Sequential organization of movement kinematics is associated with spatial orientation across scales and species

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A large part of an animals’ behavioral repertoire involves non-conditioned or spontaneously occurring behaviors (e.g., exploration, food hoarding, food protection, food handling). These behaviors are highly organized sequences of movement. In general, these movement sequences alternate between periods of fast linear speeds with little change in heading and periods of slow linear speeds with larger change in heading. This sequential organization or movement segmentation can be quantified as the correlation between linear and angular speeds. This review examines evidence that the strength of movement segmentation is related to direction estimation independent of scale when humans or rats are restricted to using self-movement cues to guide navigation and may be a novel measure of spatial orientation.

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1. Introduction

Spontaneous behaviors (e.g., exploration, food hoarding, food protection, food handling) are highly organized sequences of movement. Specifically, animals organize movement into a sequence of relatively fast non-circuitous trajectories punctuated by periods of relatively slow speed associated changes in heading. This review examines the relationship between the strength of movement segmentation and an animal’s representation of current position. Both environmental (visual, auditory, olfactory) and self-movement (vestibular, proprioceptive, efferent copies) cues can be used to update this representation. Failures in accurately updating representations of current position increase the probability of becoming topographically disoriented. Animals that are topographically disoriented do not have an accurate representation of current position to organize subsequent movement. For example, blindfolded human participants instructed to walk in a
straight line quickly exhibit circular walking paths or veering behavior (Schaeffer, 1928). Lower level factors, such as biomechanical asymmetries (e.g., leg length), have been posited to contribute to veering behavior (Bojadzian, Martin, & Danion, 1999; Lund, 1930); however, more recent work has challenged this view (Souman, Frissen, Sreenivasa, & Ernst, 2009). It is possible that an inaccurate representation of current position may contribute to veering behavior. In this context, blindfolded participants depend exclusively on processing self-movement cues to update the representation of current position. Self-movement cue processing is prone to the accumulation of error (Barlow, 1964; Gallistel, 1990; Seguinot, Maurer, & Etienne, 1993; for a review see Etienne & Jeffery, 2004); therefore, the representation of current position is continuously accruing errors. Subsequent veering behavior may emerge from a continuously drifting representation of position. Considering this work has not typically included independent assessments of spatial orientation, it is possible that disruptions in movement organization (i.e., veering behavior) may reflect topographical disorientation. Subsequent sections examine the relationship between movement segmentation and measures of spatial orientation across varied scales of movement in rats and humans.

2. Rat ambulatory scale

When a rat is exposed to a novel environment it initially engages in highly organized exploratory behavior. This behavior is focused around a home base and can be separated into searching and homeward segments (Eilam & Golani, 1989; Whishaw, Kolb, & Sutherland, 1983). The searching segment is a series of progressions and stops. Progressions are typically non-circuitous paths that vary in peak speeds or "gears" of movement (Drai, Benjamini, & Golani, 2000; Tchernichovski, Benjamini, & Golani, 1998). Stops are moments of slow speeds in which most of the segment's changes in heading occur. The correlation between the set of linear and angular speeds provides a measure of movement segmentation strength for the searching segment of an exploratory trip (see Fig. 5 in Wallace, Hamilton, & Whishaw, 2006). Rats consistently exhibit a strong inverse relationship between linear and angular speeds (−0.60) across searching segments of varying length. Interestingly, similar patterns of movement organization have been described in the human voluntary movement literature.1 The homeward segment begins after the last stop of the searching segment, is a non-circuitous progression, and ends as the rat contacts the home base. Depending on environmental cue access and familiarity, this organization can be derived from piloting and/or dead reckoning based navigational strategies (Gallistel, 1990). In general, rats use environmental (piloting) or self-movement (dead reckoning) cues to continuously or periodically update their representation of current position during the searching segment. Direction and distance estimates are derived from this representation and used to guide movement on the homeward segment. Independent of access to environmental cues, rats consistently exhibit strong movement segmentation during the searching segment and accurate estimation of direction and distance to the refuge (Wallace, Hamilton et al., 2006). Changing task demands provides an opportunity to investigate the role of performance variables that may influence the relationship between movement segmentation and spatial orientation.

Motivation is one factor that may influence the organization of movement through an environment. For example, food deprived rats are likely to move more quickly while searching an environment for randomly located food items (top panel of Fig. 1). Upon finding a relatively large food item (over 500 mg), the rat will carry the food item directly to a home base prior to consuming the food item. This organization of food hoarding behavior is observed across conditions with varied access to environmental cues (Maaswinkel & Whishaw, 1999). Similar to exploration, it is inferred that rats continuously update their representation of current position while searching for the food item, and upon finding the food item, the representation is used to estimate direction and distance to the refuge. Despite recruiting different motivational systems, the food hoarding searching paths exhibit the same level of movement segmentation (bottom panel of Fig. 1) as observed during exploratory behavior. In addition, rats are extremely accurate in estimating direction and distance to the refuge (Köppen et al., 2015). Changes in task motivation alter specific aspects of performance (e.g., moment-to-moment speeds); however, the relationship between movement segmentation and spatial orientation does not appear to be influenced by differences in motivation associated with exploration or food hoarding.

Another factor that may influence organization of movement through an environment is access to specific types of environmental information. For example, rats can be trained to follow scented strings to locate food items (Wallace, Gorny, & Whishaw, 2002). Odor tracking behavior has been shown to elicit qualitatively distinct kinematic profiles (platykurtic distribution of speeds) relative to the kinematic profiles (leptokurtic distribution of speeds) observed on homeward segments of exploratory behavior (see Fig. 4 of Wallace & Whishaw, 2003). These observed differences in movement organization were used to investigate the relationship between movement segmentation and spatial orientation during a food hoarding task (Wallace, Köppen, Jones, Winter, & Wagner, 2010). Specifically, rats trained to search for randomly located food items exhibited a relatively strong inverse relationship between linear and angular speeds (−0.6) while searching for the food item. In contrast, rats trained to follow scented strings to find food items exhibited relatively weaker movement segmentation.

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1 The two-thirds power law describes the sequential organization of human voluntary movement across multiple scales. Specifically, human participants exhibit decreases in linear speeds as path curvature increases during voluntary movement of the eyes (Lacquaniti, Terzuolo, & Viviani, 1983), hands (de'sperati & Viviani, 1997), and body (Vieilledent et al., 2001). This characteristic of human voluntary movement has been attributed to a concatenation of motor primitives guided by a central representation (Viviani & Flash, 1995). Observing that this characteristic of movement varies during development of drawing movement (Viviani and Schneider, 1991) and recovery of voluntary movement after stroke (Krebs, Aisen, Volpe, & Hogan, 1990) discounts biomechanical explanations (Sternad & Schaal, 1999) of movement organization. Work with rats has provided additional support for the view that this movement organization may depend on a representation of the animal's current position.
Fig. 1. Topographic and kinematic characteristics are plotted for a representative rat food hoarding trip (top panel). The diameter of the circles represent relative speed of the rat during the outward (blue) and homeward (red) segments of the food hoarding trip. Moment-to-moment linear (black line) and angular (grey line) speeds are plotted for the outward segment (bottom panel). Start of the outward segment (s) and end of the homeward (e) are indicated in the figure. Note: Rat ambulatory scale movement elicit linear speeds in the range of 0.0–0.6 m/s and angular speed in the range of 0.0–80°/s. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(−0.5) while scent tracking. The reduction in movement segmentation strength observed during odor tracking was associated with an increase in heading error returning to the home base with the food item. There are several possible explanations for these results. First, attention to the environmental stimuli (odor cues) may have simultaneously disrupted movement segmentation and prevented accurate updating of the representation of current position. This account does not depend on a functional relationship between movement segmentation and spatial orientation. Another possibility is that the attention to environmental stimuli directly influenced one of these variables (movement segmentation or spatial orientation) and that variable then influenced the other variable. In either account, errors in the representation influenced the ability to accurately estimate direction to the home base. Although these results fail to dissociate either explanation, work adapting the food hoarding paradigm under dark conditions to ambulatory scale in humans has provided support for a functional relationship between movement segmentation and spatial orientation.
3. Human ambulatory scale

Humans walking elliptical paths through an environment exhibit a consistent relationship between linear speeds and measures of path curvature, or the two-thirds power law (Vieilledent, Kerlirzin, Dalbera, & Berthoz, 2001). This demonstrates that human voluntary movement at the ambulatory scale exhibits organizational characteristics similar to movement segmentation observed in rats. These observations provided the foundation to investigate the relationship between movement segmentation and spatial orientation in humans. Recent work has used an ambulatory scale analogue of the rat food hoarding paradigm to investigate human dead reckoning based navigation (Wallace, Choudry, & Martin, 2006). Specifically, blindfolded human participants were instructed to use a metal detector to search for an ostensible hidden coin on a large open field. Groups searched for 30, 60, or 120 s prior to receiving instructions to return to the start position. Longer search times were associated with a progressive decline in the strength of the relationship between linear and angular speed. For example, the group that searched for 120 s exhibited stronger movement segmentation during the first 60 s than observed during the second 60 s (Fig. 2). Increases in search time were also associated with less accurate estimation of direction to the start position. These results demonstrate a relationship between movement segmentation and spatial orientation at the human ambulatory scale. It is possible that movement segmentation and spatial orientation are continuously interacting along the searching path and impact the ability to estimate direction to the start location. Initially, error gradually accumulates and influences the fidelity of the representation of the current position. Next, this poor representation of current position does not effectively guide movement segmentation. Further, subsequent weak movement segmentation amplifies the accumulation of error until the individual is no longer able to maintain spatial orientation. Longer search times afford more opportunities for weak movement segmentation to amplify the accumulation of error. This interpretation is consistent with the human ambulatory scale data; however, holding search time constant while varying search path characteristics would provide a direct test of this view.

Previous work has investigated the effects of manipulating search path topography on estimating direction and distance to the point where movement originated (Loomis et al., 1993). Specifically, blindfolded participants are led along two legs of a triangle and instructed to walk back to the start, or complete the triangle. Leg lengths (2, 4, 6 m) and the subtending angle (60, 90, 120°) were systematically combined to create 27 searching paths that each participant followed. In general, participants were observed to overestimate short lengths and small angles and underestimate long lengths and large angles. The consistency of errors observed across a variety of topographical arrangements of legs and angles prompted the development of a computational model relating these variables (Fujita, Klatzky, Loomis, & Golledge, 1993). The error-encoding model posits that the errors in direction and distance estimation reflect a bias in encoding the length of legs and the magnitude of angles. This bias in encoding the turn along the path may be related to the strength of movement segmentation experienced when following paths with varied topography. Recent work has investigated this relationship between movement segmentation and searching path topography during a manipulatory scale version of the triangle completion task for humans.

4. Human manipulatory scale

In general, human performance on dead reckoning tasks have been shown to be conserved across ambulatory and manipulatory scales (Klatzky, 1999; Wallace et al., 2010). Recent work has investigated the extent that searching path movement kinematics are related to estimating direction on the homeward segment at the manipulatory scale (Wallace et al., 2010). Specifically, blindfolded participants sat at a table and followed two lengths of string subtended by an angle that varied in magnitude across trials. Upon reaching the end of the string, participants were instructed to return to the start position. Motion capture software was used to characterize the topographic and kinematic aspects of movement on the searching and homeward segments. Participants exhibited stronger movement segmentation when following strings subtended by an obtuse angle than an acute angle. Differences in movement segmentation were associated with accuracy in estimating direction to the start position. Specifically, stronger movement segmentation (as observed in obtuse angles) was associated with smaller amounts of heading error on the homeward segment. In addition, this relationship between movement segmentation and spatial orientation has been observed to extend to a manipulatory scale version of the food hoarding task. Blindfolded participants searched the table for a randomly located piece of Velcro (Fig. 3). Once the Velcro was found, participants were instructed to return to the start position. In general, participants exhibited weaker movement segmentation on the manipulatory scale searching task relative to that observed during obtuse triangle completion trials. This weaker movement segmentation was associated with less accurate estimation of direction to the start position. Together, these observations provide further evidence for a relationship between movement segmentation and spatial orientation.

Participants in both tasks used self-movement cues to update their representation of the current position. Weak movement segmentation on the searching path contributed to encoding error into the representation of the current position. This representation was used to estimate direction to the starting position. Errors in representing the current position translated to less accurate estimates of direction in both tasks. This relationship between movement segmentation and spatial orientation provides a novel assessment to investigate the neurobiology of movement organization.
Fig. 2. Topographic and kinematic characteristics are plotted for a representative ambulatory scale dead reckoning trial from a human participant (top panel). The diameter of the circles represent relative speed of the human during the outward (blue) and homeward (red) segments of the ambulatory scale task. Moment-to-moment linear (black line) and angular (grey line) speeds are plotted for the outward segment (bottom panel). Start of the outward segment (s) and end of the homeward (e) are indicated in the figure. Note: Human ambulatory scale movements elicit linear speeds in the range of 0.0–2.5 m/s and angular speeds in the range of 0.0–30 °/s. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Rat manipulatory scale

A network of neural structures contributes to maintaining a representation of current position. Sensorimotor components of this network may differentially contribute to each scale of movement. For example, proprioception and vestibular systems contribute to ambulatory scale movement, whereas vestibular cues are less relevant for manipulatory scale movement. Convergence of multiple sensorimotor components is necessary for information processing that is common to all scales of movement (e.g., dead reckoning). Damage to a sensorimotor component of this network would be predicted to disrupt movement segmentation and measures of spatial orientation selective to that scale of movement.

Rat string pulling behavior is a highly organized manipulatory scale fine motor behavior that may provide insight to the relationship between movement segmentation and spatial orientation. String pulling behavior can be elicited in a rat by hanging a string over the edge of home cage, and reinforcement (a cashew tied to the end) promotes continued engagement.
Fig. 3. Topographic and kinematic characteristics are plotted for a representative manipulatory scale dead reckoning trial from a human participant (top panel). The diameter of the circles represent relative speed of the human during the outward (blue) and homeward (red) segments of the manipulatory scale task. Moment-to-moment linear (black line) and angular (grey line) speeds are plotted for the outward segment (bottom panel). Start of the outward segment (s) and end of the homeward (e) are indicated in the figure. Note: Human manipulatory scale movements elicit linear speeds in the range of 0.0–0.4 m/s and angular speeds in the range of 0.0–50°/s. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
Application of motion capture software to string pulling behavior has revealed the topographic and kinematic organization of forelimb movement (top panel of Fig. 4). Rats exhibit a strong inverse relationship between linear and angular speeds as forelimbs move through manipulatory space (bottom panel Fig. 4). In addition, rats exhibit relatively few misses in contacting the string. This organization depends on processing multiple sources of information to update a representation of current limb position.

Proprioceptive cues are one source of information that contributes to the organization of rat fine motor control at the manipulatory scale (McKenna & Whishaw, 1999). The sensorimotor cortex mediates proprioceptive cue processing and likely contributes to the organization of rat string pulling behavior. Recent work has examined the effects of unilateral devascularization of the sensorimotor cortex on the organization of string pulling behavior (Blackwell, Widick, Cheatwood, & Wallace, 2015). Unilateral removal of sensorimotor cortex vasculature was observed to attenuate contralateral movement segmentation and increase the number of contralateral missed string contacts relative to rats that received a control surgery (Fig. 5). These results demonstrate that damage to neural systems that mediate sensorimotor components of the representation of current position produces deficits specific to the rodent manipulatory scale and provide further evidence of a relationship between movement segmentation and spatial orientation.

Fig. 4. Topographic and kinematic characteristics are plotted for a rat’s forelimb during string pulling behavior from a representative rat (top panel). The diameter of the circles represent relative speed of the rat’s forelimb during the manipulatory scale string pulling task. Moment-to-moment linear (black line) and angular (grey line) speeds are plotted for the movement sequence (bottom panel). Start (s) and end (e) of the movement sequence are indicated in the figure. Note: rat manipulatory scale movements elicit liner speeds and the range of 0.0–1.0 cm/s and angular speeds in the range of 0.0–70°/s.
6. Convergence across scales and species

Previous sections have discussed evidence that dead reckoning based navigation guides human movement at the ambulatory and manipulatory scales. In addition, rats have been shown to use dead reckoning based navigation to guide their ambulatory scale movement. Self-movement cues originate from multiple sensory systems and likely converge on a system of brain structures that are involved in updating a representation of current position and estimating direction and distance to the point where movement originated. Traditionally the hippocampus was viewed as critical for encoding relationships among environmental cues (Morris, Garrud, Rawlins, & O’Keefe, 1982; O’Keefe & Nadel, 1978); however, multiple lines of evidence have supported a role for the hippocampus as a point of convergence in processing self-movement cues. First, rodent studies that dissociated environmental and self-movement cue processing have demonstrated that damage to the hippocampal formation (Maaswinkel, Jarrard, & Whishaw, 1999; Wallace & Whishaw, 2003; Winter, Köpken, Ebert, & Wallace, 2013; however, see Alyn & McNaughton, 1999) or to hippocampal afferent pathways (Köpken, Winter, Stuebing, Cheatwood, & Wallace, 2013; Martin & Wallace, 2007) impairs dead reckoning based navigation and spares environmental cue based navigation. Next, damage to the hippocampal formation in humans has also been shown to disrupt dead reckoning at the ambulatory scale (Philbeck, Behrmann, Levy, Potolicchio, & Caputy, 2004; however see Shrager, Kirwan, & Squire, 2008). Further, hippocampal activation has been shown to be associated with performance in a virtual reality dead reckoning task (Wolber, Wiener, Mallot, & Buchel, 2007). Finally, a history of a binge pattern of alcohol consumption during adolescence has been shown to impact structural and functional characteristics of several brain areas including the hippocampal formation in humans (Schweinsburg, McQueeney, Nagel, Eyler, & Tapert, 2010), non-human primates (Taffe et al., 2010), and rodents (He, Lee, Styner, & Crews, 2011; Crews, Braun, Hoplight, Switzer, & Knapp, 2000). Recent work has demonstrated that self-report measures of adolescent binge drinking were associated with impaired dead reckoning at the human manipulatory scale (Blankenship, Blackwell, Ebrahimi, Benson, & Wallace, 2016). These observations provide evidence that self-movement cue processing across multiple scales and species depends on the hippocampal formation.

It remains to be determined whether hippocampal damage impacts the strength of movement segmentation. Future work investigating neurodegenerative disorders that target the hippocampal formation may benefit from this type of analysis. For example, this type of analysis can be applied to characterize exploratory behavior in a rodent model of neurodegenerative diseases (e.g., Alzheimer’s disease). Observing that movement segmentation can dissociate hippocampal neuropathology in rodent models will establish a foundation to use this approach to investigate spatial orientation deficits associated with neurodegenerative disorders in humans. The results of this work will provide further insight into the relationship between spatial orientation and movement segmentation.

7. Conclusion

This review examined the relationship between movement segmentation and spatial orientation across ambulatory and manipulatory scales of movement. In general, humans and rats exhibit strong movement segmentation and accurate direction estimation independent of scale of movement when restricted to using self-movement cues to guide navigation. Several exceptions were noted. First, rats trained to track scented strings exhibit weaker movement segmentation and less accurate direction estimation relative to other modes of ambulatory scale navigation. Next, humans exhibit larger errors in direction estimation when movement segmentation was weaker at ambulatory and manipulatory scales of movement. Finally, rats with damage to the cortical areas involved in processing sensorimotor information related to the forelimb exhibited weaker manipulatory scale movement segmentation and errors in estimating direction. These observations demonstrate a relationship between movement segmentation and spatial orientation; however, a causal relationship cannot be established between these factors based on the existing literature. It is possible that movement segmentation and spatial orientation continuously interacts during a sequence of movements. This interaction may provide a relatively continuous indirect measure of spatial orientation that is observed across various scales of movement in multiple animal species. Therefore, behavioral
analysis may be useful in assessing rodent models of neurodegenerative disease, and disruptions in movement segmentation may be a prodrone of neuropathology in humans.

References


