Sex differences in virtual navigation influenced by visual factors and individual differences

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Abstract

The Morris water maze is a task adapted from the animal spatial cognition literature and has been studied in the context of sex differences in humans, particularly because of the standard design, which manipulates proximal (close) and distal (far) cues. However, there are mixed findings with respect to the interaction of cues and sex differences in virtual Morris water maze tasks, which may be attributed to variations in the scale of the space and previously unmeasured individual differences. We explore the question of scale and context by presenting participants with an outdoor virtual Morris water maze that is four times the size of the mazes previously tested. We also measured lifetime mobility and mental rotation skills. Results of this study suggest that for the small-scale environment, males and females performed similarly when asked to navigate with only proximal cues. However, males outperformed females when only distal cues were visible. In the large-scale environment, males outperformed females in both cue conditions. Additionally, greater mental rotation skills predicted better navigation performance with proximal cues only. Finally, we found that highly mobile females and males perform equally well when navigating with proximal cues.

Keywords: spatial abilities, virtual Morris water maze, sex differences, mental rotation, mobility

Males display a well-documented advantage in several spatial abilities assessments, in the majority of populations tested (Geary, 1996; Newcombe, 2010). While many hypotheses have been proposed to explain these differences, the sources of gender disparity in spatial skills remain unknown. The presented work uses the Morris water maze (Morris, 1984), a widely used spatial abilities test developed in the animal literature and adapted for humans, to examine the effects of scale and individual differences measures on the use of difference spatial cues in navigation. Our aim is to determine if the scale of the environment, and individual differences measures that may have been developed over lifetime, such as mental rotation skills and mobility experience, can help explain the previously found sex differences in the visual cues used for navigation.

The traditional Morris water maze consists of a 1-2 meter diameter pool with a small circular platform installed just below the surface of the water. Rats are placed in the pool and swim until they stumble upon the unseen platform. As the rats are looking for a way to escape the water, they are also encoding the visual cues in the room. The visual cues are generally divided into two categories, close cues, and distant cues¹. Close cues produce a greater parallax effect; meaning that when the rat changes position, the projection of close visual cues moves more than do far away cues on the retina. This effect provides information about distances and

¹ Close cues go by many different names, including proximal (Vorhees & Williams, 2006), positional (Xiaoqian J. Chai & Jacobs, 2010), landmark (Sandstrom, Kaufman, & A. Huettel, 1998) and route-based cues (Xiaoqian Jenny Chai, 2008). The discrepancy is not between the type of cues but in their suggested function. For example, Chai and Jacobs (2010) make the distinction that close cues are used to update the positional location of the viewer as they move through space. Route-based cues are similar to close cues, but researchers associate them with route strategies, in which participants navigate from cue to cue without forming a global mental representation of the space. Conversely, far cues are also known as distal (Vorhees & Williams, 2006), directional, survey, beacon and bearing cues (Xiaoqian J. Chai & Jacobs, 2010, 2012). While the function of these cues has received much attention, rules for categorizing these cues are unexplored.

arrangements of close cues more so than far cues. Distant cues display less of a parallax effect and may translate or rotate less when the rat changes location. Distant cues, therefore, primarily provide bearing information. It is suggested that when the rats are swimming around, they implicitly encode the available visual cues. This can be seen when they are again placed in the pool, and they swim back to the location where they originally found the platform. Given that the platform is not visible, researchers have argued that the rats must use other cues in the room to make relative judgments about the location of the remembered platform. The environment that the pool is located in is then manipulated to assess which types of cues the rats used. For example, experimenters may place cards around the edges of the pool to form proximal cues for a learning phase then remove the cards during the testing phase. If the rats' performance is not inhibited, then it is likely attending to distal cues such as the room's geometry or windows in the experimental space. The inverse would be true if the rats' performance decreased in that condition.

Virtual versions of this task have been adapted for humans. However, there are mixed findings in regards to the interaction of sex differences and visual cue-types. Previous work has shown that in the presence of distant or directional cues (e.g., room geometry, mountains, landscape slant, and rivers) males displayed less heading direction error (Astur, Ortiz, & Sutherland, 1998; Xiaoqian J. Chai & Jacobs, 2012) which is defined as deviation in viewing direction from the target, less overall time taken to find the target or latency (Astur et al., 1998; Astur, Tropp, Sava, Constable, & Markus, 2004; Ross, Skelton, & Mueller, 2006; Sandstrom, Kaufman, & A. Huettel, 1998) and less distance traveled to find the target (Xiaoqian J. Chai & Jacobs, 2009) than females. For prepubescent children, boys show less latency than girls in distant cue conditions (Newhouse, Newhouse, & Astur, 2007). However, the findings for virtual

environments that include close or proximal cues (e.g., close indoor objects, bushes or trees) are mixed. In one study, no sex differences were found in latency when both distal and proximal cues were present (Sandstrom et al., 1998). Chai and Jacobs (2012) found no sex difference in heading direction error when proximal cues were present. Chai and Jacobs (2009) showed that males had fewer errors in distance between a remembered location of the target and the actual target's location than females, in both distal and proximal cue conditions. However, the discrepancy between the sexes decreased in the proximal cue condition. Livinstone-Lee et al. (2011) found no difference in latency between distal and proximal in their testing trial. Furthermore, these findings, have mostly used computer-modeled environments in which the primary visual cues are created by the geometric perspective of small-scale rooms or mazes or small grassy fields. Yet these types of visual settings do not accurately simulate the types of environments in which humans acquired spatial abilities: large-scale natural landscapes. Some evolutionary hypotheses suggest that the distances males' have historically traveled is a key contributing factor to spatial abilities (Silverman et al., 2000). Yet, all previous virtual Morris mazes only test navigation accuracy in spaces smaller than 37 meters in diameter. As a result, it is unclear if maze performance in small spaces can be extended to larger spaces. Together previous work suggests that males have an advantage in navigation abilities, but further research needs to be done to determine if cue type and sex consistently interact and if these findings can be extended to large-scale natural environments.

From an evolutionary psychological perspective, theories attempt to explain sex differences in cue use by attributing sex differences to evolutionary demands that produce differences in visual cue preference (see for critical review Jones et al., 2003; see for review Low, 2001). The hunting and gathering hypothesis (Silverman et al., 2000) and the mating range

hypothesis (Gaulin, 1992) both suggest that males may use different cues to help with navigation. The hunting and gathering hypothesis proposes that ancestral males participated in hunting to a greater degree than females. Hunting is a particularly challenging navigation task that requires rapid updating of spatial orientation and anticipating shortcuts. It is suggested that males develop a cognitive map (Jacobs & Schenk, 2003) that integrates both close and far cues which enables navigation for hunting. Evolved skills in these types of demanding spatial tasks are suggested to produce the male advantage in spatial abilities tests (Silverman et al., 2000). Similarly, the mating hypothesis notes that historically humans have been a mildly polygynous species (Low, 2001), and suggests that males with larger mating ranges have more access to females and, therefore, an evolutionary advantage. Large mating ranges require the use of both close and far cues and are suggested to have either produced better spatial abilities or were a product of more developed spatial skills (Gaulin, 1992). Previous work has also shown that men and women report using different strategies when navigating. Lawton (1996) showed that men, more often than women, report using an orientation strategy when navigating, which is a strategy where directional information is primarily used. In contrast, women report using a route strategy, which is associated with navigating using turn by turn directions and landmarks and may be based more on proximal cues (Lawton, 1996).

Another approach is to focus on strategies that are developed over a lifetime that may result from individual differences in navigation or mobility experience, regardless of sex. It could be the case that spatial skills that have developed through long-term navigation practice, or lack thereof, may also significantly contribute to performance on the water maze task. Ecuyer-Dab & Robert (2004) provided evidence that some spatial abilities were related to home range size, a measure of mobility. They found that males in Montreal had larger home range sizes than

females and that a larger range size for males was correlated with higher performance on three measures of spatial skills: mental rotation abilities, object location memory and the water-level task, which tests the participant's ability to estimate the appropriate water-level for a tilted cup. For both genders, they found that range size correlated with the Group Embedded Figures Test, a spatial visualization task (Ecuyer-Dab & Robert, 2004). While their findings are promising, it may be the case that the effect of range size on women's spatial abilities was not fully revealed by the spatial measures they used. For example, they did not test navigation-dependent spatial abilities, such as those utilized in the water maze task. This task directly tests navigation accuracy and may be more affected by measures of mobility such as range size. No current studies have used a measure of mobility to predict water maze performance in order to determine if advantages may be explained by increased navigational experience.

Likewise, individual differences in mental rotation may also significantly contribute to sex differences in the maze task. In many societies tested, males have shown a strong advantage in mental rotation skills (Newcombe, 2010). However, previous work has reported inconsistent finding in regards to the relationship between mental rotation tests (MRT) and virtual maze performance. Ross et al., (2006) tested MRT in addition to maze performance but did not report correlations. Chai and Jacobs (2009) initially found MRT to be correlated with performance in both distal and proximal cue conditions, then later found no correlations in performance for either cue condition (Xiaoqian J. Chai & Jacobs, 2012). Other work has found that overall performance on the water maze task is correlated with MRT abilities (Astur et al., 2004; Burkitt, Widman, & Saucier, 2007). In addition to the inconsistencies of these findings, MRT has yet to be used in a statistical model to account for navigation performance on the maze task over and beyond the previously found sex differences and cue preference.

The aims of this study are twofold. First, we examine whether the previously found sex differences in cue preference can be generalized to a scenario that more closely simulates a real world navigation task in which humans may have evolved spatial skills, navigation in a large-scale outdoor environment. We predict that in both the large and small-scale mazes that males will show an overall advantage but in the proximal cue condition this advantage will decrease or no longer be present. These predictions would be in line with the finding of Chai and Jacobs (2009, 2012). Second, we aim to determine if performance on the maze task can be predicted by the individual differences measures of MRT and lifetime mobility. Starting with MRT, previous work has been inconsistent in regards to the relationship between this measure and performance on the virtual maze. We predict that MRT would be a significant predictor of maze performance, which would provide support for the previously reported relationship between mental rotation and navigation accuracy (Astur et al., 2004; Burkitt et al., 2007; Xiaoqian J. Chai & Jacobs, 2009). While relatively less studied, we predict that a measure of mobility over the lifetime may also predict performance on the water maze. Ecuier-Dab and Robert (2004) provided evidence that range size and some spatial abilities are correlated. Motivated by this work, we predict that males and females who are more mobile will display enhanced navigation accuracy in the virtual maze task. Through these aims, we hope to understand the effects of task parameters and individual differences on cue use in a virtual Morris maze task².

Methods

² We also collected a measure of 3D-gaming experience, to control for this in our model, as previous research has reported both to be significant strong effects (Astur, Ortiz, & Sutherland, 1998; Astur, Tropp, Sava, Constable, & Markus, 2004; Burkitt, Widman, & Saucier, 2007; Xiaoqian J. Chai & Jacobs, 2010; Hamilton, Driscoll, & Sutherland, 2002; Livingstone-Lee et al., 2011; Newhouse, Newhouse, & Astur, 2007; Ross, Skelton, & Mueller, 2006).

Participants

108 participants (54 M, 54 F) were recruited from the University of Utah undergraduate population. They were between the ages of 18 and 55, with a mean age of 23. 54 participants each randomly assigned to either the large or small-scale environments.

Apparatus

Two virtual mazes were created using video game design software (Unity 3D, 2015). A Logitech Extreme 3D Pro Joystick was used to navigate in the virtual mazes that were displayed on a Dell monitor with 1920x1080 pixel resolution in sRGB color. The speed of movement, eye height, distance from the monitor, and room conditions were constant for all participants. Participants used the joystick to move forward and turn from left to right. Backward movement and changes in camera position (looking up or down) were not permitted, for consistency with prior human and animal studies.

Virtual Mazes

In traditional virtual water maze tasks, the participants search in a small pool of water in a virtual room for a hidden platform, then their ability to return to the platform with varying visual stimuli is measured. We decided to extend this paradigm to a search task that was more closely related to a navigation task that could occur in the physical world. Our task instead had participants navigate in a large grassy field and search for a grouping of red humming birds (See Figure 1). We then tested their ability to return to the location that they found the birds, when the birds were no longer visible. Adapted from Chai and Jacobs (2009, 2010, 2012), two modified virtual Morris water mazes were created that were contained by an invisible circular fence, which the participants were aware of and could not walk through. The fence was invisible as to

not obscure cues beyond the fence or to function as a proximal cue itself. The small-scale maze was 36.6 meters in diameter, and the large-scale was four times the size of the small, 146.4 meters in diameter. Both had two conditions (proximal and distal visual cues). The proximal cue condition consisted of a grassy field with close trees, bushes and flowers of varying sizes and colors. The distal cue condition contained only cues over 100 meters beyond the edge of the fence, such as mountains, hills, sunset and clouds (See Figure 2).

Distal cue condition

Proximal cue condition

Figure 1. Example of the viewer's perspective in the distal and proximal cue conditions.

Figure 2. Schematic diagrams of the distal and proximal conditions which show the visual cues in each condition.

Lifetime Mobility

We designed a lifetime mobility questionnaire that was intended to provide a broad description of the participant's mobility. The questionnaire presented the participant with locations in Utah (local), the US (national) and outside the US (global) and asked the participant to indicate which location he or she had traveled to. The local locations were selected to provide a balanced distribution of locations that could be navigated to by car or public transportation, in addition to locations that are within walking or biking distance from the University of Utah. There were 41 locations, with a mean driving distance from the University of Utah of 91.2 miles. To assess the participant's mobility experience outside of Utah, the questionnaire prompted the participant to indicate if he or she had traveled to 13 regions in the US and 25 global regions (see Figure 3). In sum, the questionnaire included 79 locations and regions.

Figure 3. Example of the images that were shown to the participants to help them identify each of the 13 US and 25 global regions in the mobility questionnaire.

Mental Rotation Test (MRT)

We used a redrawn paper and pencil Vandenberg & Kuse MRT Test by Peters et al. (1995) created from figures originally provided by Shepard and Metzler (1971). In this test, participants selected two of four images that were rotated versions of a target image. Participants completed two sections consisting of 12 trials that were three minutes in duration each.

Performance was measured by the total number of trials in which both correct answers were selected.

3D Gaming Experience

Gaming experience was measured on a scale from 0-4, zero being “Has never played 3D games” to “Plays 3D games more than twice per week.”

Design and Procedure

A 2 (sex: male and female) x 2 (scale: large and small) × 2 (cue type: distal and proximal) mixed design with the first two factors (sex and scale) as between-subjects and the last (cue type) as within-subjects was employed. Participants were randomly assigned to the large or small virtual environment condition, containing distal cues or proximal cues first, counterbalanced for order. Each participant also completed the MRT and mobility questionnaire. After giving consent, participants were seated in front of the computer with a joystick. Distance from screen, image quality, and viewing angle were controlled for. This experiment was conducted in three phases. Phase one of this experiment was the practice period, in which participants gained experience using the equipment and joystick. Phase two was the learning period, in which participants were asked to locate a grouping of red birds in the virtual environment. Once the birds were located, participants were virtually transported back to the starting location. Phase three was the testing period, in which the birds were removed, and participants were asked to return to the location at which they found the birds, for six trials. Phase 1-3 were repeated in the second virtual environment with the other visual cue condition. Performance accuracy on this task was measured by recording x and y coordinates of their ending location and calculating the

Euclidean distance from the actual location of the birds (distance error). After completion of the water maze participants then completed the MRT and lifetime mobility questionnaire.

Results

Data analysis

Two analyses were conducted: 1) A mixed-design ANOVA, to determine if females and males performed differently when presented with distal and proximal cues in adapted Morris mazes of two different scales. 2) A linear mixed-effects analysis, to assess the influence of the participants' lifetime mobility and MRT scores on maze performance.

Virtual Maze Measures and Scale

A two-factor mixed-design ANOVA was conducted on Euclidean distance error (in meters) averaged across trials for each participant, with sex and scale as the between-subjects factors and cue type (distal cue, proximal cue) as the within-subjects factor and 3D-gaming experience as a covariate. We found that males ($M = 12.195$) significantly outperformed females ($M = 20.529$), $F(1, 103) = 20.242, p < .000$, partial $\eta^2 = .164$. Additionally, greater error resulted for both males and females when viewing only distal cues ($M = 22.59$) compared to only proximal cues ($M = 10.134$), $F(1, 103) = 39.430, p < .000$, partial $\eta^2 = .277$. The large-scale maze produced significantly larger errors ($M = 26.286$) than the small-scale ($M = 6.438$), $F(1, 103) = 287.036, p < .000$, partial $\eta^2 = .735$. There was also a significant sex x scale interaction, $F(1, 103) = 25.123, p < .000$, partial $\eta^2 = .197$, suggesting that female performance was hindered more by the large scale maze than was male performance. However, this interaction should be interpreted by assessing the significant three-way interaction; sex x scale x cue-type, $F(1, 103) =$

4.724, $p = .032$, partial $\eta^2 = .044$. To interpret this interaction, we performed post hoc t tests on individual components of the interaction. This analysis revealed that in the large scale condition, men showed less error than females when presented with both proximal cues, $t(52) = 3.324$, $p = .002$, and distal cues, $t(52) = 7.342$, $p < .000$. However, in the small-scale condition males only had significantly less error than females when viewing distal cues, $t(52) = 2.478$, $p = .017$ and not proximal $t(52) = 1.654$, $p = .106$ (See Figure 4). For the small-scale condition, this relationship replicates previous findings that only show significant differences in the distal cue condition (Xiaoqian J. Chai & Jacobs, 2009, 2012). In the large-scale condition, these findings replicate the findings that show a sex difference in both the distal and proximal cue conditions (Livingstone-Lee et al., 2011).

Figure 4. Mean absolute distance error as a function of distal or proximal cues and sex, for the small scale and large scale environments. * = $p < .05$

3.2 Maze measures, Mobility, and MRT

To analyze the relationship between the individual differences measures and the maze performance, a linear mixed effects analysis in R (R Core Team, 2012) and lme4 (Bates, Maechler & Bolker, 2012) was conducted. For this analysis, distance error in the maze was scaled by creating a ratio between the size of the environment and the size of the error. We did this by dividing the each participant's error for each trial in the large-scale environment by four, which equated for the larger scale environment being four times larger than the small. This allows for both large and small-scale environments to be equally weighted when comparing to the individual differences measures. A log transformation was also performed on distance error to reduce a skewed distribution of residuals. For clarity, we present the untransformed data in all of the graphs. In the model, we entered 3D-gaming experience, Sex, Cue, Trial number³, Mobility score, MRT score, and the interactions Sex x Cue, Sex x Mobility, Cue x Trial, Cue x Mobility, Cue x MRT, and Mobility x Sex x Cue⁴. As random effects, we added a random intercept for each subject. Table 1 shows a summary of the fixed effects that were included in our model.

Table 1

*List of fixed effects with coefficients, standard errors and p-values from the statistical model. Coefficients for interactions including cue indicate the change from distal to proximal cues. Coefficients for interactions including sex indicate the change from female to male. * = < .05*

³ Previous work has reported learning effects (Astur et al., 2004; Burkitt et al., 2007; Hamilton et al., 2002; Kallai, Makany, Karadi, & Jacobs, 2005; Livingstone-Lee et al., 2011; Ross et al., 2006; Woolley et al., 2010), suggesting that as participants gain more experience with the task that their performance increases. This main effect of learning has been reported to vary for the different cue conditions (Newhouse et al., 2007; Sandstrom et al., 1998). To control for these effects we included an interaction term to capture the difference in practice effect between distal and proximal cues (Trial x Cue).

⁴ We used the following code in R: `lmer(LogError ~ Game + Trial*Cue + MRT*Cue + Mobility*Sex*Cue + (1|Subject), REML=FALSE)`. P-values were obtained by using the normal approximations.

Fixed Effect	Estimate	Standard error	<i>t</i> -ratio	<i>p</i> -value
3D-Gaming	-0.149	0.04643	-3.21	.0013*
Sex	-0.821	0.30202	-2.72	.0065*
Cue	0.829	0.23190	3.57	.0003*
Trial	-0.051	0.01642	-3.13	.0017*
Mobility	-0.003	0.00617	-0.56	.5749
MRT	0.016	0.01109	1.46	.1416
Sex x Cue	-0.395	0.23760	-1.66	.0962
Sex x Mobility	0.010	0.00877	1.14	.2519
Cue x Trial	-0.058	0.02095	-2.79	.0052*
Cue x Mobility	-0.027	0.00490	-5.55	.0000*
Cue x MRT	-0.048	0.01490	-3.23	.0012*
Sex x Cue x Mobility	0.024	0.01177	-2.08	.0366*

Our results show a significant main effect of 3D-gaming, suggesting that as self-reported 3D-gaming increases by one level that overall errors in the distal cue condition decrease by .149 meters. There was a significant effect of trial, showing that participants performed better as the trials progressed for the distal condition, but this was qualified by a Trial x Cue interaction (See Figure 5). This interaction reveals that in the proximal cue condition errors decreased significantly more quickly as the trials progressed than in the distal cue condition. There was also a significant MRT x Cue interaction (See Figure 6). This interaction reveals that as participants increase MRT performance, their errors when navigating with proximal cues decreased at a faster rate than with distal cues.

Figure 5. Mean scaled distance error as a function of trials for the distal and proximal cue conditions.

Figure 6. Mean scaled distance error as a function of MRT scores for the distal and proximal cue conditions. The gray bands indicate 95% confidence intervals.

Finally, we found a significant three-way interaction between Sex, Cue, and Mobility (See Figure 7). To understand this interaction, we conducted a post hoc multiple linear regression analysis using a similar equation as described above but on proximal and distal cues separately; therefore interactions that included cue type had to be removed⁵. In the equation, we included 3D-Gaming, Trial, MRT, and the interaction of Mobility and Sex. Focusing on the interaction, we found a Mobility x Sex interaction for both the proximal cue condition, $t(635) = 5.315, p < .000$ and the distal cue condition, $t(635) = 2.071, p = .038$.

To understand these interactions we looked at the difference in slopes for females and males in the distal condition by computing separate linear regression equations for each sex, in which mobility predicted scaled log error. Using online software (Soper, 2015), based on a method detailed in (Cohen, Cohen, West, & Aiken, 2002), a t test was conducted showing that the male (.003) and female (-.001) slopes are not significantly different $t(636) = 1.788, p = .074$ suggesting a small but non-significant difference between male and female performance in the distal condition of the water maze task as a function of mobility. In the proximal condition we found that the female coefficient of -.014 was significantly different from the male coefficient of .001, $t(636) = 5.30, p < .000$. This suggests that female performance on the virtual maze in the proximal cue condition increases (error decreases) with mobility experience, at a higher rate than in men (males show a slight increase in error with mobility).

In sum, these analyses suggest that, for women who navigated with proximal cues, increased mobility experience throughout a lifetime may result in better performance on the virtual maze task and this performance increases at a faster rate compared to men. A simple slopes analysis showed this interaction in another way. For low indicators of mobility (1 standard

⁵ We used the following model for the distal and proximal conditions separately: $\text{lm}(\text{LogError} \sim \text{Game} + \text{Trial} + \text{MRT} + \text{Mobility} * \text{Sex})$.

deviation below the mean) changing from female to male resulted in decreased log of scaled distance error (-SD) ($b = -.183$), $t(638) = -7.752$, $p < .000$. For high indicators of mobility (1 standard deviation above the mean) changing from female to male resulted in no significant difference (-SD) ($b = -.013$), $t(638) = -.539$, $p = .590$. This suggests that highly mobile men and women performed equally well in the proximal cue conditions of the water maze.

Figure 7. Mean scaled distance error as a function of mobility scores for the males and females in the distal and proximal cue conditions. The gray bands indicate 95% confidence intervals.

4. Discussion

The current study offers two key findings; 1) Modifying the maze parameters (scale) affected performance on the virtual Morris maze. 2) Individual differences measures of MRT and

mobility predicted maze performance more in the proximal cue condition and differently for females and males. In regards to the first finding, in the small-scale maze, we replicated the previously reported sex by cue interaction, showing that males only display an advantage when navigating with distal cues. However, this pattern did not extend to the large-scale maze. In the large-scale maze, males showed a strong advantage in both the proximal and distal cue conditions, which is consistent with the work of Livingstone-Lee et al. (2011). For the second finding, we showed that the rate of improvement in the proximal cue condition was greater as mental rotation abilities increased compared to the distal cue condition. Finally, we found that women who are highly mobile perform equally well compared to highly mobile men when they are navigating with proximal cues. Furthermore, in the proximal cue condition as mobility increased the rate of female performance increased significantly more than male performance.

The finding of a sex by cue interaction for the small but not the large scale environment may be due to the method used to create the large maze as a replica of the small maze, but four times the size. The relative distances between all of the cues in the small maze were multiplied by four to create the larger maze. Typical cues were five meters apart in the small scale and 20 meters in the large scale. The attempt to keep the relative distances of the cues consistent and by not adding any additional cues to the larger maze or scaling the size of the cues may have resulted in females no longer being able to utilize their proximal cue advantage. This work suggests that two categories of cues (close and far) may not fully represent the spectrum of cues. For example, it is unclear at what distance a distal cue turns into a proximal cue or even if there is a switch in the way they are used. Chai and Jacobs (2009, 2010, 2012) propose that many cues such as mountains and the slope of the land function as a gradient of information, which provides bearing information that updates with movement. However, it remains unclear which features of

a cue are implicated with revealing the large sex difference found in both animals and humans. Further work needs to be conducted to assess the distance, size, salience, and gradient of cues in a virtual Morris water maze to determine the specific components of a cue that enables navigation differently for males and females.

Previous work has been inconsistent in regards to the relationship between mental rotation and performance on the water maze task. Our work supports the findings that MRT and maze performance are correlated, but only for the proximal cue condition (Astur et al., 2004; Burkitt et al., 2007; Xiaoqian J. Chai & Jacobs, 2009). However, our specific measure of maze performance was not consistent with that used by Astur et al. (2007). They found that mental rotation was correlated with the amount of time and distance taken to find a target, but not in their “probe” trial, which measured time spent in the correct quadrant and is their closest to our navigation accuracy measure. Burkitt et al. (2007) also found that mental rotation abilities were correlated with time taken to find a target in a virtual Morris water maze. However, both studies only used distal cues in their mazes and as a result it is unclear if correlations between both distal and proximal cue conditions would be found. Chai and Jacobs (2012) did assess the relationship between both cue conditions and MRT. They found that mental rotation abilities were correlated with navigation accuracy for both distal and proximal cues. Our findings, however, suggest that mental rotation ability primarily showed an effect in the proximal cue condition. This finding may be a product of the large distance difference between our distal and proximal cues compared to previous work. The distal cues in our mazes were a minimum of 100 meters from the participant at the closest and up to 400 meters away. Cues that are this far away move very little with respect to one another as the participant navigated. It is possible that mental rotation skills would not be particularly helpful in this circumstance. Close cues translate and rotate in

relationship to one another as the participant moves. Having the capacity to imagine the relative orientations of visual cues to predict the location of an unseen target may be enabled by the ability to mentally rotate the cues. Other spatial abilities, such as perspective taking, may be more helpful when navigating with only bearing information, such as the kind presented in our distal cue condition. Work by Kozhevnikov, Motes, Rasch, & Blajenkova (2006) suggests that perspective taking, or the ability to imagine one's self in a different location and mentally picture the scene from that location, explains unique variance in a large scale navigation task over and beyond mental rotation abilities. They suggest that perspective taking captures self-to-object relationships differently than mental rotation. It could be the case that the ability to make calculations about self-to-object relationships might be a better predictor of performance in the virtual Morris maze when cues are very far away.

Finally and interestingly, the result that women who have traveled to more places in their lifetimes have increased performance when navigating with only proximal cues did not match our original predictions. We predicted that increased mobility would be helpful for both distal and proximal cue conditions. It could be the case that females did not attend to or use the distal cues at all. A gaze analysis by Livingstone-Lee et al. (2011) showed that women primarily focus on proximal cues in a virtual Morris water maze task. It is possible that increased practice at navigation wouldn't be helpful if they didn't incorporate the cues. Further probing would be necessary to determine what strategies women were using in the distal cue condition. It could also be possible that our measure of mobility wasn't sensitive enough to the different types of navigation, which might be differentially helpful in each cue condition. For example, our mobility questionnaire did not discern if the participant was the navigator or passenger when navigating to each location. It is also unclear how frequently the participant traveled to each

location and the nature of their navigation. For example, a person that takes the same path to a location might develop fewer navigation skills than a person that frequently takes novel paths. Further studies need to be conducted to determine the nature of the interaction between mobility and performance on the water maze task.

In sum, this study supports the large body of research showing that males outperform females in some spatial abilities tests. While these sex differences are large and found in a variety of different species and human societies, our work suggests that the nature of the task and individual differences may interact with what has been suggested to be an evolutionary difference between males and females. This work proposes that skills, which may be developed through out a lifetime, may reduce some of the baseline sex differences in spatial abilities.

References

- Astur, R. S., Ortiz, M. L., & Sutherland, R. J. (1998). A characterization of performance by men and women in a virtual Morris water task:: A large and reliable sex difference. *Behavioural Brain Research*, 93(1–2), 185–190. [http://doi.org/10.1016/S0166-4328\(98\)00019-9](http://doi.org/10.1016/S0166-4328(98)00019-9)
- Astur, R. S., Tropp, J., Sava, S., Constable, R. T., & Markus, E. J. (2004). Sex differences and correlations in a virtual Morris water task, a virtual radial arm maze, and mental rotation. *Behavioural Brain Research*, 151(1–2), 103–115. <http://doi.org/10.1016/j.bbr.2003.08.024>
- Burkitt, J., Widman, D., & Saucier, D. M. (2007). Evidence for the influence of testosterone in the performance of spatial navigation in a virtual water maze in women but not in men. *Hormones and Behavior*, 51(5), 649–654. <http://doi.org/10.1016/j.yhbeh.2007.03.007>

- Chai, X. J. (2008). *Parallel Systems in Visual Spatial Cue Processing in Humans: Sex Differences, Neural Correlates and Development*. ProQuest.
- Chai, X. J., & Jacobs, L. F. (2009). Sex differences in directional cue use in a virtual landscape. *Behavioral Neuroscience*, 123(2), 276–283. <http://doi.org/10.1037/a0014722>
- Chai, X. J., & Jacobs, L. F. (2010). Effects of cue types on sex differences in human spatial memory. *Behavioural Brain Research*, 208(2), 336–342. <http://doi.org/10.1016/j.bbr.2009.11.039>
- Chai, X. J., & Jacobs, L. F. (2012). Digit Ratio Predicts Sense of Direction in Women. *PLoS ONE*, 7(2), e32816. <http://doi.org/10.1371/journal.pone.0032816>
- Cohen, J., Cohen, P., West, S. G., & Aiken, L. S. (2002). *Applied Multiple Regression/Correlation Analysis for the Behavioral Sciences, 3rd Edition* (Third edition). Mahwah, N.J: Routledge.
- Ecuyer-Dab, I., & Robert, M. (2004). Spatial ability and home-range size: examining the relationship in Western men and women (*Homo sapiens*). *Journal of Comparative Psychology* (Washington, D.C.: 1983), 118(2), 217–231. <http://doi.org/10.1037/0735-7036.118.2.217>
- Gaulin, S. J. C. (1992). Evolution of sex difference in spatial ability. *American Journal of Physical Anthropology*, 35(S15), 125–151. <http://doi.org/10.1002/ajpa.1330350606>
- Geary, D. C. (1996). Sexual selection and sex differences in mathematical abilities. *Behavioral and Brain Sciences*, 19(02), 229–247. <http://doi.org/10.1017/S0140525X00042400>
- Hamilton, D. A., Driscoll, I., & Sutherland, R. J. (2002). Human place learning in a virtual Morris water task: some important constraints on the flexibility of place navigation. *Behavioural Brain Research*, 129(1-2), 159–170.

- Jacobs, L. F., & Schenk, F. (2003). Unpacking the cognitive map: the parallel map theory of hippocampal function. *Psychological Review*, 110(2), 285–315.
- Jones, C. M., Braithwaite, V. A., & Healy, S. D. (2003). The evolution of sex differences in spatial ability. *Behavioral Neuroscience*, 117(3), 403–411.
- Kallai, J., Makany, T., Karadi, K., & Jacobs, W. J. (2005). Spatial orientation strategies in Morris-type virtual water task for humans. *Behavioural Brain Research*, 159(2), 187–196.
<http://doi.org/10.1016/j.bbr.2004.10.015>
- Kozhevnikov, M., Motes, M. A., Rasch, B., & Blajenkova, O. (2006). Perspective-taking vs. mental rotation transformations and how they predict spatial navigation performance. *Applied Cognitive Psychology*, 20(3), 397–417. <http://doi.org/10.1002/acp.1192>
- LAWTON, C. A. (1996). STRATEGIES FOR INDOOR WAYFINDING: THE ROLE OF ORIENTATION. *Journal of Environmental Psychology*, 16(2), 137–145.
<http://doi.org/10.1006/jevp.1996.0011>
- Livingstone-Lee, S. A., Murchison, S., Zeman, P. M., Gandhi, M., van Gerven, D., Stewart, L., ... Skelton, R. W. (2011). Simple gaze analysis and special design of a virtual Morris water maze provides a new method for differentiating egocentric and allocentric navigational strategy choice. *Behavioural Brain Research*, 225(1), 117–125.
<http://doi.org/10.1016/j.bbr.2011.07.005>
- Low, B. S. (2001). *Why Sex Matters: A Darwinian Look at Human Behavior*. Princeton, N.J.: Princeton University Press.
- Morris, R. (1984). Developments of a water-maze procedure for studying spatial learning in the rat. *Journal of Neuroscience Methods*, 11(1), 47–60.

- Newcombe, N. S. (2010). Picture This: Increasing Math and Science Learning by Improving Spatial Thinking. *American Educator*, 34(2), 29.
- Newhouse, P., Newhouse, C., & Astur, R. S. (2007). Sex differences in visual-spatial learning using a virtual water maze in pre-pubertal children. *Behavioural Brain Research*, 183(1), 1–7. <http://doi.org/10.1016/j.bbr.2007.05.011>
- Peters, M., Laeng, B., Latham, K., Jackson, M., Zaiyouna, R., & Richardson, C. (1995). A redrawn Vandenberg and Kuse mental rotations test: different versions and factors that affect performance. *Brain and Cognition*, 28(1), 39–58. <http://doi.org/10.1006/brcg.1995.1032>
- Ross, S. P., Skelton, R. W., & Mueller, S. C. (2006). Gender differences in spatial navigation in virtual space: implications when using virtual environments in instruction and assessment. *Virtual Reality*, 10(3-4), 175–184. <http://doi.org/10.1007/s10055-006-0041-7>
- Sandstrom, N. J., Kaufman, J., & A. Huettel, S. (1998). Males and females use different distal cues in a virtual environment navigation task. *Cognitive Brain Research*, 6(4), 351–360. [http://doi.org/10.1016/S0926-6410\(98\)00002-0](http://doi.org/10.1016/S0926-6410(98)00002-0)
- Shepard, R. N., & Metzler, J. (1971). Mental Rotation of Three-Dimensional Objects. *Science*, 171(3972), 701–703. <http://doi.org/10.1126/science.171.3972.701>
- Silverman, null, Choi, null, Mackewn, null, Fisher, null, Moro, null, & Olshansky, null. (2000). Evolved mechanisms underlying wayfinding. further studies on the hunter-gatherer theory of spatial sex differences. *Evolution and Human Behavior: Official Journal of the Human Behavior and Evolution Society*, 21(3), 201–213.

Vorhees, C. V., & Williams, M. T. (2006). Morris water maze: procedures for assessing spatial and related forms of learning and memory. *Nature Protocols*, 1(2), 848–858.

<http://doi.org/10.1038/nprot.2006.116>

Woolley, D. G., Vermaercke, B., Op de Beeck, H., Wagemans, J., Gantois, I., D’Hooge, R., ...

Wenderoth, N. (2010). Sex differences in human virtual water maze performance: novel measures reveal the relative contribution of directional responding and spatial knowledge. *Behavioural Brain Research*, 208(2), 408–414.

<http://doi.org/10.1016/j.bbr.2009.12.019>