Sex differences in virtual navigation influenced by scale and navigation experience

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Abstract

The Morris water maze is a spatial abilities test adapted from the animal spatial cognition literature and has been studied in the context of sex differences in humans. This is because its standard design, which manipulates proximal (close) and distal (far) cues, applies to human navigation. However, virtual Morris water mazes test navigation skills on a scale that is vastly smaller than natural human navigation. Many researchers have argued that navigating in large and small scales is fundamentally different, and small-scale navigation might not simulate natural human navigation. Other work has suggested that navigation experience could influence spatial skills. To address the question of how individual differences influence navigational abilities in differently scaled environments, we employed both a large (146.4 meters in diameter) and a traditional (36.6 meters in diameter) scaled virtual Morris water maze along with a novel measure of navigation experience (lifetime mobility). We found sex differences on the small maze in the distal cue condition only, but in both cue-conditions on the large maze. Also, individual differences in navigation experience modulated navigation performance on the virtual water maze, showing that higher mobility was related to better performance with proximal cues for only females on the small maze, but for both males and females on the large maze.

Keywords: virtual navigation, sex differences, navigation experience

The ability to successfully navigate in large-scale spaces is important for many daily activities, such as navigating to work or wayfinding to new locations when traveling. Successful navigation in large-scale spaces involves the ability to determine one's relative orientation to the visual cues in the environment and to form spatial memories that incorporate the cues. A growing body of literature shows sex differences in the types of visual cues used for navigation in smaller-scale spaces (e.g., Astur, Ortiz, & Sutherland, 1998; Chai & Jacobs, 2010). While these findings are robust, navigating in these small-scale spaces may be fundamentally different from navigating in large-scale spaces (Hegarty, Montello, Richardson, Ishikawa, & Lovelace, 2006; Montello, 1993). Some have argued that navigation in small spaces might not simulate natural human navigation (Learmont, Newcombe, Sheridan, & Jones, 2008). In addition, in many populations, males have larger range sizes than females (e.g., Ecuyer-Dab & Robert, 2004; Santos, McGuckin, Nakamoto, Gray, & Liss, 2011; Vashro, Padilla, & Cashdan, 2015) and studies show a relationship between spatial abilities and range size (Ecuyer-Dab & Robert, 2004; Vashro & Cashdan, 2015). To determine whether both scale and navigation experience influence sex differences in cue use during navigation, we examined performance in a traditional small-scale virtual Morris water maze (Morris, 1984), a widely used spatial abilities test developed for animals and adapted for humans, and a large-scale version, along with collecting a novel measure of self-reported navigation experience.

The traditional Morris water maze reveals sexually dimorphic visual cue-use for constructing a *cognitive map* (Tolman, 1948). The cognitive map is a spatial mental representation, defined as allocentric because it preserves object-to-object spatial relationships of cues that are not tied to the viewpoint of the observer. Visual cues used for navigation are

generally divided into two categories, close or *proximal* cues, and distant or *distal* cues[1] (O'Keefe & Nadel, 1978). Proximal cues primarily provide positional information during locomotion because of their greater effect on parallax, the apparent displacement of cues on the retina when the viewer changes location. Distal cues are more suited to providing stable bearing information as they translate and rotate less than proximal cues during movement (Knierim & Hamilton, 2011). The Morris water maze differentiates the ability to utilize cues by manipulating the visibility of each cue, then testing accuracy in returning to a remembered location. Three decades of research has shown that male rats can utilize both distal and proximal cues in the Morris water maze while females predominantly rely on proximal cues (D'Hooge & De Deyn, 2001).

Virtual adaptations of the Morris water maze have examined sex differences in cue use by humans during navigation in small scale spaces (on average around 35 m). Generally the results replicate the rodent work, with males showing greater navigational ability when presented with distal cues alone, compared to females, and a smaller or no sex difference given the presence of proximal cues (e.g., Astur et al., 1998; Chai & Jacobs, 2009; Sandstrom, Kaufman, & Huettel, 1998). However, little is known about how distal and proximal cues are used in larger scales than those used by traditional virtual Morris water mazes, an important question given that larger scales more closely approximate natural human navigation (Learmonth, Newcombe, Sheridan, & Jones, 2008). For example, the U.S. Department of Transportation reported that average 21-35-year-olds travel 37.7 miles per day, with average trip length at 9.7 miles (Santos et al., 2011) and there is evidence that males travel more than females both in the

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1 There is not consistency between terminology, classification and function of close cues (e.g, proximal (Vorhees & Williams, 2006, Knierim & Hamilton, 2011), positional (Chai & Jacobs, 2010), landmark (Sandstrom, Kaufman, & Huettel, 1998), and apparatus cues (Knierim & Hamilton, 2011)) and far cues (e.g., distal (Vorhees & Williams, 2006), directional, survey, beacon and bearing cues (Chai & Jacobs, 2010).

U.S. (Santos et al. 2011) and cross-culturally (e.g., Cashdan & Gaulin, 2016; MacDonald & Hewlett, 1999). Individual differences in egocentric and allocentric strategies are commonly used to explain the sex differences found in the Morris water maze. Generally, males more often use allocentric or orientation strategies, encoding the relative organization, directions, distances and distributions of geographic landmarks (both proximal and distal) in a cognitive map (Livingstone-Lee et al., 2011). In contrast, females more often use egocentric or route-based strategies, organizing the relative geography in relation to their current location, and thus may rely more on proximal cues (e.g., Nadel & Hardt, 2004; Choi, McKillop, Ward, & L'Hirondelle, 2006; Lawton, 1994). In a large-scale environment where there are greater distances between proximal landmarks and the distal landmarks are overall farther away (as in our current study), there may be differences in how these cues are utilized. For example, females who rely on egocentric landmark strategies may suffer on performance when proximal cues are farther apart. Implementing a large-scale maze can thus help to expand our understanding of how and when these different cues are used.

Given our focus on a large-scale environment that more closely approximates the scale of human navigation, experience with navigation—such as how much individuals travel—becomes an important variable to consider. Some research suggests that sex differences in range size can predict spatial abilities including mental rotation and object location memory in western populations (Jones, Braithwaite, & Healy, 2003; Ecuyer-Dab & Robert, 2004) as well as in hunter-gatherer societies (e.g., Vashro & Cashdan, 2015). Other related research on spatial cognitive development shows that older children, who have more practice navigating in large-scale spaces than younger children, can generalize their experience to spatial tasks in small-scale spaces while younger children show difficulty performing the same task in large and small

spaces (Learmonth et al., 2002). Thus, our goals were two-fold. First, we examined whether the established sex-difference found in maze performance with distal cues alone, but not proximal, would replicate in a large-scale maze. We expected to find sex differences in both small and large-scale mazes, but also that the difference might increase or occur in both cue-conditions in the large-scale maze. Second, we tested whether mobility experience, as assessed through self-reported travel, would modulate the predicted sex difference on maze performance. One possible outcome was that people would show enhanced navigational skills on a scale that more closely matches the scale of their natural navigation, predicting facilitatory effects of mobility only for the large-scale maze. Alternatively, highly mobile people might show better performance when navigating at both scales, consistent with a more broad relationship between mobility and spatial abilities (Ecuyer-Dab & Robert, 2004).

Method

Participants

One hundred and eight University of Utah undergraduates (54 male, 54 female, aged 18 – 55, $M = 23$ years) were tested with 54 participants (27 male, 27 female) each randomly assigned to either the large- or small-scale environments.

Apparatus

Virtual mazes were created using video game software (Unity Technologies, 2015). A Logitech Extreme 3D Pro Joystick was used to navigate in the virtual mazes that were displayed on a 1920 x 1080 pixel resolution monitor with sRGB color. The speed of movement was fixed

to 1 m/s and eye height was positioned in the center of the monitor with a viewing distance of 25

inches. Participants used the joystick to move forward and turn from left to right, which is

consistent with prior human and animal studies.

   Virtual Mazes. In traditional virtual water maze tasks, participants search in a small pool

in a virtual room with a hidden platform and then their ability to return to the platform with

varying visual stimuli is measured. We adapted this paradigm to a natural landscape more

closely related to a navigation task that could occur in the physical world. Participants navigated

in a large grassy field and searched for a grouping of red hummingbirds, which were visible (see

Figure 1). As in Chai and Jacobs (2009), the small-scale maze was 36.6 meters in diameter; the

new large-scale maze was 146.4 meters in diameter. In the proximal cue condition, the visual

cues were close trees, bushes, and flowers of varying sizes and colors. In the proximal condition,

of the larger scale maze, because it was an open field, the participant could likely detect the

presence of all of the cues from one viewing location, but it was not possible to see their specific

features or identify them without moving. The distal cue condition contained only cues past 100

meters, such as mountains, hills, sunset and clouds (See Figure 2). Each maze was contained by

an invisible circular fence that could not be passed through.

   Navigation Experience. We designed a navigation experience questionnaire that was

intended to provide a broad measure of mobility. The participants viewed a list of locations in

Utah (local) and in the United States (national) and indicated the locations that they had visited.

The local locations provided a balanced distribution of locations that could be navigated to by

car or public transportation, in addition to locations that were within walking or biking distance

from the University of Utah. For Utah, there were 41 locations, with a mean driving distance

from the University of Utah of 91.2 miles. Outside of Utah, there were 13 regions in the US

listed (See supplementary materials for full mobility questionnaire). While there are some

limitations of our lifetime mobility measure, our intention was to determine whether participants

had traveled to many locations that likely required novel navigation practice, which may be more

spatially demanding than distances or places traveled to on a daily basis (as typically tested in

measures of home range size). A mobility score was calculated by totaling the number of 41

locations in Utah and 13 regions in the US that the participant had visited.

Design and Procedure

Scale (large or small) was varied between-participants and cue-type (proximal or distal)

was varied within-participants (blocked and counterbalanced for order). After giving consent,

participants had a brief practice period to gain experience using the joystick. At the start of the

experiment, participants navigated with the joystick to locate a group of red birds in the virtual

environment. Once the birds were located, participants were instructed to look around the

environment (by rotating their viewpoint) and then they were virtually transported to a new

starting location. On six subsequent trials, participants were asked to return to the location of the

birds, which were hidden from view. On each trial, after participants indicated that they were at

the location, the birds appeared, and the participants were encouraged to look around the

environment to locate the birds. The procedure was then repeated with the second visual-cue

condition. Performance accuracy was measured by recording X and Y coordinates of end

location, which was used to calculate the Euclidean distance from the actual location of the birds

(Error). After completion of the water maze tasks, participants completed the lifetime mobility

questionnaire and a measure of video gaming experience (rating 0-4, never played 3D games to

play 3D games more than twice per week). Participants also completed a battery of spatial

abilities tasks as part of a larger project, but these were not analyzed in the context of the goals of the present study.

Results

To test the effect of maze scale and navigation experience (Mobility) on sex differences in cue use in the virtual Morris water maze, we conducted a linear mixed-effects analysis on the small-scale and large-scale maze error separately[2]. In each analysis, lme4 in R (Bates, Maechler & Bolker, 2012) was used to calculate the regression weights and 3D video game experience (Gaming) was entered as a covariate. Trial sequence (Trial Number), proximal and distal block order (Block Order), Sex, Cue Type (Cue), Mobility score (Mobility), and the interactions between Trial Number, Block Order, Sex, Cue, and Mobility were used to predict maze performance (Error)[3]. A random intercept was included for each subject.

Table 1 shows a summary of the regression coefficients for the small-scale maze. After accounting for the significant effect of Gaming our results showed a main effect of Trial Number revealing that participants' errors decreased over the sequence of trials but there was no interaction between Sex and Trial, replicating other work on practice effects (e.g., Chai & Jacobs, 2009). There was also a significant Cue x Sex interaction (See Figure 3) along with a Cue x Mobility interaction, which are both qualified by the significant three-way interaction between Cue, Mobility, and Sex (See Figure 4). To understand the Cue x Sex interaction, we

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2   Because overall chance of error was inherently greater for the large- versus small-scale maze, we did not initially run the omnibus analysis with both scales included together. However, an additional analysis was conducted where maze error for the large-scale environment was divided by four to allow for direct comparisons between the scales. The findings of this analysis were consistent with the presented results.

3   We used the following code in R: lmer (Error ~ Game + Trial Number*Sex +Block Order*Sex + Mobility*Gender*Cue + (1|Subject)). *P*-values were obtained by using normal approximations.

conducted post hoc *t*-tests on the individual components of the interaction. We found that when navigating with distal cues, males ($M = 8.45$ $SE = .75$) had significantly fewer errors than females ($M = 10.80$, $SE = .56$), $t(52) = 2.478$, $p = .017$, 95% CI [0.44, 4.24]. However there was no sex difference when navigating with proximal cues, $t(52) = 1.65$, $p = .107$, 95% CI [-0.30, 3.10]. This relationship replicates previous findings that showed significant sex differences only for the distal cue condition (e.g., Chai & Jacobs, 2009). To examine the relationship between Cue, Mobility and Sex, we computed separate linear regression equations for each sex and tested for the interaction between Cue and Mobility. There was a significant interaction for females, ($b = -0.10$), $t(320) = -2.06$, $p = 0.039$, 95% CI [-0.19, -0.004], revealing that mobility was associated with decreased navigation errors for females in the proximal condition more than in the distal condition. However, Cue and Mobility did not interact for males ($b = 0.05$), $t(320) = 1.08$, $p = 0.28$, 95% CI [-0.04, 0.16][4]. This suggests that navigation experience is particularly advantageous for women when proximal cues are available. It could also be the case that many females did not attend to or use the distal cues at all (Livingstone-Lee et al., 2011) and thus the effects of mobility experience only appeared in our proximal cue condition.

The same mixed effects analysis was conducted for the large-scale maze (see Table 2). Our results showed that males ($M = 18.87$, $SE = 1.56$) had significantly fewer navigation errors than females ($M = 33.66$, $SE = 1.72$; See Figure 5). However, there was no interaction between sex and cue as found in the small-scale analysis, suggesting that the male advantage was consistent across both cue conditions. In addition, there was a significant Cue x Mobility interaction (See Figure 6), revealing that Mobility reduced errors in the proximal condition more than the distal condition across both males and females. The difference in results of the two

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4   There was also no significant main effect of mobility for males.

scales suggests that mobility experience affected navigation performance for both males and

females in the larger scale, but specifically affected female performance on the smaller scale.

Mobility may not have facilitated male performance on the small-scale maze because of the

overall reduced error level for males, particularly for the proximal cue condition.

General Discussion

In our small-scale maze, we replicated the work of Chai and Jacobs (2009), showing that

males display superior performance compared to females when navigating with distal cues and

that there was no sex difference when navigating with proximal cues. In the large-scale maze, we

found that males displayed superior performance when navigating with both distal and proximal

cues compared to females. These findings support the argument that spatial abilities used in

small-scale spaces may not generalize fully to spatial abilities used in larger scale spaces

(Hegarty et al., 2006; Learmonth et al., 2002; Montello, 1993; Wolbers & Wiener, 2014). Much

of the previous work on navigation and memory across different scales has distinguished

between *vista* spaces—smaller, typically "room-size" spaces that can be fully seen from a single

viewing location—and *environmental* spaces, larger spaces where it is necessary to traverse the

space in order to view all of the cues (Montello, 1993). In this sense, scale and visibility are often

confounded—smaller spaces have cues visible from a single viewpoint and studies with larger

spaces have been designed with paths or rooms that do not share visible cues (Meilinger et al.,

2014). Our study is a beginning step to examine the influence of scale on navigation independent

of visibility. The current results that are based on a very large open space where cues are at least

visible (if not memorable), add to the growing literature on spatial abilities across different scales

by showing that individual differences do not fully generalize from small to large scales, even

when the visual cues are very similar.

Although the same cues were used in the small and large-scale mazes, the *utility* of the cues may have changed (See Figure 7 for a screenshot of the proximal cues in the large scale maze). This could explain the sex difference in the proximal-cue condition found for the large maze (but not the small maze or previous related work). To keep the relative distances, sizes, and quantity of the cues consistent across scale, we multiplied the distances between the cues in the small-scale maze by four. This increased the distances between the proximal cues by roughly 15 meters. The longer distance between cues may have resulted in females no longer being able to use their proximal cue strategies effectively in the large-scale maze. To our knowledge, there are no studies that identify distances that differentiate proximal and distal cues. In an extensive review, Knierim and Hamilton (2011) define proximal cues operationally as those inside the maze apparatus, whereas distal are those outside the apparatus. However, cues outside the apparatus can be both relatively close (e.g., Sandstrom et al., 1998), and far (e.g., Chai & Jacobs, 2009). In addition to the distance from the viewer, the distinct effects of salience and visual angle for proximal and distal cues are unclear. Future work is needed to define the properties and context of distal and proximal cues that enable male and female navigation abilities.

We did find an influence of navigation experience on cue use in both the large- and small-scale mazes. Overall, we found that navigation experience related positively to accuracy on the maze and interacted with effects of sex, but there were differences between the two scales. In the small-scale maze, for females only, error decreased as mobility experience increased for the proximal cue condition. In the large maze, all participants showed improved performance with increased mobility experience, but again only in the proximal cue condition. While we had no predictions of how navigation experience might differentially affect the cue conditions, the results suggest that strategies that are developed through experience with travel to new places

rely more on the information gained from proximal cues.

It is also possible that our measure of navigation experience was unable to identify important components of mobility that might influence navigation with distal cues. For example, being the navigator or the passenger, locomoting by different means (e.g., car, plane, bike, on foot), or using GPS devices could yield different types of navigation experience. Although additional work needs to be conducted to develop our measure of navigation experience and to understand which components of travel may influence spatial skills, the current findings are suggestive of a positive relationship between navigation experience and navigational skills that help to explain some of the disparities typically seen between women and men in large-scale navigation tasks.

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Distal cue condition

Proximal cue condition

Figure 1. Example of the viewer's perspective in the distal (top) and proximal (bottom) cue conditions.
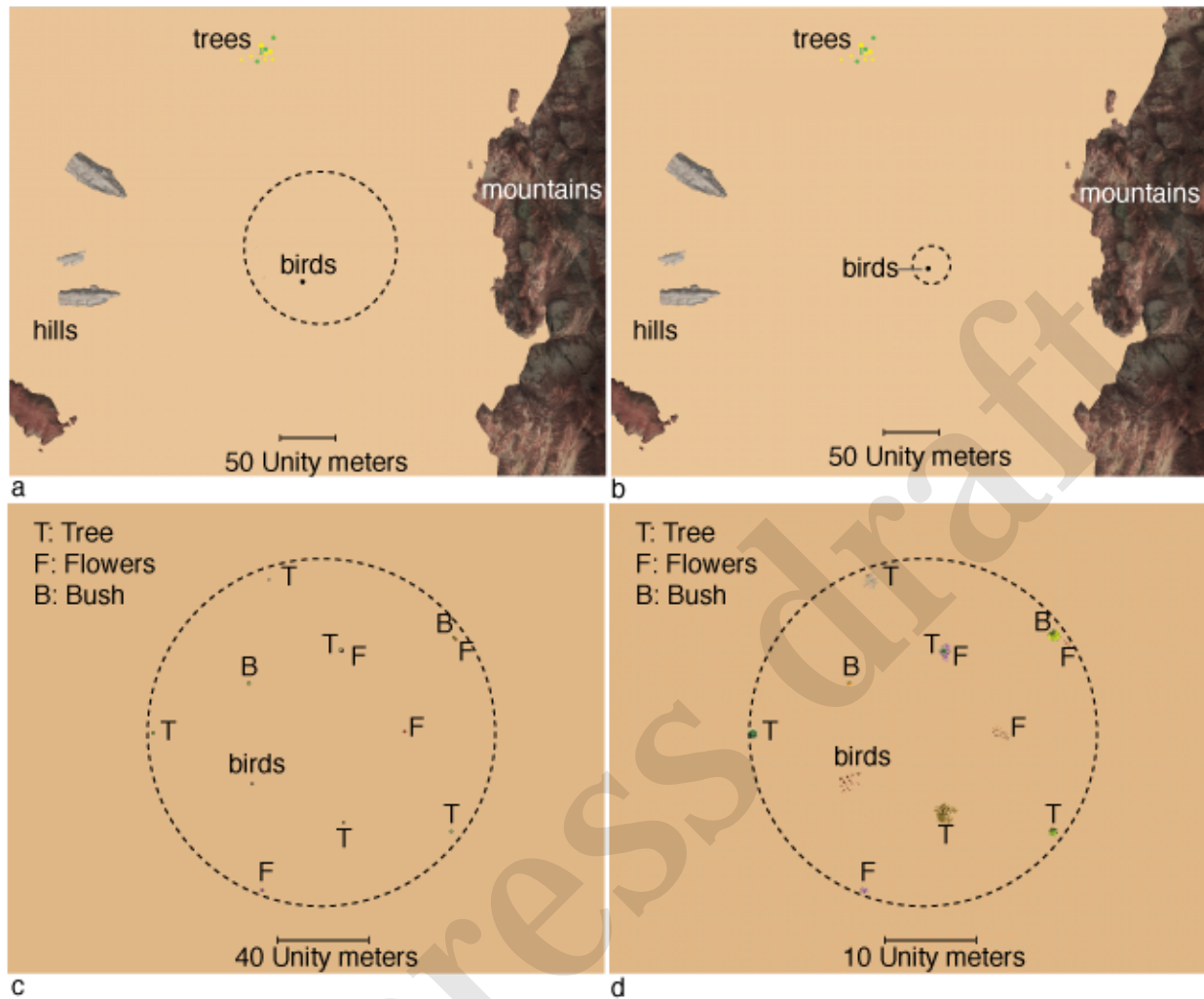
Figure 2. A. Distal large scale. B. Distal small scale. C. Proximal large scale. D. Proximal Small Scale. Schematic diagrams, which show the visual cues and their locations from a top-down perspective in each condition. Participants never saw these diagrams.
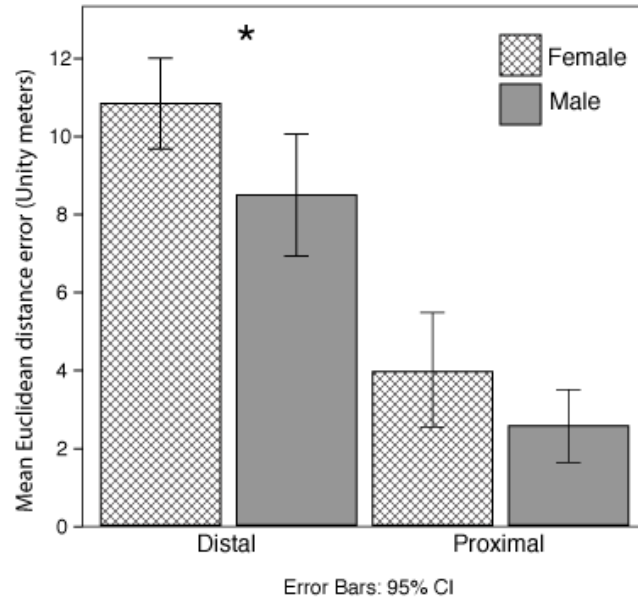
Figure 3. Euclidean distance error as a function of distal or proximal cues and sex, for the small-scale maze. Error bars represent 95% confidence intervals. * = $p < .05$
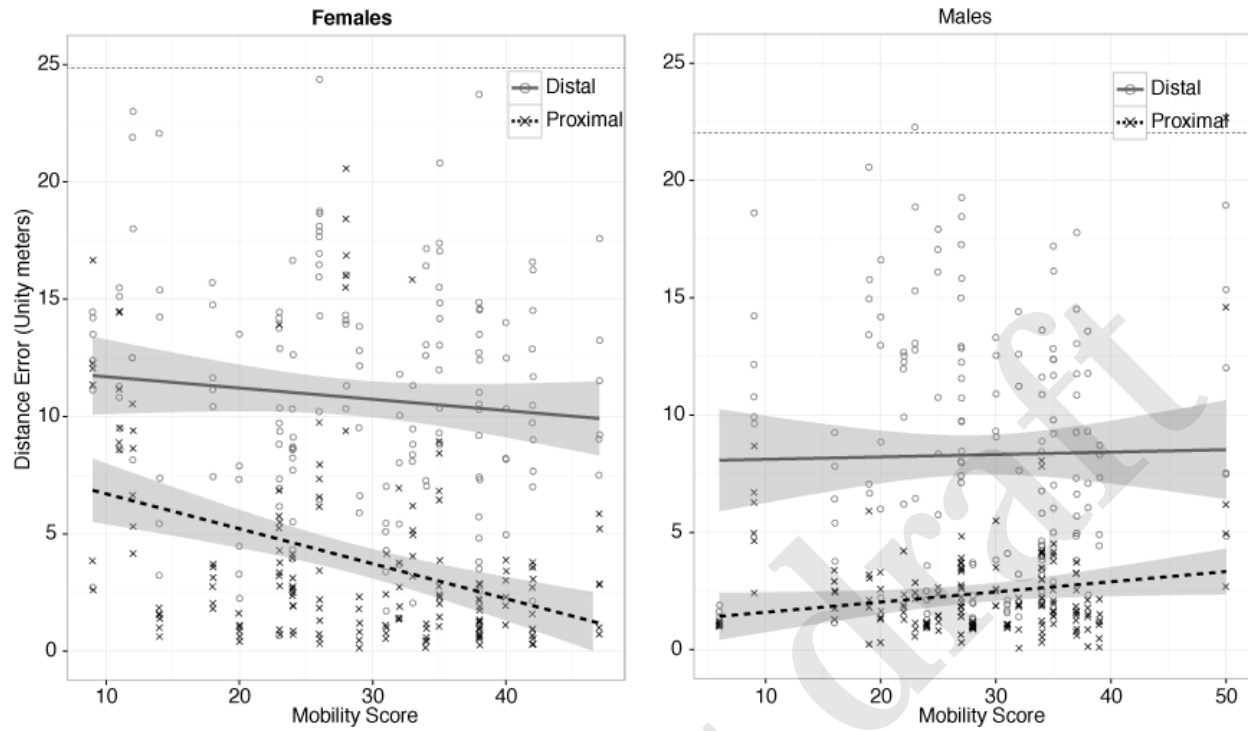
Figure 4. Euclidean distance error as a function of mobility scores (as assessed by self-report of number of locations traveled) for the males and females in the distal and proximal cue conditions for the small-scale maze. The gray bands indicate 95% confidence intervals. Dotted line at the top of the figure represents 3 SD above mean error.
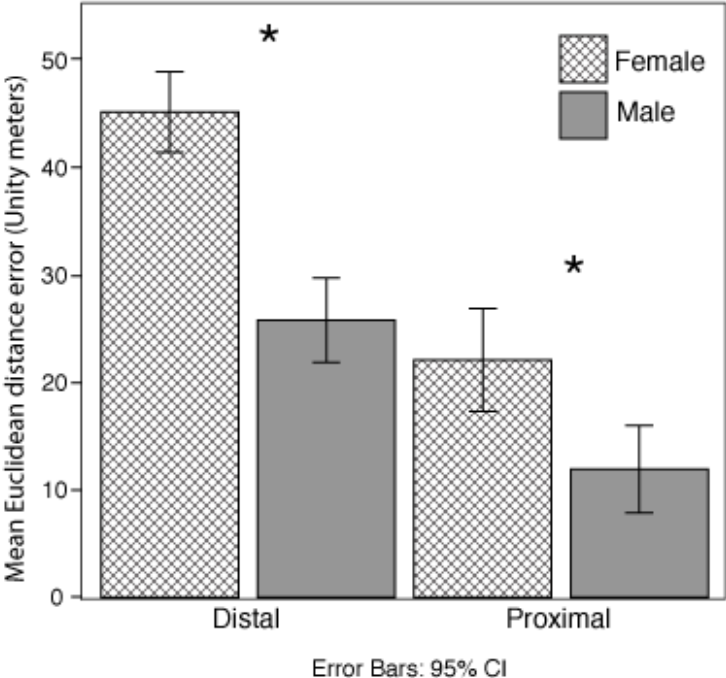
Figure 5. Euclidean distance error as a function of sex, for the large-scale maze. Error bars represent 95% confidence intervals. * = *p* < .05
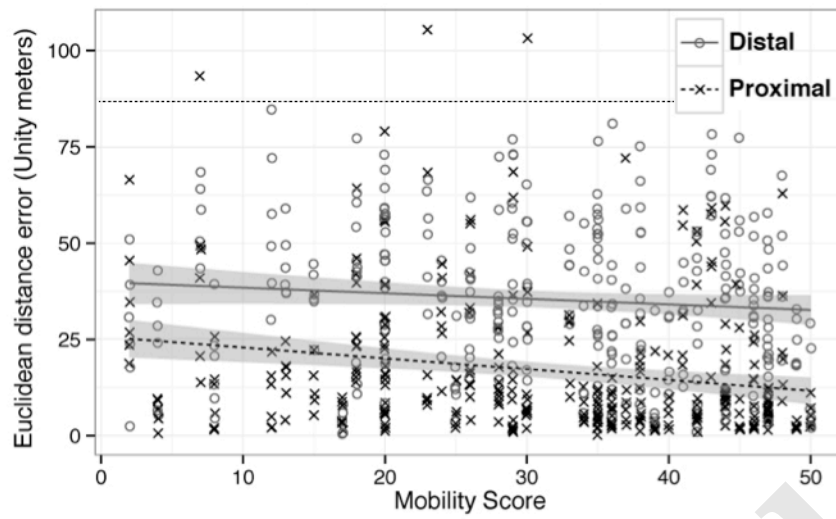
Figure 6. Euclidean distance error as a function of mobility scores for the proximal and distal cue conditions, in the large-scale maze. The gray bands indicate 95% confidence intervals. Dotted line at the top of the figure represents 3 SD above mean error.
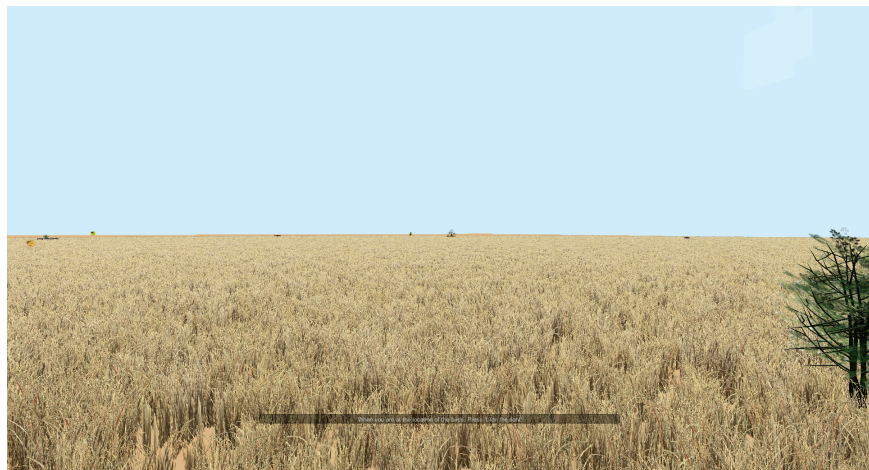
Figure 7. Screenshot of large scale proximal condition, which shows eight cues.

Table 1
*List of fixed effects with coefficients, standard errors, p-values and 95% confidence intervals
from the statistical model for the small-scale maze. 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. Coefficients for interactions including Block Order
indicate the change from proximal then distal to distal then proximal * = < .05*

Fixed Effect	Estimate	Standard error	*t*-ratio	*p*-value	95% CI
Sex	-3.86	2.45	-1.57	.115	(-8.68 , 0.95)
Cue	-3.98	1.26	-3.13	.001*	(-6.46 , -1.49)
Mobility	-0.06	0.04	-1.26	0.20	(-0.15 , 0.03)
Trial Number	-0.28	0.12	-2.31	0.02*	(-0.52, -0.04)
Gaming	-0.75	0.35	-2.15	0.03*	(-1.44 , -0.06)
Block Order	-1.21	0.92	-1.32	0.18	(-3.02, 0.58)
Sex x Cue	-3.61	1.85	-1.94	0.05*	(-7.24 , 0.02)
Sex x Mobility	0.05	0.07	0.79	0.42	(-0.08, 0.20)
Sex x Block Order	2.38	1.27	1.87	0.06	(-0.10, 4.88)
Sex x Trial Number	-0.17	0.17	-1.00	0.31	(-0.51, 0.16)
Cue x Mobility	-0.10	0.04	-2.41	0.01*	(-0.18, -0.01)
Sex x Cue x Mobility	0.15	0.06	2.58	.009*	(0.03, 0.28)

Table 2

List of fixed effects with coefficients, standard errors, p-values, and 95% confidence intervals from the statistical model for the large-scale maze. 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. Coefficients for interactions including Block Order indicate the change from proximal then distal to distal then proximal * = < .05

Fixed Effect	Estimate	Standard error	t-ratio	p-value	95% CI
Sex	-20.85	7.29	-2.85	.004*	(-33.65, -6.69)
Cue	-13.71	3.88	-3.53	.000*	(-21.32, -6.10)
Mobility	0.04	0.13	0.33	0.73	(-0.22, 0.32)
Trial Number	-1.84	0.49	-3.70	.000*	(-2.42, -1.06)
Gaming	-3.31	1.23	-2.69	.007*	(-5.72, -0.90)
Block Order	4.13	3.00	1.37	.168	(-1.75, 10.02)
Sex x Cue	2.25	6.24	0.36	0.71	(-9.99, 14.50)
Sex x Mobility	0.15	0.20	0.77	0.44	(-0.24, 0.56)
Sex x Block Order	0.67	4.21	0.15	0.87	(-7.58, 8.92)
Sex x Trial Number	0.19	0.69	0.27	0.78	(-0.64, -0.10)
Cue x Mobility	-0.37	0.13	-2.69	.006*	(-0.64, -0.10)
Sex x Cue x Mobility	0.29	0.20	1.49	0.13	(-0.09, 0.69)