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# Eye tracking, strategies, and sex differences in virtual navigation

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ABSTRACT

Reports of sex differences in wayfinding have typically used paradigms sensitive to the female advantage (navigation by landmarks) or sensitive to the male advantage (navigation by cardinal directions, Euclidian coordinates, environmental geometry, and absolute distances). The current virtual navigation paradigm allowed both men and women an equal advantage. We studied sex differences by systematically varying the number of landmarks. Eye tracking was used to quantify sex differences in landmark utilisation as participants solved an eight-arm radial maze task within different virtual environments. To solve the task, participants were required to remember the locations of target objects within environments containing 0, 2, 4, 6, or 8 landmarks.

We found that, as the number of landmarks available in the environment increases, the proportion of time men and women spend looking at landmarks and the number of landmarks they use to find their way increases. Eye tracking confirmed that women rely more on landmarks to navigate, although landmark fixations were also associated with an increase in task completion time. Sex differences in navigational behaviour occurred only in environments devoid of landmarks and disappeared in environments containing multiple landmarks. Moreover, women showed sustained landmark-oriented gaze, while men's decreased over time. Finally, we found that men and women use spatial and response strategies to the same extent. Together, these results shed new light on the discrepancy in landmark utilisation between men and women and help explain the differences in navigational behaviour previously reported.



## 1. Introduction

The ability to successfully navigate through known and novel environments is essential in modern life. Finding one's way to and from locations such as school, work, and home, or orienting oneself in a new city are necessary for daily functioning. However, there is a large variance in the ability to successfully navigate when placed in a novel environment. In particular, numerous studies have found sex differences in navigational ability, some favouring women and others favouring men depending on the method used (Andreano & Cahill, 2009; Astur, Ortiz, & Sutherland, 1998; Astur, Tropp, Sava, Constable, & Markus, 2004; Driscoll, Hamilton, Yeo, Brooks, & Sutherland, 2005; Malinowski, 2001; Sakthivel, Patterson, & Cruz-Neira, 1999; Sandstrom, Kaufman, & Huettel, 1998; Saucier et al., 2002; Silverman & Eals, 1992; Spiers, Sakamoto, Elliott, & Baumann, 2008).

To reach a particular location, one can rely upon two distinct strategies. A *spatial strategy* involves the construction of a cognitive map of an environment, in which the relative positions of multiple landmarks in space are encoded as the navigator moves. Functional neuroimaging and lesion studies in humans as well as in animals have consistently identified the hippocampus' role in spatial memory (Bohbot, Iaria, & Petrides, 2004; Hartley, Maguire, Spiers, & Burgess, 2003; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Maguire et al., 2003). Conversely, a *response strategy* involves learning sequences of body movements in response to a stimulus, such as a starting position or a particular environmental feature. Functional neuroimaging studies have associated this response strategy with activation in the striatum, particularly the caudate nucleus (Bohbot et al., 2004; Hartley et al., 2003; Iaria et al., 2003; Packard, Hirsh, & White, 1989; White & McDonald, 2002). Women and men were found to be using spatial and response strategies in equal proportions (Bohbot et al., 2004; Iaria et al., 2003; Levy, Astur, & Frick, 2005), suggesting that the male advantage in using Euclidian maps or the female advantage in landmark utilisation does not impact the spontaneous use of spatial and response strategies.

Saucier et al. (2002) were able to determine differences in men and women's preferential cue utilisation in a real-world navigation task. Participants searched for various locations by following two types of instructions, either landmark- or Euclidian-based directions. It was found that women made fewer errors and took

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less time to complete the task when they were asked to navigate by following landmarks than when they were instructed to use distances and cardinal directions. Men performed equally well using either method. Astur et al. (2004) tested men and women on two virtual spatial memory tests, the Radial Arm Maze and the Morris Water Maze. In both tasks, men took less time to find targets than women, though actual distance traveled did not differ significantly between men and women. The authors hypothesised that these differences in performance reflected different navigational methods between men and women. Similarly, Sandstrom et al. (1998) manipulated the availability of landmarks and room geometry. Men and women were trained in a virtual Morris Water Maze that featured unique room geometry and landmarks. The shape of the room or surrounding landmarks was altered to differentiate which cues were used by participants. While men were able to navigate using either landmarks or room geometry, women's performance was impaired when landmarks were removed. Levy et al. (2005) did not find sex differences in strategies used in a "T maze" or in performance on a radial arm maze task that contained landmarks later in training. Interestingly, early in training, they found a small but significant bias in women using a spatial strategy consistent with the fact that they used landmarks to orient themselves. Together, these studies suggest that while men and women perform with similar accuracy, they differ in their reliance on landmarks. Men can make use of Euclidian coordinates (Dabbs, Chang, Strong, & Milun, 1998; Lambrey & Berthoz, 2007; Saucier et al., 2002), environmental geometry (Sandstrom et al., 1998), absolute distances (Dabbs et al., 1998; Postma, Jager, Kessels, Koppeschaar, & van Honk, 2004; Ruggiero, Sergi, & Iachini, 2008), and mental rotation (Malinowski, 2001) in order to orient themselves, and are therefore able to perform equally well when one type of environmental information is missing. Conversely, women seem to rely more on landmarks when navigating (Dabbs et al., 1998; Lambrey & Berthoz, 2007), and their performance decreases when none are available.

In the present study, we tracked eye movements to examine whether variations in gaze behaviour underlie the specific differences in navigational behaviour between men and women. We manipulated the impact of landmark availability on gaze and navigational behaviour by systematically increasing or decreasing the number of landmarks in the environment. It was hypothesised that a sex difference in gaze behaviour would be observed, as previous research has shown differences in eye movement allocations between men and women (Campagne, Pebayle, & Muzet, 2005; Miyahira, Morita, Yamaguchi, Morita, & Maeda, 2000; Miyahira, Morita, Yamaguchi, Nonaka, & Maeda, 2000; Mueller, Jackson, & Skelton, 2008). Campagne et al. (2005) followed individuals' eye movements as they performed a simulated driving task. Following a prolonged navigation period, a sex difference was observed in the gaze pattern. Specifically, whereas men quickly reduced the frequency of glances to an attentional target, the frequency of glances in women did not decrease as quickly, indicating differences in gaze allocation to attentional targets. In accordance with these results, a study by Mueller and colleagues (2008) found that men's fixation durations decreased faster than women's in a virtual Morris Water Maze task, where participants had to learn the spatial features of an environment in the learning trials. Moreover, men were found to visually explore more space early in the task than women, which the authors argue is an indication that men were encoding spatial relations between features of the environment more so than women. However, there were no significant sex differences in the amount of time spent looking at environmental features. In a study by Miyahira et al. (2000), the authors investigated sex differences in the distribution of eye movements when viewing fixed scenes. By tracking eye movements using head-mounted video cameras, visual exploration could be accurately measured across four stimuli of increasing complexity, from blank circles to landscape scenes. It was found that eye movements for the scene were significantly different from the simpler stimuli, and mean gazing time of women was higher than that of men. The literature therefore suggests that the distribution of eye movements between men and women differs when a high attentional demand is required or when the complexity of the visual target increases.

If the ability to remember previously visited places depends on the type of information used in the environment, it was hypothesised that this would be reflected in the distribution of gaze to the visual stimuli used as reference points. It was thought that differences in navigational method might result in different visual search patterns, as determined by the frequency and length of landmark-directed eye movements. Specifically, because men typically rely on multiple sources of information to orient themselves, such as room geometry, Euclidian coordinates, or distance from a particular reference point, we hypothesised that this would result in an overall low allocation of visual gaze to landmarks. Conversely, as women usually orient themselves by forming associations between the various landmarks that make up an environment and their position in relation to them, there should be an associated increase in landmark-directed gaze. We therefore expected to see a greater number of landmark-directed eye movements in women than men.

## 2. Methods

### 2.1. Participants

Seven (four men, three women) members of the student population of McGill University and staff of the Douglas Mental Health University Institute volunteered for the experiment. Participants were between 21 and 37 years old (mean age = 28.17 ± 5.67) and had normal or corrected-to-normal vision. Video game experience was determined for each participant and was correlated with age, sex, strategy, latency, and number of fixations. Informed consent was obtained from all participants in accordance to the guidelines of the local ethics committee.

### 2.2. Behavioural paradigm

A modified version of the 4-on-8 virtual maze (Iaria et al., 2003) was administered to participants. Five distinct virtual environments were made using the editor program of a commercially available computer game (Unreal Tournament 2003; Epic Games, Inc.) and displayed on a 17" monitor with a resolution of $1280 \times 1024$ pixels. Each virtual environment was composed of a maze consisting of a central platform branching out into eight equally distant pathways (Fig. 1). The maze was surrounded by a different landscape in each of the five virtual environments and contained a different number of landmarks; 0, 2, 4, 6, or 8 landmarks. The order of presentation of the different environments was semi-randomized so that the environments would not be presented in order of increasing number of landmarks. The same order of environments was presented to all participants. All participants started at the centre of the radial arm maze, always facing the same direction. There were three trials in each virtual environment, totaling 15 trials for each participant (Fig. 2). A trial consisted of two parts. In the first part, 4 of the 8 pathways were open and contained an object, while the remaining 4 pathways were closed by barriers. At the end of each pathway were stairs leading to a pit where participants could retrieve an object. Participants were instructed to remember the location of these objects. In the second part, all 8 pathways were open, and participants were asked to avoid previously visited pathways in order to retrieve the objects, which were moved to the pathways that were

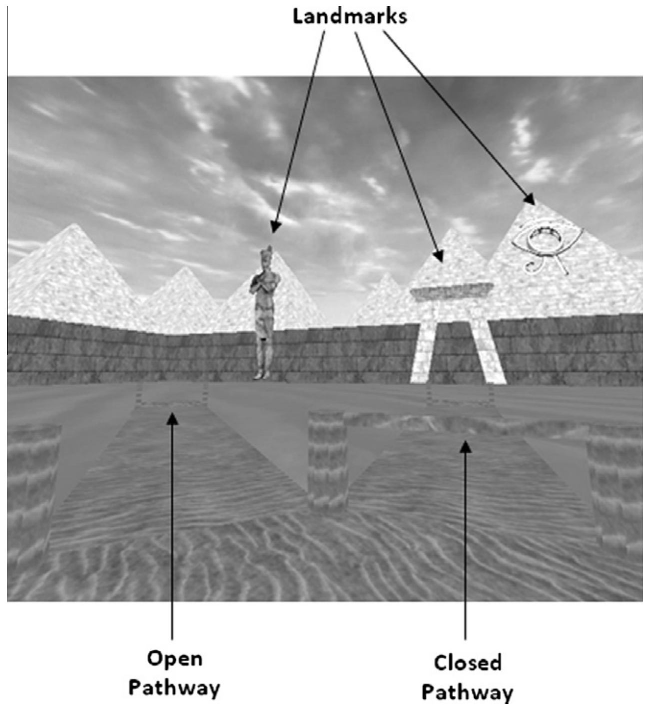


**Fig. 1.** Participant's point of view in one of the environments of the 4-on-8 virtual maze, demonstrating open (left) and closed (right) pathways as well as the landmarks (arch, eye, and statue) used as reference points. The background refers to anything that is not distinctive (pyramids, wall, and sky).

initially closed. The platform array was enclosed by a short wall, surrounded by visible landmarks. The position and type of landmarks differed between each environment. Detailed verbal reports were taken from participants at the end of the task which served to inform us of the exact strategy used. They enabled us to determine whether a given individual used a spatial or response strategy for each virtual environment, and how many landmarks were used. If several landmarks were reported as having been used in the verbal report, and if the participant did not mention any response strategy, then the participant was assigned a spatial strategy for that particular virtual environment. The term navigational method is used to describe the elements participants used to solve the task (e.g., landmarks, Euclidian coordinates, absolute distances, cardinal direction, etc.), however this term does not correspond with navigational strategy.

All participants were first asked to navigate in a new habituation environment to get used to the controls on the keyboard and to ensure that they all started with equal experience using the Unreal platform. The habituation environment consisted of a radial maze similar to the ones in the experimental tasks. However, there were no landmarks and no objects at the end of the paths. It was simply used to accustom participants with the maze and to get them to navigate with ease between the different arms.

### 2.3. Procedure

Eye movements were tracked using an ASL 504 Remote Mounted Camera. This camera operates on the principles of retinal retroreflection and corneal reflectivity to plot the angle of the eye with respect to the stimuli presented. The ASL Eye Tracker 5000 EYEHEAD Integration System was used to process and calculate gaze information as well as to control camera operations. As participants navigated on one computer, a second was used to track eye movements, while a third combined both types of input into one video file (Fig. 3). Research participants were seated at a fixed viewing distance of 64 cm from the navigation screen, with the screen positioned at eye level. The camera was placed directly below this screen and both were housed in a custom-designed stand. A main computer utilised the Gazetracker program to combine eye tracking, navigation information, and to record participants' trials for subsequent analysis. A remote sensor was affixed to a headband and placed on the participant's head, above the eye to be tracked (usually the right eye). The camera was then focused and centred on the pupil of the tracked eye. Accuracy of the eye tracking system was achieved by adjusting the eye's fixation point across a 9-point calibration on the computer screen. Once the camera interface was calibrated, the behavioural task began. No time constraints were placed on individuals as they navigated through the virtual environments. An experimental session lasted approximately 3 h.

### 2.4. Analysis of eye-movement data

The GazeTracker EyeTracking Analysis Software was specifically designed to measure a person's point of gaze on a video stream. We used GazeTracker to combine eye tracking information with the video displayed on the computer monitor as people navigated. We examined the time spent looking at landmarks over the total navigation time, giving us a measure of *resource use* for each trial completed. Analysis of eye tracking data was a laborious enterprise as every navigation path is unique, representing the places visited by each participant. It was therefore necessary to perform a frame by frame analysis for each participant's navigation trials. Since we recorded 30 frames per second and the length of recorded videos was approximately 125 min, a participant's navigation session averaged 225,000 frames, requiring over 63 h of pre-analysis coding of eye tracking data for each participant. For this reason, eye tracking analysis of free navigation data is typically done on small groups of five to ten participants (Hollands, Patla, & Vickers, 2002; Imai, Moore, Raphan, & Cohen, 2001).

For each frame we noted whether the participant's gaze fell upon the landmarks contained within each environment. The classification of *fixation* was attributed if the gaze landed on or around the landmark within a zone equal to 50% of its size (allowing for foveal variability) for three or more consecutive frames (0.1 s or more). There is a large variability in the differentiation between glances, fixations, short fixations, steady fixations, and long fixations in the literature. For example, a study by Inhoff, Topolski, and Wang (1992) attributed a value between 50 and 150 ms for short duration fixations, while Rayner (1998) determined a length of 200–300 ms for short fixations. Further, fixation length is also dependent on the stimulus presented (words versus scenes). Rayner (1998) attributes a lower range (between 200 and 250 ms) for reading English words, and admits individual differences play a part in biasing this range (under 100 ms to over 500 ms). Some studies also discard any eye movements of less than 50 ms (Over, Hooge, Vlaskamp, & Erkelens, 2007). We contend that information gathered from these shorter eye movements are as valid as longer ones, and may help to identify sex differences in visual search during navigation. We therefore chose to use a cutoff of 100 ms to define fixations. For every trial, we also examined each landmark's contribution as a reference point during navigation by calculating the time spent looking at each landmark over the time dedicated to looking at all landmarks (*landmark use*).

The probability of each landmark to be used is equal, and so the probability of any one landmark to be used is 100% divided by the number of landmarks present in the environment. Thus, for the condition containing 4 landmarks, a landmark was considered to be utilised if eye movements directed towards it represented 25% and above of total landmark-directed gaze. Similarly, for the environments containing 6 and 8 landmarks, the threshold was set to 16.67% and 12.5%, respectively. For the condition in which only 2

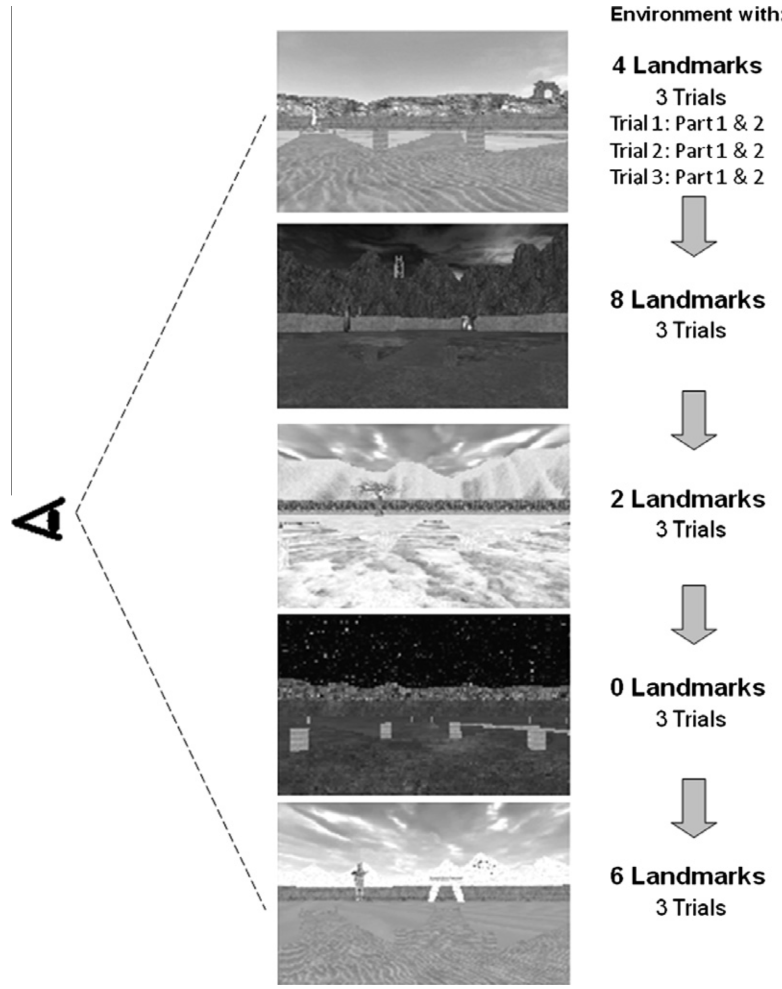


**Fig. 2.** Experimental design. participants navigated through five distinct environments differing in the landscape and number of landmarks while their eye was being tracked. Order of presentation was semi-randomized to control for learning effects.

landmarks were available, we used a 40% threshold. A minimal threshold of 50% was unrealistic due to the fact that there were only 2 landmarks and that both would have to have been fixated upon exactly 50% of the time in order to be considered as having been utilised. Therefore we set a lower threshold in this condition. This means that, if a landmark was viewed only 35% of the time, it was not considered as being used. The number of landmarks that exceeded their set threshold was taken to determine the number of landmarks used. We also considered the number of landmarks that were reported to be used in the verbal reports.

### 2.5. Statistics

The SPSS program (Version 11.5) was used to perform all statistical analyses. Variables (total time, total errors, resource use, landmark use, number of fixations) were considered for each individual trial as well as for each part of a trial. Each participant therefore had 15 data points if the data were considered for each trial (5 conditions × 3 trials), and 30 data points if they were considered for each part of a trial (5 conditions × 3 trials × 2 parts). Each of these data points were considered to be independent of each other because they were collected in different environments under different conditions or in different parts of the learning curve. Statistics were computed using multivariate analyses of variance (MANOVAs) and Mixed Model ANOVAs. Landmark number was the within-subjects measure because all participants participated in all of the conditions (0, 2, 4, 6, 8 landmarks) and sex was the between-subjects factor. Independent samples *t*-tests were conducted to compare the number of fixations/s between men and women as well as landmark use between spatial and response learners for each trial. Pearson correlations were performed to investigate the link between various variables.

## 3. Results

### 3.1. Navigational performance

Men and women differed in their performance on the 4-on-8 virtual maze. Overall, women took longer to complete the task on a given trial ($F_{1,198} = 44.171$, $p < 0.001$) and made more errors ($F_{1,206} = 6.396$, $p < 0.05$) than men. There were no sex differences in the 8-landmark condition in terms of the number of errors or latencies. However, when the number of landmarks was reduced, performance-related sex differences emerged. Women took more time to complete a given trial in the 0-, 2-, 4- and 6-landmark conditions (0 landmarks: $F_{1,40} = 22.793$, $p < 0.001$; 2 landmarks: $F_{1,40} = 19.225$, $p < 0.001$; 4 landmarks: $F_{1,36} = 7.433$, $p < 0.01$; 6 landmarks: $F_{1,38} = 6.537$, $p < 0.05$) (Fig. 4). There was a significant negative correlation between the number of landmarks and latencies in women only ($r = -0.209$, $p < 0.05$) (Fig. 4). Women made more errors per trial than men in the 0-landmark condition only ($F_{1,40} = 6.226$, $p < 0.01$) (Fig. 5). A correlation was conducted between errors and

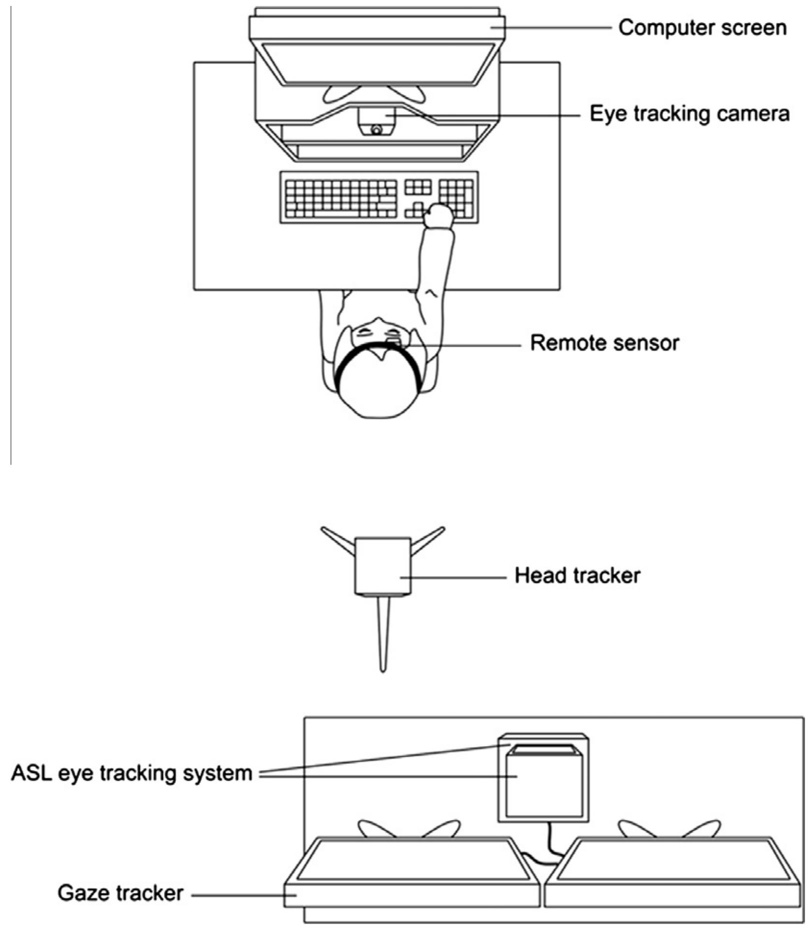


**Fig. 3.** Overhead depiction of the experimental setup of eye tracking equipment. One computer was used to display the virtual environment with a camera used to measure eye movements just below the computer screen. A second computer, placed behind participants, was connected to the ASL 504 to track participants' eye movements as they navigated in virtual environments and a third computer next to it, was used to operate the gaze tracker program that combined the live display and gaze information. A head tracking device, placed behind participants, kept track of head movements relative to a remote sensor adjusted to the participant's head, approximately 8 cm above the tracked eye.

landmarks available in the environment. The correlation was non-significant for both men ($p > 0.05$) and women ($p > 0.05$) (Fig. 5).

### 3.2. Navigational strategies

Since this task could be solved using a spatial or response strategy, sex differences were analyzed according to spontaneous navigational strategies. We assessed strategy based upon the verbal reports of participants. Understanding the spatial relationship of multiple stimuli in the environment is required for the construction of the cognitive map; therefore, we asked whether those who look at more landmarks also adopt a hippocampal-based spatial strategy to solve this task. An equal proportion of men and women used spatial (55%) and response (45%) strategies at the beginning of testing, as expected from our earlier work (Iaria et al., 2003). Throughout the experiment, there was an increase in the use of response strategies, in equal proportion of men and women, as 66% of the trials performed by the participants involved a response strategy (spatial: 8 trials for men vs. 6 for women; response: 16 trials for men vs. 12 for women), consistent with previous research (Iaria et al., 2003).

### 3.3. Gaze and navigation

A sex-based dissociation in eye movements was detected throughout the experiment. Overall, women made more landmark fixations than men ($F_{1,157} = 7.980$, $p < 0.005$). Specifically, more fixations were performed by women than men in environments containing 2 and 6 landmarks ($F_{1,40} = 8.127$, $p < 0.01$ and $F_{1,39} = 9.557$, $p < 0.05$, respectively) (Fig. 6). Importantly, the number of fixations correlated with the time to complete the task across all conditions (women: $r = 0.630$, $p < 0.001$; men: $r = 0.589$, $p < 0.001$) (Fig. 6). Independent samples *t*-test revealed no difference between men and women in the number of fixations/s ($p > 0.05$) or landmark use ($p > 0.05$).

### 3.4. Gaze and strategies

We also looked at resource use (i.e. time spent looking at landmarks over total time) according to strategy. Independent samples *t*-tests were conducted to investigate whether spatial and response learners differed in resource use at different time points during learning. The three trials of all five conditions were considered together. In the first trial, spatial learners had significantly greater resource use than response learners, ($t(50) = -1.67$, $p < 0.05$) (Fig. 7). This was not significant in the second trial ($t(50) = 1.41$, $p > 0.05$) and in the third trial ($t\ (52) = -\ 0.05$, $p > 0.05$). Thus, spatial learners spent more time than response learners looking at landmarks at the beginning of learning on the first trial, but not on subsequent trials, until the end of testing in a particular environment.

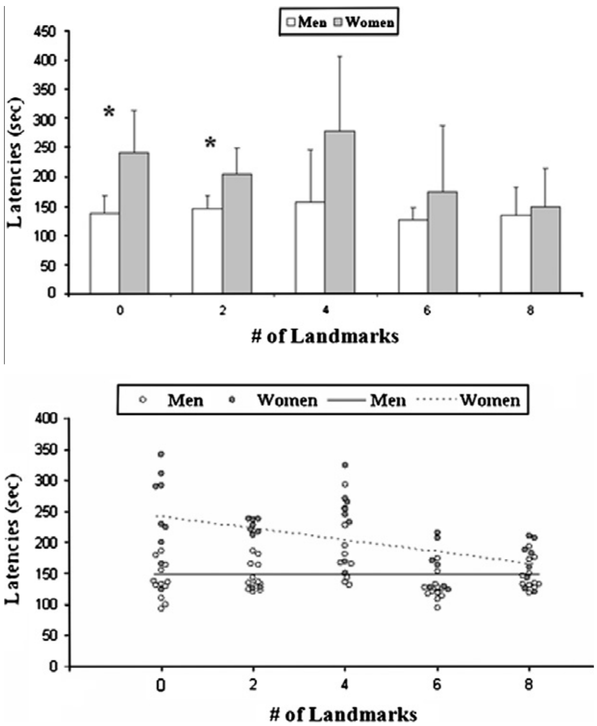


**Fig. 4.** Top: Navigation behaviour differences between men and women. Men completed trials more quickly than women in the 0, 2, 4, and 6 landmark conditions. There were no sex differences in the 8-landmark condition. Bars indicate the standard error of the mean (SEM), *: $p < 0.05$. Bottom: Men took less time than women in the 0, 2, 4, and 6 landmark conditions. These sex differences disappear when the number of landmarks increases. Points on the graph were shifted along the *x*-axis to distinguish between overlapping points. There was a significant correlation between the number of landmarks and latencies in women only ($r = -.209$, $p < 0.05$).

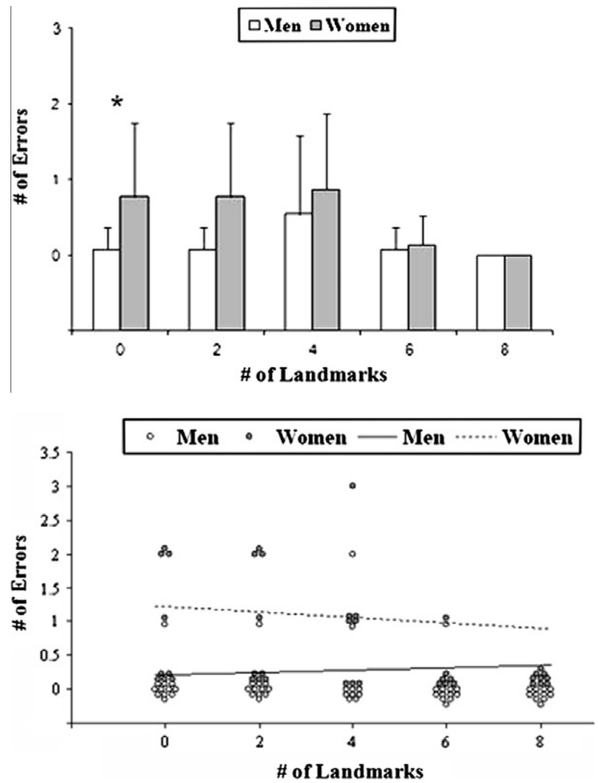


**Fig. 5.** Top: Navigation errors in men and women. Women made more errors in the 0-landmark condition only. There were no sex differences in the 2, 4, 6, and 8 landmark conditions. Bars indicate the standard error of the mean (SEM), *: $p < 0.05$. Bottom: Men made fewer errors than women in the 0-landmark condition only. These sex differences disappear when the number of landmarks increases. Points on the graph were shifted along the *x*-axis to distinguish between over-lapping points.

### *3.5. Environmental landmarks*

Navigation trials were analyzed in order to determine whether any gaze behaviour pattern was preserved across participants throughout testing. Irrespective of sex, participants spent less than 10% (8.14% ±0.417) of total navigation time looking at landmarks (i.e. resource use). This pattern was preserved across all conditions and resource use increased as the number of landmarks increased and leveled off at 6 landmarks (2 landmarks: 4.29% ±0.322; 4 landmarks: 7.33% ±0.814; 6 landmarks: 11.5% ±0.845; 8 landmarks: 9.65% ±0.799). In fact, there was a significant correlation between resource use and number of landmarks ($r = 0.447$, $p < 0.001$). Analysis of individual recorded trials revealed that approximately 90% of participants' gaze was not spent gazing at the landmarks, but was directed towards the arena floor, upcoming pathways, or random points in the visual field instead. Orientation-related eye movements represented a relatively small proportion of total navigation time compared to locomotion- and goal-related eye movements. Since there were no differences in resource use between men and women, there were no differences in the time spent looking at other things in the virtual environment.

Correlations were performed to explore whether landmark use (i.e. time spent looking at each landmark over the time dedicated to looking at all landmarks) changed as the number of landmarks available in the environment increased. Landmark use positively correlated with the number of landmarks in each condition, i.e. the more landmarks available in the environment, the more landmarks participants used according to percent of time spent fixating on these landmarks ($r = 0.739$, $p < 0.001$). This effect was significant for both men ($r = 0.718$, $p < 0.001$) and women ($r = 0.785$, $p < 0.001$). Similarly, the number of landmarks participants reported using significantly correlated with the number of landmarks available in the environment ($r = 0.337$, $p < 0.001$).

Additionally, there was a significant correlation between the number of landmarks reported and strategy used, i.e. the more landmarks were reported, the more participants used a spatial strategy ($r = 0.792$, $p < 0.001$). However, this was to be expected because these two variables are dependent on each other. The number of landmarks used according to gaze behaviour (landmark use) and the number of landmarks reported correlated significantly ($r = 0.24$, $p < 0.005$).

Correlations were performed to investigate whether any change occured in total time spent looking at landmarks over time. The correlation between trials and total time spent looking at landmarks was found to be significant: throughout the experiment, total time spent looking at landmarks decreased significantly ($r = -0.168$, $p < 0.05$). We then looked at whether this was modulated by sex. We performed a correlation between trials and total time spent looking at landmarks for each sex. Men showed a significant negative correlation ($r = -0.385$, $p < 0.001$), while women did not show such a correlation ($r = 0.008$, $p > 0.05$). Thus, over time, men spent less time looking at landmarks, whereas time spent looking at landmarks did not change for women.

### *3.6. Video game experience*

Video game experience did not correlate with sex ($r = 0.41$; $p = 0.939$), strategy ($r = 0.695$; $p = 0.126$), time ($r = 0.624$; $p = 0.185$), or number of fixations ($r = 0.382$,, $p = 0.455$), degrees of freedom = 6, n.s.

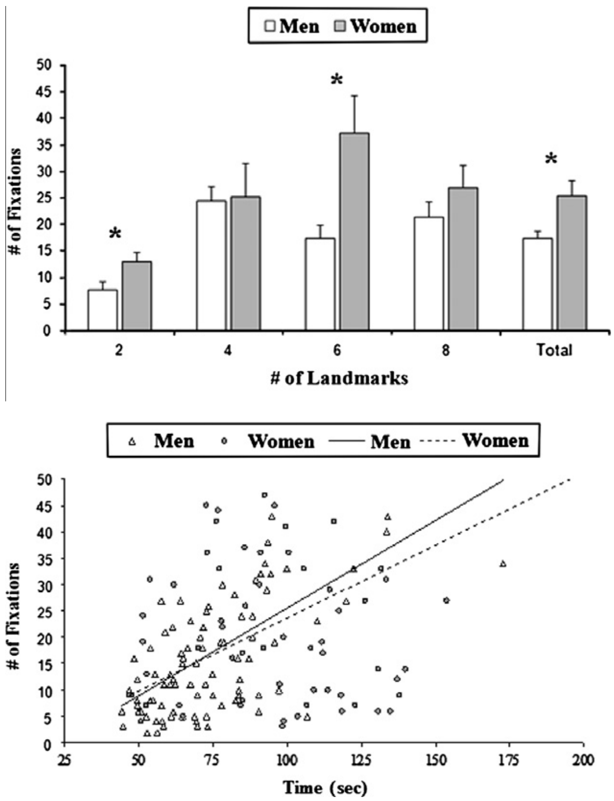


**Fig. 6.** Top: Eye movement differences between men and women. Overall, women made more landmark-oriented fixations than men. Women made more landmark-oriented fixations than men in the 2- and 6-landmark condition. Bars indicate the standard error of the mean (SEM), *: $p < 0.05$. Bottom: Correlation between latencies and the number of fixations in the 4-on-8 virtual maze across sex. As individuals took more time to complete the task, so did the number of fixations aimed at the surrounding landmarks.

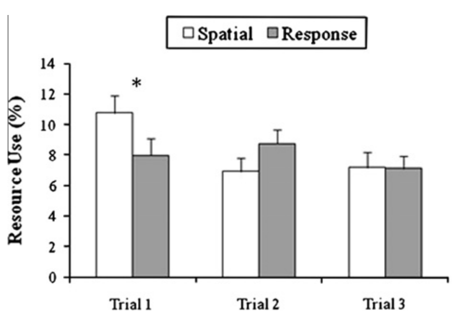


**Fig. 7.** Resource use is shown for spatial and response learners for each of the three trials, averaged over all conditions. Spatial learners exhibited more resource use than response learners during Trial 1, but showed the same amount of resource use for Trials 2 and 3.

## 4. Discussion

Eye tracking technology was employed to measure eye movements as participants completed a navigation task that could be solved by using a spatial or response strategy. The purpose of this experiment was to examine the differences in visual acquisition of relevant orientation-related information and navigational behaviour between men and women as the number of landmarks systematically varied.

### *4.1. Navigational performance*

Overall, women made more errors and took more time to complete the task relative to men. However, this effect was modulated by the number of landmarks present in the virtual environment. While we replicated earlier findings in which men completed the task in less time, these previous studies did not demonstrate differences in performance between men and women (Astur et al., 2004; Sandstrom et al., 1998). Since we controlled for practice effects by reordering the presentation of the same task, using different environments that systematically varied in terms of the number of landmarks, the sex differences that emerged are likely due to the changes in the number of landmarks. We were able to identify sex differences in navigational behaviour when all environmental features potentially used as reference points were removed. Specifically, women performed equally well as men when landmarks were present but they were impaired in the 0-landmark condition. Men were not affected by changes in landmark availability. These behavioural differences indicate that landmarks play a more critical role in navigation for women than men, whereas men are able to utilise additional information from the environment such as room geometry, Euclidian coordinates, or cardinal directions. Gron, Wunderlich, Spitzer, Tomczak, and Riepe (2000) studied sex differences in human navigation using fMRI. The study showed that while both men and women activated the right hippocampus, men additionally activated the left hippocampus while women activated the right parietal and right prefrontal cortex. The authors conclude that women use landmarks more predominantly then men and that the activation of prefrontal areas in women reflects the need to hold landmark information in working memory during navigation.

### *4.2. Gaze and navigation*

Our results indicate that women navigate better when their environment is rich in detail, such as when a high number of landmarks can be recruited as reference points. Since women's performance was affected to a greater extent by changes in the environment, this would suggest that there is a sex difference in the way people use visual information for navigation. In our study, the total number of fixations was higher in women than men. Since men and women spent the same proportion of time looking at landmarks when they navigated, as measured by the number of fixations/s and resource use, the higher number of fixations in women relative to men could explain the increased latencies typically found in the literature (Astur et al., 2004; Iaria et al., 2003; Levy et al., 2005). Together, these results indicate that women spent more time acquiring landmark-related visual information during navigation. This is supported by the fact that over time, men spent less time looking at landmarks, while it did not change for women. The differences in navigational behaviour reported above can thus be attributed to differences in gaze behaviour; women took more time to complete a given trial because they spent more time looking at surrounding landmarks. These results are in line with the study by Barkley and Gabriel (2007) that showed that women took longer then men to identify matching photograph pairs when proximal pinpoint cues were removed from one of the photographs. Moreover, they were better than men at identifying landmarks that were isolated from the background of previously shown photographs.

We provided evidence that men made significantly fewer errors than women when navigating in a virtual environment with no landmarks present, i.e. in the 0-landmark condition. This suggests that men use extra-landmark information during navigation. For example, other studies in the literature suggest that men could be using distances and polar coordinates, room geometry, Euclidian coordinates or an internal compass (Sakthivel et al., 1999; Sandstrom et al., 1998; Saucier et al., 2002; Silverman & Eals, 1992). The fact that men completed the task quicker is potentially related to the use of extra-landmark information during navigation. Since women did not use these non-landmark cues, it was necessary for them to visually sample the landmarks more often to construct an accurate representation of the environment, thus extending the period of each trial. These results show clear evidence that when provided with their preferred stimuli women perform equally well as men on a navigational task.

The female advantage in object location memory tasks found in numerous studies (Andreano & Cahill, 2009; Barnfield, 1999; De Goede & Postma, 2008; Lejbak, Vrbancic, & Crossley, 2009; Levy et al., 2005; Silverman, Choi, & Peters, 2007; Silverman & Eals, 1992; Spiers et al., 2008; Tottenham, Saucier, Elias, & Gutwin, 2003) may explain the preferential use of landmarks in women. Although a few studies have challenged this well-known female advantage (Iachini, Sergi, Ruggiero, & Gnisci, 2005; Saucier, Lisoway, Green, & Elias, 2007), our study suggests that women may form cognitive maps by encoding the relationship between the location of landmarks as they would encode objects in an object location memory task.

### 4.3. Navigational strategies

Confirming our previous work (Iaria et al., 2003), we found that there was no interaction between sex and navigational strategy. In other words, women and men used spatial and response strategies in equal proportions. Currently there is a question in the literature as to whether women are biased towards using non-spatial or response navigational strategies (Lovden et al., 2007). Studies that have suggested that women may be more likely to use a non-spatial strategy may have been finding spatial memory deficits in women because of a lack of environmental landmarks, rather than a deficit in spatial cognition. In addition, these tasks may not allow for cognitive mapping, and thus, the use of landmarks and their relationship to one another. For example, Lovden et al. (2007) administered a maze task where participants had to reach different targets. Such a maze requires the learning of a series of right and left turns to find the way to a target location, and therefore, a response strategy is needed. The finding that women took more time than men to learn the shortest route to a target cannot therefore be explained by the preference of women to use a response strategy. In fact, the evidence seems to point to the opposite interpretation, i.e. women may be using hippocampal-dependent spatial strategies to a greater extent then men. Although spatial learners were comprised of an equal proportion of men and women, the evidence suggests that men were more flexible at using non-spatial strategies than women when tested in the 0-landmark condition. Since women made more errors and took more time than men in the 0-landmark conditon, this indicates a greater reliance on landmarks, i.e. the spatial strategy. This is also supported by (1) the fact that women spent more time than men looking at landmarks and (2) with time, women show sustained attention to landmarks relative to men. Volumetric studies of the hippocampus support this hypothesis because spatial strategies, which are sensitive to hippocampal lesions (Bohbot et al., 2004), have also been associated with increased grey matter in the hippocampus (Bohbot, Lerch, Thorndycraft, Iaria, & Zijdenbos, 2007), and women have been reported to have equal or greater hippocampal volumes than men (Cahill, 2006; Goldstein et al., 2001; Pruessner, Collins, Pruessner, & Evans, 2001).

Finally, it is interesting that resource use, or the percentage of time that participants spent looking at landmarks, was greater in spatial learners than in response learners on the first trial of the 4-on-8 virtual maze, but that this difference disappeared in the subsequent trials. One interpretation of these findings is that spatial learners look significantly more at landmarks than response learners in the beginning of the task, while they are forming a cognitive map. However, once the cognitive map is formed, they no longer need to look at landmarks to the same extent. This interpretation is consistent with virtual navigation neuroimaging studies whereby spatial learners showed significant fMRI activity in the hippocampus only at the beginning of the task whereas response learners did not (Etchamendy et al., in press; Iaria et al., 2003). Furthermore, since spatial strategies were associated with greater fMRI activity and grey matter in the hippocampus (Bohbot et al., 2007; Iaria et al., 2003), these data are consistent with environment enrichment studies where rodents reared in environments rich with objects had greater hippocampal grey matter (see Kolb, Gorny, Soderpalm, and Robinson (2003) for a review).

## 5. Conclusion

In summary, the present study found evidence of sex differences in the acquisition of visual information and the way it is applied to solve a 4-on-8 virtual maze. Gaze and navigation behaviour are not static processes but are modulated by many factors, in particular the number of landmarks and time. For example, as the number of landmarks available in the environment increases, the proportion of time spent looking at landmarks and the number of landmarks used increases. The sex differences in navigational behaviour observed in the current study occurred only in environments devoid of visual landmarks and were eliminated in rich visual environments containing multiple landmarks. Furthermore, eye tracking confirmed that women spend more time looking at landmarks than men during navigation. Finally, we showed that the percentage of time that participants spent looking at landmarks was greater in spatial learners than in response learners on the first trial, during cognitive map formation. Together, these results confirm the discrepancy in cue utilisation between men and women and may explain the differences in navigational behaviour previously reported.

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