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Analysis of Movement Kinematics on Analogous Spatial Learning Tasks Demonstrates Conservation of Direction and Distance Estimation Across Humans (Homo sapiens) and Rats (Rattus norvegicus)

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This series of experiments evaluates the nature of the representation that mediates human (*Homo sapiens*) and rat (*Rattus norvegicus*) movement characteristics on analogous spatial learning tasks. The results of Experiment 1 demonstrated that self-movement cues were sufficient to guide the performance of human participants during place training and matching-to-place testing tasks adapted to tabletop or manipulatory scale. Experiment 2 investigated the effect of manipulating access to environmental cues during place training on the nature of the representation used to guide performance. Blindfolded human participants appeared to encode the absolute location of the goal, whereas participants with access to environmental cues appeared to encode the relative location of the goal. The results of Experiment 3 demonstrated that human participants with access to environmental cues exhibited a similar response tendency (as observed in Experiment 2) after half as many trials of place training. During Experiment 4, rats exhibited movement characteristics in the water maze that were similar to movement characteristics observed in human participants who were provided access to environmental cues. These observations provide evidence that direction and distance estimation processes mediate performance on spatial tasks that are conserved across humans and rats.

Keywords: translational, comparative cognition, cognitive map, self-movement cues, proprioception

Spatial orientation depends on accurate processing of environmental (e.g., visual, auditory, olfactory) and self-movement (e.g., vestibular, proprioceptive, optic flow, motor efferent copies) cues. Disruptions in spatial orientation are commonly observed with neurological disorders (Aguirre & D'Esposito, 1999). For example, closed head injury or stroke localized to the right hemisphere typically results in sensory and motor neglect for the contralateral side of the body, severely disrupting spatial orientation (Heilman, Watson, & Valenstein, 2003). Further, during the progression of dementia of the Alzheimer's type, at least 60% of the patients will become lost in familiar environments (e.g., homes or neighbor-hoods), resulting in episodes of wandering (Rabins, Mace, & Lucas, 1982). Developing a translational model of spatial orientation that uses behavioral tasks to dissociate environmental and self-movement cue processing has the potential to characterize the neuropathology that produces disruptions in spatial orientation associated with neurological disorders.

For the past 30 years, performance of rats in the water maze has been the preferred behavioral technique for investigating the neurobiology of spatial orientation (Morris, Garrud, Rawlins, & O'Keefe, 1982). Previous studies have provided evidence that environmental (Morris, 1984; Sutherland & Dyck, 1984; Maurer & Derivaz, 2000) and self-movement (Burešová, Homuta, Krekule, & Bures, 1988; Semenov & Bures, 1989; Liu, Turner, & Bures, 1994) cues contribute to performance in the water maze; however, explanations of water maze performance continue to be dominated by the theories that posit rats encode relationships among multiple environmental cues, or encode a cognitive map (Tolman, 1948; O'Keefe & Nadel, 1978). For example, disruptions in learning the location of the hidden platform (i.e., place response) in the water maze, associated with compromised hippocampal-formation function, are typically attributed to impaired cognitive mapping based navigation (Morris et al., 1982; Morris, Anderson, Lynch, & Baudry, 1986; Moser, Krobert, Moser, & Morris, 1998; Feigenbaum & Morris, 2004). In contrast, both nonspatial pretraining (Cain, Saucier, Hall, Hargreaves, & Boon, 1996) and modified

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training procedures (Whishaw & Tomie, 1997; Day, Weisand, Sutherland, & Schallert, 1999) have been shown to eliminate performance impairments associated with manipulations that compromise hippocampal-formation function. These observations are consistent with a role for the hippocampal formation in water maze performance; however, the navigational strategy mediated by the hippocampal formation in the water maze remains to be determined.

Like most spatial tasks, place and directional responses are confounded in the traditional water maze task (Blodgett, McCutchan, & Mathews, 1949; Skinner et al., 2003; Hamilton, Akers, Weisend, & Sutherland, 2007). It is possible to dissociate which response is mediating performance by shifting the apparatus relative to stable environmental cues. Specifically, subsequent to hidden platform training in the water maze, the pool is shifted in the testing room such that a rat can swim to the absolute location in relation to room cues (place response) or swim to the relative location in relation to apparatus cues (direction response). During the shift probe, rats exhibit a strong bias to swim toward the relative location of the hidden platform in relation to the apparatus—or a directional response (Hamilton et al., 2007). Only specific training conditions (i.e., elimination of visual cues associated with the pool wall) are sufficient to elicit a tendency to swim toward the absolute location in relation to the testing room—or a place response (Hamilton et al., 2008; Hamilton, Akers, et al., 2009; Hamilton, Johnson, Redhead, & Verney, 2009). Considering these observations, a translational model of spatial orientation must also be able to dissociate the nature of the representation that mediates performance in spatial tasks.

Previous work has shown that humans and rodents have the ability to estimate direction and distance to the point where movement was initiated, when restricted to online processing of self-movement cues or dead-reckoning-based navigation (Mittelstaedt & Mittelstaedt, 1980; Etienne, 1980; Potegal, 1982; Etienne, Maurer, Saucy, & Teroni, 1986; Séguinot, Maurer, & Etienne, 1993; Maaswinkel & Whishaw, 1999; Loomis et al., 1993; Klatzky, 1999; Worsley et al., 2001; Philbeck, Behrmann, Levy, Potolicchio, & Caputy, 2004; Shettleworth & Sutton, 2005; Wallace, Choudhry, & Martin, 2006; Wolbers, Wiener, Mallot, & Büchel, 2007; Wallace, Köppen, Jones, Winter, & Wagner, 2010). Several lines of evidence have shown that self-movement cue processing is sufficient to support performance during tasks in which direction or distance estimates remain consistent across training trials. First, under dark conditions, rats display a decrease in the latency to locate the hidden platform in the water maze, provided the start and goal locations maintain a fixed relationship (Moghaddam & Bures, 1996). Next, during training on nonvisually guided reaching tasks, humans learn to scale their peak speeds to the distance between the start and goal locations (Bock & Eckmiller, 1986; Gordon, Ghilardi, Cooper, & Ghez, 1994). As of yet, it remains to be determined whether self-movement cues are sufficient to support the performance of humans in behavioral tasks analogous to the water maze.

Experiment 1 examined the movement characteristics of blindfolded human participants with a tabletop (i.e., manipulatory scale) analogue of the water maze. Participants were given 20 trials with the goal in a fixed location (i.e., place training) prior to shifting the goal location every other trial (i.e., matching-to-place testing) for six trials. Experiment 2 investigated the movement characteristics

of blindfolded and sighted human participants during a place training task in the bead maze and the subsequent shift probe to characterize the nature of the representation (i.e., cognitive mapping or directional/vector) mediating performance. Experiment 3 examined whether overtraining in the sighted human participants contributed to the group differences observed in the second experiment. Finally, Experiment 4 examined whether rat movement characteristics associated with performance during place training and shift probe in the water maze was similar to that exhibited by human participants in the preceding experiments. These studies continue a line of research establishing a translational model of spatial orientation (Wallace et al., 2006, 2010).

Experiment 1

The current experiment examined whether self-movement cues generated at the manipulatory scale are sufficient to guide the performance of human participants in spatial tasks that parallel place training and matching-to-place testing procedures used in the water maze literature (Morris et al., 1982; Sutherland, Kolb, & Whishaw, 1982; Whishaw, 1985).

Method

Participants. Northern Illinois University undergraduate students were recruited from introduction to psychology classes and given supplemental course credit for their participation. Female ($n = 10$) and male ($n = 10$) participants ranged in age from 19 to 26 years, with the average age being 21.5 years old. Eighteen of the participants were right-handed and two of the participants were left-handed. Throughout the experiment, participants were instructed to use their dominant hand to perform the task. All of the procedures in this study were approved by the local Institutional Review Board, which follows the standards set by the U.S. Office for Human Research Protections guidelines.

Apparatus. Participants were seated in an adjustable chair, with wheels such that their forearms were resting comfortably on the surface of the table (61.0 cm × 91.0 cm). The testing apparatus was a circular well (48.3 cm in diameter and 2.5 cm deep) cut into two sheets of foam board, with a third sheet of foam board serving as the base. A small piece of hook-type Velcro tape (1 cm × 1 cm) was attached to the surface of the base. A bullet camera attached to a DVD recorder was positioned above the participant, allowing the entire surface of the table to be within view of the camera. Darkened swimming goggles were used to blindfold participants.

Procedure. Prior to testing, participants were seated in a chair, instructed to put the blindfold on, and then rolled into the testing room. During place training and matching-to-place testing, participants were seated at one side of the table and instructed to use their index finger to search for the piece of Velcro tape while maintaining contact with the base of the apparatus. Once the participants found the Velcro tape, the experimenter asked them to remove their finger from the maze and place their hand on their lap. The next trial began after the experimenter guided the participants' hand to one of the eight possible start locations around the perimeter of the circular well. Start locations pseudorandomly varied across trials. During the 20 place training trials, the Velcro tape remained in the same location in the center of one of the arena's quadrants. Matching-to-place testing began on the 21st

trial and continued until the 26th trial, such that the location of the Velcro tape shifted to the center of a new quadrant every two trials. Between place training and matching-to-place trials, the participants remained blindfolded and noise was made to simulate moving the location of the Velcro tape.

Data analysis. Performance of the participants was recorded on DVDs. Each trial was converted into a digital computer file using the Peak Performance System (Vicon, Centennial, Colorado) at 30 frames per second. The position of the finger was digitized every other frame by selecting a pixel corresponding to a marker placed on the fingertip of the participant. Several measures were used to quantify the performance observed across trials. Both the latency and distance traveled while searching for the Velcro tape were calculated for each trial. Heading error characterized the ability of participants to estimate direction to the Velcro tape on each trial and was calculated as the angle subtended by the following three points: (a) Velcro tape, (b) start position, and (c) first peak in speed on the path. Previous work has demonstrated that scaling of moment-to-moment speeds reflects distance estimation. For example, humans scale their moment-to-moment speeds during nonvisually guided reaching to the length of the movement extent (Bock & Eckmiller, 1986; Gordon et al., 1994). In addition, movement scaling has been observed in humans and rats on dead reckoning tasks (Wallace et al., 2010). The present study used movement scaling to index participant's estimation of the distance to the Velcro tape. Movement scaling was quantified by calculating the correlation between the peak speeds (i.e., highest moment-to-moment speed of a path) and minimum distances (i.e., shortest distance between the start and end points of a path) for a set of paths. Latency, distance, and heading error were averaged into four blocks of five trials during place training. These measures were averaged during matching-to-place testing across trials in which the Velcro tape was shifted (Block 1) and trials in which it remained in the same quadrant (Block 2). The correlations between peak speeds and minimum distances were calculated for sets of trials that corresponded to the blocks previously described.

Results

Place training. Topographic characteristics of searching behavior are plotted for a representative participant's first, second, third, and fourth blocks (see panels A, B, C, and D of Figure 1) of place training. In general, participants gradually became more accurate in finding the Velcro tape as training progressed (see the left-hand panels of Figure 2). Mixed-design analysis of variance (ANOVA) was used to evaluate whether sex of the participant influenced these changes in performance observed across trials. The ANOVA conducted on latency to find the Velcro tape revealed a significant effect of block, $F(3, 54) = 8.829$, $p < .001$, $\eta_p^2 = .329$; however, neither the effect of sex, $F(1, 18) = 0.259$, $p = .617$, $\eta_p^2 = .014$, nor the Sex $\times$ Block interaction, $F(3, 54) = 0.170$, $p = .916$, $\eta_p^2 = .009$, were significant. Post hoc analysis conducted on the latency to find the Velcro tape revealed a significant linear trend, $F(1, 18) = 16.315$, $p = .001$, $\eta_p^2 = .475$, across the four blocks. The ANOVA conducted on distance traveled while searching for the Velcro tape revealed a significant effect of block, $F(3, 54) = 8.359$, $p < .001$, $\eta_p^2 = .317$; however, neither the effect of sex, $F(1, 18) = 0.161$, $p = .693$, $\eta_p^2 = .009$, nor the Sex $\times$ Block interaction, $F(3, 54) = .439$, $p = .726$, $\eta_p^2 =$
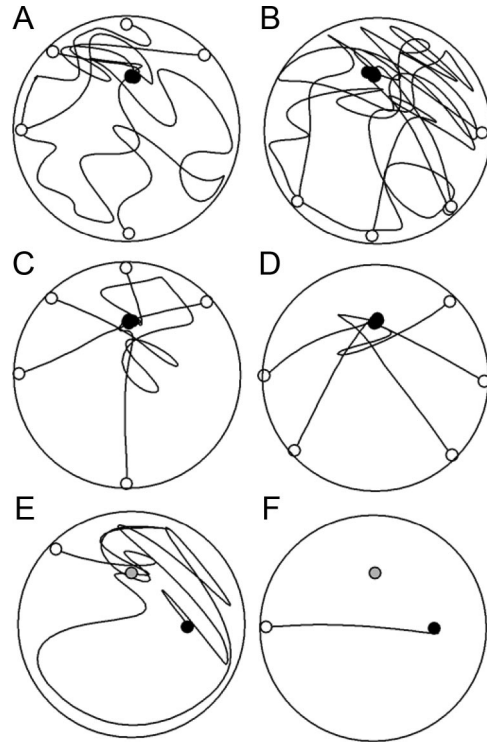

Figure 1. The start position (white circle), searching path, and position of Velcro tape (black circle) are plotted for a representative participant's first (A), second (B), third (C), and fourth (D) blocks of place training trials. Performance on the first (E) and second (F) trials of matching-to-place is plotted for a representative participant.

.024, were significant. Post hoc analysis conducted on distance traveled revealed a significant linear trend, $F(1, 18) = 16.953$, $p = .001$, $\eta_p^2 = .485$, across the four blocks. The ANOVA conducted on heading error revealed a significant effect of block, $F(3, 54) = 16.000$, $p < .001$, $\eta_p^2 = .471$; however, neither the effect of sex, $F(1, 18) = .179$, $p = .677$, $\eta_p^2 = .010$, nor the Sex $\times$ Block interaction, $F(3, 54) = .123$, $p = .946$, $\eta_p^2 = .007$, were significant. Post hoc analysis conducted on heading error revealed a significant linear trend, $F(1, 18) = 39.197$, $p < .001$, $\eta_p^2 = .685$, across the four blocks.

As place training progressed, participants displayed a tendency to scale their moment-to-moment speeds to the minimum distance required to reach the Velcro tape (see panels A and B of Figure 3). Specifically, longer minimum distances to reach the Velcro tape were associated with higher peak speeds. Recall that a participant's movement scaling was quantified by calculating the correlation between minimum distances and peak speeds for each block of five trials. The ANOVA conducted on correlations between peak speed and minimum distance revealed a significant effect of block, $F(3, 54) = 3.106$, $p = .034$, $\eta_p^2 = .147$; however, neither the effect of sex, $F(1, 18) = 0.000$, $p = .988$, $\eta_p^2 = .000$, nor the Sex $\times$ Block interaction, $F(3, 54) = 1.033$, $p = .385$, $\eta_p^2 = .054$, were significant. Post hoc analysis on the correlations between peak speeds and minimum distances revealed a significant linear trend, $F(1, 18) = 6.176$, $p = .023$, $\eta_p^2 = .255$, across blocks.

Matching-to-place testing. Topographic characteristics of searching behavior are plotted for a representative participant's
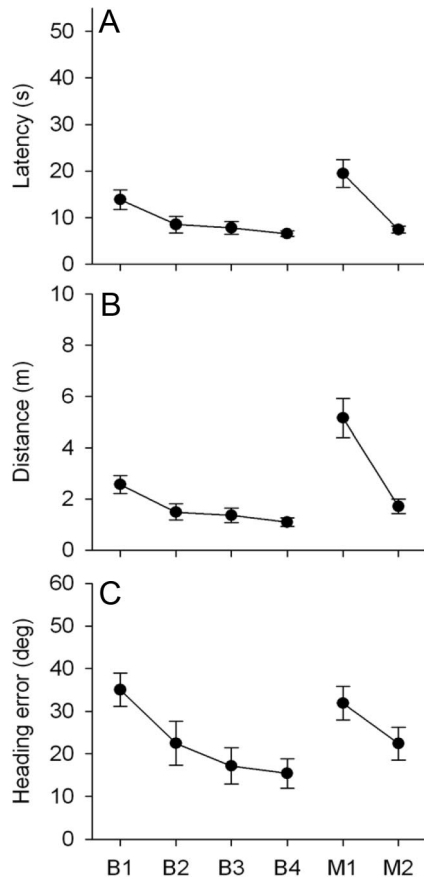
Figure 2. Average latency to reach the platform (A), distance traveled (B), and heading error (C) is plotted for the four blocks of place training. The average for these measures are also plotted for the first (M1) and second (M2) trials of matching-to-place performance.

first and second trials (see panels E and F of Figure 1) during matching-to-place testing. In general, participants' performance significantly improved on the second trial when the Velcro tape remained in the same position as experienced on the preceding trial (see right-hand panels of Figure 2). The ANOVA conducted on latency to find the Velcro tape revealed a significant main effect of block, $F(1, 18) = 21.472$, $p < .001$, $\eta_p^2 = .544$, no significant main effect of sex, $F(1, 18) = 0.707$, $p = .411$, $\eta_p^2 = .038$, and no significant Sex $\times$ Block interaction, $F(1, 18) = 3.488$, $p = .078$, $\eta_p^2 = .162$. The ANOVA conducted on distance traveled to find the Velcro tape revealed a significant effect of block, $F(1, 18) = 23.241$, $p < .001$, $\eta_p^2 = .564$; however, neither the effect of sex, $F(1, 18) = 0.167$, $p = .687$, $\eta_p^2 = .009$, nor the Sex $\times$ Block interaction, $F(1, 18) = 2.174$, $p = .158$, $\eta_p^2 = .108$, were significant. The ANOVA conducted on heading error revealed a significant effect of block, $F(1, 18) = 10.897$, $p = .004$, $\eta_p^2 = .377$; however, neither the effect of sex, $F(1, 18) = 0.177$, $p = .679$, $\eta_p^2 = .010$, nor the Sex $\times$ Block interaction, $F(1, 18) = 0.147$, $p = .706$, $\eta_p^2 = .008$, were significant.

A change in scaling of moment-to-moment speeds was observed when comparing performance observed during the first and second blocks of matching-to-place testing (see panel C of Figure 3).

Specifically, participants reliably exhibited higher peak speeds with longer minimum distances on the second block of matching-to-place testing. The ANOVA conducted on correlations between peak speed and minimum distance revealed a significant effect of block, $F(1, 18) = 7.016$, $p = .016$, $\eta_p^2 = .28$; however, neither the main effect of sex, $F(1, 18) = 2.184$, $p = .157$, $\eta_p^2 = .108$, nor the Sex $\times$ Block interaction, $F(1, 18) = 0.001$, $p = .976$, $\eta_p^2 = .000$, were significant.

Discussion

This experiment demonstrated that self-movement cues (i.e., proprioception and motor efferent copies) generated at the manipulatory scale were sufficient to support improvements in performance in tasks that parallel traditional water maze procedures. In general, participants took less time and traveled shorter distances to find the Velcro tape across place training blocks. Although participants began searching for the Velcro tape from different points around the perimeter of the apparatus, their heading error decreased across place training blocks. Finally, as training progressed, participants began to scale their movement kinematics to the distance between the start location and the Velcro tape. These
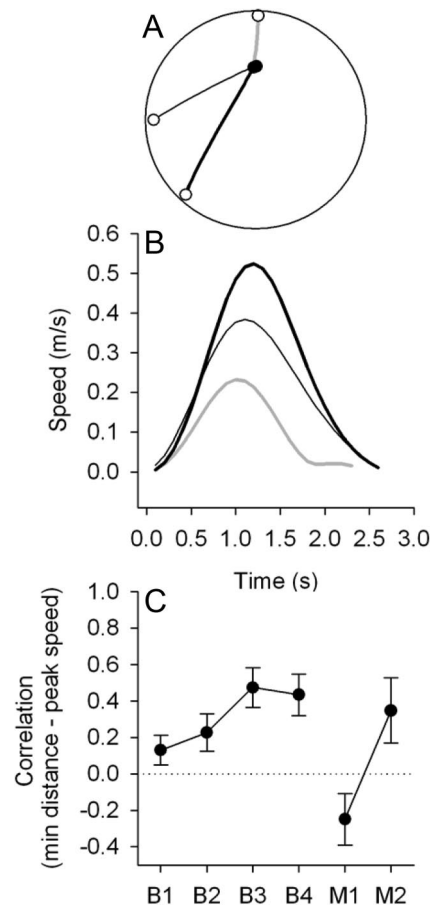

Figure 3. Topographic (A) and kinematic (B) characteristics are plotted for three paths that vary in distance between the start and Velcro tape. The average correlation between peak speed and minimum distance is plotted for each block of place training and matching-to-place testing (C).

observations are evidence that participants encoded the location of the Velcro tape.

Improvements in performance were also observed during matching-to-place testing. Recall that the Velcro tape was shifted to a new quadrant of the bead maze every other trial. Participants took less time and traveled shorter distance to locate the Velcro tape on the second block relative to the first block. In addition, heading error decreased as scaling of movement kinematics increased from the first block to the second block. These observations demonstrate that self-movement cues are sufficient to update the representation of the Velcro tape position.

Experiment 2

Experiment 1 demonstrated that self-movement cues were sufficient for encoding and updating the location of the Velcro tape. The goal of this experiment was to characterize the nature of the representation guiding performance.

Method

Participants. Northern Illinois University undergraduate students (female, $n = 9$; male, $n = 9$) were recruited from introduction to psychology classes and given supplemental course credit for their participation. Considering that sex differences were not observed on any measures in Experiment 1, that variable was excluded from subsequent analyses. Participants ranged in age from 18 to 26 years, with 19.6 years being the average age. Seventeen of the participants were right-handed and one of the participants was left-handed. Throughout the experiment, participants were instructed to use their dominant hand to perform the task. All of the procedures in this study were approved by the local institutional review board, which follows the standards set by the U.S. Office for Human Research Protection guidelines.

Apparatus. Participants were seated at the same apparatus used in Experiment 1, except the circular well was filled with small plastic beads. The beads prevented sighted participants from using visual cues associated with the Velcro tape to guide performance.

Procedure. The procedure was similar to the place training described in Experiment 1, with several exceptions. First, participants were randomly assigned to the sighted ($n = 8$) or blindfolded ($n = 10$) groups, with equivalent numbers of females and males assigned to each group. Next, during the first 20 place training trials, the bead maze was laterally offset half of the radius of the circular arena relative to the participants' preferred hand (i.e., to the left if the participant was right-handed; see Panel A of Figure 5). Start locations pseudorandomly varied across trials, and the Velcro tape remained in the same location in the center of an arena quadrant. Between trials, participants remained seated at the table to minimize stimulation of self-movement cues, and participants in both groups wore blindfolds while the beads were repositioned for the next trial. Intertrial intervals were approximately 30 s. Finally, on the 21st trial, the Velcro tape was removed, the apparatus was laterally shifted (i.e., half of the diameter of the circular arena) in the opposite direction of the offset, participants started from the same southern position and searched for 30 s prior to being instructed to remove their hand from the bead maze.

Data analysis. The measures used to characterize performance during the first 20 place training trials were the same as

those used during Experiment 1: latency, distance traveled, heading error, and correlation between minimum distance and peak speed. These measures were averaged (i.e., latency, distance, heading error) or calculated (i.e., correlation between minimum distance and peak speed) for each block of five trials.

Two additional measures were developed to characterize the nature of the response observed during the 21st trial in which the Velcro tape was removed and the apparatus was shifted laterally. Signed heading direction was calculated as the angle subtended by the following three points: (a) the center of the bead maze, (b) the start position, and (c) the point at which the first peak in speed occurred on the path. The signed heading direction was assigned a negative value if the initial peak in speed was left of center (absolute response) and a positive value if the initial peak in speed was right of center (relative response). Percent time spent searching the absolute side of the bead maze was calculated for the first and second 15 s of the 21st trial.

Results

Place training. In general, participants became more accurate in finding the Velcro tape as training progressed, and providing access to visual cues facilitated performance on the task (see panels A, B, and C of Figure 4). Mixed-design ANOVAs were used to evaluate group differences in performance observed during place training. The ANOVA conducted on latency to find the Velcro tape revealed a significant effect of group, $F(1, 16) = 10.613$, $p = .005$, $\eta_p^2 = .399$, block, $F(3, 48) = 29.077$, $p < .001$, $\eta_p^2 = .645$, and Group $\times$ Block interaction, $F(3, 48) = 6.241$, $p = .001$, $\eta_p^2 = .281$. Post hoc analysis conducted on the latency to find the Velcro tape revealed a significant linear trend, $F(1, 16) = 30.963$, $p < .001$, $\eta_p^2 = .659$, across the four blocks. The ANOVA conducted on the distance traveled while searching for the Velcro tape revealed a significant effect of group, $F(1, 16) = 11.591$, $p = .004$, $\eta_p^2 = .420$, block, $F(3, 48) = 22.076$, $p < .001$, $\eta_p^2 = .580$, and Group $\times$ Block interaction, $F(3, 48) = 4.921$, $p = .005$, $\eta_p^2 = .235$. Post hoc analysis conducted on distance traveled revealed a significant linear trend, $F(1, 16) = 25.691$, $p < .001$, $\eta_p^2 = .616$, across the four blocks. The ANOVA conducted on heading error revealed a significant effect of group, $F(1, 16) = 12.311$, $p = .003$, $\eta_p^2 = .435$, block, $F(3, 48) = 42.773$, $p < .001$, $\eta_p^2 = .728$, and Group $\times$ Block interaction, $F(3, 48) = 3.643$, $p = .019$, $\eta_p^2 = .185$. Post hoc analysis conducted on heading error revealed a significant linear trend, $F(1, 16) = 85.973$, $p < .001$, $\eta_p^2 = .843$, across the four blocks.

Both groups began to scale their moment-to-moment speeds to the minimum distance to reach the Velcro tape (panel D of Figure 4) as place training progressed. The ANOVA conducted on correlations between peak speed and minimum distance revealed a significant effect of block, $F(3, 48) = 4.053$, $p = .012$, $\eta_p^2 = .202$; however, neither the effect of group, $F(1, 18) = 3.924$, $p = .065$, $\eta_p^2 = .197$, nor the Group $\times$ Block interaction were significant, $F(3, 48) = 0.369$, $p = .776$, $\eta_p^2 = .023$. Post hoc analysis conducted on the correlations between peak speeds and minimum distances revealed a significant linear trend, $F(1, 16) = 7.474$, $p = .015$, $\eta_p^2 = .318$, across blocks.

Shift probe. Response topography differed between groups during the shift probe (see panels B and C of Figure 5). The initial heading of the blindfolded group was directed toward the left side
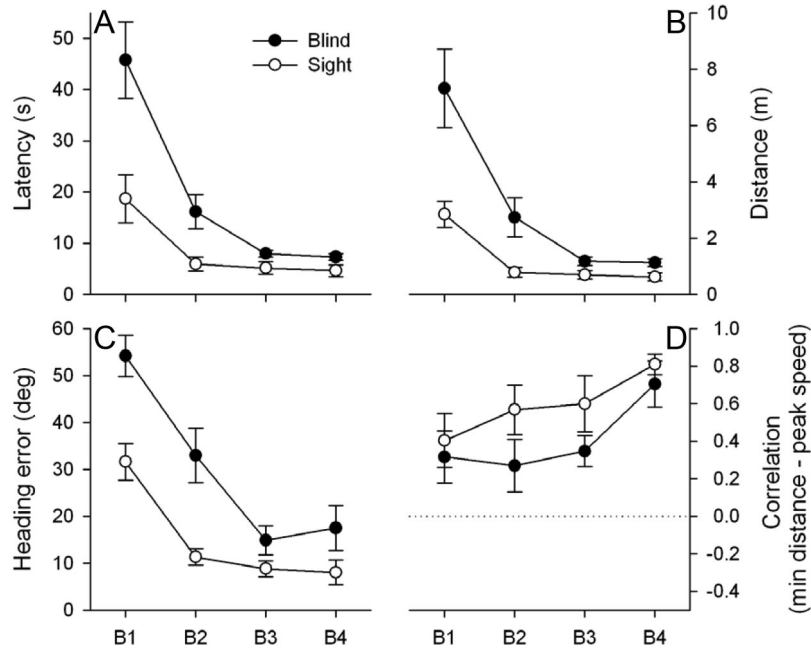
Figure 4. Each group's average latency to reach the platform (A), distance traveled (B), heading error (C), and correlation between peak speed and minimum distance (D) is plotted for the four blocks of place training.

of the bead maze (i.e., absolute response), whereas the initial heading of the sighted group was directed toward the right side of the bead maze (i.e., relative response). The independent samples *t* test conducted on the signed heading direction demonstrated that groups significantly differed in their initial heading direction, $t(16) = 2.190$, $p = .044$, $d = 1.315$. After the initial heading trajectory, each group showed a distinct searching pattern during the 30-s shift probe. The blindfolded group searched the left side of the bead maze before searching the right side of the bead maze. In contrast, the sighted group searched the right side of the bead maze prior to searching the left side of the bead maze. The ANOVA conducted on percent time spent on the left side of the bead maze resulted in a significant Group × Time interaction, $F(1, 16) = 6.675$, $p = .020$, $\eta_p^2 = .294$; however, nether the main effect of group, $F(1, 16) = .217$, $p = .647$, $\eta_p^2 = .013$, nor the main effect of time, $F(1, 16) = .130$, $p = .724$, $\eta_p^2 = .008$, were significant.

Discussion

This experiment demonstrated that access to visual cues influenced several aspects of performance in the bead maze. First, access to visual cues facilitated acquisition on measures of general performance (i.e., latency and distance) and direction estimation (i.e., heading error); however, access to visual cues did not significantly influence acquisition on measures of distance estimation (i.e., correlation between minimum distance and peak speed). Next, groups displayed significant differences in performance during the shift probe. The initial heading of blindfolded participants was left of the midline, or an absolute response, whereas sighted participants' initial heading was right of the midline, or a relative response. Finally, after the first progression, groups exhibited contrasting search strategies. The blindfolded group initially

searched in the left half of the bead maze (i.e., continuing to exhibit an absolute response) prior to searching the right half of the bead maze. In contrast, the sighted group initially searched the right half of the bead maze (i.e., continuing to exhibit a directional response) prior to searching the left half of the bead maze.

These observations are consistent with cue availability influencing the response elicited. Restricting participants to using self-movement cues elicited a place response. Providing participants with access to visual and self-movement cues elicited a directional response. These varying response profiles are consistent with the blindfolded group encoding the absolute location of the Velcro tape relative to certain environmental cues (i.e., body) and the sighted group encoding the direction and distance to the Velcro tape relative to other environmental cues (i.e., bead maze).

Experiment 3

Experiment 2 demonstrated that providing access to visual cues resulted in qualitatively different response characteristics during the shift probe. The current study examined whether participants with access to visual cues will still exhibit a directional response during the shift probe after half as many training trials to evaluate whether the effect was due to overtraining.

Method

Participants. Northern Illinois University undergraduate students were recruited from introduction to psychology classes and given supplemental course credit for their participation. Female (*n* = 14) and male (*n* = 9) participants ranged in age from 18 to 26 years, with 19.7 years being the average age. Twenty-one of the participants were right-handed and two of the participants were
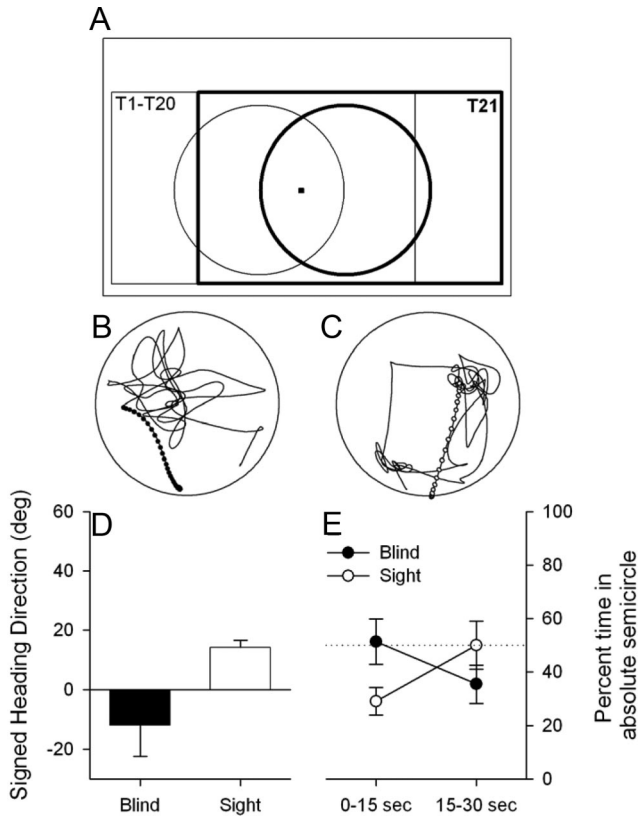
Figure 5. A schematic (A) is presented of the apparatus position during training (thin line) and the shift probe (heavy line). A searching path is plotted for a representative participant from the blindfolded (panel B) and sighted (C) groups during the shift probe. The initial trajectory until the first stop (dotted line) and subsequent searching path (solid line) is plotted for each participant. The average signed heading direction for the initial trajectory is plotted for each group (D). The average percent time spent searching the absolute semicircle is plotted for each group for the first and second 15 s (E).

left-handed. Throughout the experiment, participants were instructed to use their dominant hand to perform the task. All of the procedures in this study were approved by the local institutional review board, which follows the standards set by the U.S. Office for Human Research Protection guidelines.

Apparatus. Participants were seated at the same apparatus as used in Experiment 2.

Procedure. The procedures were similar to those used in Experiment 2, with two exceptions. First, all participants were sighted and only given 10 place training trials prior to the probe trial. Next, during the probe trial, participants were randomly assigned to either experience the bead maze in the same position ($n = 11$) or shifted position ($n = 12$). Participants were given 30 s to search for the Velcro tape (which had been removed after the last place training trial) prior to being instructed to remove their hand from the bead maze.

Data analysis. The measures used to characterize performance during the first 10 place training trials were the same as those used in Experiments 1 and 2: latency, distance traveled, heading error, and correlation between minimum distance and

peak speed. These measures were averaged (i.e., latency, distance, heading error) or calculated (i.e., correlation between minimum distance and peak speed) for the first and second blocks of five trials.

The two measures developed to characterize performance on the 21st trial of Experiment 2 were also used to characterize performance on the 11th trial of the current experiment: signed heading direction and percent time spent searching the absolute side of the bead maze. Considering that both groups may exhibit similar signed heading directions, despite making topographically distinct responses, the x- and y-coordinates associated with each participant's first peak in speed were obtained for the 11th trial. Values obtained for each coordinate was independently evaluated for group differences.

Results

Place training. In general, participants became more accurate in finding the Velcro tape across the two place training blocks (see Figure 6). Considering that groups experienced the same procedures on the first 10 trials, group differences were not evaluated for place training. Paired sample *t* tests were used to evaluate whether performance significantly changed across training blocks. The paired samples *t* test conducted on latency, $t(22) = 8.119$, $p < .001$, $d = 1.693$, distance traveled, $t(22) = 6.789$, $p < .001$, $d = 1.416$, and heading error, $t(22) = 6.804$, $p < .001$, $d = 1.419$, all revealed a significant improvement in performance across blocks.

Participants began to scale their movements early in training. The paired samples *t* test conducted on correlations between peak speed and minimum distance did not significantly change across blocks, $t(22) = -1.34$, $p = .194$, $d = .279$; however, single
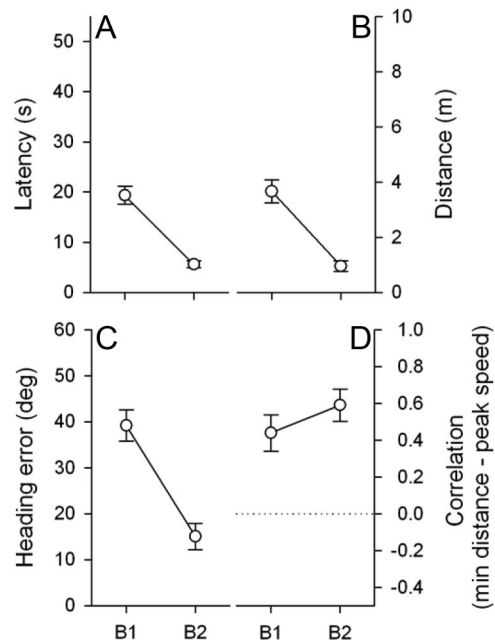

Figure 6. The average latency to reach the platform (A), distance traveled (B), heading error (C), and correlation between peak speed and minimum distance (D) are collapsed across groups and plotted for both blocks of place training.

samples *t* tests revealed that the average correlations were significantly larger than zero on Block 1, $t(22) = 4.470$, $p < .001$, $d = .932$, and Block 2, $t(22) = 6.734$, $p < .001$, $d = 1.404$.

Shift probe. Response topography was similar for both groups during the shift probe (see panel A of Figure 7). Both groups' initial heading was directed toward the right side (i.e., relative response) of the bead maze. The independent sample *t* test conducted on signed heading direction did not reveal significant differences in their initial heading direction, $t(21) = 1.432$, $p = .167$, $d = .589$; however, both the shift group, $t(11) = 5.509$, $p < .001$, $d = 1.590$, and the no-shift group, $t(10) = 3.169$, $p = .010$, $d = .956$, had signed heading directions that were significantly larger than zero. After the initial heading trajectory, both groups searched the right side of the bead maze prior to searching the left side of the bead maze. The ANOVA conducted on percent time spent on the left side of the bead maze resulted in a marginally significant main effect of time, $F(1, 21) = 4.373$, $p = .049$, $\eta_p^2 = .172$; however, neither the main effect of group, $F(1, 21) = .646$, $p = .431$, $\eta_p^2 = .030$, nor the Group × Time interaction, $F(1, 21) = 1.996$, $p = .172$, $\eta_p^2 = .087$, were found to be significant.

The average starting location and peak speed location are plotted for both groups (see panel A for Figure 7). An independent samples *t* test conducted on peak speed location revealed significant group differences on the *x*-axis, $t(21) = 20.804$, $p < .001$, $d = 7.016$; however, groups did not significantly differ on the *y*-axis, $t(21) = .238$, $p = .815$, $d = .086$. These results are consistent with both groups having peak speed locations that were the same distance from the starting position; however, the shifted group exhibited a directional response that was shifted with the apparatus in absolute space.

Discussion

This experiment was designed to evaluate whether the directional response observed during the probe trial in the sighted group of Experiment 2 was an artifact of overtraining. In general, performance improved during the two place training blocks. One exception was the failure to observe a significant change in correlation between peak speed and minimum distance across blocks. Interestingly, both groups had average correlations that were significantly larger than zero. Therefore, participants may have been encoding the position of the Velcro tape early in training and were using their distance estimates to scale their peak speeds.

During the shift probe, both groups exhibited several movement characteristics consistent with encoding the direction and distance to the Velcro tape. First, both groups' initial heading was directed toward the relative side of the apparatus. This demonstrates that the initial direction estimate was anchored to the bead maze apparatus rather than the body of the participant or other stable environmental cues. Next, location of the peak speed on the *y*-axis did not differ between groups and was largely restricted to the midpoint between the start location and the position of the Velcro tape. This observation is also consistent with distance estimates being anchored to the bead maze rather than the participant's body or other stable environmental cues. Finally, both groups searched the relative side of the apparatus prior to shifting to search the absolute side of the apparatus. The tendency to initially search the relative side prior to searching the absolute side is further evidence that performance of participants with access to visual and self-movement cues is mediated by a representation that encodes the direction and distance to the Velcro tape.

Experiment 4

Experiment 1 demonstrated that water maze procedures can be adapted to the human manipulatory scale and that self-movement cues are sufficient to guide performance. Experiments 2 and 3 provided support for the view that participants encode a vector that represents the direction and distance to a location while performing in spatial tasks analogous to the water maze (Blodgett et al., 1949; Cheng, 1989; Skinner et al., 2003; Hamilton, Akers, et al., 2009; Hamilton, Johnson, et al., 2009). Support for the directional component was observed during the shift probe when participants exhibited a response bias toward the relative half of the bead maze. Support for the distance component was observed when participants began to scale their peak speeds to the distance required to reach the Velcro tape. The current experiment examined whether rats exhibited scaling of movement kinematics during place training, a relative response bias during the shift probe, and sexually dimorphic performance on either of these components.

Method

Subjects. Twelve naïve Long-Evans female ($n = 6$) and male ($n = 6$) rats (*Rattus norvegicus*) served as subjects for the current
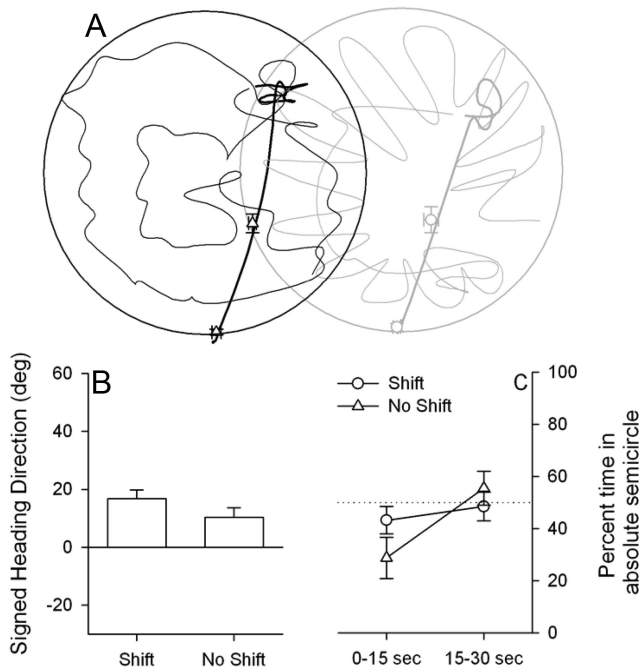

Figure 7. Searching paths are plotted for a representative participant from the shift (black line) and no-shift (gray line) groups during the probe trial (A). The shift (triangle) and no-shift (circle) groups' average start location and first peak in speed location are plotted relative to the *x*-axis and the *y*-axis. The average signed heading direction for the initial trajectory is plotted for each group (B). The average percent time spent searching the absolute semicircle is plotted for each group for the first and second 15 s (C).

study and were housed in same-sex pairs in plastic cages. The colony room was maintained at 20 to 21 °C and on 12-hr light–dark cycle. Throughout testing, rats were provided ad lib access to rat chow (5L42 Rodent Breeder Diet food pellets; PMI Nutritional International, Brentwood, Missouri) and water. The Institutional Animal Care and Use Committee at Northern Illinois University, which follows the guidelines set by the Office of Laboratory Animal Welfare, approved all the procedures described in this experiment.

Apparatus. The apparatus was a circular tub (1.73 m in diameter and 0.60 m deep) filled with water such that the hidden platform (0.28 m tall) was hidden 2 cm below the surface of the water. White nontoxic tempura paint was used to make the water opaque, further limiting the visibility of the platform. The pool was located in a room (4.36 m by 2.74 m) with multiple visual cues (e.g., posters, sink, door frames, a large metal cabinet) and a bullet camera positioned above the pool. The camera was connected to a DVD recorder, providing a record of the rats' performance for offline analysis. During nonspatial pretraining, a ceiling-to-floor black curtain was hung around the water maze.

Procedure. All rats experienced 4 days of nonspatial pretraining prior to the 5 days of place training. The shift probe occurred the day after the last place training trial. The nonspatial pretraining was included to limit the effects of sexually dimorphic stress responses on water maze performance (Beiko, Lander, Hampson, Boon, & Cain, 2004). During nonspatial pretraining, rats were given three trials per day to find a hidden platform that moved to a new location each trial. Place training involved giving rats four trials per day to locate the hidden platform, in which the platform remained in a consistent location. During the shift probe, the hidden platform was removed and the position of the water maze was shifted a distance equal to the pool radius (0.865 m). For each

day, rats were tested in a random order, and all rats received their first trial prior to any rat experiencing its second trial; therefore, the intertrial interval was approximately 20 min. During a trial, rats were released facing the wall of the water maze from multiple locations along the periphery. If a rat did not find the hidden platform within 60 s, the experimenter used a strainer to guide the rat to the hidden platform. After the rat reached the hidden platform, it was left there for 30 s prior to returning it to the transport cage. Subsequent to each trial, the water was stirred and strained to limit the availability of odor cues.

Data analysis. The measures used to characterize rat performance in the water maze during place training were the same as those used during Experiments 1, 2, and 3: latency, distance traveled, heading error, and correlation between minimum distance and peak speed. These measures were averaged (i.e., latency, distance, heading error) or calculated (i.e., correlation between minimum distance and peak speed) for each day of place training.

The same two measures developed to characterize performance during the shift probe of Experiments 2 and 3 were adapted for the shift probe of the current study: signed heading direction and percent time spent searching the absolute side of the water maze.

Results

Place training. In general, rat water maze performance improved during the nine days of training with the hidden platform (see Figure 8). Mixed-design ANOVAs were used to evaluate differences between female and male rats observed during place training. The ANOVA conducted on latency to find the hidden platform revealed a significant effect of sex, $F(1, 10) = 15.633$, $p = .003$, $\eta_p^2 = .610$, and day, $F(8, 80) = 18.779$, $p < .001$, $\eta_p^2 = .653$; however, the Sex $\times$ Day interaction, $F(8, 80) = 0.479$, $p =$
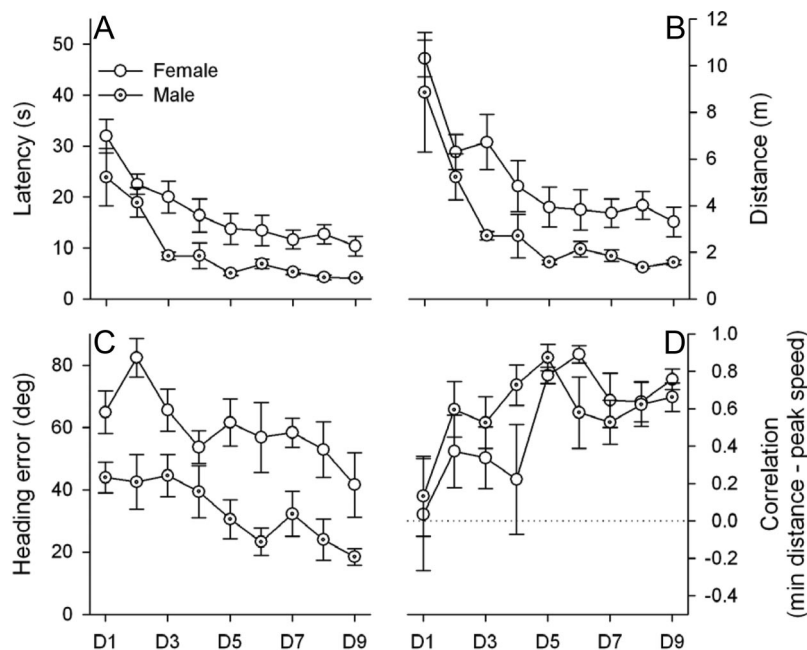

Figure 8. Female and male rats' average latency to reach the platform (A), distance traveled (B), heading error (C), and correlation between peak speed and minimum distance (D) is plotted for each day of place training.

.868, $\eta_p^2 = .046$, was not significant. Post hoc analysis conducted on the latency to find the platform revealed a significant linear trend, $F(1, 10) = 64.311$, $p < .001$, $\eta_p^2 = .865$, across days. The ANOVA conducted on distance traveled while searching for the hidden platform revealed a significant effect of sex, $F(1, 10) = 9.361$, $p = .012$, $\eta_p^2 = .484$, and day, $F(8, 80) = 15.882$, $p < .001$, $\eta_p^2 = .614$; however, the Sex × Day interaction, $F(8, 80) = 0.547$, $p = .818$, $\eta_p^2 = .052$, was not significant. The post hoc analysis conducted on distance traveled revealed a significant linear trend, $F(1, 10) = 41.067$, $p < .001$, $\eta_p^2 = .804$, across days. The ANOVA conducted on heading error revealed a significant effect of sex, $F(1, 10) = 16.047$, $p = .002$, $\eta_p^2 = .616$, and day, $F(8, 80) = 5.789$, $p < .001$, $\eta_p^2 = .365$; however, the Sex × Day interaction, $F(8, 80) = 0.887$, $p = .531$, $\eta_p^2 = .081$, was not significant. The post hoc analysis conducted on heading error revealed a significant linear trend, $F(1, 10) = 26.554$, $p < .001$, $\eta_p^2 = .726$, across days. Each of these measures demonstrated that performance improved across days; however, the performance of male rats was significantly better than the performance of female rats.

Female and male rats began to scale their moment-to-moment speeds to the minimum distance to reach the hidden platform as place training progressed (see panel D of Figure 8). The ANOVA conducted on correlations between peak speed and minimum distance revealed a significant effect of day, $F(8, 80) = 4.096$, $p < .001$, $\eta_p^2 = .291$; however, neither sex, $F(1, 10) = .469$, $p = .509$, $\eta_p^2 = .045$, nor the Sex × Day interaction, $F(8, 80) = 1.179$, $p = .322$, $\eta_p^2 = .105$, were found to be significant. The post hoc analysis conducted on correlations between peak speed and minimum distance revealed a significant linear trend, $F(1, 10) = 23.053$, $p = .001$, $\eta_p^2 = .697$, across days. These results were consistent with improved performance that did not significantly differ between males and females.

Shift probe. In general, rats displayed a bias to make a relative response that did not significantly differ between female and male rats (see Figure 9). The t tests conducted on initial heading, $t(10) = 1.431$, $p = .183$, $d = 1.044$, percent time spent on the left side of the water maze during the first half, $t(10) = -0.619$, $p = .550$, $d = .354$, and second half, $t(10) = 0.077$, $p = .940$, $d = .043$, of the shift probe failed to reveal significant differences between female and male rats. Failure to observe sex differences during the shift probe prompted collapsing across females and males for subsequent analyses. The single sample t test conducted on initial heading, $t(11) = 1.174$, $p = .265$, $d = .339$, failed to reveal a significant difference from zero; however, percent time spent on the left side of the water maze during the first half, $t(11) = -3.690$, $p = .004$, $d = 1.065$, and second half, $t(11) = -5.940$, $p < .001$, $d = 1.715$, of the shift probe were significantly different from 50%. Although the initial heading of rats was variable, both females and males spent significantly more time searching the right side (i.e., relative half) of the water maze.

Discussion

This experiment examined whether movement characteristics observed in human participants at the manipulatory scale are also observed in rats performing analogous spatial tasks. First, both species appear to use distance estimation to guide performance. During place training, rats developed a scaling of peak speeds that varied with the distance to the hidden platform. A similar move-
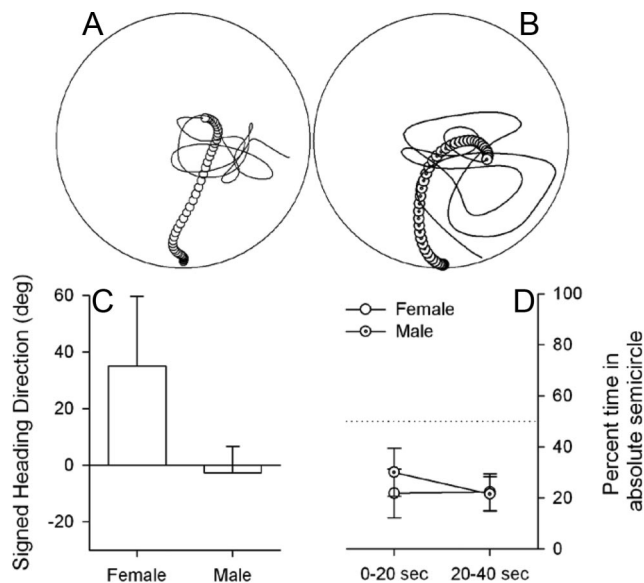

Figure 9. Searching paths are plotted for a representative female (A) and male (B) rat during the shift probe. The average signed heading direction for the initial trajectory is plotted for female and male rats (C). The average percent time spent searching the absolute semicircle is plotted for female and male rats during the first and second 20 s (D).

ment characteristic was observed in human participants during place training at the manipulatory scale (see Experiments 1, 2, and 3). Second, both species appear to use direction estimation to guide performance. During the shift probe, rats exhibited a tendency to search the relative half of the water maze. This observation is similar to previous work with rats in the water maze (Hamilton et al., 2007, 2008; Hamilton, Akers, et al., 2009), human participants in the virtual reality domain (Hamilton, Johnson, et al., 2009), and human participants at the manipulatory scale (see Experiments 2 and 3). These observations are consistent with the view that humans and rats use distance and direction components of a vector representation to guide performance during analogous spatial tasks.

One aspect of behavior that varied between humans and rats was presence of sex differences in performance. Although human performance did not vary as a function of the sex of the participant, male rats found the hidden platform faster, swam shorter distances, and had lower heading errors relative to female rats. Interestingly, not all aspects of behavior were similarly influenced by the sex of the rat. Female and male rats were equivalent in their development of peak speed scaling and response bias during the shift probe. In addition, both female and male rats exhibited a similar response bias during the shift probe. These observations are evidence that sex differences do not uniformly influence spatial orientation. The possible explanations for this dissociation of sex differences observed between humans and rats, as well as differential effects observed within rats, will be considered in the general discussion.

General Discussion

This series of experiments examined the kinematic and topographic characteristics of movement observed in humans and rats

as they performed analogous spatial tasks. The first experiment demonstrated that blindfolded human participants have the capacity to encode the position of the Velcro tape during place training and matching-to-place testing in a manipulatory scale version of the water maze. The second experiment investigated the nature of the representation mediating human performance in the bead maze at the manipulatory scale. Shifting the bead maze laterally revealed that blindfolded participants' searching was directed toward the absolute position (place response), whereas sighted participants' searching was directed toward the relative position (directional response). The tendency to make a directional response during the shift probe was observed after half as many trials in Experiment 3, thereby discounting the role of overtraining in determining the nature of the response observed. In each of these experiments, human participants demonstrated improved performance on standard water maze measures (latency, distance traveled, heading error) as well as a novel measure of distance estimation (scaling of peak speeds to the distance between the start position and the Velcro tape). The fourth experiment examined whether water maze performance differed between female and male rats during acquisition with a hidden platform and the shift probe. Sex differences were observed on standard measures of water maze performance; however, female and male rats exhibited similar rates of acquisition of movement scaling and a similar response bias (directional) during the shift probe. These observations provide evidence in support of the development of a translational model of spatial orientation that dissociates cues and the strategies used to guide movement.

Nature of the Representation

Spatial orientation can be derived from self-movement or environmental cues. Several representational systems have been advanced to describe the use of environmental cues to guide movement during a place response. The cognitive map view posits that animals encode a symbolic representation of relationships between environmental cues, and operations can be performed on this representation (Tolman, 1948; Gallistel, 1990). For example, rats exhibit instantaneous transfer by running down an alley directly leading to a goal when the trained route to the goal was blocked (Tolman, Ritchie, & Kalish, 1946). The cognitive map view was further supported by the discovery of place cells in the hippocampus (O'Keefe & Dostrovsky, 1971) and led to the development of the hippocampus as a cognitive map theory (O'Keefe & Nadel, 1978). In addition, observing that hippocampal lesions disrupted acquisition of a place response in the hidden platform version of the water maze task provided further evidence that the hippocampus mediates the encoding of relationships between environmental cues (Morris et al., 1982, 1986; Moser et al., 1998; Feigenbaum & Morris, 2004). Several observations from the first experiment are consistent with blindfolded participants possibly using a map-based representation to guide movement. First, performance improved despite participants starting from multiple points around the edge of the apparatus. Using multiple start locations resulted in varied response topography, thereby limiting use of a single movement sequence to locate the Velcro tape. Next, rapid improvement in performance was observed during matching-to-place testing. This one trial transfer is also consistent with the process of updating the goal location in a map-based representation. Although

these results are consistent with participants using a map-based representation to guide movement, alterative explanations have been advanced to account for performance observed in mazes.

One alterative explanation posits that animals encode the direction of the goal relative to environmental or apparatus cues (Blodgett et al., 1949). During most spatial tasks, place and directional responses result in the same movement sequence; however, shifting the apparatus in the room has been shown to dissociate these responses. Previous work has demonstrated that rats performing on a dry maze (Skinner et al., 2003) or in a water maze (Hamilton et al., 2007) display a strong bias for a direction response. Human participants also exhibit a strong directional response bias in a virtual reality analogue of water maze procedures (Hamilton, Johnson, et al., 2009). The results of the current study demonstrate that the bias of human participants to exhibit a directional response depends on access to environmental cues. Only participants who performed without a blindfold exhibited directional responding. Although the performance of blindfolded participants was consistent with a place response, restricting access to self-movement cues might have fostered encoding the direction of the Velcro tape relative to the body rather than the apparatus. A parallel encoding system has been advanced to explain the improved water maze performance observed when rats were tested under dark conditions, whereby rats encode the direction of the hidden platform relative to the start location (Moghaddam & Bures, 1996). In addition, changing the direction of the hidden platform under dark conditions has an effect limited to the first trial (see Figure 8 of Moghaddam & Bures, 1996). This is similar to the performance observed across the first and second trials of matching-to-place testing in the current study (see panels E and F of Figure 1). These results are consistent with humans and rats encoding the direction to the goal that is anchored to environmental cues; however, direction is not sufficient to explain all aspects of performance.

Human and rat movement kinematics were observed to systematically change across training trials in the current study. Early in training, neither species scaled their peak speed to the distance between the start and goal locations; however, movement scaling was observed in both species as training progressed. Similar movement scaling has been observed in other tasks independent of amount of training. For example, human participants have been shown to exhibit movement scaling subsequent to training on nonvisually guided reaching tasks (Bock & Eckmiller, 1986; Gordon et al., 1994). In addition, movement scaling has been observed in humans and rats on dead reckoning tasks that depend on trial unique processing of self-movement cues (Wallace et al., 2010). These observations are consistent with humans and rats using a vector representation (deriving direction and distance information from either online or mnemonic processes) to guide movement during spatial tasks.

Previous work has provided evidence that directional/distance vector-based navigation is highly conserved across many species. For example, hamsters trained to search for food in a consistent location relative to two fixed landmarks search a consistent direction and distance from each landmark when they are moved apart (Collett, Cartwright, & Smith, 1986). Similar performance has been observed on the expansion test in human children (MacDonald, Spetch, Kelly, & Cheng, 2004; Marsh, Spetch, & MacDonald, 2011), marmoset monkeys (MacDonald et al., 2004), orangutans

(Marsh et al., 2011), and pigeons (Spetch, Cheng, & MacDonald, 1996; Spetch, Cheng, MacDonald, & Linkenhoker, 1997). The performance of human adults represents an exception to this response topography. Specifically, human adults will search between the landmarks during the expansion test, rather than searching a consistent direction and distance from each landmark (Spetch et al., 1996, 1997). This response bias to search the middle has been attributed to human adults encoding a map-based representation of the relationships between the landmarks, rather than a directional/distance vector-based representation. Although this interpretation of performance does not generalize to the current set of studies with human adults, future work examining the effects of providing discrete landmarks or training with a cued Velcro tape in the bead maze may provide an opportunity to integrate both lines of research.

Sex Differences in Spatial Orientation

Sexually dimorphic performance on spatial tasks has been observed across multiple animal species (Jones, Braithwaite, & Healy, 2003). For example, male rats typically exhibit faster acquisition on the hidden platform version of the water maze relative to female rats (Roof, 1993; Isgor & Sengelaub, 1998; Blokland, Rutten, Prickaerts, 2006; however, see Bucci, Chiba, & Gallagher, 1995). A similar pattern of results has been observed in human participants while performing a virtual reality analogue of the hidden platform version of the water maze (Astur, Ortiz, & Sutherland, 1998; Astur, Tropp, Sava, Constable, & Markus, 2004; Newhouse, Newhouse, & Astur, 2007; Mueller, Jackson, & Skelton, 2008; however, see Sandstrom, Kaufman, & Huettel, 1998). Several mechanisms have been advanced to explain the different levels of performance observed between females and males. One view posits that sexually dimorphic performance reflects a differential preference for a specific navigational strategy. For example, when male and female participants are restricted to using geometric cues in a virtual reality version of the water maze, males were more accurate in locating the hidden platform compared with females (Sandstrom et al., 1998). In addition, providing instructions for ambulatory or manipulatory scale spatial tasks that emphasize geometric characteristics of the task has also been shown to facilitate the performance of males compared with females (Saucier et al., 2002). These results are consistent with male participants demonstrating a preference for using the geometric characteristics of the task or relationships between distal cues compared with female participants; however, as previously discussed, direction and place responses are confounded in those spatial tasks.

A recent study used the shift probe to investigate the nature of the representation mediating performance in these virtual reality spatial tasks (Hamilton, Johnson, et al., 2009). During the shift probe, both female and male participants made directional responses when the pool wall was visible and made place responses when the pool was invisible. The failure to observe sexually dimorphic performance despite observing directional and place responses parallels the results obtained in the current study. First, female and male participants did not differ on traditional measures of learning (i.e., latency to find the platform, distance, or heading error). Next, blindfolded participants exhibited a place response during the shift probe, whereas sighted participants exhibited a directional response during the shift probe. Taken together, both studies demonstrate that factors that influence the nature of the response do not interact with the sex of the participant; therefore, the view that males preferentially use geometric cues to guide performance on spatial tasks does not account for the results of either study. Defining the task factors that interact with sex of the participant will be critical in understanding the mechanisms that produce sexually dimorphic performance on spatial tasks.

Rats exhibited sexually dimorphic performance in the current study; however, these differences were restricted to the traditional measures of learning in the water maze. First, male rats took less time, swam shorter routes, and had smaller heading error during training with the hidden platform compared with female rats. Next, during acquisition, both female and male rats exhibited a similar increase in movement scaling. Specifically, as training progressed, peak speeds increased as the distance between the start location and goal location increased. Previous work has shown that humans and rats spontaneously exhibited movement scaling during dead reckoning tasks (Wallace et al., 2010). These observations are consistent with distance estimation being continuously updated by online processes or derived from a representation acquired across multiple trials. The results of the current study demonstrate that the latter process does not appear to interact with sex of the subject. Next, female and male rats did not differ in their response characteristics observed during the shift probe. Both sexes exhibited a response consistent with encoding the direction to the hidden platform rather than the absolute position. Although male heading error throughout acquisition was significantly lower than female heading error, direction estimation did not interact with sex during the shift probe. These results demonstrate that sex differences were restricted to general measures of performance in the water maze, whereas direction and distance estimations did not vary between female and male rats. This dissociation may reflect that aspects of movement organization vary between male and female rats, whereas direction and distance estimation are not sexually dimorphic processes. Sex differences in movement organization have been observed in food protection behavior (Field, Whishaw, Pellis, 1996) and have been shown to depend on organization effects of gonadal hormones (Field, Whishaw, Forgie, & Pellis, 2004). In addition, work has demonstrated that differences in body morphology between females and males are not mediating the sexually dimorphic movement organization (for a review, see Field & Pellis, 2008). Application of a similar analytic technique to the swimming behavior of rats in the water maze may provide further insight to the nature of the observed sex differences.

Translational Model of Spatial Orientation

The present study was conducted to further develop a model that can more accurately translate the neural basis of spatial orientation in rats to understanding human spatial orientation. The water maze remains an important tool in the investigation of the neurobiology of mnemonic processes; however, standard procedures and measures are not able to dissociate the cues or navigational strategies that are mediating performance. There continues to be a need to evaluate the novel therapeutic treatments for cognitive impairments associated with neurodegenerative disorders. A number of advances have been made in the behavioral assessments used to investigate the neurobiology of spatial orientation (for a review,

see Wallace, Martin, & Winter, 2008). For example, food-hoarding tasks have been shown to behaviorally dissociate environmental and self-movement cue processing in rats (Maaswinkel & Whishaw, 1999). Studies using the food-hoarding paradigm have demonstrated that disruption of hippocampal formation function spares use of environmental cues, whereas use of self-movement cues is impaired (Whishaw & Maaswinkel, 1998; Maaswinkel, Jarrard, & Whishaw, 1999; Martin & Wallace, 2007). Subsequent work has provided evidence that the contribution of the hippocampal formation to self-movement cue processing is conserved in humans (Worsley et al., 2001; Philbeck et al., 2004; Wolbers et al., 2007); however, a set of behavioral tasks that can dissociate use of environmental and self-movement cues has yet to be developed for humans.

Several aspects of movement at the manipulatory scale make it an attractive domain for developing a translational model of spatial orientation. First, spatial orientation can be examined with minimal risk to the participant. The probability of falling and sustaining an injury increases with age; therefore, it is untenable to investigate the effects of aging or neurodegenerative disorders on ambulatory scale spatial orientation. Next, humans and rats appear to apply similar navigation strategies to environmental cues. For example, in the current study, when humans and rats were provided access to environmental and self-movement cues, both species exhibited a directional response during the shift probe, consistent with using a directional/distance vector to guide performance. Finally, humans and rats exhibit a similar capacity to use self-movement cues to guide performance. Both species have been shown to continuously process self-movement cues to plot a direct path to the point at which movement was initiated (i.e., dead reckoning; Wallace et al., 2010). In addition, the present study demonstrates that humans, like rats (Moghaddam & Bures, 1996), can use self-movement cues to encode the position of a goal. These observations demonstrate that manipulatory scale spatial tasks provide a robust behavioral tool to investigate human spatial orientation.

Additional work is needed to further develop this translational model of spatial orientation. First, rats trained with a water maze that shifts position in the room each trial exhibit a tendency to make a place response during the shift probe (Hamilton et al., 2008). It remains to be determined whether similar results would be obtained in humans at the manipulatory scale and the extent to which sexually dimorphic performance might be observed during acquisition. Next, the addition of proximal cues has been shown to dissociate responding in water maze procedures. For example, hippocampal lesions disrupt water maze performance with a hidden platform, whereas performance with a cued platform is spared (Morris et al., 1982; Pearce, Roberts, & Good, 1998). In addition, proximal cues have also been shown to developmentally dissociate water maze performance in humans (Overman, Pate, Moore, & Peuster, 1996) and rats (Akers & Hamilton, 2007). Varying the stability or quality of manipulatory environmental cues may provide additional evidence that navigational strategies are conserved across different species and scales of movement.

Conclusion

The current set of studies demonstrated that humans and rats use the same navigational strategies to guide movement. Specifically,

as training progresses, both species begin to scale movement kinematics to the distance between the start and goal locations, consistent with using distance estimation to guide movement. In addition, both species search for the hidden platform/Velcro in the relative position during the shift probe, consistent with using direction estimation to guide movement. These observations provide additional evidence that humans and rats use a directional/distance vector representation, rather than a cognitive map representation, to guide performance in water maze tasks.

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