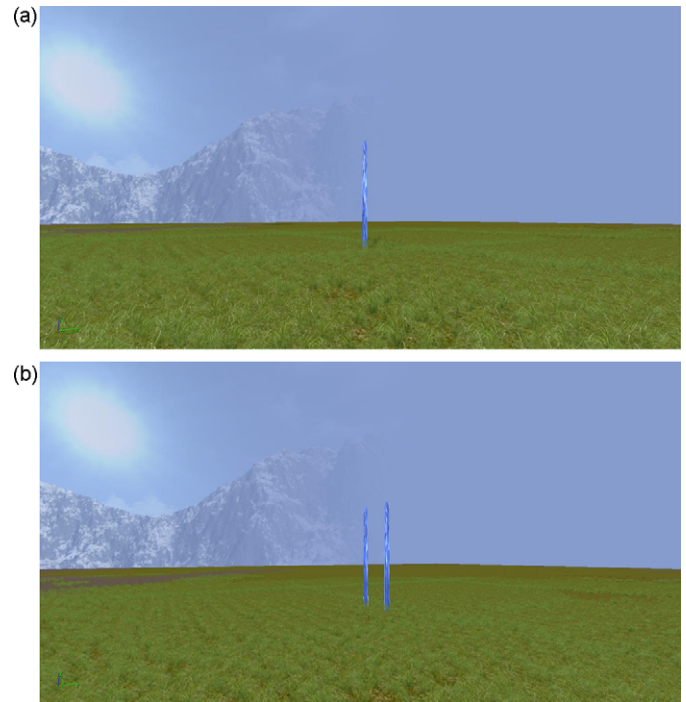


Fig. 2. An example of the virtual environments in Task B: (a) training phase and (b) probe phase.

female performance, would erase any overall sex differences in performance, but that the additional of the slant would increase the male advantage and hence the overall sex difference in performance on this condition.

2.5.2. Apparatus and procedures

The environment consisted of a large open field within a mountain landscape and a visible sun. The target was a tall blue crystal, with an identical blue crystal as the decoy. A virtual stopwatch on the top-left corner of the screen indicated remaining time for each trial (Fig. 2).

Each trial consisted of a training phase followed immediately by a probe phase. During the training phase, participants were instructed to remember the location of the target (i.e., the tall crystal) in the field. During the probe phase, a second, identical decoy crystal was placed at variable distances (2.5 m, 5 m, 10 m, 15 m, in virtual units) from the target. Participants were instructed to choose the original target from the two identical crystals, by a single touch. The probe phase ended once a crystal had been touched. Participants started from the same location in the

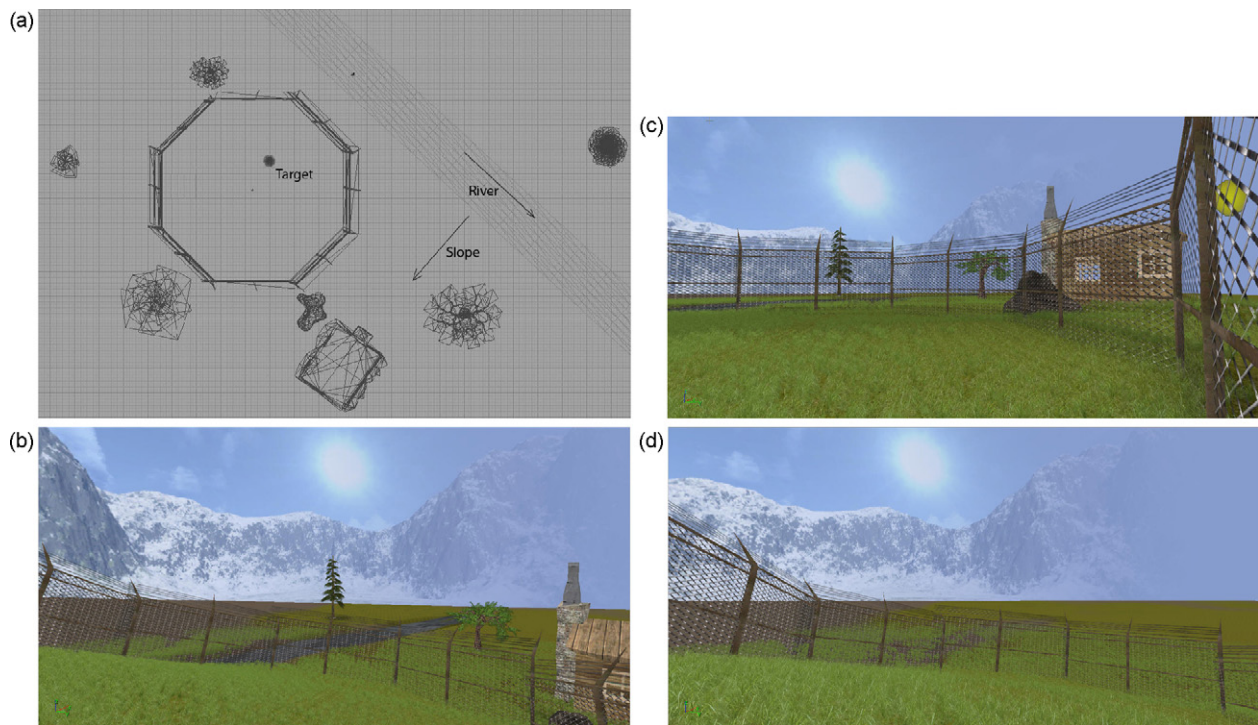


Fig. 3. Virtual environments used in Task C. (a) Layout of the training environment from the virtual engine editor showing the fence, objects surrounding the test arena, and the target in the middle. Screenshot of the training environment is shown in (b), positional-cue removal probe in (c), directional-cue removal probe in (d). The fence was not visible during the task.

training phase and probe phase. The training phase was 20 s and probe phase were 45 s long in duration. There were a total of six trials (15 m, 10 m, 5 m, 2.5 m, 2.5 m with trees, and 2.5 m with slant), with 2 s inter-trial intervals. For the easier target-decoy distance conditions (5 m, 10 m and 15 m), there were no additional cues in the environments. For the most difficult target-decoy distance (2.5 m), there were three trials: (a) no additional cues; (b) two additional positional cues (two trees placed close to the target); (c) additional geographical slant of approximately 30°. The order of trials was pseudo-random.

2.5.3. Results

The number of participants who chose the target correctly in each condition is shown in Table 2. There were no differences between the number of males and females who successfully identified the target for any of the target-decoy distances, without additional cues (Fisher's exact test, p 's > .2). However, at the smallest distance (2.5 m), a sex difference emerged with the added cue of a geographical slant. Here a greater number of males than females correctly identified the target location (Fisher's exact test, $p = .02$; Table 2).

To measure the possible effects of video gaming experience, we used the Mann–Whitney test to compare video game scores in participants who found the target versus those who did not, for each test condition. For the slope condition, the groups did not differ in 3D gaming ($p = .52$), joystick use ($p = .65$), or 2D gaming ($p = .72$). These measures did not differ between groups in any of the other conditions (3D gaming, p 's > .2; joystick use p 's > .6; 2D gaming, p 's > .4). These data suggest that video game experience did not predict the success of identifying the target from the decoy object and did not contribute to the sex difference pattern observed here.

In addition to accuracy of the choice, latency and path length to the crystal for each trial were recorded. Overall, the average latency for males tends to be slightly shorter than females, however, this difference was not significant in any trial (t -test, p 's > .2; Fig. s2). Path length was also similar between males and females (p 's > .3; Fig. s3).

2.6. Task C: hidden target memory with cue removal

2.6.1. Rationale

The first goal of this task was to assay sex differences in spatial memory in a naturalistic 3D environment in the presence of both cue types. The second goal was to measure the effects of cue removal on sex differences in performance. Because this design was adapted from those used to measure sex differences in rodents, we also designed the maze to be comparable to these studies and also to prior studies of human performance in virtual mazes. We therefore modeled our task structure after the water maze task of Morris et al. [25], but included both positional cues around the boundary of the test arena, and additional directional cues in the environment. Prior virtual water mazes usually did not have cues in or near the maze boundary

to serve as positional cues. Such virtual mazes usually produce a male advantage [1,2]. In the present study, we predicted that the removal of directional cues would impair males more than females, and that removing positional cues would have the opposite effect.

2.6.2. Apparatus and procedure

The training environment was a large outdoor grassy terrain and an octagonal-shaped arena that was located on a small hill of ~30° slant (Fig. 3a and b). The arena was surrounded by an invisible fence 18.3 m in radius and positional cues (four trees, a rock, a cabin and a shrub). The sun, sky, river and slope served as directional cues. The fence was invisible to ensure an unbroken view of the surrounding cues to the participant. The target was a tall, spiked blue crystal. Once the participant reached the vicinity of the hidden target's location, the crystal slowly appeared from the ground and then was present for 10 s before disappearing. The probe environments were modified from the training environment with either positional cues removed, or a directional cue (terrain slant) removed (Fig. 3c and d).

Training trials commenced immediately after practice trials. Participants were instructed to search for the target in each trial, located somewhere on the hill in the environment (Fig. 3b). They were given seven training trials from different start locations. The trial ended when the target was found, up to a cut-off time of 90 s. Between trials, participants were instructed to focus on a white cross that was displayed for 10 s centered on a black screen. After the training trials, participants received two probe tests (removal of positional or directional cues) with new start locations, in counterbalanced order, separated by two training trials with all cues present. The location of the hidden target remained the same in all trials.

2.6.3. Results

To analyze the degree of success in finding the hidden target, we calculated the total distance traveled before reaching the target for each trial per participant. Total distance traveled was used as a measure for the efficiency of the target search. The first training trial was not included since the location of the target had not been revealed and therefore the search was random. Hence the training trial distance was calculated from the average of trial 2 to trial 6. In probe tests, the mean distance to target was compared to this training average, to assess the effect of cue removal on navigation performance. The distance scores were analyzed using a two-factor mixed-design ANOVA, with trial number as the within-subject factor and sex as the between-subject factor.

The learning curves for both groups in the training trials are shown in Fig. 4. There was a significant main effect of trial ($F(5,225) = 5.33$, $p < .001$), showing a learning effect of the target location. Neither the trial-by-sex interaction ($p = .84$) nor the main effect of sex ($p = .3$) was significant. Performance on each training trial did not differ between women and men (p 's > .2).

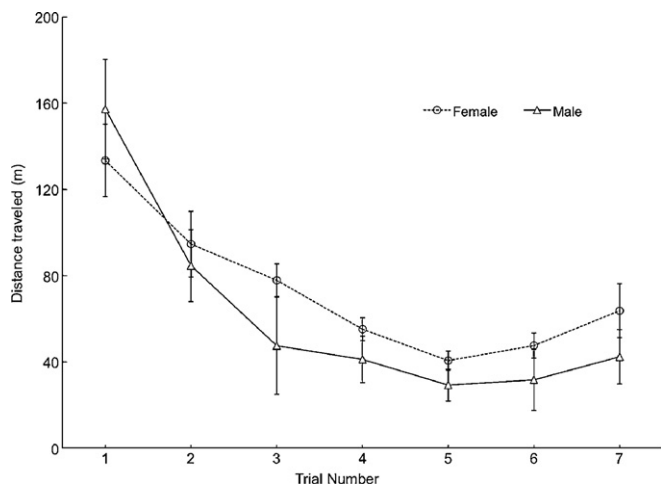


Fig. 4. Performance during training in Task C. Total distance (virtual meters) traveled before finding the hidden target is plotted against the trial number. Error bars are one standard error above and below the mean.

For the probe test with directional-cue-removal, there was a significant sex-by-trial-type interaction ($F(1,44)=5.26, p=.027$), indicating the manipulation of the directional cue affected females and males differently (Fig. 5a). Post hoc pairwise comparison revealed a decrease of performance after cue removal in males ($t(21)=2.14, p=.02$), but not in females. To exclude the possibility that sex differences observed in this task resulted from a male advantage in video game experience, we repeated the mixed-design ANOVA with 3D video game experience and joystick use as covariates. Neither 3D gaming ($F(1,42)=.82, p=.79$) nor joystick use ($F(1,42)=.47, p=.82$) had an effect on navigation performance. The sex-by-cue-type interaction was still significant ($F(1,42)=4.9, p=.02$).

When positional cues were removed, there was a significant main effect of sex ($F(1,45)=5.14, p=.028$) (Fig. 5b). The interaction between sex and trial type was not significant ($p=.3$). A post hoc *t*-test revealed, however, that females traveled farther when positional cues were removed compared to the distance traveled in the training trials ($t(24)=2.18, p=.03$). The main effect for trial type was also significant ($F(1,45)=5.65, p=.02$), indicating that the removal of positional cues made the task more difficult and therefore increased overall search distance. To control for the effect of video gaming scores, we included them as a covariate in the ANOVA but this did not change the pattern of the results. Once again, neither 3D gaming ($p=.48$) nor joystick use ($p=.9$) had a significant effect on navigation performance.

3. Discussion

The present study complements prior research on sex differences in spatial memory by examining in more detail the role of functional classes of cues on performance in virtual versions of classical rodent and human spatial memory tasks. Our results support the hypothesis that females and males depend differentially on cues giving primarily directional or positional information. When both directional cues and positional cues were present, females and males were equally efficient in learning the location of the hidden target (Task C) and identifying the target from decoy loca-

tion (Task B). We found reliable evidence that males depend more on directional cues than females in these tasks. In the virtual spatial delayed-match-to-sample task (Task B), adding a directional cue (geographical slant) to the environment helped males more than females to discriminate the target from the decoy object. In the hidden target task (Task C), when a directional gradient cue (terrain slant) was removed, male performance was affected to a greater extent than that of females. These findings are consistent with the male advantage reported in navigation studies when positional cues were not available and participants had to rely on cues such as geometric information and distal objects [1,24,31]. This is also in congruent with the male preference on orientation strategy or survey knowledge in self-reported way-finding strategies [19] and virtual environment navigation [5]. Our current findings indicate that directional cues such as geographical slant, are utilized more and perhaps encoded more effectively by males than females in spatial memory tasks.

The expected female advantage in positional cue use, however, was less robust. As predicted, when positional cues were removed from the environment in the hidden target task (Task C), females were more affected, although the sex-by-cue type interaction was not significant. In the virtual object location memory task (Task A), however, we did not find the expected female advantage. This negative result is not inconsistent with the history of studies of sex differences in multiple object location. While some studies [15,21,37] have replicated the female advantage in object location memory originally reported by Silverman and Eals [35], others have failed to reproduce this result [8,9,11,29]. The results seem to be sensitive to test conditions such as the type of objects included, the nature of the task format and how the stimulus is presented [38]. A recent study demonstrated that the outcome of an object location memory task depended on whether the stimulus was presented to the participants in peri-personal space or extra-personal space [32]. A female advantage in performance emerged when the object array was presented on an 11 in. \times 17 in. paper on a tabletop (peri-personal space). However this sex difference disappeared when the object array was projected onto a large white wall (extra-personal space). In light of this sensitivity to experimental details, our negative results suggest that several factors in task design will influence the outcome of object switching tasks. To our knowledge, ours is the first study to approach this question using a simulation of the natural experience: employing first-person perspective while studying the locations of three-dimensional objects in a naturalistic (albeit virtual) environment. Yet all of these factors could be contributing to the emergence of sex differences in the task. It is important, therefore, that future studies dissociate these factors to determine their relative contribution and interaction.

Finally, we were limited by the risk of data loss, as discussed earlier, to testing participants on the three tasks in a fixed order. Although we cannot definitively rule out order effects, in a prior study using similar methods, the same pattern for male advan-

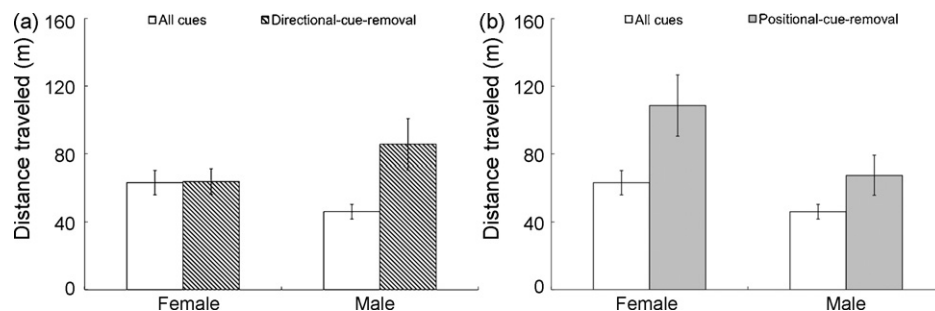


Fig. 5. Task C results. Total distance traveled before finding the hidden target (navigation efficiency) when a directional cue (terrain slant) (a), and positional cues (b) were removed compared to average training trials when all cues were present. Error bars are one standard error above and below the mean.

tage in directional cue use emerged when the condition order was counterbalanced [6].

The two studies, taken together, provide strong evidence for the dissociation of directional and positional cues in men and women. In the prior study, we demonstrated that males showed more accurate navigation in the presence of directional cues [6]. Much work still needs to be done to pinpoint the physiological and cognitive mechanisms underlying these disassociations. Sex differences in spatial cue use appears to be typical of polygamous mammal species where females and males differ in their use of space, such as in wild rodents [13,34] and laboratory rodents [33], that are derived from polygamous rodent species. Clearly in humans, many other factors will contribute to the expression of sex differences in cognitive performance. In the case of navigation, these factors include experience and environmental contributions [7,20]. Lawton [20] showed that when giving directions, men are more likely to use cardinal directions, whereas women are more likely to refer to landmarks. However in areas where roads are arranged in grid-like patterns, both women and men are more likely to refer to cardinal directions. Future research needs to look into the interaction of genetic, developmental and environmental factors on performance [36].

Our findings also provide new insights for future research on the neural basis of spatial navigation and sex differences. Previous brain imaging studies have identified a number of brain regions, including the hippocampus parietal and frontal regions, that are active during navigation [22]. However, it is still largely unknown how these regions work together to process different spatial information during navigation. Here we demonstrated that directional and positional cues are dissociable behaviorally in men and women. In the parallel map model, two classes of cues are hypothesized to be mediated by different structures in the brain [14]. Although data from human studies is still lacking, there have been a number of studies of hippocampal function in laboratory rodents that lend support to this model [17,28]. Furthermore, cortical regions outside of the hippocampus such as the posterior parietal cortex have been shown to play an important role in processing topological information from positional cues (see [18]). Future human brain imaging studies are needed to address the question of whether different components of the spatial environment have different neural signatures in the hippocampus and other cortical regions, and whether sex differences in spatial navigation performance are associated with neural activities specific to different cue types.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.bbr.2009.11.039.

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