

# Comparative Analysis of Movement Characteristics During Dead-Reckoning-Based Navigation in Humans and Rats

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Human and rat movement organization was investigated as they searched for randomly located rewards without access to visual information. Under dark conditions, rats foraged for randomly located food pellets (Experiment 1). Blindfolded humans were instructed to search for an ostensible hidden coin using a metal detector (Experiment 2). After locating the food pellet, rats carried it back to the refuge, and after a designated searching time, humans were instructed to return to the start location. Although both species exhibited a high degree of similarity in searching path movement organization and ability to return to the start location, disruption of human searching path organization was associated with impairments in returning to the start location. These results support the vestibular “gain” account of movement organization during dead-reckoning-based navigation.

*Keywords:* spatial navigation, movement kinematics, topographical disorientation, two thirds power law, path integration

Accurate spatial orientation is critical for obtaining resources and avoiding predation. When an animal becomes disoriented while foraging for food, the animal’s ability to return to the safety of the nest is compromised, thereby increasing risk of predation and decreasing the efficiency of foraging. Therefore, it is not surprising that animals have evolved multiple navigational strategies to maintain spatial orientation. The specific navigational strategy that is used reflects the availability of environmental information, the animal’s familiarity with the environment, and the predictive value of landmarks in the environment (Masswinkel & Whishaw, 1999; Shettleworth & Sutton, 2005). In novel environments or environments in which allothetic cues (visual, auditory, or olfactory landmarks) may become unreliable, dead-reckoning-based navigation is particularly useful. Dead reckoning involves the continuous or online processing of self-movement information (vestibular cues, proprioceptive cues, motor efferents, or optic flow) generated as an animal moves through an environment. Evaluation of this self-movement information within the temporal context in which the movements occurred provides direction and distance information associated with the location where movement was initiated (Barlow, 1964; Darwin, 1873; Gallistel, 1990; Pote-

gal, 1982; Shettleworth, 1998). Therefore, self-movement information can be used to maintain spatial orientation with respect to the animal’s nest or refuge independent of allothetic cue availability or familiarity.

Several lines of evidence suggest a role for the vestibular system in dead-reckoning-based navigation. First, vestibular nucleus lesions, but not enucleation, impair a rat’s ability to return to a start location after passive transport (Miller, Potegal, & Abraham, 1983). Second, damage to the vestibular system produces deficits in food-hoarding tasks when allothetic cues are either absent (testing under dark conditions) or allothetic cues conflict with previous experience (testing with the home base in a new location; Wallace, Hines, Pellis, & Whishaw, 2002). Third, many of the computational models that have been advanced to explain the errors observed in dead-reckoning-based navigation posit a role for the vestibular system in updating the animal’s current position (Barlow, 1964; Benhamou, Sauve, & Bovet, 1990; Fujita, Klatzky, Loomis, & Golledge, 1993; Mittelstaedt & Mittelstaedt, 1973; Muller & Wehner, 1988; for a review of models see Maurer, 1998; Maurer & Seguinot, 1995). Most of these models assume that errors in detecting linear and angular accelerations while moving through an environment contribute to the error in returning to the starting location; however, only a few studies have been conducted to actually examine the kinematic and topographic characteristics of nonhuman animals’ movements while using dead-reckoning-based navigation (Wallace, Hines, et al., 2002; Wallace & Whishaw, 2003). No studies have been conducted to examine the kinematic and topographic characteristics of movement while humans use dead-reckoning-based navigation. Therefore, investigating these characteristics of movement may provide critical constraints for future development of computational models of dead reckoning.

Rodent exploratory behavior has proven to be a valuable tool for studying the kinematic and topographic characteristics of move-

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ment during dead-reckoning-based navigation. Rats' exploration of an environment has been characterized as a set of trips organized around a home base (Drai, Benjamini, & Golani, 2000; Eilam & Golani, 1989; Tchernichovski, Benjamini, & Golani, 1998; Whishaw, Kolb, & Sutherland, 1983). Each exploratory trip is composed of a tour and a return segment. The tour segment is a circuitous path through the environment consisting of a number of progressions and stops. The return segment is a single noncircuitous progression directed towards the home base (Wallace & Whishaw, 2003). Observing exploratory trip organization independent of environmental familiarity and visual-cue availability has supported a role for dead reckoning in guiding this behavior. Rats use the self-movement information generated in the tour segment to plot the trajectory of the return segment. A recently observed inverse relationship between linear speed and path curvature on the tour segment has been suggested to enhance the processing of self-movement information (Wallace, Hamilton, & Whishaw, in press). Restricting changes in heading direction to discrete locations along the tour, rather than gradual changes in heading direction over the course of the tour, may increase the likelihood that the semicircular canals of the vestibular system will detect angular accelerations encountered during the tour. Transduction of angular acceleration by the vestibular system and the subsequent process of integration are sensitive to the accumulation of errors (Barlow, 1964). Therefore, the indirect relationship between linear speed and path curvature may function to increase the gain of the vestibular system and reduce errors inherent in dead-reckoning-based navigation. Observing that disruptions in the relationship between linear speed and path curvature are associated with impairments in dead reckoning would provide evidence in support of the vestibular gain account of movement organization.

Another possible explanation of the relationship between linear speed and path curvature reflects the motivational state of the rat. During an exploratory trip, rats make a series of slow, direct progressions with changes in heading direction occurring at stops. In the absence of a known food source, this provides a low effort mode of exploring the environment. That is, more effort is required to travel at high speeds during high path curvature; therefore, movement produced during exploration reflects that the rat is minimizing effort. Observing that changes in task demands or motivational state (i.e., exploration vs. searching for food) influence the relationship between linear speed and path curvature would support an effort minimization account of movement organization. Observing the same relationship between linear speed and path curvature under different motivational conditions would conflict with the effort minimization account and provide indirect support for the vestibular gain account of movement organization.

The first experiment evaluates both the increased vestibular gain and effort minimization accounts of the relationship between linear speed and path curvature by examining movement characteristics observed while rats hoard food items under environmental conditions shown to require dead-reckoning-based navigation. Rats' proclivity to carry large food items to a home base for consumption has been used to examine the use of multiple navigational strategies (Whishaw, Coles, & Bellerive, 1995). Manipulating visual-cue availability during food hoarding has been used to dissociate allothetic (piloting) and idiothetic (dead reckoning) navigational strategies (Maaswinkel & Whishaw, 1999). Although

observing a failure to influence the relationship between linear speed and path curvature on the searching path with changing task demands would conflict with an effort minimization account, this would, in essence, only reflect a null effect and require further evidence to support an enhanced gain explanation of movement organization.

Additional support for the increased vestibular gain account of the relationship between linear speed and path curvature could be obtained by demonstrating that this relationship systematically varies with the ability to dead reckon. A recent experiment has demonstrated that when humans were blindfolded and given a metal detector to search for a hidden coin in an open field, their ability to return to the start location (i.e., their ability to dead reckon) varied as a function of searching time (Wallace et al., 2004). Several explanations can be advanced to account for the observed time-dependent spatial disorientation. First, the increasing searching time may be associated with longer travel distances and larger cumulative changes in heading direction thereby exceeding the computational abilities of the dead-reckoning system in humans. Second, a time-dependent change in the relationship between linear speed and path curvature may compromise the ability of the vestibular system to detect changes in linear and angular speed. Although these explanations may not be mutually exclusive, observing a time-dependent change in the relationship between linear speed and path curvature would provide further evidence that the movement organization on the search path is, at least, related to spatial orientation. As of yet, no studies have directly examined the contribution of kinematic and topographic characteristics of human movement to the use of dead-reckoning-based navigation. The second experiment evaluates the relationship between linear speed and path curvature as blindfolded humans search for an ostensible hidden coin for 30, 60, or 120 s and their ability to return to the start location. Both experiments provide converging approaches to evaluate the role of the relationship between linear speed and path curvature for maintaining spatial orientation.

Although both experiments evaluate different aspects of the increased vestibular gain account of movement organization, the comparative approach is critical for the development of an animal model of spatial orientation. In general, work examining the neurobiology of spatial orientation has focused on allothetic-cue-based navigation (O'Keefe & Nadel, 1978). Recent studies have suggested a role for deficits in processing idiothetic information (e.g., radial optic flow) in spatial disorientation observed in Alzheimer's disease (Kavcic & Duffy, 2003; Tetewsky & Duffy, 1999). Therefore, examining the extent that humans and rats display similar movement characteristics on tasks thought to tap dead-reckoning-based navigation may further aid in the development of an animal model of spatial orientation.

## Experiment 1: Rat Food Hoarding

### Method

*Subjects.* The subjects were 4 female Long-Evans rats (*Rattus norvegicus*) weighing approximately 250–300 g. Rats were housed in groups of 2 in plastic cages in the colony room with the temperature maintained at 20–21 °C and with a 12-hr light–dark cycle. Prior to testing, feeding was restricted to maintain the rats at 85% of their expected body weight, and we

provided several 1-g banana food pellets (Bio-Serv, Frenchtown, NJ) each day to habituate the rat to the novel food item. After daily testing, rats were provided with supplemental rat chow (5L42 Rodent Breeder Diet food pellets; PMI Nutrition International, Brentwood, MO) in their home cages. All experimental procedures in this study were approved by the local Institutional Animal Care and Use Committee, which follows the standards set by the National Institutes of Health guidelines.

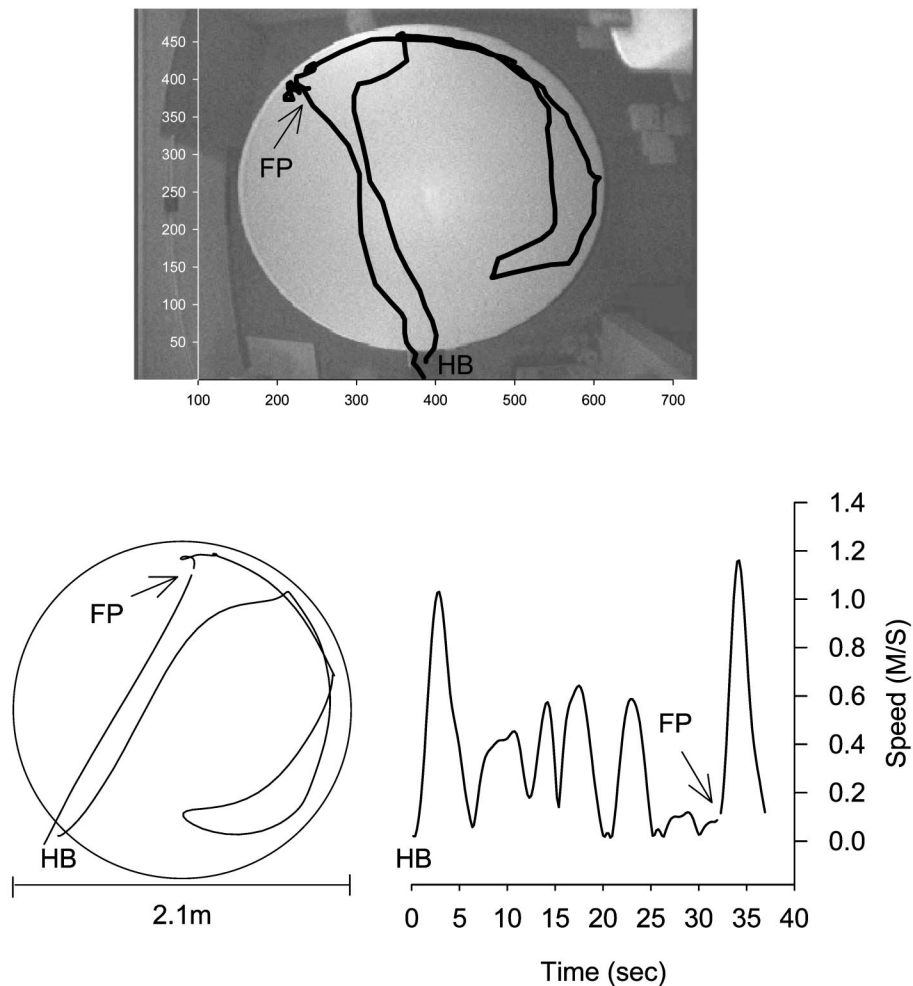
**Apparatus.** The apparatus was a wooden circular table without walls measuring 200 cm in diameter. The table was painted white and was located in a large room that could be illuminated or made completely dark. The testing room was light proof, such that when the lights were turned off during dark testing conditions, the room was completely dark. An infrared camera was positioned perpendicular to the table, and two infrared emitter banks were attached on different walls (see the top panel of Figure 1 for the resulting field of view for the rat experiment). This provided sufficient infrared illumination in the room such that the rat and testing apparatus were visible on the camera under dark conditions. The experimenter used

an infrared spotter to test the rat under complete dark conditions. Infrared is a wavelength that the rat is not able to detect (Neitz & Jacobs, 1986).

A small Plexiglas box (17 cm  $\times$  26 cm  $\times$  12 cm) with an oval opening (7 cm in diameter) in one of the short sides was placed on the edge of the table to be used as a refuge by the rat. The surface of the table was approximately 83 cm above the floor. The table was rotated between rats and wiped down with Windex after testing each rat, thereby limiting the salience of odor cues for spatial orientation.

**Procedure.** Throughout testing, rats were transported under dark conditions from the colony room to the testing room via a circuitous path that varied from day to day. The transport cage was rotated several times during transportation. Prior to formal testing, rats were habituated to the refuge and table by being placed in the refuge and left for 1.5 hr to explore the table under normal light conditions.

Rats were trained to leave the refuge and search for randomly located 1-g banana food pellets under normal light conditions. Initially, the food pellet was placed close to the refuge; however, over days, the distance



*Figure 1.* The top panel is a photograph of the rat testing environment with the camera perspective used throughout testing. A sample path is plotted over the photograph reflecting the raw data coordinate system. The bottom left panel plots the same path after the coordinate system transformation that reflects a camera position that is perpendicular to the testing environment (the camera was already perpendicular to the testing environment). The bottom right panel plots the moment-to-moment speeds of the same path. The location of the food pellet (FP) and the home base (HB) are indicated in each panel.

between the refuge and the food pellet was gradually increased. Food pellets were individually placed on the table. After locating the food pellet, the rat carried it to the refuge for consumption. While the rat was still in the refuge, the second food pellet was placed on the table. This procedure was repeated until four food pellets were placed on the table. Daily training continued until the rat carried four food pellets that were at least halfway across the table (100 cm) to the refuge (over 14 days). Subsequently, rats received 2 days of testing in which all aspects of the experiment were the same as experienced during food hoarding training, except they searched for food items under completely dark conditions.

**Data analysis.** The digital video tapes of rat behavior were converted to digital computer files using the Peak Performance system (Peak Performance Technologies, Englewood, CO) at a sampling rate of 60 Hz. Rat movements were tracked by selecting one pixel every five frames that corresponded to the midpoint between the rat's forelimbs. The resulting  $x$  and  $y$  coordinates from rats were scaled to real world units and used to calculate moment-to-moment speeds (see Figure 1).

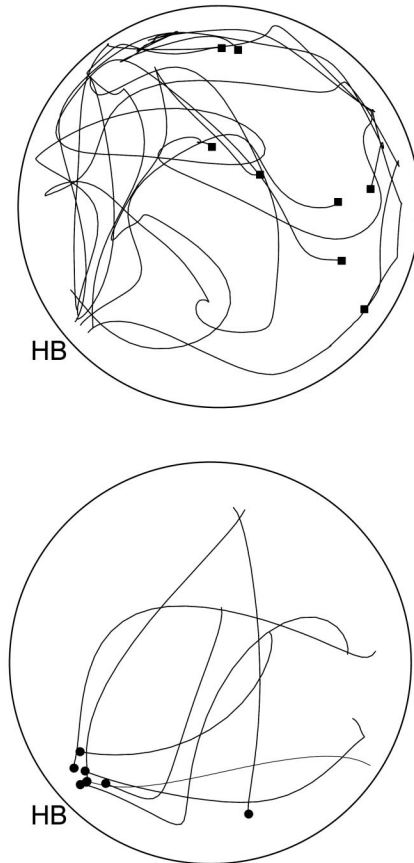
A single food hoarding trial was segmented into searching and homeward paths. The searching path was defined as all of the movements that displaced the rat from the refuge until locating the food pellet. The homeward path was defined as all of the movements occurring after locating the food pellet until the rat stopped (speed decreased below 0.1 m/s). Path distance, path circuitry, and average path speed were calculated for searching and homeward paths. Searching paths were further decomposed into progressions and stops. Progressions were defined as at least 10 frames in which movement exceeded 0.1 m/s, and stops were reflected as movement below 0.1 m/s (Wallace et al., in press). Average progression distance, progression circuitry, and progression speed were computed for rats' searching paths. Distance reflects the actual distance traveled by the rat on the searching or homeward path and progressions. Path circuitry is indicated by the ratio of the distance of the line that connects the first point to the last point of a path or progression to the actual distance traveled on the path or progression. Relatively direct paths are associated with values of 1.0 to 0.8. As the path or progression becomes progressively more circuitous, values decrease to 0.0. Searching path or progression speed reflects the distance traveled within the given time frame.

Head directions of the homeward path were measured for each rat's eight food hoarding trips. The heading direction was defined as the angle subtended by the point centered on the opening of the refuge, the point corresponding to where the food pellet was located, and the point on the periphery associated with the termination of the homeward path. Circular statistics were used to evaluate differences in heading direction (Batschelet, 1981).

Moment-to-moment measures of searching path curvature were computed for each searching path. Path curvature for the first three points of the searching path was obtained by calculating the angle subtended by the points and dividing it 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. This continued until moment-to-moment path curvatures were computed for the entire searching path. The resulting set of moment-to-moment path curvatures was smoothed using the Loess local smoothing technique (Cleveland, 1979; Cleveland & Devlin, 1988).

## Results

**Searching and homeward path topography.** Figure 2 plots eight searching paths (top panel) and their associated homeward paths from a representative rat. Searching paths originate at the home base, cover different regions of the table, and terminate when the food pellet is located. Homeward segments originate at different locations on the table and terminate after the rat's speed decreases below 0.1 m/s.



**Figure 2.** The top panel plots one rat's eight searching paths that originate at the home base (indicated by HB) and terminate where the food pellet was located (indicated by a black square). The bottom panel plots the rat's homeward paths that originate where the food pellet was located and terminate when the rat's speed decreases below 0.1 m/s (indicated by black circle).

Mean distances for searching paths, homeward paths, and searching path progressions are listed in Table 1. The paired-samples  $t$  test revealed that searching paths were significantly longer than homeward paths,  $t(3) = 4.352$ ,  $p < .05$ ; however, mean searching path progressions were not significantly longer than homeward paths,  $t(3) = 1.789$ ,  $ns$ . Rat mean path circuitry for searching paths, homeward paths, and searching path progressions are listed in Table 1. The paired-samples  $t$  test revealed that the searching paths were significantly more circuitous than homeward paths,  $t(3) = -9.058$ ,  $p < .05$ ; however, mean searching path progressions were not significantly more circuitous than homeward paths,  $t(3) = 1.692$ ,  $ns$ . Table 1 lists the mean speed from searching paths, homeward paths, and searching path progressions observed in rats. Paired-samples  $t$  tests revealed that mean speeds on homeward paths were faster than searching paths,  $t(3) = 10.117$ ,  $p < .05$ , and searching path progressions,  $t(3) = 8.900$ ,  $p < .05$ . Searching paths were significantly longer and more circuitous than homeward paths; however, searching path progressions were similar in distance and circuitry to homeward paths. Mean homeward path speeds were significantly faster than searching paths and searching path progressions.

Table 1  
*Topographical Characteristics of Rat Food Hoarding Behavior*

Characteristic	Distance (m)	Path circuitry	Speed (m/s)
Searching path	7.08 (2.21)	0.44 (0.11)	0.32 (0.03)
Homeward path	2.51 (0.27)	0.90 (0.04)	0.59 (0.07)
Searching progressions	1.97 (0.34)	0.85 (0.02)	0.35 (0.05)

*Note.* Values reflect the mean for each variable collapsed across each rat's eight food hoarding trips. The associated standard deviations are indicated parenthetically.

Although the rat searching time was not manipulated in the current experiment, regression analysis conducted on the relationship between searching path duration and measures of searching path topography (i.e., path length and circuitry) provides a comparison with human performance observed in Experiment 2. Searching path length and circuitry are plotted as a function of searching path duration for each rat's food hoarding trials in Figure 3. All rats displayed a significant increase in path length with longer searching times: Rat 1,  $F(1, 6) = 13.23, p < .05$ ; Rat 2,  $F(1, 6) = 79.79, p < .05$ ; Rat 3,  $F(1, 6) = 41.99, p < .05$ ; Rat 4,  $F(1, 6) = 151.88, p < .05$ . In general, path circuitry increased with longer searching durations; however, only 3 rats displayed a significant increase in path curvature with longer searching times: Rat

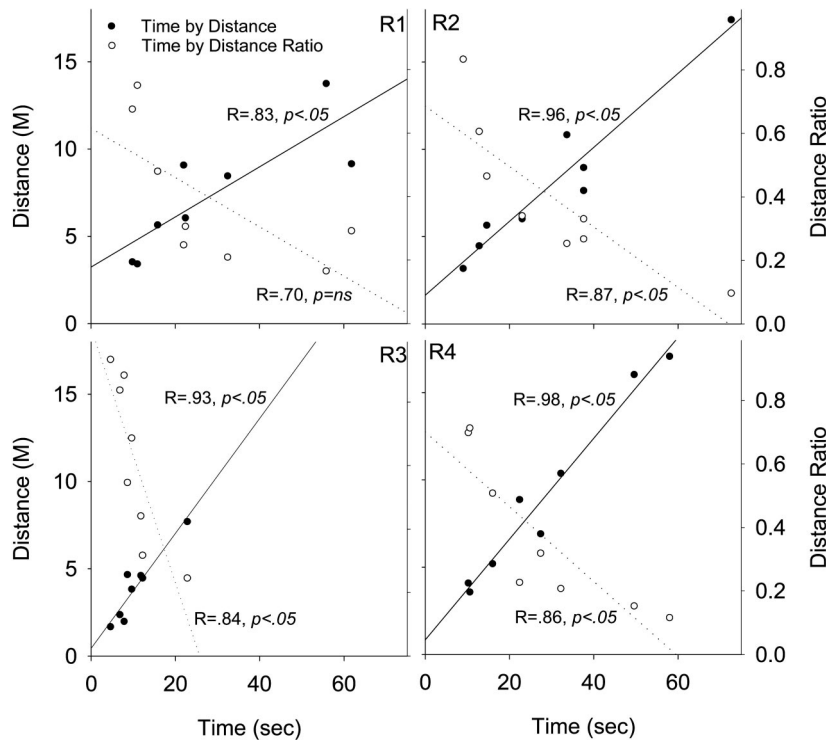
1,  $F(1, 6) = 5.76, ns$ ; Rat 2,  $F(1, 6) = 15.24, p < .05$ ; Rat 3,  $F(1, 6) = 14.47, p < .05$ ; Rat 4,  $F(1, 6) = 17.33, p < .05$ . In general, as each rat spent more time searching for the food item, path length and path circuitry increased.

*Heading directions.* Figure 4 plots each rat's set of heading directions (black dots) and mean heading directions (white dots). The single-sample  $t$  test revealed that the mean parameter of concentration ( $M = .90, SEM = .05$ ) was significantly different from 0.0,  $t(3) = 16.854, p < .05$ . After finding the food pellet, rats consistently returned directly to the refuge.

*Searching path kinematics.* The top panel of Figure 5 plots the moment-to-moment linear speeds and path curvatures for a representative searching path. During periods of path curvature, linear speed is minimized. The average correlations between searching path moment-to-moment linear speeds and path curvature for each rat are plotted in the bottom panel of Figure 5. Each rat's average correlation was significantly different from 0.0: Rat 1,  $t(7) = -25.322, p < .05$ ; Rat 2,  $t(7) = -26.701, p < .05$ ; Rat 3,  $t(7) = -5.310, p < .05$ ; Rat 4,  $t(7) = -16.018, p < .05$ . This inverse relationship between moment-to-moment linear speeds and path curvatures was observed across all rats' searching paths.

*Discussion*

Under completely dark conditions, rats searched for randomly located food pellets. Upon locating a food pellet, rats carried it



*Figure 3.* Searching path time by distance scatter plots (black dots) and the associated regression function (solid line) are plotted for each rat (R1, R2, R3, and R4). Searching path time by distance ratio scatter plots (white dots) and the associated regression function (dotted line) are plotted for each rat (R1, R2, R3, and R4). As the duration of the searching path increases, rats travel longer distances (left y axis), and the searching path becomes more circuitous (right y axis).

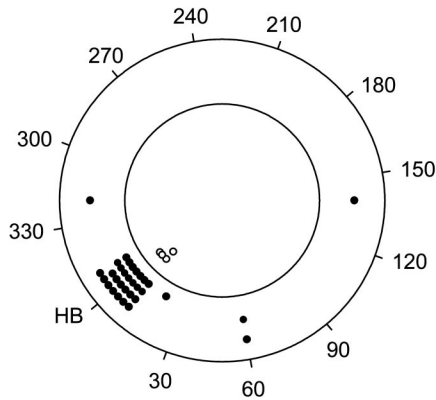


Figure 4. The outer ring plots each rat's heading directions from the eight trips. The inner ring plots each rat's mean heading direction. The location of the home base (HB) was transformed for each rat to facilitate comparison.

directly back to the refuge and immediately consumed it. Several characteristics of movement observed during food hoarding under completely dark conditions parallel behavior reported in studies examining rat exploratory behavior (Wallace et al., in press). First, searching and return progressions were similar in length, and both were noncircuitous paths. Rather than traveling in a large arc, changes in searching path heading direction occurred at distinct locations. Second, after locating the food pellet in the absence of visual information, rats accurately returned to the refuge. This ability to return directly to the refuge independent of visual-cue availability or environmental familiarity has been suggested to support a role for dead reckoning in organizing exploratory behavior (Wallace et al., in press; Wallace, Hines, & Whishaw, 2002; Wallace & Whishaw, 2003). Finally, searching path linear speeds and path curvature were inversely related. As rats moved faster, path curvature decreased and vice versa. Observation of this relationship between linear speed and path curvature in rat exploratory behavior has been suggested to enhance processing of self-movement information by increasing the gain associated with linear and angular accelerations (Wallace et al., in press). Observing similar movement characteristics under different task demands, conflicts with an effort minimization account of movement organization. One direct prediction from the vestibular gain account of movement organization suggests that disruption in searching path movement organization should be related to a rat's ability to accurately return to the refuge. Therefore, Experiment 2 examines this hypothesis in blindfolded humans performing a similar navigational task.

## Experiment 2: Human Searching Task

### Method

**Participants.** Students were recruited from introductory psychology courses and provided with supplemental course credit for their involvement. Male ( $n = 12$ ) and female ( $n = 18$ ) participants were an average of 22.5 years old, with the youngest participant being 18 and the oldest being 32 years old. On the basis of self-report, 27 of the participants were right handed, 2 were left handed, and 1 reported to be ambidextrous. All

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.

**Testing area and related equipment.** The testing area was a 21 m  $\times$  12 m rectangle located on the practice football field on the main campus of Northern Illinois University. The close proximity of Huskie Stadium to the practice field permitted the video recording of participants from the stadium's top bleachers. The resulting field of view for the second experiment is located in the top panel of Figure 6. Orange cones (0.30-m tall) were used to indicate the boundaries of the testing area. The ground was a level, grassy terrain.

A Sony mini-digital camera (DCR-TRV38) was used to record trips for all of the participants during the experiment. The camera was attached to a tripod such that it could be held in a stable position within and between testing sessions.

Two-way radios were used to communicate with the participant without providing auditory directional information. One two-way radio was attached to a string that was placed around the participants' necks. A second two-way radio was used by the experimenter to communicate instructions to the participants. Participants were provided with a handheld metal detector that was adjusted to their height. The experimenter demonstrated that the metal detector made a brief tone when passing over a coin on the ground. Subsequently, participants were blindfolded with darkened swimming goggles and a scarf tied around their head.

**Procedures.** Participants were randomly assigned to one of three groups: 30-s search, 60-s search, or 120-s search. Participants were blind-

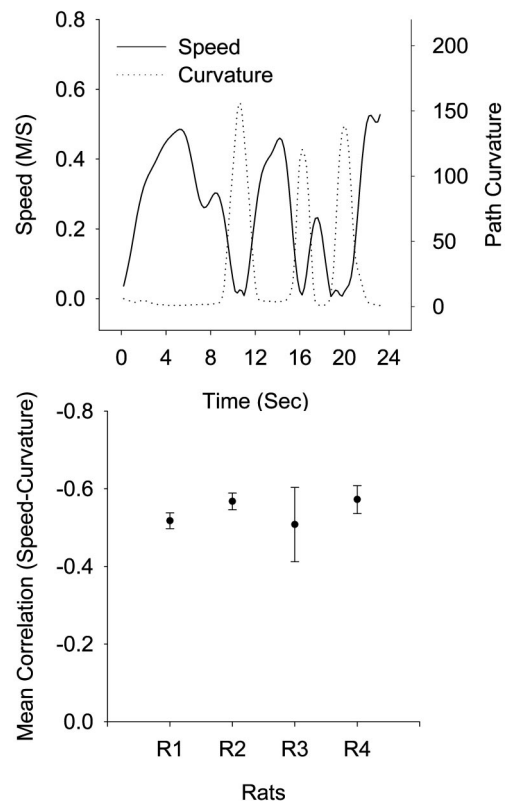
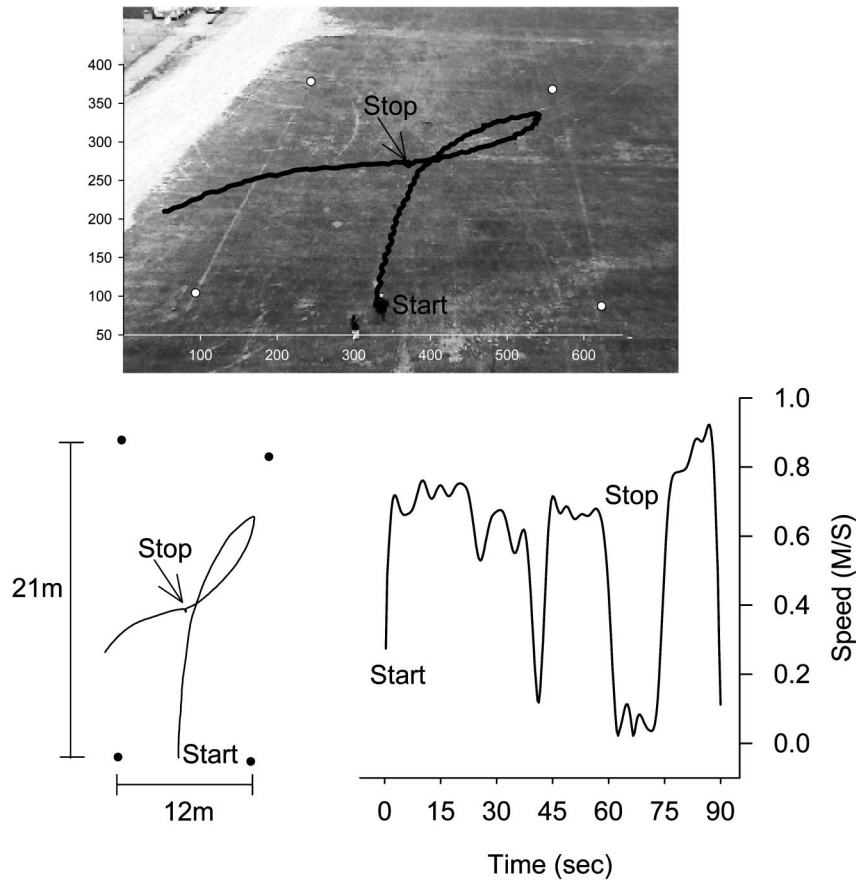


Figure 5. The top panel plots the moment-to-moment linear speeds (solid line) and path curvatures (dotted line) for a representative searching path. The bottom panel plots each rat's (R1, R2, R3, and R4) average correlation between moment-to-moment speeds and path curvature collapsed across the eight searching paths. Error bars represent standard error.



*Figure 6.* The top panel is a photograph of the human testing environment with the camera perspective used throughout testing. A sample path is plotted over the photograph reflecting the raw data coordinate system. The bottom left panel plots the same path after the coordinate system transformation that reflects a camera position that is perpendicular to the testing environment. The bottom right panel plots the moment-to-moment speeds of the same path. The start corresponds to where and when the participant was instructed to begin searching for the hidden coin. The stop corresponds to when the participant was asked to stop prior to being instructed to return to the start location.

folded (approximately 10 m away from the start location) and led to the start location. Prior to the first searching trial, participants were instructed to stop and raise their hand upon locating the hidden coin. They were also informed that if they began to leave the testing area, they would be prompted to stop and then would be informed of the direction to turn such that they would return to the testing area. After the designated searching time had elapsed, participants were instructed to stop, return to the location where they initiated the search, and stop when they reached that location. Homeward paths were terminated by the experimenter if the participant began to leave the testing area. At the conclusion of the homeward path, participants were led to a location outside of the testing area where they waited for the experimenter to move the hidden coin. Next, the experimenter led participants to the start location and asked if they felt comfortable continuing the experiment (no participants indicated that they felt uncomfortable). Upon approval, they were prompted to initiate their search. These procedures were repeated until each participant had completed three trials. Participants remained blindfolded throughout the entire experiment. The experimenter debriefed participants after the completion of testing as to the lack of a hidden coin and the purposes of the experiment.

*Data analysis.* Digital video tapes of participants' behavior were converted to digital computer files using the Peak Performance system (Peak Performance Technologies) at a sampling rate of 60 Hz. Participant movements were tracked by selecting one pixel every 10 frames that corresponded to the participant's right shoulder. The participants'  $x$  and  $y$  coordinates (see top panel of Figure 6) were transformed via projective scaling. Projective scaling uses the apparent perspective of fixed landmarks (orange cones) such that the camera perspective was shifted to a position that is perpendicular to the plane of movement (see bottom left panel of Figure 6). The resulting transformed  $x$  and  $y$  coordinates from participants were scaled to real world units and used to calculate moment-to-moment speeds (see bottom right panel of Figure 6).

A single trial was segmented into searching and homeward paths. The searching path was defined as all of the movements that displaced the participant from the start location until the designated searching time elapsed. The homeward path was defined as all of the movement occurring after the participant was instructed to return to the start location until either the participant stopped or the experimenter stopped the participant as he/she left the testing area. Similar to Experiment 1, we calculated path distance, path circuitry, and average path speed for searching and homeward

paths. Searching paths were further decomposed into progressions and stops. Progressions were defined as at least 10 frames in which movement exceeded 0.3 m/s, and stops were reflected as movement below 0.3 m/s. Average progression distance, progression circuitry, and progression speed were computed for participants' searching paths.

Homeward path heading directions were measured for each participant's three trials. The heading direction was defined as the angle subtended by the point centered on the start location, the point corresponding to where the participant was instructed to stop, and the point associated with the termination of the homeward path. Circular statistics were used to evaluate differences in heading direction (Batschelet, 1981). Moment-to-moment measures of searching path curvature were computed as indicated in the first experiment.

## Results

*Searching and homeward path topography.* Participants' searching (top panels) and homeward (bottom panels) paths from the first trial are presented for each group in Figure 7. The search paths originate at the start location and radiate into the open field. Homeward paths originate at varied locations throughout the open field. Table 2 presents each group's mean distance, path circuitry, and speed for searching paths, homeward paths, and searching path progressions.

The analysis of variance (ANOVA) conducted on each group's mean searching and homeward path distance revealed significant main effects of path segment,  $F(1, 27) = 144.257, p < .05$ , and group,  $F(2, 27) = 21.954, p < .05$ . The Group  $\times$  Path Segment interaction was also found to be significant,  $F(2, 27) = 35.338, p < .05$ . Post hoc comparisons revealed that the searching path distances were significantly longer than the homeward path distance for the 60-s and 120-s groups; however, no differences in path distance were observed in the 30-s group (Tukey's Least Significant Difference [LSD]). The ANOVA conducted on each group's mean path circuitry revealed a significant main effect of path segment,  $F(1, 27) = 104.672, p < .05$ , and group,  $F(2, 27) = 23.571, p < .05$ . The Group  $\times$  Path Segment interaction was also found to be significant,  $F(2, 27) = 12.496, p < .05$ . Post hoc comparisons revealed that both the 60-s and 120-s groups had significantly more circuitous searching paths relative to homeward paths; however, the difference in path circuitry was not significant in the 30-s group (Tukey's LSD). The ANOVA conducted on mean searching and homeward path speeds revealed a significant main effect of path segment,  $F(1, 27) = 317.680, p < .05$ , and a significant Group  $\times$  Path Segment interaction,  $F(2, 27) = 3.570, p < .05$ . The main effect of group was not significant,  $F(2, 27) = 0.263, ns$ . Post hoc analysis revealed that speeds were significantly faster on the homeward path relative to the searching path for each group (Tukey's LSD).

In general, searching progressions are direct paths of varying length and direction. A substantial portion of the searching path's circuitry is the result of directional changes occurring during discrete locations along the path. To examine the extent that these characteristics were observed across all groups, ANOVAs were conducted on mean distance, path circuitry, and speed observed on searching progressions and homeward paths.

The ANOVA conducted on mean progression distance failed to reveal a significant main effect of group,  $F(2, 27) = 0.772, ns$ ; path segment,  $F(1, 27) = .016, ns$ ; or Group  $\times$  Path Segment

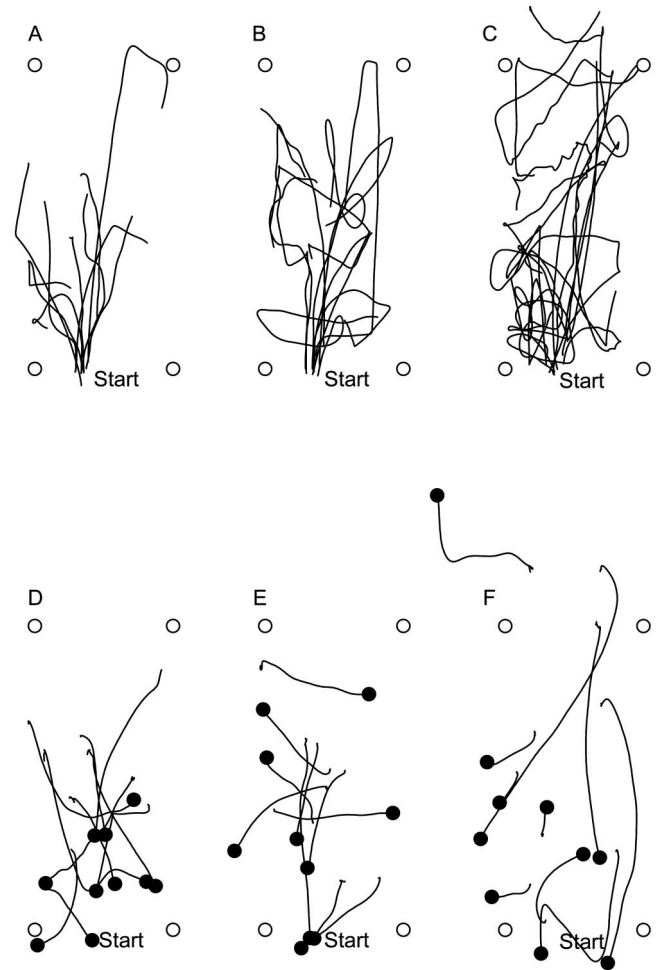


Figure 7. The first searching (A, B, & C) and homeward (D, E, & F) paths are plotted for the 30-s group (A & D), 60-s group (B & E), and 120-s group (C & F). Searching paths originate at the same location then terminate at different locations in the environment (A, B, & C). Homeward paths are initiated where the searching paths ended and continue until terminated (see black dots).

interaction,  $F(2, 27) = 0.310, ns$ . There were no significant differences in the distance traveled on searching progressions and homeward paths. The ANOVA conducted on the mean progression path circuitry failed to reveal a significant main effect of group,  $F(2, 27) = 0.215, ns$ ; path segment,  $F(1, 27) = 0.717, ns$ ; or Group  $\times$  Path Segment interaction,  $F(2, 27) = 0.780, ns$ . Groups' searching progressions and homeward paths were noncircuitous paths. Although the ANOVA conducted on mean searching progression and homeward path speed revealed a significant main effect of path segment,  $F(1, 27) = 33.688, p < .05$ , both the main effect for group,  $F(2, 27) = 0.357, ns$ , and the Group  $\times$  Path Segment interaction,  $F(2, 27) = 1.518, ns$ , were not significant. Mean progression speeds were faster on homeward paths relative to searching progressions across all groups.

*Heading directions.* A participant's ability to return to the starting location is reflected in the mean heading direction and the



Table 2  
*Topographical Characteristics of Human Searching Behavior*

Group and characteristic	Distance (m)	Path circuitry	Speed (m/s)
30 s			
Searching path	20.73 (6.87)	0.79 (0.12)	0.56 (0.22)
Homeward path	16.94 (5.02)	0.91 (0.03)	0.74 (0.21)
Searching progressions	14.52 (8.20)	0.94 (0.09)	0.65 (0.18)
60 s			
Searching path	36.77 (13.08)	0.44 (0.22)	0.49 (0.10)
Homeward path	12.35 (3.05)	0.88 (0.13)	0.74 (0.15)
Searching progressions	12.67 (6.04)	0.90 (0.06)	0.63 (0.18)
120 s			
Searching path	62.19 (13.86)	0.30 (0.11)	0.47 (0.15)
Homeward path	15.73 (6.48)	0.83 (0.12)	0.73 (0.16)
Searching progressions	13.26 (7.79)	0.90 (0.07)	0.55 (0.07)

*Note.* Values reflect the mean for each variable collapsed across each participant's three searching trips. The associated standard deviations are indicated parenthetically.

variability in heading directions across trials. Figure 8 plots each participant's homeward path heading directions obtained from the three trials (black dots) and participant's mean heading direction (white dots) from the three trials. Evaluating group differences in heading direction depends on similar variability in heading direction between groups. The bar graph in Figure 8 plots each group's mean heading direction parameter of concentration. The ANOVA conducted on the parameter of concentration revealed a significant effect of group,  $F(2, 27) = 4.817, p < .05$ . Post hoc analysis revealed a significant linear trend in the parameter of concentration across groups,  $F(2, 27) = 9.578, p < .05$ . Finally, single-sample  $t$  tests conducted on the group mean heading direction parameter of concentration revealed that the 30-s, 60-s, and 120-s groups were significantly different from zero,  $t(9) = 19.497, p < .05$ ;  $t(9) = 14.517, p < .05$ ; and  $t(9) = 8.681, p < .05$ , respectively. Although increasing searching times produced significantly more variability in participants' heading directions, all of the groups' heading directions differed significantly from chance. This effect is consistent with a progressive impairment in returning to the start location with increased searching time; however, all groups had a bias in returning to the start location. Significant group differences in heading direction variability precluded analysis of group differences in mean heading direction (Batschelet, 1981).

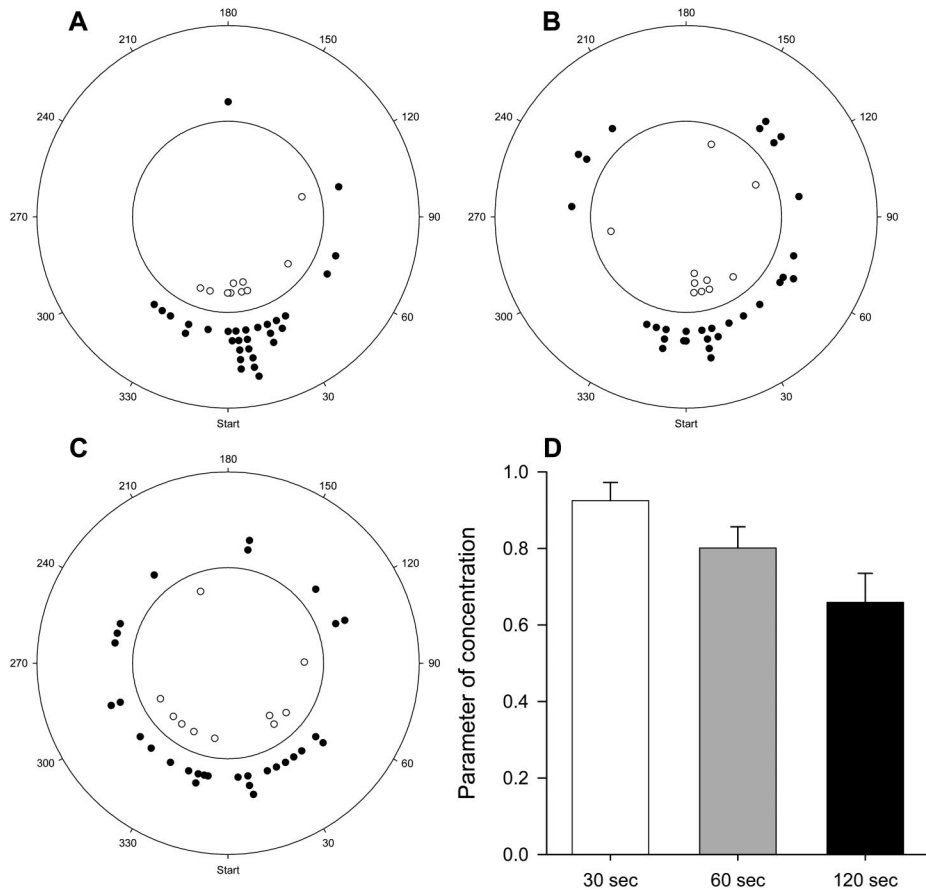
*Searching path kinematics.* Humans segment their searching paths into linear progressions punctuated by bouts of angular movements (see Panel A of Figure 9). The kinematics observed during the searching path further supported this segmentation of movement (see Panel B of Figure 9). Calculating the correlation between moment-to-moment linear speed and path curvature provides a measure of the extent that the searching path is segmented into linear progressions and bouts of angular movements. Each group's mean correlation between moment-to-moment linear speed and path curvature is plotted in Panel C of Figure 9. The ANOVA conducted on searching path correlations revealed a significant main effect of group,  $F(2, 27) = 3.711, p < .05$ . Post hoc analysis revealed a significant linear trend across group mean correlations,  $F(1, 27) = 7.247, p < .05$ . As participants searched for longer times, the relationship between moment-to-moment

linear speeds and path curvature decreased. Further inspection of the relationship between searching path moment-to-moment linear speed and path curvature suggested that the limited variability in path curvature observed during increased linear speeds may have contributed to our obtained results. Therefore, correlations between moment-to-moment linear speed and path curvature were calculated during periods of high path curvature (greater than  $2.5^\circ$  per second) and lower path curvature (less than  $2.5^\circ$  per second) for each participant's searching path. The bars in Panel D of Figure 9 plot each group's mean correlation during periods of high path curvature. The ANOVA conducted on searching path correlations during periods of high path curvature revealed a significant main effect of group,  $F(2, 27) = 12.084, p < .05$ . A subsequent post hoc analysis revealed a significant linear trend across the groups' mean searching path correlations,  $F(1, 27) = 24.358, p < .05$ . The scatter plots in Panel D of Figure 9 plot each group's mean correlation during periods of low path curvature. The ANOVA conducted on searching path correlations during periods of low path curvature failed to reveal a significant effect of group,  $F(2, 27) = 0.324, ns$ . As the duration of searching path increased, there was a progressive disruption of the searching path's segmentation into linear progressions and angular movements. The disruption was selective to periods of high path curvature.

The decreased strength in the relationship between linear speed and path curvature observed in the 120-s group may be selective to the second half of the searching path. Correlations were generated for each bout of high path curvature observed on the 60-s and 120-s groups' searching paths. Figure 10 plots mean correlations collapsed across each period of high path curvature (above  $2.5^\circ$  per second) for the entire searching path of the 60-s group, the first half of the searching path of the 120-s group, and the second half of the searching path of the 120-s group. The independent-samples  $t$  test conducted on searching path correlations from the 60-s group and the first half of the 120-s group was not significant,  $t(18) = -0.824, ns$ . The paired-samples  $t$  test conducted on the searching path correlations for the first 60 s and the second 60 s from the 120-s group was significant,  $t(9) = -3.799, p < .05$ . These results demonstrate that the disruption in movement kinematics is specific to the second half of the searching path of the 120-s group.

## Discussion

In the absence of visual information, human participants searched for a hidden coin for varying amounts of time prior to being instructed to return to the start location. As one might anticipate, increases in searching time were associated with longer path distances and increased path circuitry. The observed increase in searching path circuitry does not occur continuously throughout the path, however. Changes in searching path heading direction occur at discrete locations along the path. Although human participants displayed a general tendency to return to the start location when prompted, this ability varied as a function of searching time. Analysis of searching path kinematics revealed that disruptions in the inverse relationship between linear speed and path curvature also varied as a function of searching time. In addition, these disruptions were specific to the second half of the 120-s group's searching path. It should be noted that the disruption in the relationship between linear speed and path curvature was due to



*Figure 8.* Heading directions (black dots) obtained across participants' three trials are plotted for the 30-s group (A), 60-s group (B), and 120-s group (C). Average heading directions (white dots) are also plotted for each participant. Heading directions of zero degrees correspond to an accurate return to the start location. Panel D plots each group's average parameter of concentration. Error bars represent standard error.

the participants' behavior observed on longer trials and was not the result of experimenter manipulations. It is possible that disruptions in searching path organization impaired the participant's ability to detect changes in angular and linear speed. Therefore, processes involved in dead reckoning were compromised, resulting in increased variability in plotting a path to the start location. These observations provide support for the increased gain account of movement organization (Wallace et al., in press).

### General Discussion

The current study evaluated the claim that searching path organization functions to increase the gain associated with changes in linear and angular speeds (Wallace et al., in press). First, a consistent relationship between linear speed and path curvature was observed under dark conditions in which rats were actively searching for randomly located food pellets. These observations occurred under different motivational and task demands from those previously reported (Wallace et al., in press). Provided that movement organization reflects the rats' motivation to minimize the effort needed for moving through an environment, then changing task

demands should influence the organization of the searching path. The obtained results were inconsistent with predictions from an effort minimization account of path organization. Second, disruptions in the searching path organization were associated with impairments in the humans' ability to accurately return to the start location. Although these results are consistent with the increased gain account of searching path organization, further work is required to determine the mechanism (or mechanisms) that contributes to the disruption in the relationship between linear speed and path curvature.

### Potential Mechanisms of Searching Path Organization

One model of dead reckoning posits that systematic errors in encoding of linear and angular components encountered during the searching path impair navigational ability (Fujita et al., 1993). This encoding-error theory was advanced to explain triangle completion performance observed in humans (Loomis et al., 1993). Observing that searching path organization varied as a function of searching duration suggests that encoding errors may not be static. For example, during initial segments of the searching path (i.e., when

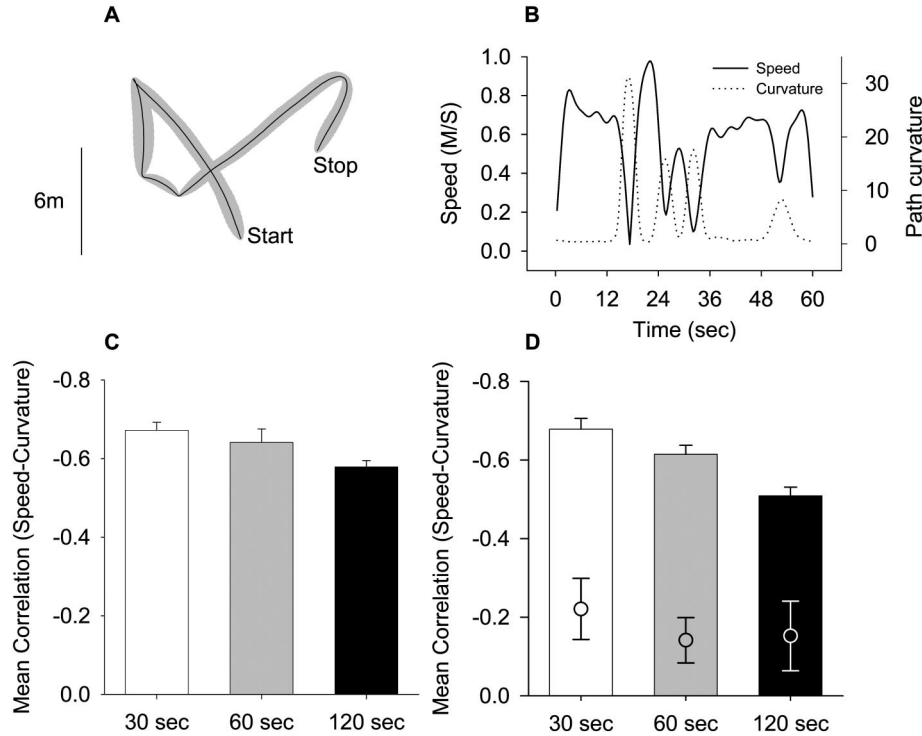


Figure 9. A: Searching path topography (black line) and relative moment-to-moment speeds (width of the gray region) are plotted for a representative participant in the 60-s group. B: Moment-to-moment speed (solid line) and path curvature (dotted line) for the same searching path. C: Each group's mean correlation between moment-to-moment speeds and path curvature for the entire searching path. D: Mean correlation between moment-to-moment speeds and path curvatures during high (bars) and low (scatter) periods of path curvature. Error bars represent standard error.

movements are still organized), participants' encoding of the path reflects consistent encoding errors. As the searching path progresses, these encoding errors increase in magnitude because the gain associated with angular components of the searching path

organization is reduced. Although application of the encoding-error model to the current data set is beyond the scope of this study, the segmentation of both human and rat movements on the searching paths lends itself to evaluating these parameters of the model.

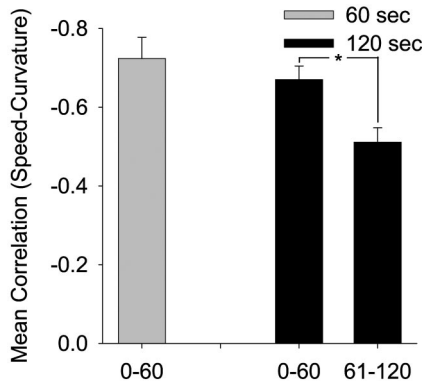


Figure 10. Mean correlation between moment-to-moment speeds and path curvature collapsed across periods of high path curvature are plotted for the 60-s group's searching path, the first 60 s of the 120-s group's searching path, and the second 60 s of the 120-s group's searching path (\* $p < .05$ ). Error bars represent standard error.

The relationship observed between linear speed and path curvature during searching paths has also been observed during hand drawing movements (Viviani & Terzuolo, 1980), visual tracking (de'Sperati & Viviani, 1997), and walking (Vieilledent et al., 2001). In this literature, the relationship has been formalized as the two thirds power law (Lacquaniti, Terzuolo, & Viviani, 1983). Considerable debate exists regarding the nature of this relationship. One view suggests that the relationship between linear speed and path curvature reflects lower level organizing principles such as the biomechanical properties of moving end effectors through space (Sternad & Schaal, 1999). Provided that the physics of end effectors was the sole basis of the relationship between linear speed and path curvature, then the strength of the relationship should be independent of searching path duration. Observing that longer searching paths were associated with decreases in the strength of the relationship between linear speed and path curvature is inconsistent with the lower level biomechanical account of moving end effectors through space. Another view suggests that the central representation of a movement command involves the

concatenation of simple movement primitives (Viviani & Flash, 1995). The latter view has found support in examining the development of hand writing (Viviani & Schneider, 1991) and the kinematics of continuous movements after an individual has suffered a stroke (Krebs, Aisen, Volpe, & Hogan, 1999). These studies have demonstrated the presence of simple movement primitives as well as deficits in sequencing or concatenating movement primitives. The current study demonstrated similar findings in humans. Although progression distance, circuitry, and speed did not vary as a function of searching path duration, the sequencing of progressions deteriorated with longer searching path durations. Whether a compromised central representation disrupted the organization of the searching path or vice versa remains to be determined.

The high degree of similarity in movement organization observed between humans (during shorter searching times) and rats in the current set of studies is consistent with both species using parallel mechanisms for dead-reckoning-based spatial orientation, thus suggesting that dead reckoning is a phylogenetically old adaptation for spatial orientation. In addition, research has suggested that dead reckoning in rats and humans may be mediated by similar anatomical structures (Maaswinkel, Jarrard, & Whishaw, 1999; Philbeck, Behrmann, Levy, Potoicchio, & Caputy, 2004; however see Alyan & McNaughton, 1999; Spiers et al., 2001). The differences in performance may reflect the co-opting of navigational strategies that are better suited for the animal's environmental niche. For example, rats are nocturnal animals, and navigational strategies that operate independent of visual landmarks may be of strong adaptive value. Therefore, dead reckoning observed in rats reflects a gradual tuning of a single navigational strategy by evolutionary processes. In contrast, humans are diurnal animals and have access to both visual landmarks and idiothetic information during navigation. Under these conditions, visual landmarks may function to correct or calibrate the use of idiothetic cues. Although dead-reckoning-based navigation in rats has not experienced the same environmental pressures as experienced in humans, research has demonstrated that allothetic cues interact with idiothetic cues in both species (Etienne, Maurer, & Seguinot, 1996; Maaswinkel & Whishaw, 1999; Shettleworth & Sutton, 2005). Future work examining the use of allothetic and idiothetic cues in two species of the same phylogenetic family that occupy different environmental niches may provide additional insight to the evolution of dead-reckoning-based spatial orientation.

### *Rat Model of Spatial Orientation*

Spatial disorientation is associated with many acute and neurodegenerative disorders. Aguirre and D'Esposito (1999) suggest that spatial disorientation reflects a class of heterogeneous syndromes, rather than a general impairment in spatial orientation. In general, previous research investigating the neurobiology of spatial orientation has focused on the use of allothetic information (O'Keefe & Nadel, 1978); however, recent investigations into the spatial disorientation observed in patients diagnosed with dementia of the Alzheimer's type (DAT) have suggested that deficits in processing idiothetic information may contribute to wandering behavior. Specifically, patients diagnosed with DAT demonstrate significant impairments in detection of radial optic flow (Tetewsky

& Duffy, 1999). Radial optic flow is one source of self-movement information that may contribute to dead reckoning. The present study builds a foundation for future human and rat studies that may contribute to the understanding of wandering observed in DAT (Rabins, Mace, & Lucas, 1982) and the evaluation of the effectiveness of cognitive enhancing drugs used to treat DAT (Logsdon et al., 1998).

### *Role of Nonvisual Allothetic Cues for Spatial Orientation*

There is another possible explanation for the behavior observed in the current set of experiments. Humans and rats may be using nonvisual allothetic cues to remain oriented during the searching path. For example, humans had access to somatosensory (e.g., the sensation of the sun or wind on one side of the face) and auditory cues in the environment during the searching path. If participants were using environmental stimuli for orientation, then the ability to reliably return to the start location would be independent of searching path duration. Humans exhibited a decrease in their ability to reliably return to the start location with increased path duration, which conflicts with a nonvisual allothetic-cue basis of spatial orientation.

In the rodent literature, previous studies have demonstrated that rats can be trained to track self- and conspecific-generated odor trails (Wallace, Gorny, & Whishaw, 2002). It is possible that the spatial orientation observed in the current study reflects the rats' use of odor-tracking-based piloting rather than dead reckoning. The observation that rats' homeward paths do not retrace searching paths conflicts with an odor-tracking-based piloting account of spatial orientation. In addition, the kinematics associated with odor tracking are qualitatively different from those observed during dead reckoning (Wallace & Whishaw, 2003). These differences in movement kinematics reflect slow halting movements and lateral head scans as a rat is using an odor trail to navigate. In the current study, homeward path speeds were significantly faster than searching path speeds, and rats did not display the typical lateral head scans while returning to the refuge. Therefore, the characteristics of the behavior observed on the homeward path are inconsistent with an odor-tracking-based piloting account of spatial orientation.

### *Conclusion*

This study examined the similarities in movement characteristics observed while humans and rats searched for a hidden object (humans) or a food pellet (rats) and their ability to return to the point where the search was initiated without access to visual information. In general, both humans and rats displayed a similar organization of searching behavior. Furthermore, disruptions in the behavioral organization observed in human searching were associated with a decreased ability to reliably return to the start location. These results provide evidence for the increased vestibular gain account of movement organization during dead-reckoning-based navigation (Wallace et al., in press). Developing techniques that enhance spatial orientation in humans may further characterize an understanding of spatial disorientation and provide tools to assess the effectiveness of therapies used to treat spatial disorientation.

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### Call for Nominations

The Publications and Communications (P&C) Board has opened nominations for the editorships of **Journal of Applied Psychology**, **Psychological Bulletin**, **Psychology of Addictive Behaviors**, **Journal of Personality and Social Psychology: Interpersonal Relations and Group Processes (IRGP)**, and **Journal of Educational Psychology** for the years 2009-2014. Sheldon Zedeck, PhD, Harris Cooper, PhD, Howard J. Shaffer, PhD, Charles S. Carver, PhD, and Karen R. Harris, PhD, respectively, are the incumbent editors.

Candidates should be members of APA and should be available to start receiving manuscripts in early 2008 to prepare for issues published in 2009. Please note that the P&C Board encourages participation by members of underrepresented groups in the publication process and would particularly welcome such nominees. Self-nominations are also encouraged.

Search chairs have been appointed as follows:

- **Journal of Applied Psychology**, William C. Howell, PhD and J Gilbert Benedict, PhD
- **Psychological Bulletin**, Mark Appelbaum, PhD and Valerie F. Reyna, PhD
- **Psychology of Addictive Behaviors**, Linda P. Spear, PhD and Robert G. Frank, PhD
- **Journal of Personality and Social Psychology: IRGP**, David C. Funder, PhD
- **Journal of Educational Psychology**, Peter A. Ornstein, PhD and Leah L. Light, PhD

Candidates should be nominated by accessing APA's EditorQuest site on the Web. Using your Web browser, go to <http://editorquest.apa.org>. On the Home menu on the left, find "Guests". Next, click on the link "Submit a Nomination," enter your nominee's information, and click "Submit."

Prepared statements of one page or less in support of a nominee can also be submitted by e-mail to Susan J.A. Harris, P&C Board Search Liaison, at [sjharris@apa.org](mailto:sjharris@apa.org).

Deadline for accepting nominations is **January 10, 2007**, when reviews will begin.