Sex Differences in Directional Cue Use in a Virtual Landscape

Xiaoqian J. Chai and Lucia F. Jacobs
University of California, Berkeley

How males and females differ in their use of cues for spatial navigation is an important question. Although women and men appear to respond differently to close and distant objects, object features and the geometry of spaces, the common denominator of these sex-specific cue preferences is unknown. By constructing virtual landscapes from either directional (graded, gradient) or positional (pinpoint) cues, the authors tested the hypothesis that sex differences arise from preferences for cues that provide primarily direction or position, as predicted by the parallel map model of the cognitive map. Women and men learned a target location in the presence of either one or the other class of cues. Men were more accurate in estimating the target location overall, but the navigation accuracy difference between men and women was greater in the presence of directional cues. Our findings provide support for the parallel map model and suggest that the previously reported male advantage in the presence of distant objects and geometric cues derives from their function as directional cues.

Keywords: spatial navigation, sex differences, hippocampus, cue use, virtual environment

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To establish how cognitive processes are affected by gender is a question of both theoretical and practical importance (Halpern, 1997; Spelke, 2005). Under natural and laboratory conditions, sex differences in spatial cognition have been found in a variety of mammalian species where females and males use space differently (Barkley & Jacobs, 2007; Galea & Kimura, 1993; Gaulin & Fitzgerald, 1986). What is important and interesting is not only are there ecological differences in how female and male mammals use space, but that the sexes appear to utilize spatial information from visual cues in markedly different ways. Females are notably sensitive to the unique features of discrete objects whereas males are sensitive to the geometry of the enclosure [laboratory rats (Saucier, Shultz, Keller, Cook, & Binsted, 2008; Williams, Barnett, & Meck, 1990; Williams & Meck, 1991); three species of wild kangaroo rats (Barkley & Jacobs, 2007; Langley, 1994)]. In a classic rat radial-maze learning study by Williams et al. (1990), performance dropped in males but not in females when the geometry of the room was altered. When the locations of extramaze objects were randomized, female performance declined while male performance was unaffected. Similar results have been shown in humans, using a variety of experimental methods, including paper-and-pencil and flat screen two-dimensional tasks (Jones & Healy, 2006; Kelly & Bischof, 2005) and recent three-dimensional (3-D) computer-generated virtual environment (VE) tasks which closely resemble those used in animal studies (Astur, Ortiz, & Sutherland, 1998; Sandstrom, Kaufman, & Huettel, 1998). For example, in a virtual water maze where the geometry of the room and the presence of unique featured landmarks was disassociated, Sandstrom et al. (1998) found that male performance was less affected by the absence or randomization of landmarks when shape of the room provided stable geometric information. Moffat, Hampson, and Hatzipantelis (1998), using a virtual complex maze, found that men achieved a higher level of accuracy more quickly than did women, a result parallel to sex differences seen in meadow voles solving a similar maze (Gaulin & Fitzgerald, 1986).

What is still not clear, despite decades of research (for recent reviews, see Coluccia & Louse, 2004; Halpern & LaMay, 2000), is the exact nature of the difference. A recent cognitive map model proposed by Jacobs and Schenk (2003), the parallel map model, may provide new insights into the cognitive and neural mechanisms of these differences. The parallel map model postulates that the cognitive map is an integration of two parallel map components that are constructed from two distinct classes of cues: directional cues and positional cues, respectively; and the two map components are supported by different subregions of the hippocampus and associated brain structures. Directional (compass) cues include gradient cues such as odor and light, geographical slant information, as well as geometric cues and distal pinpoint cues such as distant landmarks, which polarize the environment but do not provide precise positional information. Positional cues are proximate unique pinpoint objects, which can provide more precise positional information within the local cue array. The spatial representation of the environment is formed by integrating local maps constructed from the positional cues onto the larger, coarser map built from directional information. There is growing

evidence for this model from recent animal studies (Kemp & Manahan-Vaughan, 2008; Poirier, Amin, & Aggleton, 2008; Goodrich-Hunsaker, Hunsaker, & Kesner, 2008; Save, Paz-Villagran, Alexinsky, & Poucet, 2005). Kemp and Manahan-Vaughan (2008) recorded hippocampal local field potentials in freely moving rats and found that large directional cues in the environment facilitated long-term depression (LTD) in the dentate gyrus, whereas small local cues facilitated LTD in the CA1 subfield of the hippocampus. Similarly, the dissociation of proximal cues and distal cues has been shown in associative parietal cortex and dorsal hippocampus lesioned rats (Parron, Poucet, & Save, 2004; Save et al., 2005; Goodrich-Hunsaker, Hunsaker, & Kesner, 2005). In humans, although recent brain imaging studies have begun to reveal the neural correlates of navigation (Maguire et al., 1998; Hartley, Maguire, Spiers, & Burgess, 2003; Shelton & Gabrieli, 2002; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Wolbers & Buchel, 2005), how different navigational cue types are encoded in the human hippocampus has not been investigated.

The goal of the present study was therefore to examine the predictions of the parallel map model for human navigation, using sex differences in navigation as a natural dissociation of the two mapping systems. Sex differences in navigation probably emerge from evolutionary processes involved in mate competition (Jacobs, 1996). In the present study, we postulated that the sexes rely differentially on the two mapping systems, with males depending more on directional information and females depending more on positional information. For example, in a recent study on cue perception, Barkley and Gabriel (2007) contrasted men and women's responses to photographs with directional gradient (e.g., distant skylines) and to pinpoint cues (e.g., trees). Participants were shown a pair of photographs where the cue of interest was deleted from the second photo and were asked to compare the two photos. As predicted by the parallel map model, women were slower when local pinpoint cues were deleted from the pictures. Sex differences in directional and positional cue use in navigational settings, however, have not been directly tested in humans. Moreover, the literature on the neural basis of sex differences in humans is limited. By creating and testing a virtual navigation task that can dissociate directional and positional cues, the goal of the present study was to lay the foundation for brain imaging studies on the neural basis of sex differences in navigation.

We constructed a naturalistic landscape for orientation and made the structure of the task—remembering the location of a reward—parallel to that of the Morris water maze (Morris, Garrud, Rawlins, & O'Keefe, 1982) to facilitate comparison with prior studies of humans (VE) and nonhuman animals in mazes (Astur, Tropp, Sava, Constable, & Markus, 2004; Sandstrom et al., 1998; Saucier et al., 2008; Williams et al., 1990; Williams & Meck, 1991). We tested navigation in VE landscapes containing either all directional cues or all positional cues to examine how women and men differ in using these two classes of cues. We included a gradient cue (terrain slant) in this study as one of the directional cues. Terrain slant is an important environmental cue for orientation and has been reported to facilitate navigation in humans (Restat, Steck, Mochnatzki, & Mallot, 2004) and to orient hippocampal place fields in laboratory rats (Jeffery, Anand, & Anderson, 2006). How the sexes differ in using slant information during navigation has not been previously studied, however, either in laboratory animals or humans. We predicted women and men

would show different strengths in the presence of different cue classes, with men orienting more accurately with directional cues, while women would have an advantage in the all-positional cue condition. Finally, we examined sex differences in self-reported spatial strategies and administered a test for mental rotation (Peters et al., 1995; Vandenberg & Kuse, 1978), an important component of spatial ability, to assess whether there were typical sex differences in spatial abilities in our test cohort.

Method

Participants

A total of 84 undergraduate students, aged 18 to 25 years (41 females, mean age = 19.8, SD = 1.9; 41 males, mean age = 19.2, SD = 1.1) participated in the study. All male participants and 24 female participants were undergraduate students at University of California, Berkeley. Seventeen female participants were additionally recruited from the MIT summer undergraduate research program (see Supplementary Material for details). All participants were right-handed and had normal or corrected-to-normal vision. One participant (Berkeley female) did not complete the experiment due to dizziness, and her data were excluded from the analyses.

Apparatus

We constructed computerized 3-D VEs using a commercially available video game engine (Unreal Engine 2 by Epic Games, Raleigh, NC). These environments were presented on a 21-inch computer monitor with participants sitting approximately 55 cm in front of the monitor. Horizontal field of view was approximately 39 degrees, and vertical field of view was approximately 30 degrees. Participants used a joystick (Cyborg Evo by Saitek, Bristol, U.K.) 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.

Virtual Environments (VEs)

The task was modeled after the logic of the Morris water maze task, in which the participant must search for a single hidden target in a circular arena. As seen in Figure 1, the VE was a large grassy terrain that contained a test arena surrounded by an octagonal invisible fence that was 18.3 virtual meters in radius. The fence was invisible to ensure an unblocked view of the surrounding cues. The target was a blue spike-like crystal. Two types of environments were constructed, one with all directional cues and one with all positional cues. In the directional-cue environment, the test arena was located on a small hill with a terrain slant of approximately 30 degrees. Other directional cues included a river running at the bottom of the slope and a cloud-filled sky (Figure 1a, c). In the positional-cue environments, the test arena was situated on a flat terrain with positional cues such as rocks, small plants, wooden barrels and mushrooms forming clusters of different configurations within the arena. The target was located in one of the clusters. Because duplicates of the same objects were found at different locations, the task could not be solved by simply associating the target location with a single object (Figure 1b, d).

a

b

c

d
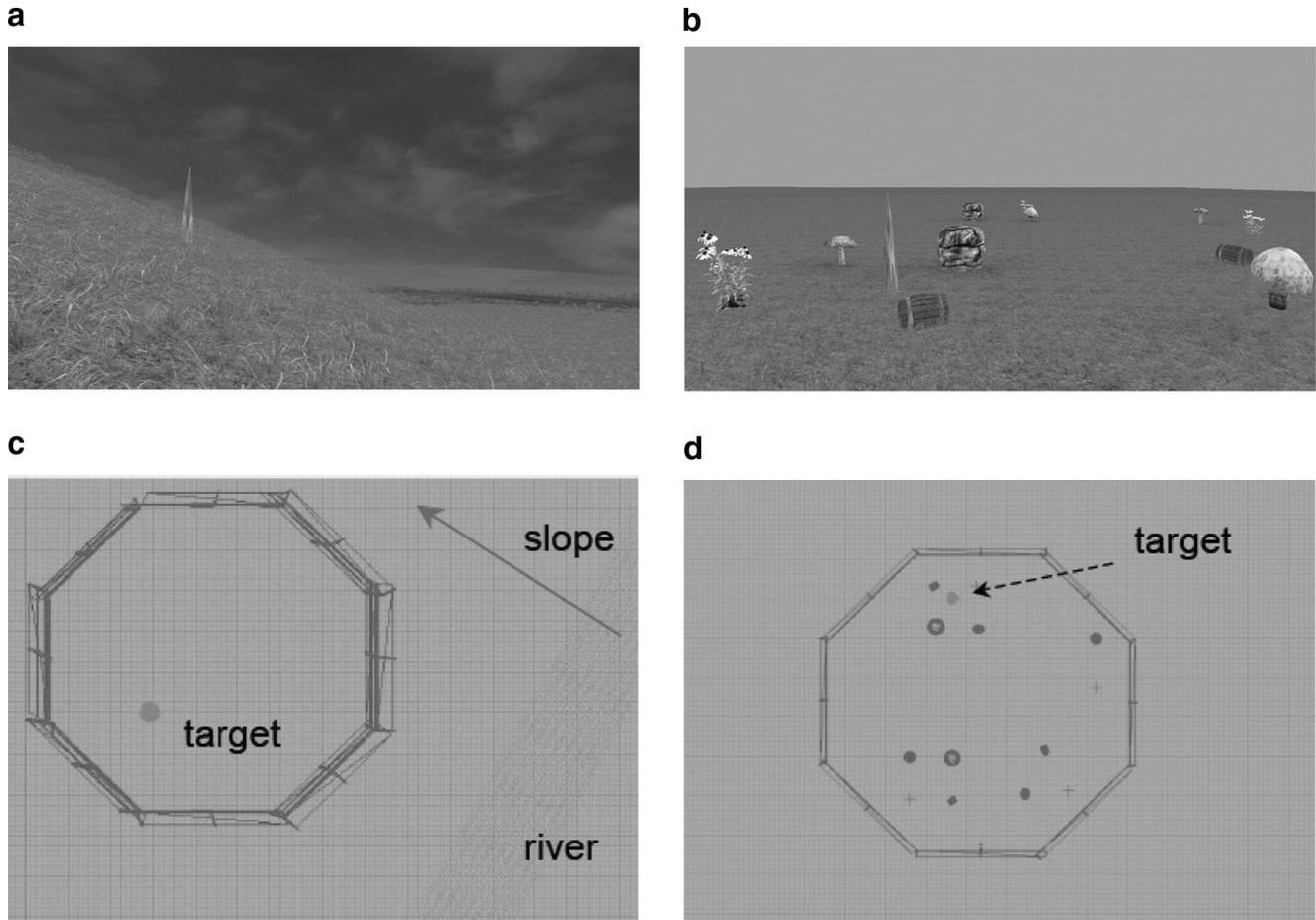
Figure 1. Representative virtual environments for the different cue class trials. Screenshot of (a) directional-cue trial; (b) positional-cue trial. Schematic of (c) directional-cue trial, (d) positional-cue trial (the arrow points up the slope). The blue crystal (target) was located in one of the cue clusters in positional-cue trials and on the slope in directional-cue trials. The target was not present in the probe trials. Actual view perspective of the participant was lower than shown here.

Procedure

Prior to starting the navigation trials, participants were shown how to use the joystick in two demonstration environments, which closely resembled the testing environments in terms of directional and positional cues, respectively. Participants were then given a short practice session to familiarize themselves with the VE interface and to practice moving with the joystick. The practice environment was an obstacle course situated on a grassy landscape similar to the test environments, with 10 blue crystals of different shapes scattered across the arena. The participants completed two practice trials, one situated in an environment similar to the directional-cue testing environment, the other one situated in an environment similar to the positional-cue testing environment. Participants were told to move toward the crystals and "collect" them by running over them. If the participant felt like he or she needed more practice, a second practice trial was given. All participants reported they were comfortable with moving in the VE at the end of the practice trials.

Navigation trials commenced immediately after practice trials. There were six trials for each type of cue environment. Each trial consisted of two phases: a training phase and a probe phase, each 25 s in duration. In the training phase, the target was visible throughout the trial. Participants were told to explore the area and try to memorize the location of the target. Each training phase was followed immediately by the probe phase. The probe phase environment was the same as training except that the target was invisible. Participants had 20 s to approach as closely as possible to the goal location. The starting point of the participant was different in the training phase and the probe phase. A timer was displayed on the top left corner of the screen to help participants keep track of time. At the end of the 20 s, the crystal reappeared for 5 s to give participants feedback on their performance. There was then a 10 s intertrial fixation on a centered cross on the monitor. The location of the target was different in each of the six trials for both directional-cue and positional-cue trials. Each positional-cue trial used different object cues and different object loca-

tions. The trials were presented in pseudorandom order. We measured navigation success as the distance between the target location and participant's position just before the feedback period in the probe phase. Participants were given the following verbal instructions prior to starting the navigation trials:

> There are two parts in each trial. In Part one, you will be placed in an environment in which there is one blue crystal. You have 25 seconds to explore the area and memorize the crystal location. In Part two, you will be directed to the same environment as part one except this time the crystal is not visible. Your job is to go back to where the crystal was in part one. Try to get to the crystal as close as possible. When you are done searching, you should stop moving and wait for the crystal to emerge from the ground to give yourself feedback on how you did. There is a timer on the upper-left corner of the screen indicating how much time is left. Please note you will be starting from different locations each time so your initial views of the environments might be different. In some trials, there will be objects around the crystal to help you remember its location, in some trials there won't be any objects and you will be placed on a small hill. Please direct your attention to the cross on the screen between trials.

After the virtual navigation task, participants completed a series of questionnaires that measured computer and video gaming experience, handedness, as well as any strategy they may have employed during the virtual navigation task. A 7-point scale was used to assess the frequency of 2-D and 3-D 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). An overall video game experience score was calculated by combining the 2-D and 3-D gaming scores.

Mental Rotation Test (MRT)

We used the redrawn version of the mental rotation test originally constructed by Vandenberg and Kuse (1978) (Peters et al., 1995). The object images from the original written test were scanned into jpeg files and displayed on the computer screen. Each problem consisted of one original object and four possible choices, two of which were rotated versions of the original image. Participants were given 3 min to pick the rotated images for 24 problems. One point was given if both correct images were picked.

Spatial Strategy Questionnaire

Prior studies using paper and pencil questionnaires have detected two ways of navigation, survey (global layout, map-like representation), and route (remembering routes and turns; Lawton, 1994; Tversky, 1991). Yet the preference to use a survey representation, which depends on directional cues, or a landmark-centered strategy, that uses positional information from landmarks, has not been linked to sex differences. Pazzaglia, Cornoldi, and De Beni (2000) identified five factors in spatial strategies based on data from 285 participants, representing general sense of direction, compass directions in orienting tasks, preference for route, landmark-centered, and survey spatial representations. To investigate sex differences in survey and landmark strategies, we included questions related to preference for survey and landmark spatial representations from the original questionnaire in our study. For each question, participants ranked how often they used a certain strategy (1 to 5). For each participant, two scores were calculated from the answers to the questions, one that represented a survey representation strategy and one that represented a landmark-centered spatial strategy (see Supplementary Material for details of the questionnaire).

Results

Virtual Navigation Performance

To measure navigation accuracy, we calculated the distance of the participant's position from the target at the end of each probe trial. For each participant, two average scores were computed from the directional-cue trials and the positional-cue trials, respectively, and analyzed using a two-factor mixed-design ANOVA with sex as the between-subjects factor and cue type (positional cue, directional cue) as the repeated-measure factor.

The main effects were significant for sex, $F(1, 80) = 38.51$ $p < .001$, and cue type, $F(1, 80) = 195.44$, $p < .001$. There was also a significant sex-by-cue interaction, $F(1, 80) = 7.31$, $p = .008$. Post hoc t tests revealed that men arrived closer to the target location than did women under both the directional-cue condition, $t(80) = 6.39$, $p < .001$ and the positional-cue condition, $t(80) = 3.71$, $p < .001$. However, the difference between male-female navigation accuracy was greater in the directional-cue trials (see Figure 2).

To assess how often the correct positional-cue clusters were identified, we calculated the percentage of trials in which the participant correctly identified the cluster of objects that contained the target. Men had higher percentage ($M = 81.91$, $SD = 3.05$) than women ($M = 74.19$, $SD = 3.29$), but this difference was not significant, $t(80) = 1.72$, $p = .09$; see Figure 3.

Males reported more 3-D video game experience, $t(80) = 5.25$, $p < .001$ than did females. There were no differences in 2-D game experience, $t(80) = 1.38$, $p = .17$, or joystick use, $t(80) = 1.60$, $p = .11$. To exclude the possibility that sex differences in virtual
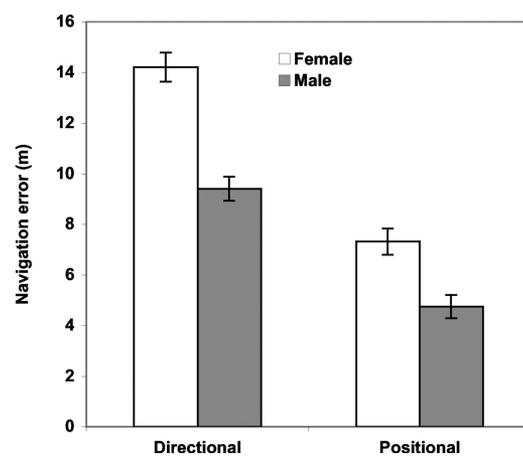

Figure 2. Virtual navigation performance. Mean navigation error (in virtual meters) under directional and positional-cue conditions, defined as the mean distance ($\pm$SEM) of the participant's position from the target location at the end of the trial. Navigation error was higher in directional-cue trials. Men were more accurate than women overall. There was a significant sex by cue type interaction.
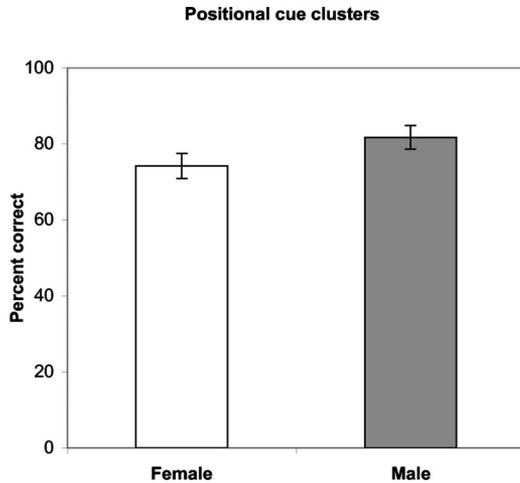
Positional cue clusters

Figure 3. Mean percentage of the positional-cue trials (±SEM) in which the correct cue cluster that contained the target was identified.

navigation resulted from this male advantage in video game experience, we repeated the mixed-design ANOVA with 3-D video game experience a covariate. Gaming experience had no effect on navigation accuracy, $F(1, 79) = 1.14$, $p = .29$. The main effect of sex, $F(1, 79) = 23.20$, $p < .001$, and the sex-by-cue-type interaction, $F(1, 79) = 6.00$, $p = .017$ were still significant. Similarly, 2-D game, joystick use, and overall game experience had no effects on the navigation results.

Trial-by-Trial Analysis of Navigation Performance

To examine possible sex differences in learning rate from trial to trial, individual trial data were analyzed using a two-factor mixed-design ANOVA with sex as the between-subjects factor and trial number as the repeated-measure factor. For directional-cue trials, the main effect of learning approached significance, $F(5, 385) = 2.23$, $p = .051$, the main effect of sex was significant, $F(1, 77) = 36.93$, $p < .001$. However, the interaction between sex and trial was not significant, $F(5, 385) = .15$, $p = .91$, which suggests that men and women did not differ in their learning rate. The difference in male-female performance was similar throughout the experiment. For positional-cue trials, there was a significant main effect of sex, $F(1, 78) = 13.45$, $p < .001$. Neither main effect of learning, $F(5, 390) = 1.42$, $p = .22$, nor the interaction between sex and trial, $F(5, 390) = .20$, $p = .96$, was significant (see Figure 4).

Search Time in Probe Trials

To test the possibility that women were simply slower when navigating to a previously learned location, we calculated how much time each participant used to search for the target in the probe phase of each trial (see Figure 5). The average time that the female and male groups spent on searching the target was similar for directional-cue trials (female = 16.95 s, male = 16.83 s, $t(80) = .37$, $p = .71$) and for positional-cue trials (female = 16.84 s, male = 16.49 s, $t(80) = 1.04$, $p = .30$). We then compared search time for each individual trial between males and females. We found no sex differences in this measure in any of the six posi-

tional cue trials. Females were equally fast as males on 5 out of the 6 directional-cue trials and were slower only on the first directional-cue trial, in which the average female search time was under the time limit ($M = 18.51$ s, $SD = 0.37$). Finally, we compared the percentage of trials in which the full 20 s was used to search the target for each participant. Again men and women did not differ in this measure, in either the directional-cue (female = 23.4%, male = 24%, $t(80) = .14$, $p = .89$) or positional-cue trials (female = 18.9%, male = 21.5%, $t(80) = .58$, $p = .56$).

MRT and Spatial Strategy

Performance on the MRT differed between the sexes, as expected, with a male advantage, $t(76) = 4.27$, $p < .001$. The average score for men was 6.59 ($SD = 2.17$), and the average score for women was 4.37 ($SD = 2.41$).

Spatial strategy scores were analyzed using the Mann–Whitney test. For each participant, the landmark-strategy score was subtracted from the survey-strategy score to represent preference for survey strategy. This differential score was higher in males ($U = 515.5$, N1 = 41, N2 = 41, $p = .002$), suggesting a male preference for survey representation strategy. Post hoc tests revealed that men ranked higher than women on survey-representation questions ($U = 547.5$, N1 = 41, N2 = 41, $p = .018$); however, scores on landmark-centered strategy did not differ between women and men ($U = 776$, N1 = 41, N2 = 41, $p = .54$) (see Figure 6). Across all subjects, survey-strategy scores correlated positively with navigation accuracy in directional-cue trials ($r = .30$, $p = .007$).
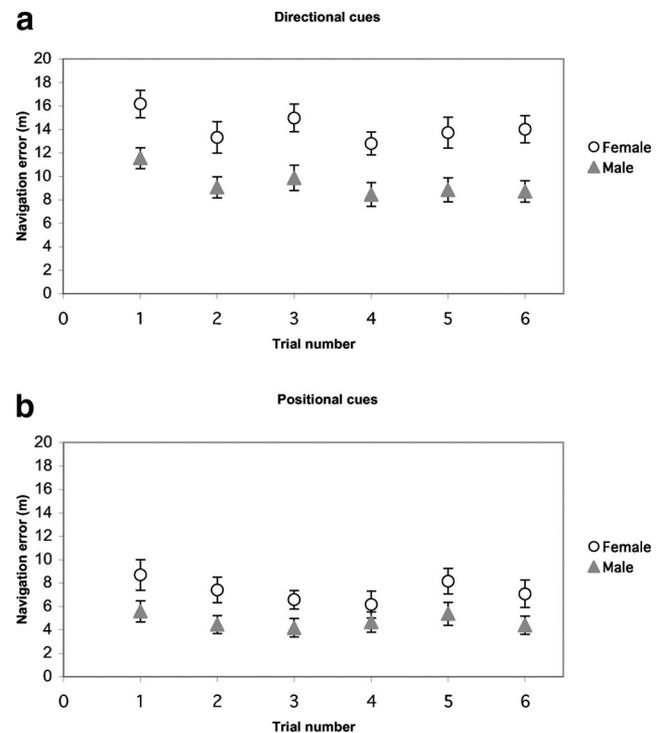
a   **Directional cues**

b   **Positional cues**

Figure 4. Trial-by-trial virtual navigation performance. Mean navigation error (±SEM), defined as the mean distance (±SEM) of the participant's position from the target location at the end of the trial.
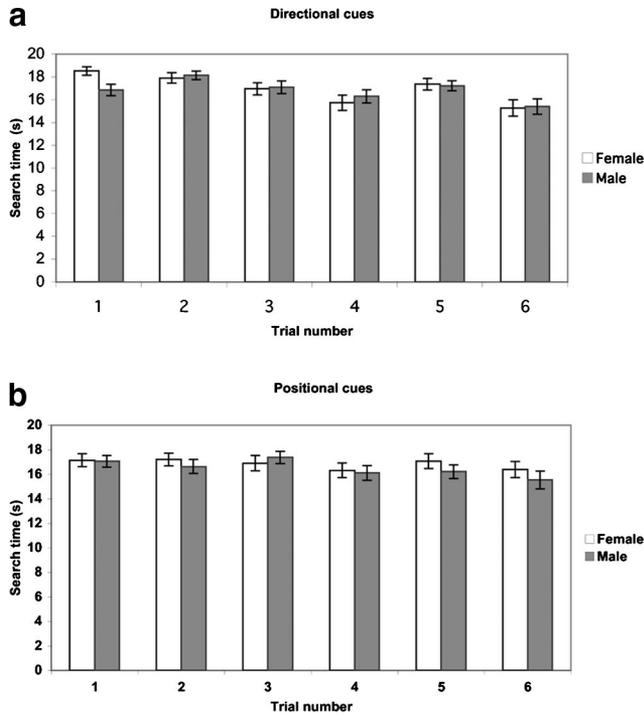
Figure 5. Mean (±SEM) time used to search the target in probe phase of the trials. (a) directional-cue trials, (b) positional-cue trials.

Overall, MRT scores were positively correlated with navigation accuracy in both directional-cue ($r = .37$, $p = .001$) and positional-cue ($r = .38$, $p = .001$) trials. The difference between the survey-strategy score and the landmark-strategy score was also correlated with MRT ($r = .30$, $p = .007$). Within the female group, MRT was correlated with navigation accuracy in positional-cue trials ($r = .36$, $p = .02$). No other correlations were found.

Discussion

The goal of our study was to examine the hypothesis that men and women differ in their use of directional and positional cues when navigating 3-D virtual landscapes, as predicted by the cognitive map model of Jacobs and Schenk (2003). Specifically, following up on the work of Barkley and Gabriel (2007), we asked if in a naturalistic 3-D environment, sex-specific perception of gradient and pinpoint cues transfers to navigational cue use. We therefore constructed two extreme cases of landscapes—all directional or all positional cues—that were nonetheless landscapes that can be found under natural conditions. In each case the participants had the same goal of encoding and recalling the reward location. We found that men were more accurate in finding the target location in both cue conditions but that the male advantage was larger when only directional cues were available. Women and men did not differ in identifying the correct positional cues that predicted the target location. Self-reported spatial strategy revealed the same pattern with men reporting higher preference scores on survey representation in navigation.

Our results are consistent with the male advantage reported in prior virtual navigation studies where positional cues were not

available and participants had to rely on cues such as geometric information and distant objects (Astur et al., 1998; Moffat et al., 1998; Sandstrom et al., 1998). Our results also indicate that men encoded gradient cues such as terrain slant more effectively than women during navigation. What seems to be the common denominator among cues that produce this male performance advantage is the degree to which cues provide directional information. Geometric shape, distant objects, and gradient cues cannot define the precise location of the target, but because they polarize the environment, they can provide directional information. Our results thus provide evidence for the hypothesis that males depend more on directional cues during navigation, as predicted by Jacobs and Schenk (2003).

In contrast to our original hypothesis, we did not see the expected female navigation advantage in the positional-cue condition. Men were more accurate in estimating the position of the target in both cue environments, although the male advantage was smaller when only positional cues were present. However, tasks that require an accurate measurement of distance have been shown to favor men (Iachini, Sergi, Ruggiero, & Gnisci, 2005; Postma, Izendoorn, & De Haan, 1998). Iachini et al. (2005) studied object location memory in a 3-D real environment and found no sex differences in object recognition, yet men recalled the distance between objects and the size of the layout more accurately than did women. A number of other studies have also reported that men prefer to use euclidean information (i.e., cardinal directions and distance) during navigation (Dabbs, Chang, Strong, & Milun, 1998; Saucier et al., 2002). Therefore in our study, both genders may have been equally good at identifying the targeted "cluster" of positional cues, but men estimated the distance more accurately between the target and the surrounding positional cues. We indeed found no sex difference in the identification of the correct positional-cue cluster. Furthermore, the pattern of self-reported spatial strategy is consistent with this interpretation of the virtual navigation data. Men reported higher scores on survey (global) representation, which depends heavily on directional cues, whereas scores on landmark-centered strategies did not differ between the genders. If men rely more on a survey-centered strategy than do women, they should outperform women in environments where there are few or no positional cues, as we observed. The lack of difference in landmark-
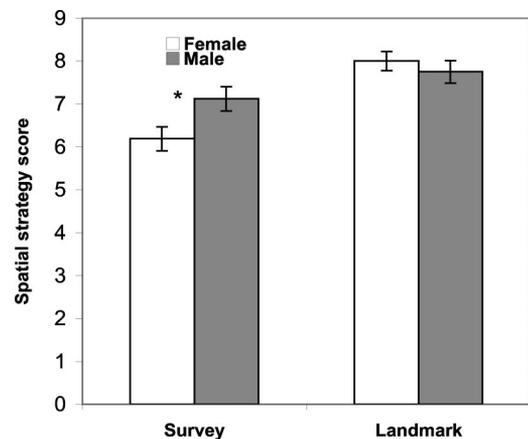

Figure 6. Mean (±SEM) scores from the self-reported spatial strategy questionnaire.

centered strategy scores indicates that both genders make use of positional cues in navigation. Overall, high scores in survey-strategy correlated with better navigation performance in the directional-cue trials. Within either male or female group, we did not find any correlation between spatial strategy scores and navigation. This may be due to the relatively small variation in the spatial strategy scores in both groups. Another possibility is that men and women may solve the positional-cue and directional-cue trials in different ways. Women may be associating the target location with particular positional-cue configurations, whereas men could be using positional cues to estimate euclidean distance from the target. Likewise, females might use a particular directional cue (such as the river) as a positional cue.

Women in our study reported similar landmark preference scores to those of men on the spatial strategy questionnaire. On the surface, these results are inconsistent with several prior studies demonstrating women's proficiency in learning routes and landmarks (Choi, McKillop, Ward, & L'Hirondelle, 2006; Dabbs et al., 1998; Galea & Kimura, 1993; Lawton, 1994). For example, in a study of direction giving, Dabbs et al. (1998) found that women were more likely to use more concrete terms such as turning left/right and describing landmarks along the way. However, these previous studies did not differentiate route and landmark-centered strategies. Pazzaglia et al. (2000) were able to differentiate landmark-centered representation from route and survey representations. Landmark-centered representation focuses on identifying landmarks in the environment that do not necessarily connect a set of routes. The questionnaire used in this study (adapted from Pazzaglia et al., 2000) included only the landmark-centered questions, which may explain the similar scores we found in women and men. Route-learning is only one of the several components of navigation and there are many navigation tasks in which route-learning does not apply, for example, navigation in a large, open environment with few routes. Therefore even though women may be biased toward a route strategy and have better memories for landmarks along the routes, but it is not necessarily true that they generally use landmarks more than men during navigation, especially in open environments like the one used in our study. The nature of navigation tasks used in our study were not targeted toward route-learning, and for that reason may not have shown the same female biases toward landmark-use as have other navigation studies involving route-learning.

Performance in spatial tasks is hormonally dependent in laboratory animals (Williams et al., 1990) and has been shown to fluctuate across the menstrual cycle in women (Epting & Overman, 1998; Hampson, 1990). Although the design of the present study did not address the question of hormonal influences, future studies could use within-subject assays of hormone levels and navigational performance to delineate the interaction of hormones and navigational cue types.

An alternative explanation for sex differences in performance could be greater speed of memory retrieval by men than women. In this scenario, women would be slower but not less accurate as they required more time to compute the target location in the directional-cue trials. However, our analysis on target search time showed no difference between groups, suggesting that the time allotted for performance was sufficient for both groups to retrieve the target location. Furthermore, our unpublished data in another study with self-paced VE navigation trials show a similar male advantage, even when females were under no time constraint (unpublished data,

Chai & Jacobs). It therefore seems less probable that sex differences in navigation accuracy observed in our study were due to speed of location retrieval but rather from a difference in representation of the target location. The lack of correlation between video gaming experience and navigation accuracy also suggests that the effect observed here was not due to females having difficulty moving in VE. Although our study does not definitively exclude the hypothesis that female navigation accuracy in directional-cue trials is time-limited, the results are consistent with our hypothesis that sex differences in the use of directional cues underlie sex differences in navigation performance in humans.

The present study demonstrated that directional and positional cues can be dissociated behaviorally in men and women, thereby lending support to the parallel map model of hippocampal function. The study therefore lays the behavioral foundation for future brain imaging studies of humans on the neural correlates of sex differences in cue use in navigation. Based on the parallel map model, directional and positional cues are subserved by dissociable hippocampal subregions, a prediction that can be directly tested using functional imaging and VE tasks such as the one described here. Our initial results with such methods indeed support such subregion dissociation (unpublished data, Chai, Jacobs, & Gabrieli). A series of recent studies are also consistent with this model of hippocampal function (Doeller & Burgess, 2008; Doeller, King, & Burgess, 2008). In a VE navigation task, navigation using a single intramaze landmark was dissociated from navigation using boundary information. Boundary-related learning was associated with right posterior hippocampal activation while intramaze landmark-related learning was associated with dorsal striatum activation. The intramaze landmark was similar to the positional cues in our experiment, which were also located within the test arena. Boundary information, together with distant objects, can be used as a directional cue. Such studies, combined with the results described here, point to a new refinement of brain imaging studies that can pinpoint the exact neural signatures of brain networks that mediate and underlie spatial navigation.

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