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Navigating With Fingers and Feet: Analysis of Human (*Homo sapiens*) and Rat (*Rattus norvegicus*) Movement Organization During Nonvisual Spatial Tasks

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The current set of studies examines the contribution of movement segmentation to self-movement cue processing for estimating direction and distance to a start location in humans and rats. Experiments 1 and 2 examined the extent that ambulatory dead reckoning tasks can be adapted to the manipulatory scale in humans. Experiments 3 and 4 investigated the performance of rats in similar tasks at their ambulatory scale. Movement segmentation had differential effects on absolute heading error for humans and rats when only comparing performance on specific tasks; however, movement segmentation had similar effects for both species when performance was examined across all tasks. In general, magnitude of movement segmentation was associated with absolute heading error in both humans and rats. In contrast, both species modified homeward segment kinematics based on the distance to the start location in all tasks, consistent with the use of self-movement cues to estimate distance. The current study provides evidence for a role of movement segmentation in processing self-movement cues selective to direction estimation and develops a foundation for future studies investigating the neurobiology of spatial orientation.

Keywords: dead reckoning, path integration, translational neuroscience, two thirds power law, spatial orientation, wayfinding

Spatial orientation is essential for the survival of an animal. Considering the dynamic nature of environments, an animal is more likely to avoid predation and locate resources in the environment if it can use multiple sources of information to maintain spatial orientation. Information used to maintain spatial orientation can be classified based on how it originates. One source of information involves stimuli present in the environment (e.g., visual, auditory, olfactory). Animals can learn to use a single landmark or the relationships between multiple landmarks as stimuli to guide movement through an environment (Tolman, Ritchie, & Kalish, 1946; Blodgett, McCutchan, & Mathews, 1949; O'Keefe & Nadel, 1978; Gallistel, 1990). Using landmarks to guide movement depends on previous experience in the environment and may become less accurate if access to familiar landmarks is limited. Under situations in which environmental information is novel or not accessible, animals can use another source of information to guide movement. Self-movement cues, or the information generated as the animal moves through the environment (e.g., vestibular, proprioception, optic flow), can also be used to maintain spatial orientation. An animal uses self-movement cues to update an

online representation of its current direction and distance traveled. In addition, these representations can be used to plot a path to the point where movement originated, a navigational strategy referred to as path integration or dead reckoning (Darwin, 1873; Murphy, 1873; Barlow, 1964; Gallistel, 1990). Spatial orientation depends on the ability of the animal to process both environmental and self-movement sources of information.

Disruption in spatial orientation is commonly observed in acute and chronic neurological disorders. For example, during the progression of dementia of the Alzheimer's Type (DAT), 60% of patients will become lost in familiar environments such as their home or neighborhood resulting in wandering behavior (Rabins, Mace, & Lucas, 1982). As of yet, it is not known whether wandering behavior reflects a general deficit in spatial orientation or a deficit selective to processing either environmental or self-movement cues. Considering the physical limitation associated with neurological disorders, advances in understanding the nature of the deficit mediating wandering behavior will depend on the development of tasks at the manipulatory scale and on translational models of spatial orientation.

Early work developing a translational model of spatial orientation supported a role for the hippocampus in encoding a symbolic representation of the relationships between environmental cues (O'Keefe & Dostrovksy, 1971; O'Keefe & Nadel, 1978; Muller & Kubie, 1987; Morris, Garrud, Rawlins, & O'Keefe, 1982). More recent work has challenged this view, supporting a role for the hippocampus in processing self-movement cues. First, self-movement cues have been shown to contribute to the firing characteristics of place cells (Quirk, Muller, & Kubie, 1990; Knierim, Kudrimoti, & McNaughton, 1998). Next, hippocampal lesions

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have been shown to spare rats' use of environmental cues in dry land mazes (Gaffan, Bannerman, & Healey, 2000; Gaffan, Bannerman, & Healey, 2003) and with modified training protocols in the water maze (Whishaw & Jarrard, 1996). Finally, hippocampal lesions have been shown to selectively impair self-movement cue processing in a food hoarding task (Maaswinkel, Jarrard, & Whishaw, 1999). These observations have clear parallels in the human literature. For example, accuracy in estimating direction to a start location in a virtual reality version of the triangle completion task was associated with stronger activation of the right hippocampus (Wolbers, Wiener, Mallot, & Buchel, 2007). In addition, damage to the medial temporal lobe has been shown to impair performance on ambulatory triangle completion tasks when participants were restricted to using self-movement cues (Worsley et al., 2001; Philbeck, Behrmann, Levy, Potolicchio, & Capoty, 2004; however, see Shrager, Kirwan, & Squire, 2008). Further, in one of the few lines of research investigating spatial orientation in DAT, patients showed impaired use of radial optic flow to determine direction of movement (Tetewsky & Duffy, 1999). It remains to be determined whether this impairment is selective to radial optic flow or if it reflects a more general impairment in dead reckoning based navigation. Use of self-movement cues to maintain spatial orientation and the role of the hippocampus in processing self-movement cues appear to be highly conserved across both species providing a foundation for understanding spatial disorientation.

Dead reckoning is a system of parallel processes operating on self-movement cues resulting in an estimate of the direction and distance to the point where movement was initiated (see Wallace, Martin, & Winter, 2008, for review). The ability to estimate direction based only on self-movement cues has been observed in ants (Muller & Wehner, 1988), gerbils (Mittelstaedt & Mittelstaedt, 1980), rats (Maaswinkel & Whishaw, 1999), dogs (Seguinot, Cattet, & Benhamou, 1998), and humans [at ambulatory (Loomis et al., 1993) and manipulatory scales (Klatzky, 1999)]. For example, dead reckoning has been suggested to mediate the organization of rat exploratory behavior (Wallace, Hines, & Whishaw, 2002). While exploring a novel environment, rats have been observed to segment their movement into periods of fast linear speed along paths with low curvature and periods of slow linear speed along paths with high curvature (Wallace, Hamilton, & Whishaw, 2006). Movement segmentation has been suggested to facilitate processing of self-movement cues by increasing the gain associated with detecting changes in heading. Support for this claim was found in a recent study showing that weaker movement segmentation was associated with disruptions in spatial orientation (Wallace, Choudhry, & Martin, 2006). The current set of studies examines whether movement segmentation has a similar relationship to direction estimation on tasks at the manipulatory scale in humans and the ambulatory scale in rats.

In addition to estimating direction, there is evidence that animals use self-movement cues to estimate distance. This ability has been observed in invertebrates (see Collett & Collett, 2000, for a review) and vertebrates (Séguinot, Maurer, & Etienne, 1993; Gothard, Skaggs, & McNaughton, 1996; Séguinot et al., 1998; Mittelstaedt & Mittelstaedt, 2001; Terrazas et al., 2005). Distance estimation may reflect an online representation of recently experienced self-movement cues. For example, after exploration of a novel environment, rats will scale the moment-to-moment speeds of their homeward trajectory such that the peak in speed occurs at

the midpoint of the path (Wallace, Hamilton, et al., 2006). This scaling of moment-to-moment speeds is observed independent of the distance of the path. Similar movement characteristics have been observed in human nonvisually guided reaching tasks (Bock & Eckmiller, 1986; Gordon, Ghilardi, Cooper, & Ghez, 1994); however, this performance depends on encoding the distance between the start and the goal. As participants become familiar with reaching for a specific distance, a consistent temporal pacing of moment-to-moment linear speeds is observed with the peak speed occurring at the middle of the path. Manipulating movement distance results in participants rescaling their movement kinematics such that the peak speed occurs at the midpoint of the new path length. The current set of studies examines whether online processing of self-movement cues would be sufficient for distance estimation in humans and rats.

The first experiment investigated the ability of blindfolded human participants to accurately estimate direction and distance to a start location after searching for a piece of Velcro tape on the surface of a table. Groups varied in the distance between the Velcro tape and the start location. The second experiment restricted the blindfolded human participants' searching behavior by requiring them to follow strings attached to the surface of the table. Groups varied in the angle subtended by the two strings. Both of these tasks were conducted at the human manipulatory scale; therefore, estimating direction and distance to the start location depended on self-movement information (i.e., proprioceptive cues) generated as the result of limb movement.

The third and fourth experiments modified the rat food hoarding paradigm to parallel the demands of the human tasks. Under completely dark conditions, rats searched a large table for food pellets to carry back to the refuge for consumption. The distance between the food pellet and the refuge varied across trials. Also, under completely dark conditions, rats were trained to follow scented strings to locate food pellets. The angle subtended by the two scented strings varied across trials. Both of these tasks were conducted at the rat ambulatory scale; therefore, estimating direction and distance to the start location depended on self-movement information (i.e., vestibular and proprioceptive cues) generated as the result of full body movement. Characterizing the similarities and differences in performance of both species on these dead reckoning tasks represents a critical step in developing a translational model of spatial orientation.

Experiment 1

This experiment examined the ability of human participants to use self-movement cues generated while searching the surface of a table to estimate direction and distance to the point where movement originated on that trial. The distance between the start point and the Velcro tape was varied across the three groups (short, medium, and long).

Methods

Participants. Northern Illinois University undergraduate students were recruited from psychology courses and provided supplemental course credit for their involvement. Male ($n = 15$) and female ($n = 15$) participants were an average age of 22.8 years old, with the youngest being 20 and the oldest being 34 years old.

Based on self report, 28 of the participants were right-handed, and two were left-handed. Participants were instructed to use their preferred hand throughout testing. All of the procedures in this study were approved by the local Institutional Review Board, which follows the standards set by the United States Office for Human Research Protections guidelines.

Apparatus. Participants were seated in an adjustable chair with their forearms resting comfortably on the surface of a rectangular table ($0.61\text{ m} \times 0.91\text{ m}$). A bullet camera attached to a DVD recorder was positioned above the participant such that the entire surface of the table was within view of the camera. A small piece of hook type Velcro tape ($2.5\text{ cm} \times 2.5\text{ cm}$) was attached to the surface of the table. Location of the Velcro tape varied across trials with distance from the start position varying among groups. Darkened swimming goggles and a scarf tied around the head was used to blindfold participants.

Procedures. Participants were randomly assigned to one of three groups based on the distance experienced between the start location and Velcro tape: Short (0.18 m), Medium (0.42 m), and Long (0.57 m). Upon entering the lab, participants were seated at the testing table, basic demographic characteristics (sex, age, and handedness) were collected, and a practice searching trial was given. After the participant was blindfolded the Velcro tape was attached to the table and the participant's finger was placed at one of the three start locations (see Figure 1). Participants were instructed to search for the Velcro tape without lifting their finger from the surface of the table. After locating the Velcro tape, participants were instructed to return to the starting location. Participants were asked to place their hand at their side while the table was set for the next trial. Participants started from each of the three locations twice. The goal was offset in a different direction each trial. Therefore each participant experienced six start-goal configurations. After completion of the six trials, participants

removed the blindfold and were debriefed about the purpose of the experiment.

Data analysis. Videos of participants' behavior were converted to digital computer files using the Peak Performance system (Peak Performance Technologies). Participant movements were tracked by selecting one pixel every other frame that corresponded to the tip of the participant's index finger. The participants' x- and y-coordinates were scaled to real world units and used to calculate moment-to-moment speeds.

Each trial was divided into outward and homeward segments. The outward segment was defined as the path the finger followed until locating the Velcro tape. Two measures were used to characterize the organization of the outward segment: time elapsed and movement segmentation. Time elapsed was calculated from the participants' scaled x- and y-coordinates. Movement segmentation depends on calculating the correlation between moment-to-moment linear speeds and path curvature observed on the outward segment. Path curvature was obtained by calculating the angle subtended by the first three points and dividing that value by the corresponding temporal interval. This calculation was repeated on the last two points from the previous calculation and the point that immediately followed the original three points. Calculations continued until path curvatures were computed for the entire outward segment. Then path curvatures were interpolated using the Loess local smoothing technique (Cleveland, 1979; Cleveland & Devlin, 1988). Previous work has shown that disruptions in movement segmentation occurred during periods of high path curvature (Wallace, Choudhry et al., 2006). Therefore, the correlation between moment-to-moment linear speeds and path curvatures were calculated only during times of high path curvature (i.e., path curvatures that exceeded the 25th percentile for the corresponding outward segment).

The homeward segment was defined as the path of the finger followed after the participant was instructed to return to the start location. Two measures were used to characterize the accuracy of the homeward segment. The absolute heading error reflected the angle subtended by the start location, location of the Velcro tape, and the midpoint of the homeward segment. The peak speed or maximum moment-to-moment speed was recorded from each homeward segment.

Results

Topographic and kinematic characteristics of a single trial are plotted for representative participants in the Short (left panels of Figure 1), Medium (middle panels of Figure 1), and Long (right panels of Figure 1) groups. In general, outward segments were circuitous paths with varied moment-to-moment speeds; whereas, homeward segments were noncircuitous paths with a single peak in speed. Mixed-design ANOVAs were used to evaluate differences in outward and homeward segment characteristics. It was noted earlier that groups differed in the distance to the start location after locating the Velcro tape. The observation that participants varied in the complexity of the outward segment prior to finding the Velcro tape prompted an analysis of outward segment path circuitry on performance. Path circuitry was calculated by dividing outward segment travel distance by the distance between the start and end of the path. As the ratio approached zero, the outward segment became more circuitous. Each participant's six

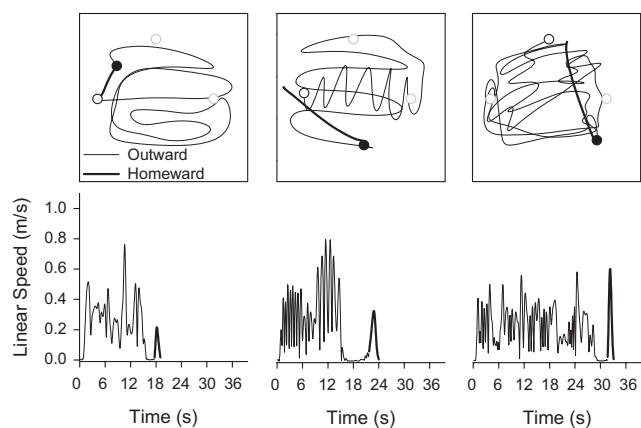


Figure 1. Topographic (top panels) and kinematic (bottom panels) profiles of a representative searching trial are provided for participants in the Short (left panels), Medium (middle panels), and Long (right panels) groups. A single trial involves the participant starting from one (black circles) of three positions (other two starting positions are indicated by gray circles), searching for the Velcro tape (black circle), and returning to the start location. The location of the start and Velcro tape varies across trials. Each trial has been divided into an outward (thin line) and homeward (heavy line) segments.

trials were sorted based on outward segment path circuitry: the two trials with highest circuitry were classified as high circuitry (M : 0.04), the next two trials were classified as medium circuitry (M : 0.09), and the last two trials were classified as low circuitry (M : 0.32). The data were analyzed with one between subject factor (i.e., Short, Medium, and Long distance to the start location) and one within subject factor (i.e., high, medium, low outward segment path circuitry).

Outward segment characteristics. The ANOVA conducted on time elapsed (see Table 1) revealed a significant main effect of path circuitry [$F(2, 54) = 34.808, p = .000, \eta_p^2 = .563$]; however, neither the main effect of group [$F(2, 27) = 3.276, p = .053, \eta_p^2 = .195$] nor the Group by Path Circuitry interaction [$F(4, 54) = 1.134, p = .350, \eta_p^2 = .078$] was found to be significant. Post hoc analysis conducted across the three levels of path circuitry revealed a significant linear trend in time elapsed [$F(1, 27) = 39.191, p = .000$]. These results demonstrate that increases in outward segment path circuitry were associated with participants spending more time searching for the piece of Velcro tape.

The ANOVA conducted on movement segmentation (see Table 1) failed to reveal a significant main effect of path circuitry [$F(2, 54) = 3.009, p = .058, \eta_p^2 = .100$], group [$F(2, 27) = 1.571, p = .226, \eta_p^2 = .104$], or Path Circuitry by Group interaction [$F(4, 54) = 1.621, p = .226, \eta_p^2 = .107$]. These effects demonstrate neither path circuitry nor distance from the start location influenced movement segmentation.

Homeward segment characteristics. The ANOVA conducted on absolute heading error revealed a significant main effect of path circuitry [$F(2, 54) = 3.633, p = .033, \eta_p^2 = .119$]; however, neither the main effect of group [$F(2, 27) = 0.550, p = .583, \eta_p^2 = .039$] nor Path Circuitry by Group interaction [$F(4, 54) = 1.649, p = .175, \eta_p^2 = .109$] were found to be significant. Post hoc tests conducted across the three levels of path circuitry revealed a significant linear trend in absolute heading error [$F(1, 27) = 4.942, p = .035$]. These results demonstrated that increases in outward segment path circuitry were associated with increases in absolute heading error of the homeward segment.

The ANOVA conducted on peak speed revealed a significant main effect of group [$F(2, 27) = 20.899, p = .000, \eta_p^2 = .608$]; however, neither the main effect of path circuitry [$F(2, 54) = 1.715, p = .190, \eta_p^2 = .060$] nor Path Circuitry by Group interaction [$F(4, 54) = 1.759, p = .151, \eta_p^2 = .115$] were found to be significant. Although post hoc analyses conducted across the three groups revealed that peak speed of the short group was significantly slower relative to the medium and long groups, the medium and long groups did not differ from each other. These results demonstrated that increasing the distance to the start location significantly increased the peak speed observed on the homeward segment.

Discussion

This experiment examined humans' ability to use self-movement cues to dead reckon at the manipulatory scale. Increases in outward segment circuitry were associated with increases in absolute heading error. There are at least two possible explanations for this observation. First, direction estimation may depend on an online representation of direction that is updated by self-movement cues generated from limb movements. Small errors in updating this representation will have a cumulative effect that grows with increases in outward segment path circuitry. Second, at the beginning of each trial, participants may encode the position of the start location in manipulatory space. Increases in outward segment path circuitry were associated with increases in time elapsed. Therefore, it is possible that disruptions in direction estimation may reflect limitations in mnemonic processing. For example, memory for the direction to the start location may decay with time or become increasingly susceptible to interference. Path circuitry of the outward segment was observed to be independent of the participants' ability to modify peak speed on the homeward segment. These results are consistent with explanations associated with either errors in self-movement cue processing or limitations in mnemonic processing having effects selective to direction estimation.

Another characteristic that influenced performance on the homeward segment was the distance between the Velcro tape and the start location. Groups with longer distances between the Velcro tape and start location had faster peak speeds on the homeward segment. These results parallel studies showing that increases in movement distance was associated with increases in movement speed during nonvisually guided reaching in humans (Bock & Eckmiller, 1986; Gordon et al., 1994). These observations have been interpreted as participants using force, rather than position, to represent movement distance. Therefore, it is possible that participants were using self-movement cues to determine the force required to return to the start location. Observing that distance to the start location did not influence homeward segment absolute heading error provides further evidence that direction and distance estimation are mediated by separate parallel systems.

The current experiment did not show that variations in movement segmentation were associated with the magnitude of absolute heading error. There are several possible explanations for the failure to observe a relationship between heading error and movement segmentation in the current experiment. First, it is possible that the temporal intervals required to locate the Velcro tape were not sufficient to induce disorientation. On average, the most circuitous trials only took approximately 45 seconds before the

Table 1
Humans Searching Task Outward Segment Characteristics

Group	Time		Movement segmentation	
	M	95% CI	M	95% CI
Circuitry				
Short				
High	22.46	[4.16, 40.76]	-0.50	[-0.58, -0.44]
Medium	8.72	[2.48, 14.97]	-0.51	[-0.58, -0.44]
Low	3.85	[-0.02, 7.72]	-0.41	[-0.48, -0.34]
Medium				
High	44.31	[26.01, 62.61]	-0.42	[-0.50, -0.35]
Medium	18.36	[12.12, 24.60]	-0.47	[-0.54, -0.40]
Low	9.80	[5.93, 13.67]	-0.46	[-0.53, -0.39]
Long				
High	45.31	[27.01, 63.61]	-0.52	[-0.59, -0.44]
Medium	19.63	[13.39, 25.87]	-0.54	[-0.61, -0.47]
Low	11.49	[7.62, 15.36]	-0.49	[-0.56, -0.42]

Note. Values represent the mean for each variable collapsed across each participant's set of searching trips; 95% confidence intervals are indicated parenthetically.

Velcro tape was located. In contrast, disruptions in movement segmentation at the ambulatory scale were only observed after participants had searched for 60 seconds (Wallace, Choudhry et al., 2006). Next, it is possible that movement segmentation is only critical for navigation that involves activation of the vestibular system. In the current experiment, participants remained seated and were restricted to using proprioceptive self-movement cues. Therefore, movement segmentation may not significantly contribute to self-movement cue processing at the manipulatory scale. Finally, movement segmentation was not systematically manipulated in the current study. Sorting trials based on the path circuitry of the outward segment may not have been sufficient to detect a relationship between movement segmentation and direction estimation. Using a task in which movement segmentation can be manipulated independent of other factors may provide further insight to its contribution to dead reckoning.

The results of the current experiment are consistent with participants using self-movement cues to estimate direction and distance to the start location. To further evaluate this claim, Experiment 2 was designed to equate groups for mnemonic processing demands while systematically varying the magnitude of movement segmentation. The outward segment involved participants following strings of equal length; however, groups experienced paths with differing moment-to-moment path curvatures. Observing that performance on the homeward segment varies as a function of path curvature will provide further evidence that dead reckoning tasks can be adapted to the manipulatory scale.

Experiment 2

This experiment examined the ability of human participants to estimate direction and distance to the start point after following two legs of a triangular path. The angle experienced between the two legs was manipulated across the three groups (acute, right, and obtuse).

Methods

Participants. Undergraduate students at Northern Illinois University were recruited from psychology courses and provided supplemental course credit for their involvement. Male ($n = 6$) and female ($n = 24$) participants were an average age of 22.2 years old, with the youngest participant being 20 and the oldest being 46 years old. Based on self report, 28 of the participants were right-handed and 2 were left-handed. Participants were instructed to use their preferred hand throughout testing. All of the experimental procedures in this study were approved by the local Institutional Review Board, which follows the standards set by the United States Office for Human Research Protections guidelines.

Apparatus. The apparatus was identical to that used in Experiment 1, except participants followed strings (100% cotton butcher twine approximately 1 mm in diameter). Two strings of equal length (25 cm) were used to form the two legs of the triangle. An overhand knot was tied in one end of the first string and served as the starting position. The end of the first string and the end of the second string was inserted through a small hole (2 mm) at the center of the table. An overhand knot was tied at the other end of the second string and served as the goal. The angle subtended by the knot of the first string, the small hole at the center of the table,

and the knot of the second string varied across groups. As with Experiment 1, participants were blindfolded with darkened swimming goggles and a scarf tied around their heads.

Procedures. Participants were randomly assigned to one of three groups based on the angle subtended by the two strings: Acute (35°), Right (90°), and Obtuse (145°). Upon entering the lab, participants were seated at the testing table, basic demographic characteristics (sex, age, and handedness) were collected, and a practice trial was given. Participants were not blindfolded during the practice trial and were required to follow strings, find the second knot, and return to the start location. If the participant began to follow the string back to the start, the participant was stopped and instructed to return directly to the start location. Next, participants were blindfolded, instructed to follow the string, and upon finding the knot in the end, they were told to await further instructions. After locating the final knot, participants were instructed to return to the start location. Then participants were asked to place their hand at their side while the table was set for the next trial. Similar to Experiment 1, participants were started from three locations with the goals located in one of two positions. Each participant experienced all six start and goal location configurations once. After completion of the six trials, participants removed the blindfold and were debriefed about the purpose of the experiment.

Data analysis. Conversion of the video and the process of tracking participants' movements were the same as described in Experiment 1; however, participant movements were tracked by selecting one pixel every third frame that corresponded to the tip of the participant's index finger. The participants' x- and y-coordinates were scaled to real world units and used to calculate moment-to-moment speeds. Each trial was divided into outward and homeward segments. The outward segment was defined as all of the movements that displaced the participant from the start location until locating the final knot in the string. Two measures were used to characterize the organization of the outward segment: time elapsed and movement segmentation. The homeward segment was defined as all of the movement occurring after the participant was instructed to return to the start location. Two measures were used to characterize the accuracy of the homeward segment: absolute heading error and peak speed.

Results

Topographic and kinematic characteristics of a single trial are plotted for representative participants in the Acute (see left panels of Figure 2), Right (see middle panels of Figure 2), and Obtuse (see right panels of Figure 2) groups. In general, participants accurately followed the string until locating the knot. Accuracy of the homeward segment varied as a function of the angle followed on the outward segment.

Outward segment characteristics. The ANOVAs conducted on outward segment characteristics (see Table 2) failed to reveal a significant main effect of group for time elapsed [$F(2, 27) = 0.326, p = .724, \eta_p^2 = .024$]. In contrast, a significant main effect of group was observed for movement segmentation [$F(2, 27) = 3.682, p = .039, \eta_p^2 = .214$]. Post hoc analyses conducted on movement segmentation revealed a significant linear trend across groups [$F(1, 27) = 7.210, p = .012$]. Although groups did not differ in time elapsed; the extent that participants segmented their

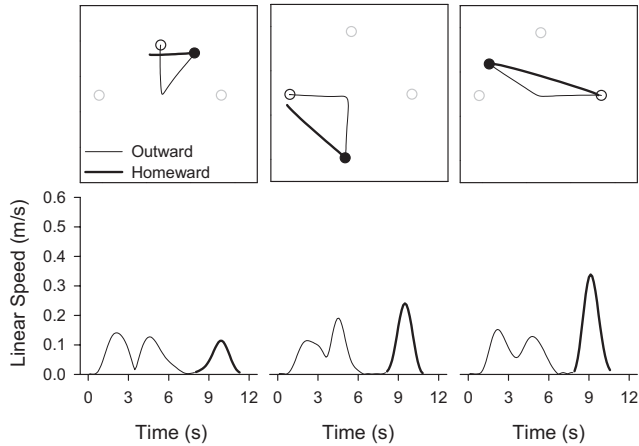


Figure 2. Topographic characteristics (top panels) are plotted for a representative string following trial from participants in the Acute (left panels), Right (middle panels), and Obtuse (right panels) groups. A single trial involves the participant starting from one (black circles) of three positions (other two starting positions are indicated by gray circles), the string to the second knot (black circle), and returning to the start location. The kinematic characteristics (bottom panels) associated with each representative trial are also provided. Each trial has been divided into an outward (thin line) and homeward (heavy line) segments.

movements varied as a function of the angle that subtended the two legs of the triangle.

Homeward segment characteristics. Several measures were used to characterize the accuracy of the homeward segment. The ANOVA conducted on heading error revealed a significant main effect of group [$F(2, 27) = 13.651, p = .000, \eta_p^2 = .503$]. Post hoc analyses conducted on absolute heading error revealed a significant linear trend across groups [$F(1, 27) = 26.250, p = .000$]. Next, the ANOVA conducted on the peak speed revealed a significant main effect of group [$F(2, 27) = 17.694, p = .000, \eta_p^2 = .567$]. Post hoc analyses conducted on peak speed revealed a significant linear trend across groups [$F(1, 27) = 34.514, p = .000$]. These effects demonstrated that the angle experienced on the outward segment significantly influenced performance on the homeward segment.

Discussion

This experiment examined human participants' use of self-movement cues while following strings attached to the surface of the table. Groups differed in the angle connecting the two strings resulting in differences in path curvature experienced on the outward segment. Therefore, strength of movement segmentation increased with larger angles. Although time elapsed associated with the outward segment did not vary across groups, distance to the start location increased with larger angles. These characteristics in outward segment organization were associated with differences in performance observed on the homeward segment.

The absolute heading error was one aspect of performance on the homeward segment that varied as a function of the angle experienced on the outward segment. Decreasing the angle experienced on the outward segment was associated with an increase in the absolute heading error observed on the homeward segment. A

mnemonic account was advanced as a possible explanation for the differences in absolute heading error observed in Experiment 1. In the current study, searching paths were equivalent in time elapsed, equating groups for mnemonic demands. A strict mnemonic account fails to explain the group differences in absolute heading error observed in the current study. In addition, the average time elapsed on the outward segment was shorter than most of the values observed for the searching segments of Experiment 1. Providing further evidence that the lack of movement segmentation observed in Experiment 1 cannot be accounted for by mnemonic processes or a failure to produce disorientation. Observing that movement segmentation varied with absolute heading error on the homeward segment is consistent with its role in accurate processing of self-movement cues. These results demonstrate that manipulation of path curvature may be critical to observe the influence of movement segmentation on direction estimation at the manipulatory scale.

Peak speed was the other aspect of performance on the homeward segment that varied with the angle experienced on the outward segment. Increases in angle experienced on the outward segment produced longer distances to the start location. Participants' peak speeds on the homeward segment increased with longer distances to the start location. These observations parallel the results of Experiment 1 and provide further evidence that participants were using self-movement cues to determine distance to the start location. Additional studies are needed to determine whether an estimate of distance to the start location was represented as the force required to return to the start location.

Humans appear to use self-movement cues generated at the manipulatory scale to estimate direction to a start location. Magnitude of movement segmentation appears to influence self-movement cue processing related to direction estimation; however, the generality of its role remains to be determined. Previous work has shown that rats exhibit a similar quality of movement segmentation during voluntary movement in an open field. As of yet, no studies have shown an association between the magnitude of movement segmentation and performance on dead reckoning tasks. In addition to direction estimation, humans use self-movement cues to estimate distance to a start location. Relatively little work has investigated the kinematics of movement related to distance estimation in rats. Observing that rats modulate their moment-to-moment speeds in relation to the distance to get back to the start location would provide a novel technique to investigate distance estimation. The following rat experiments adapted the procedures used in the previous human experiments to further develop a translational model of spatial orientation.

Table 2
Human Triangle Task Outward Segment Characteristics

Triangle	Time		Movement segmentation	
	<i>M</i>	95% CI	<i>M</i>	95% CI
Acute	10.65	[9.01, 12.29]	-0.54	[-0.58, -0.51]
Right	10.41	[8.76, 12.05]	-0.56	[-0.60, -0.53]
Obtuse	11.29	[9.65, 12.93]	-0.61	[-0.64, -0.57]

Note. Values represent the mean for each variable collapsed across each participant's set of triangle completion trips; 95% confidence intervals are indicated parenthetically.

Experiment 3

This experiment examined direction and distance estimation in rats when restricted to using self-movement cues. The natural tendency of rats to carry food to a refuge was used to examine the contribution of movement segmentation to estimating direction and the extent that moment-to-moment speeds are scaled to the distance experienced between the refuge and the food pellet.

Methods

Subjects. Seven naïve female Long-Evans rats (*Rattus norvegicus*) pair housed in plastic cages served as subjects for the current study. The colony room was maintained at approximately 20–21 °C and on a 12-hr light–dark cycle. Before training began, rats were fed supplemental rat chow (5L42 Rodent Breeder Diet food pellets; PMI Nutrition International, Brentwood, MO) to maintain them at 80% of their free-feeding weight. In addition to daily feeding, rats were given a 1 g banana pellet each day to habituate the rats to the food item used in the experiment. The local Institutional Animal Care and Use Committee, which follows the guidelines set forth by the Office of Laboratory Animal Welfare, approved all procedures used in this experiment.

Apparatus. The apparatus was a wooden circular table (2.13 m in diameter) without walls that was painted white. The surface of the table was approximately 83 cm above the floor. This table was located in a square room that was prepared so that light could not penetrate when testing under dark conditions. To observe the rat's behavior under dark conditions, experimenters wore night-vision goggles, a night-vision camera was attached to the ceiling of the testing room, and infrared emitters were positioned along the walls. Previous work has demonstrated that rats are not able to detect infrared wavelengths (Neitz & Jacobs, 1986). The night-vision camera was connected to a DVD recorder located in an adjacent room providing a permanent record of the rat's behavior for subsequent analysis. The refuge was a Plexiglas box (17 cm × 26 cm × 12 cm) with a ramp leading up to an edge of the open top. A wooden support held the refuge just below the surface of the table such that the rat could exit the refuge and explore the surface of the table.

Procedure. A cage with opaque sides, bottom, and a wire mesh top was used to transport rats from the colony to the testing room. During transportation, lights were turned off, the cage was rotated, and the experimenter walked a circuitous path that varied across days. This limited the rats' ability to learn the location of the testing room relative to the colony. During each session, a rat was placed in the refuge and given 30 minutes access to the surface of the table. The first eight sessions were conducted under normal light conditions. Rats were trained to leave the refuge and search the table for randomly placed food pellets. The following three sessions were conducted under complete dark conditions with food pellets placed varying distances from the refuge. After the rat located the first food pellet and carried it to the refuge, a second food pellet was placed on the table. This continued until the rat had retrieved five food pellets. At the conclusion of a session, the rat was removed from the refuge, returned to the colony, and the table was rotated and cleaned with Windex.

Data analysis. The Peak Performance System was used to convert video of rats' behavior to digital computer files. Rat

movements were tracked by selecting one pixel every third frame that corresponded to the middle line of the body at the level of the forelimbs. The rats' x- and y-coordinates were scaled to real world units and used to calculate moment-to-moment speeds. Each trial was segmented into outward and homeward segments. The outward segment was defined as all of the movements that displaced the rat from the refuge until locating the food pellet. As with the previous experiments, two measures were used to characterize the organization of the outward segment: time elapsed and movement segmentation. The homeward segment was defined as all of the movement occurring after the rat located the food pellet until returning to the refuge. Two measures were used to characterize the homeward segment: absolute heading error and peak speed.

Results

Topographic and kinematic characteristics were plotted for representative trials in which the food pellet was a short (see left panels of Figure 3), medium (see middle panels of Figure 3), or long (see right panels of Figure 3) distance from the refuge. In general, outward segments were circuitous paths with varied moment-to-moment speeds; whereas, homeward segments were noncircuitous paths with a single peak in speed. Two separate analyses were used to characterize the performance of rats in the searching task. The first analysis examined the effect of varying the distance of the food pellet from the start location on outward and homeward segment characteristics. Food pellets were placed short (~0.95m), medium (~1.54m), and long (~2.10m) distances from the start location. Subsequent analyses capitalized on the variability in path circuitry observed prior to rats locating the food pellet. Each rat's set of trials was sorted into high (0.18), medium (0.41), and low (0.77) outward segment path circuitry categories, and differences in performance observed on outward and homeward segment characteristics were evaluated.

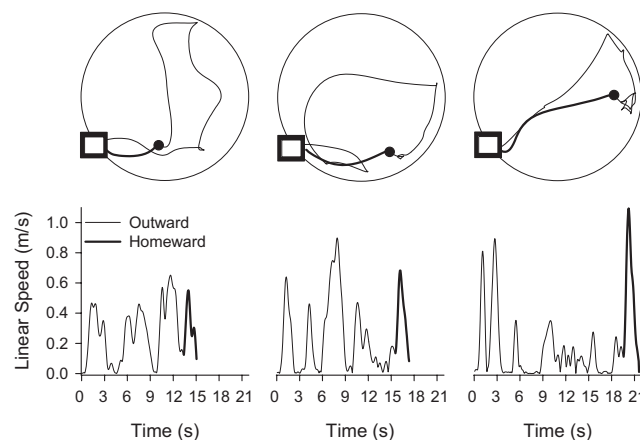


Figure 3. Topographic (top panels) and kinematic (bottom panels) profiles of a representative searching trial are provided for a representative rat after placing the food pellet a short (left panels), medium (middle panels), or long (right panels) distance from the refuge. A single trial involves the rat departing from the refuge (square), searching for the food pellet (black circle), and carrying the food pellet to the refuge. Each trial has been divided into an outward (thin line) and homeward (heavy line) segments.

Food pellet to refuge distance. The ANOVAs conducted on outward segment characteristics (see Table 3) failed to reveal significant main effects of food pellet to refuge distance on time elapsed [$F(2, 12) = 1.187, p = .338, \eta_p^2 = .165$] or movement segmentation [$F(2, 12) = 0.610, p = .559, \eta_p^2 = .092$]. Varying the distance the food pellet was located relative to the refuge did not significantly influence any of the outward segment characteristics.

Two measures were used to characterize performance on the homeward segment as the distance between the food pellet and refuge varied. Absolute heading error [$F(2, 12) = 0.964, p = .409, \eta_p^2 = .138$] did not significantly differ across varying distances. In contrast, peak speed [$F(2, 12) = 17.800, p = .000, \eta_p^2 = .748$] significantly varied as a function of distance between the food pellet and refuge. Post hoc analysis conducted on distance revealed a significant linear trend in peak speed [$F(1, 6) = 26.960, p = .002$]. Although heading error did not vary as a function of distance, peak speeds significantly increased as the distance between the food pellet and refuge increased consistent with rats' ability to estimate distance.

Outward segment path circuitry. Each rat's set of trials was sorted and classified based on the circuitry of the outward segment: high circuitry, medium circuitry, and low circuitry. The ANOVAs conducted on outward segment characteristics (see Table 3) revealed significant main effects of path circuitry on time elapsed [$F(2, 12) = 54.364, p = .000, \eta_p^2 = .901$] and movement segmentation [$F(2, 12) = 7.111, p = .009, \eta_p^2 = .542$]. Post hoc analyses revealed significant linear trends for both measures. Sorting trials based on the path circuitry of the outward segment resulted in significant differences in the time elapsed and movement segmentation observed on the outward segment.

Two measures were used to characterize performance on the homeward segment as path circuitry of the outward segment varied. The ANOVA conducted on absolute heading error [$F(2, 12) = 4.379, p = .037, \eta_p^2 = .422$] revealed a significant effect of outward segment path circuitry. Post hoc analysis conducted on path circuitry revealed a significant linear trend in absolute heading error [$F(1, 6) = 6.785, p = .040$]. In contrast, the ANOVA conducted on peak speed [$F(2, 12) = 3.775, p = .053, \eta_p^2 = .386$] failed to reveal a significant effect of outward segment path circuitry. Path circuitry on the outward segment significantly influenced absolute heading error, but not peak speed, associated with

the homeward segment. These observations are consistent with path circuitry influencing direction estimation, but not distance, in rats.

Discussion

This experiment examined rats' ability to use self-movement cues to estimate direction and distance to the refuge during a food hoarding task. Performance on the homeward segment was influenced by two characteristics. When trials were sorted based on the distance between the food pellet and the refuge, rats were observed to increase their homeward segment peaks with longer distances. Distance to the refuge did not influence absolute heading error observed on the homeward segment. These results are consistent with rats using self-movement cues generated on the outward segment to estimate the distance to the refuge.

Upon sorting trials based on the path circuitry of the outward segment, rats were observed to increase their heading error with more circuitous outward segments. Although both distance traveled and time elapsed increased with more circuitous outward segments, movement segmentation also varied with path circuitry. Specifically, the correlation between linear speed and path curvature became weaker with more circuitous searching paths. Homeward segment peak speed did not vary as a function of outward segment path circuitry. These results are consistent with the potential role for movement segmentation in rats using self-movement cues to estimate direction to the refuge. However, time elapsed varied with movement segmentation on the outward segment; therefore, a mnemonic account cannot be excluded from explaining the variability in absolute heading error observed on the homeward segment.

Experiment 4

This study was designed to vary the movement segmentation experienced on the outward segment while holding mnemonic demands of the outward segment constant. Rats were trained to track a scented string of a fixed length that was arranged into acute, right, and obtuse angles. This manipulation was intended to manipulate the magnitude of movement segmentation, thereby influencing the rats' ability to use self-movement cues to estimate direction to the refuge.

Methods

Subjects. Eleven naïve female Long-Evans rats (*Rattus norvegicus*) pair housed in plastic cages served as subjects for the current study. Animal husbandry and food restriction were the same as described for Experiment 3.

Apparatus. The apparatus was similar to that described in Experiment 3; however, a slightly larger wooden circular table (2.35 m in diameter) was used. As before, the refuge was located just below the surface of the table so that the rats could exit the refuge and explore the surface of the table. Rats were trained to track a string (100% cotton butcher twine approximately 2 mm in diameter) scented with their own odor relative to a vanilla scented string. Rat odors were applied to the strings by gently rubbing the string on the rat's body for five consecutive days. Vanilla odor was applied to the string by dipping the string in vanilla extract, wiping

Table 3
Rat Searching Task Outward Segment Characteristics

	Time		Movement segmentation	
	<i>M</i>	95% CI	<i>M</i>	95% CI
Distance				
Short	22.77	[7.61, 37.92]	-0.59	[-0.62, -0.56]
Medium	35.97	[16.73, 55.21]	-0.61	[-0.65, -0.56]
Long	31.67	[23.13, 40.22]	-0.59	[-0.61, -0.56]
Path circuitry				
High	53.54	[38.36, 66.72]	-0.55	[-0.58, -0.52]
Medium	25.93	[18.10, 33.77]	-0.62	[-0.66, -0.58]
Low	11.86	[4.95, 18.78]	-0.60	[-0.63, -0.58]

Note. Values represent the mean for each variable collapsed across each rat's set of searching trips; 95% confidence intervals are indicated parenthetically.

off excess extract, and letting the string dry overnight. Strings were stored in individual jars when not being used. Metal thumbtacks were used to attach the strings to the surface of the table.

Procedure. As describe in Experiment 3, rats were transported from the colony room to the testing room under dark conditions via a circuitous path that varied across days. Odor tracking behavior was shaped in three phases prior to formal testing. Rats had to successfully complete three trials a day for two days prior to advancing to the next phase of training. The first phase was conducted under standard light conditions. Rats were exposed to the refuge, table, 100 cm string scented with their own odor, and 100 cm string scented with vanilla. Both strings originated at the refuge and radiated in different directions. Food pellets were placed only along the string scented with the rat's own odor. The second phase of training began after rats were reliably locating food pellets at the end of the self scented string. During the second phase, rats were given three trials to use the self scented string to locate the food pellet. A trial involved a rat exiting the refuge, following the string to the end, picking up the food pellet, and carrying it to the refuge for consumption. A cover was placed on the refuge while the rat was consuming the food pellet so that position of the strings could be changed across trials. If the rat located the food pellet without following the string, the rat was picked up, the food pellet was removed from the rat's mouth, and the rat was returned to the refuge. The third phase of training began after rats were reliably following the self scented string as it changed positions across trials. During the third phase, rats were trained to follow strings that were twice as long (200 cm) under standard light conditions. After rats were reliably locating the food pellet at the new length, the lights were turned off for subsequent training and testing. Testing began after rats were reliably scent tracking under dark conditions. During testing, rats were presented with the string they were trained to follow arranged into two legs (100 cm) of a triangle separated by a single angle. Within a day, rats would receive three trials in which the angle subtending the legs would either be acute, right, or obtuse. The order in which angles were experienced varied across days. The size of the table and necessity to work under completely dark conditions limited the precision in forming specific angles. At the conclusion of a session, the rat was removed from the refuge, returned to the colony, and the table was rotated and cleaned with Windex.

Data analysis. Only trials in which the rat followed the scented string and located the food pellet were included in the analysis. The Peak Performance System was used to convert video of rats' behavior to digital computer files. Rat movements were tracked by selecting one pixel every third frame that corresponded to the middle line of the body at the level of the forelimbs. The rats' x- and y-coordinates were scaled to real world units and used to calculate moment-to-moment speeds. Each trial was segmented into outward and homeward segments. The outward segment was defined as all of the movements that displaced the rat from the refuge until locating the food pellet. As with the previous experiments, two measures were used to characterize the organization of the outward segment: time elapsed and movement segmentation. The homeward segment was defined as all of the movement occurring after the rat located the food pellet until returning to the refuge. Two measures were used to characterize the accuracy of the homeward segment: absolute heading error and peak speed.

Results

Topographic and kinematic characteristics are plotted for representative trials in which a rat followed strings arranged into an acute angle (see left panels of Figure 4), a right angle (see middle panels of Figure 4), and an obtuse angle (see right panels of Figure 4). Considering the difficulty in reliably arranging the strings on the table into a specific angle, trials in which rats followed the string were sorted and classified as acute ($M: 69^\circ; SD: 4.8$), right ($M: 93^\circ; SD: 9.3$), and obtuse ($M: 131^\circ; SD: 7.57$). Rats accurately followed the string for at least three trials at each angle.

Outward segment characteristics. The ANOVAs conducted on outward segment characteristics (see Table 4) failed to reveal a significant main effect of angle for time elapsed [$F(2, 20) = 1.572, p = .232, \eta_p^2 = .136$], and for movement segmentation [$F(2, 20) = 0.260, p = .774, \eta_p^2 = .025$]. Outward segment time elapsed and movement segmentation did not vary across the angles of varying magnitude.

Homeward segment characteristics. Peak speeds and heading error were used to characterize the accuracy of the homeward segment. The ANOVA conducted on the peak speeds revealed a significant main effect of angle [$F(2, 20) = 9.153, p = .002, \eta_p^2 = .478$]. Post hoc analysis conducted on angle revealed a significant linear trend in peak speed [$F(1, 10) = 16.888, p = .002$]. In contrast, the ANOVA conducted on heading error failed to reveal a significant main effect of angle [$F(2, 20) = 0.538, p = .592, \eta_p^2 = .051$]. Although angle experienced on the outward segment did not significantly influence the absolute heading error, homeward segment peak speed increased as outward segment angle increased. These observations are consistent with distance estimation in rats.

Discussion

This experiment examined the ability of rats to use self-movement cues to return to the refuge after following a string to locate a food pellet. Outward segments did not vary in the time

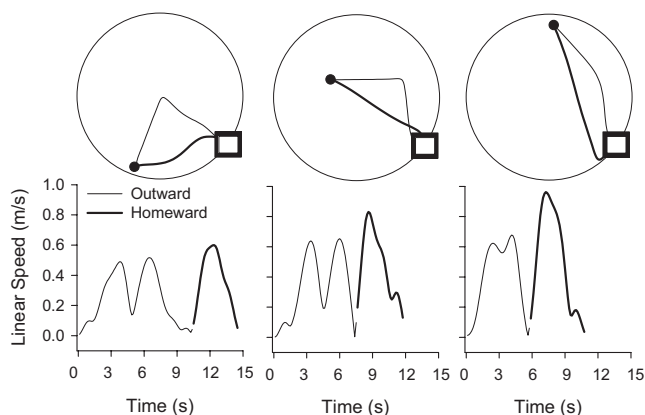


Figure 4. Topographic characteristics (top panels) are plotted for a representative scent tracking trial from rats following strings arranged into acute (left panels), right (middle panels), or obtuse (right panels) angles. The kinematic characteristics (bottom panels) associated with each representative trial are also provided. Each trial has been divided into an outward (thin line) and homeward (heavy line) segments.

Table 4
Rat Triangle Task Outward Segment Characteristics

Triangle	Time		Movement segmentation	
	<i>M</i>	95% CI	<i>M</i>	95% CI
Acute	9.79	[8.87, 10.70]	-0.50	[-0.55, -0.44]
Right	9.87	[7.29, 12.44]	-0.52	[-0.59, -0.46]
Obtuse	8.42	[7.52, 9.32]	-0.52	[-0.58, -0.46]

Note. Values represent the mean for each variable collapsed across each rat's set of triangle completion trips; 95% confidence intervals are indicated parenthetically.

elapsed or movement segmentation observed across the three classes of angles; however, distance to the refuge increased with larger angles. These characteristics of the outward segment will be considered in light of the performance observed on the homeward segment.

The absolute heading error did not vary as a function of the characteristics of the outward segment. This result is relevant for explanations advanced to account for differences in absolute heading error observed in previous experiments. Time elapsed did not vary across the different angles experienced on the outward segment; therefore, mnemonic demands were equivalent. The similar mnemonic demands across outward segments may explain the failure to observe differences in absolute heading error. Varying the angle experienced on the outward segment was intended to manipulate movement segmentation; however, movement segmentation did not vary as a function of the angle experienced on the outward segment. Under these conditions, errors in using self-movement cues to update a representation of direction would have been equal across angles. Therefore, the lack of differences in absolute heading error cannot discount the role of movement segmentation in the accurate processing of self-movement cues related to direction estimation.

Homeward segment peak speeds were observed to vary as a function of the angle experienced on the outward segment. Specifically, larger angles were associated with faster peak speeds. These observations parallel the results of Experiment 3 and provide further evidence that rats use self-movement cues to estimate distance to the refuge.

General Discussion

This series of experiments examined dead reckoning in humans at the manipulatory scale and rats at the ambulatory scale. Similarities and differences were observed in both species' ability to use self-movement cues to estimate direction and distance. For example, both species scaled their moment-to-moment speeds to the varying distances experienced between the start of the homeward segment and goal locations across tasks. This observation suggests that online processing of self-movement cues was sufficient for distance estimation in both species and in both tasks. In contrast, movement segmentation on the searching segment was only associated with heading error on the triangle completion task in humans and the searching task in rats. One possible explanation for these differences is that an animal's range of movement segmentation values was limited by the demands of the task. In the

triangle completion task, humans display a large range of movement segmentation values, relative to the restricted range observed in rats. Therefore, a within task analysis of the relationship between movement segmentation and heading error is a less sensitive approach, relative to a between task analysis that captures a larger range of movement segmentation values. A more detailed discussion of these observations and their implications for understanding spatial orientation are presented in the following sections.

Estimating Direction

Previous work has demonstrated animals use self-movement cues to maintain spatial orientation in the absence of environmental cues (Mittelstaedt & Mittelstaedt, 1980; Etienne, 1980; Loomis et al., 1993; Maaswinkel & Whishaw, 1999; Shettleworth & Sutton, 2005; Wallace, Hamilton et al., 2006; Wallace, Choudry et al., 2006). One aspect of performance in these studies involves estimating direction to the start location. Animals must continuously update an online representation of direction with self-movement cues. Although this navigational strategy has adaptive value in novel environments or in the absence of environmental cues, it is prone to the accumulation of errors (Barlow, 1964). A variety of models have been advanced to explain the error in estimating direction associated with dead reckoning based navigation (see Maurer & Ségunoit, 1995, for a review). One model posits that errors in estimating direction to the start location reflects inaccuracies in encoding recently experienced changes in heading (Fujita, Klatzky, Loomis, & Golledge, 1993). The model has accounted for human performance under conditions in which distance traveled and changes in heading experienced on the outward segment were systematically manipulated. The model has yet to be applied to situations in which the outward segment was not structured by the experimenter. Provided that movement segmentation facilitates detection of changes in heading, the model would predict that the magnitude of movement segmentation should influence the absolute heading error observed on the homeward segment.

Previous work has demonstrated that rat movement segmentation is highly consistent (approximately -0.60) across spontaneous exploration and food hoarding paradigms (Wallace, Hamilton et al., 2006; Wallace, Choudry et al., 2006). The variation in rat movement segmentation observed in the current tasks is novel. Several factors may have contributed to observing this variation in rat movement. First, previous studies analyzed movement segmentation for all trips independent of the circuitousness of the outward segment. Experiment 3 demonstrated that as outward segments become more circuitous movement segmentation decreased in magnitude. Second, the disruption in movement segmentation observed in Experiment 3 is due to using different behavioral testing procedures. Specifically, rats in Experiment 4 were trained to track odor scented strings. This training resulted in a quantitative difference in movement segmentation. The performance of rats in both tasks demonstrated that movement segmentation was associated with heading error of the homeward segment.

The viability in movement segmentation observed across tasks was different for human participants. During the searching task, human movement segmentation was equally weak across the different level of outward segment path circuitry; however, movement segmentation varied with the string arrangements in the string following task. Given these differences, a within task analysis does

not yield consistent relationships between movement segmentation and heading error across both species. However, a between task analysis reveals a consistent relationship across species. To characterize the consistency of these relationships between tasks, scatter plots were generated for each outward segment characteristic (see Figure 5). Disruptions in movement segmentation were associated with increased absolute heading error in both humans and rats. Time elapsed on the outward segment also varied with absolute heading error observed in humans. Consistent with previous research (Wallace, Choudhry et al., 2006), time elapsed was not observed to be strongly associated with rats' absolute heading error. This pattern of results is consistent with both movement segmentation and mnemonic processes influencing humans' ability to use self-movement cues to estimate direction; whereas, only movement segmentation influenced rats' ability to estimate direction. This is an exploratory analysis with relatively few data points contributing to each scatter plot. Therefore, the influence of outliers on the observed correlations cannot be excluded. The magnitude of movement segmentation was the only outward segment characteristic that was strongly associated with performance in both species; further work is needed to investigate its contribution to spatial orientation.

A similar type of movement segmentation has been observed in human voluntary movements at the manipulatory (Viviani & Ter-

zuolo, 1982; de'Sperati & Viviani, 1997) and ambulatory (Vieilledent, Kerlirzin, Dalbera, & Berthoz, 2001) scales. These tasks involve participants following paths that continuously vary in path curvature. The nature of the representation mediating movement segmentation in these tasks has been debated. A bottom-up view posits that movement segmentation emerges from lower level processes related to the biomechanics of moving end effectors through space (Sternad & Schaal, 1999). In contrast, a top-down view posits that voluntary movements are mediated by a central representation (Viviani & Flash, 1995). Translating this central representation to action involves the concatenation of simple movement primitives. The top-down view posits that factors that influence the central representation should also influence movement segmentation. In contrast, the bottom-up view posits that movement segmentation should be observed independent of factors that influence a central representation. Several lines of evidence support the top-down view. First, movement segmentation at the manipulatory scale follows a developmental sequence (Viviani & Schneider, 1991). Humans develop the ability to maintain a central representation of the movement. Prior to the development of this ability, weaker movement segmentation is observed. Next, brain damage that impairs the individual's ability to maintain a central representation, results in weaker movement segmentation (Krebs, Aisen, Volpe, & Hogan, 1999). Further, recall that disrupt-

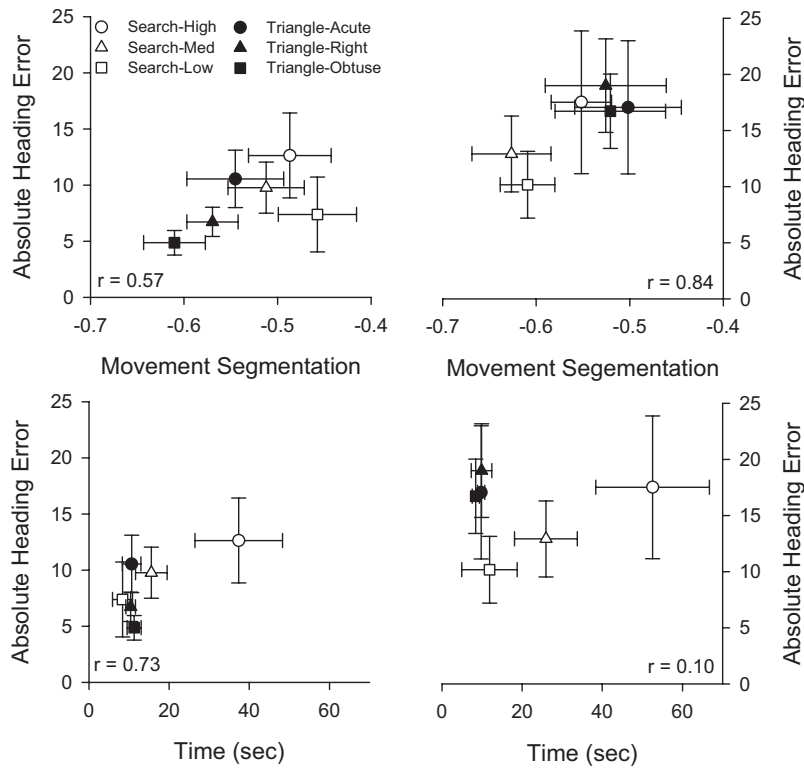


Figure 5. The relationship between characteristics of the outward segment and homeward segment absolute heading error were plotted for humans (left panels) and rats (right panels). Outward segment movement segmentation (top panels) was strongly associated with absolute heading error in both species. Outward segment time elapsed (bottom panels) was only strongly associated with absolute heading error in humans. Error bars reflect the 95% confidence interval associated with each point. Note: The correlation values in each graph were calculated from the average outward segment characteristic and homeward segment absolute heading error observed across each condition in the searching and string following tasks ($n = 6$).

tions in spatial orientation during an ambulatory dead reckoning task were associated with weaker movement segmentation (Wallace, Choudhry et al., 2006). Finally, the results of the current studies also demonstrate that movement segmentation can vary in magnitude. It remains to be determined whether it is a failure to accurately update the current representation of direction that leads to weaker movement segmentation, vice versa, or a combination of both.

Estimating Distance

Distance estimation also contributes to maintaining spatial orientation. Studies have shown that animals use multiple sources of information to estimate distance to a goal. In the absence of visual information, humans have been shown to use self-movement information to encode the distance to a goal location. Nonvisually guided reaching involves using self-movement cues to encode the distance to a goal (Gordon et al., 1994). As participants become familiar with reaching for a specific distance, a consistent scaling of moment-to-moment linear speeds is observed with the peak speed occurring at the middle of the path. Manipulating movement distance results in participants rescaling their movement kinematics such that the peak speed occurs at the midpoint of the new path length. These observations are consistent with humans using self-movement cues to encode the distance to a goal.

In the absence of specific training, animals use self-movement cues to continuously update an online representation of distance. For example, rats organize their exploratory behavior under dark conditions into a series of trips (Wallace et al., 2002; Wallace, Hamilton et al., 2006). Each trip is divided into searching and homeward segments. The searching segment is a sequence of slow linear progressions. The homeward segment is characterized by consistent temporal pacing of moment-to-moment linear speeds with the peak speed occurring at the midpoint of the path. Each outward segment is a unique set of self-movement, therefore estimating distance to the refuge depends on continuous processing of self-movement cues.

The current study provides further evidence that animals use self-movement cues to estimate distance. Humans and rats increased their homeward segment peak speed as the length of their homeward segment increased. Recall that the behavior of human participants occurred at the manipulatory scale, limiting their access to self-movement cues to those associated with limb movement (i.e., proprioception). In contrast, rat behavior occurred at the ambulatory scale, providing access to multiple sources of self-movement cues (i.e., vestibular and proprioceptive). Despite these differences, both species modulated their homeward segment peak speeds. Therefore, it is possible that distance estimation is conserved across both species.

Further support for a distance estimation system that is conserved across species is found in studies investigating the neural basis of spatial disorientation associated with neurodegenerative disorders. Several lines of evidence support the possibility that limitations in processing self-movement cues mediate wandering behavior associated with the progression of Alzheimer's disease. First, recall that patients with Dementia of the Alzheimer's Type (DAT) show deficits in detecting radial optic flow (Tetewsky & Duffy, 1999; O'Brien et al., 2001). Next, degeneration of the basal forebrain cholinergic system (provides cholinergic projections to

the hippocampal formation) is associated with the cognitive decline observed with the progression of DAT (Davies & Maloney, 1976; Perry, Perry, Blessed, & Tomlinson, 1977). Translational research investigating the effects of selective cholinergic deafferentation of the hippocampus on spatial orientation has shown a sparing of mnemonic functions and navigation based on external cues (Vuckovich, Semel, & Baxter, 2004; Bizon, Han, Hudon, & Gallagher, 2003; Cahill & Baxter, 2001; Dornan et al., 1997). Recent work has demonstrated that similar damage to the hippocampal cholinergic system impairs rats' use of self-movement cues while sparing external cues during a food hoarding task (Martin & Wallace, 2008). Further work is needed to determine the extent that these impairments are selective to distance estimation.

Caveat

Eliminating access to visual information in the current set of experiments was intended to force both species to use self-movement cues to guide performance. The consistent ability of humans and rats to return to the start location was attributed to both species using self-movement cues to estimate direction and distance. It is possible that human participants had access to an additional source of information to guide navigation. Specifically, humans could have used their torso as a consistent reference point throughout a trial. In contrast, rats did not have constant access to one reference point throughout a trial. The relatively small number of trials in combination with the use of multiple start points was designed to minimize this ability in humans. Although continuous access to a reference was not an issue for humans engaging in dead reckoning at the ambulatory scale (Wallace, Martin, & Choudhry, 2006), the pragmatics of testing DAT patients requires the development of spatial orientation tasks at the manipulatory scale. Therefore, future work should investigate whether using the torso as a reference point is sufficient to guide navigation.

Conclusion

Both humans and rats use self-movement cues to estimate direction and distance to the location where movement initiated. Although evidence for a role for movement segmentation depended on the task and the species, its effects were selective to direction estimation. Modifying the distance to the start location significantly influenced movement kinematics. Increases in distance resulted in increases in homeward segment peak speeds, independent of task or species. This series of studies builds a foundation for future work using translational neuroscience to understand spatial disorientation associated with neurodegenerative diseases.

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