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Reprint of “Sequential organization of movement kinematics is associated with spatial orientation across scales and species”[☆]

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ABSTRACT

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.

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 disorientated. Animals that are topographically disorientated 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 (Boyadjian, 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

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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 (-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.

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, 1999) 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.

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